# The Effects of Landscape Heterogeneity and Change on Beetle Community Composition

PhD Biological Sciences

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**November 2018**

**Declaration of original authorship**

I confirm that, aside from the contributions of co-authors, this is my own work; the use of all material from other sources has been properly and fully acknowledged.

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26th November 2018

**ABSTRACT**

Biodiversity conservation in anthropogenically modified landscapes requires consideration of the interactions between communities of species, the spatial heterogeneity of landscapes and their change through time. The significance of insects for understanding the biodiversity crisis is well known. However, we lack even basic information about the vast majority of insects and the response of many taxa to landscape heterogeneity is poorly understood. Several groups of beetles, especially ground beetles (Carabidae), are frequently employed as indicators in landscape-scale studies. To more fully understand the range of responses to landscape heterogeneity and change in beetles, this thesis considers three beetle communities in varied landscape contexts. A novel application of historical land use data was used to consider time lag in woodland ground beetles' response to landscape change. Flower-visiting beetles and coprophilous beetles were considered in the context of an agriculture-dominated landscape mosaic and on a gradient of urban land use, respectively. All three communities were modified to some degree by landscape heterogeneity, with responses mediated by traits such as body size, dispersal ability and feeding guild. Woodland ground beetle communities were more strongly linked to landscape patterns in the 18th and 19th centuries, providing evidence for an extinction debt that may be on the order of 200 years. Flower-visiting beetle communities were shaped by mesoscale landscape composition, especially the amount of tree cover and gardens in the surrounding 200 metres. A widespread but little-studied genus of flower-visiting beetles (Scraptiidae: *Anaspis*) displayed heterogeneous sex ratios among the sites visited; the distribution and sex ratios of two species were linked to local habitat composition and structure, measured using LiDAR data. Coprophilous beetles were less species-rich in urban sites, but some species appeared to benefit from urbanisation. Potential applications of these results are considered along with suggestions for future research in landscape entomology.

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# 1. General Introduction: The Effects of Landscape Heterogeneity and Change on Beetle Community Composition

## 1.1. Landscape Ecology and Conservation

Land use changes have driven declines in abundance and species richness and modified species assemblages globally, especially where anthropogenic land use is most intense (Newbold et al., 2015). Further conversion of land for agriculture (and intensification) is estimated to result in future potential losses of 30% of terrestrial vertebrate species (Kehoe et al., 2017). Comparable estimates for invertebrates are difficult to calculate due to insufficient knowledge of the true number of species (Gaston, 1994; Stork, 2018) and their distribution, abundance and sensitivity to environmental change (Didham et al., 2010; Cardoso et al., 2011), though a recent estimate suggests that as many as one-fifth of invertebrate species may be threatened with extinction globally (Collen et al., 2012).

At a regional level, land use changes may modify species communities but not necessarily change the number of species a landscape can support (Parody et al., 2001). In some cases local and even regional species richness can be enhanced by anthropogenic land use (Sattler et al., 2011; Martínez et al., 2015; Theodorou et al., 2017; Brüning et al., 2018), but at the expense of phylogenetically unique native species (Knapp et al., 2017). In order to predict and manage the effects of land use change, we need to understand current patterns of land use and biodiversity (Pimm et al., 1995) and how these are linked. Spatial ecology is concerned with the spatial extent of any ecological processes (Wiens, 1989), whilst the landscape scale (and thus landscape ecology) always encompasses multiple patches and land cover types at the level of inference, i.e., it is fundamentally concerned with heterogeneity (Farina, 2006).

The importance of spatial and landscape ecology has increased since the publication of the theory of island biogeography (MacArthur & Wilson, 1967), growing out of an understanding that larger patches (where a patch is a relatively homogenous area of habitat) are likely to host more species (MacArthur & Levins, 1964). The world island is now applied most commonly not to oceanic islands but to isolated fragments of habitat surrounded by a 'matrix' of non-habitat (Fernández-Juricic & Jokimäki, 2001; Donald & Evans, 2006; Fattorini et al., 2018).

Metapopulation dynamics is the second important paradigm in spatial ecology (Levins, 1969; Hanski & Gilpin, 1991; Hanski, 1994), in which the maintenance of a metapopulation requires a flow of individuals between patches, maintaining genetic diversity and in the event of patch-level extinction events recolonising low-quality 'sink' patches from higher-quality 'source' habitat (Pulliam, 1988; Eriksson, 1996) . Metapopulation extinction occurs where a landscape does not meet the necessary habitat and connectivity thresholds for metapopulation persistence, ultimately

structuring metacommunities (Mouquet & Loreau, 2003; de la Sancha et al., 2014; Alignier, 2018). Non-immediacy of extinction or recolonisation in each patch adds complexity to the temporal dimension of biodiversity responses to landscape change (Hanski & Ovaskainen, 2000a, 2002; Talluto et al., 2017). In this way, habitat fragmentation is not static; it is the dynamic change in connectivity through time that is important for population persistence (Rosenzweig, 1995; Martensen et al., 2017), and landscape heterogeneity is the product of spatial and temporal changes in land use. To fully assess landscape heterogeneity effects, attention has increasingly turned to the importance of matrix habitats (i.e., non-focal habitats in the surrounding landscape: Pearson, 1993; Ricketts, 2001; Cook et al., 2002; Bender & Fahrig, 2005), with a greater focus on landscape 'mosaics' (Debinski et al., 2001; Fahrig, 2003; Bennett et al., 2006; Haslem et al., 2008).

Conservation projects increasingly operate at a landscape scale, in part because of a perception that it is more cost-effective but also out of a genuine filtering through of spatial ecology principles to the policy level (Lawton et al., 2010). However, our knowledge of how biodiversity in the broadest sense is shaped by landscape is far from complete. This chapter will review our understanding of how landscape heterogeneity, expressed in terms of change through space and time, impacts biodiversity. It begins with a consideration of the broad effects of landscape heterogeneity on biodiversity. It then considers the place of insects in current research, particularly beetles, the most diverse order of insects, of which several families are commonly used as indicator groups.

## 1.2. Landscape Heterogeneity (Composition and Configuration)

Spatial landscape heterogeneity can be described as the combination of landscape composition and landscape configuration. Landscape composition simply describes the amounts of different types of land cover in a given area, whilst landscape configuration describes the spatial arrangement of those land cover patches (Bennett et al., 2006), measuring factors such as patch size and isolation.

### 1.2.1. Local vs. Landscape

Landscape factors are certainly not always more important than properties of the local environment (Van Halder et al., 2008; Philpott et al., 2014; Otoshi et al., 2015), but are rarely completely unimportant (but see Krämer et al., 2012; Fuller et al., 2018), and the relative balance varies between taxa (Sjödin et al., 2008). For example, both habitat quality and patch isolation may determine butterfly distributions (Thomas et al., 2001), but for specialist species habitat quality or local habitat amount is more important than any feature of the wider landscape (Thomas et al., 2001; Krauss et al., 2003). In any case, local habitat quality can be modified by the properties of the surrounding landscape (Jorgensen et al., 2014) and landscape also mediates the effectiveness of conservation measures locally (Rubene et al., 2017). Overall, species richness in a patch is

determined by the synergistic effects of local, landscape and regional factors (Götmark et al., 2011).

### 1.2.2. Habitat Amount, Patch Size and Fragmentation

For more mobile species groups such as birds, the amount of their focal habitat in the landscape, i.e., landscape composition, is generally found to be more important than landscape configuration (Angelstram, 2004; Mortelliti et al., 2010; Broughton et al., 2013; Neumann et al., 2016a), though some bird species depend on larger habitat patches (Tilghman, 1987; Broughton et al., 2010) and Lamb et al. (2016) predicted that larger patches are more important for birds in land-sparing scenarios. More mobile insects are also not limited by dispersal, according to population genetics studies (Francuski et al., 2013; Schauer et al., 2018), and therefore do not always respond to habitat fragmentation; similarly, habitat amount is more important than fragmentation for some grassland plants (Cousins et al., 2007). Response to both habitat amount and patch size is not always linear (Angelstram, 2004; Radford et al., 2005; Suarez-Rubio et al., 2013), linked to territory size in birds or the size of patch that can sustain a viable population for localised invertebrates or plants (Steffan-Dewenter & Tscharntke, 2002; Lindgren & Cousins, 2017). Individuals may actually preferentially move toward larger patches, as observed in *Chrysolina graminis*, a flightless leaf beetle (Chapman et al., 2007).

For low-mobility species, connectivity may therefore only be beneficial once the habitat threshold is exceeded (Mortelliti et al., 2011); landscapes with small patches and low total cover are likely to be dominated by high-mobility, generalist species (Öckinger & Smith, 2006). Whether aspects of landscape configuration are a proxy for habitat amount may also simply be a question of spatial scale. For example, Barbaro et al. (2007) concluded that landscape configuration at the 'mesoscale' (hundreds of metres) was a proxy for landscape composition for predicting ground beetle community composition, whilst Neumann et al. (2016b) found that ground beetle communities were predicted best by a model that included hedgerows as linear connecting features, working at a kilometres wide scale.

Fahrig (2013) suggested the 'habitat amount' hypothesis, whereby fragmentation is always a proxy for habitat amount and there is no practical difference between patch isolation and patch size effects. Seibold et al. (2017) confirmed the hypothesis for saproxylic beetles, whilst Haddad et al. (2017) found it was not supported for woody plants in Mediterranean forests. Lindgren & Cousins (2017) found that larger, less isolated semi-natural grassland remnants were more valuable for plants, supporting island biogeography over habitat amount, while Tulloch et al. (2015) highlighted the value of both small and large patches to maintaining biodiversity. The debate over the true nature of fragmentation effects is very much ongoing (Fletcher Jr et al., 2018).

There is in any case direct evidence for the use of connecting features by ground beetles (Burel, 1989; Petit & Burel, 1998a; Jopp & Reuter, 2005) with the relative importance of connecting features mediated by mobility (Jopp & Reuter, 2005), though potential dispersal corridors such as road verges do not always mitigate fragmentation (Wilson et al., 2016). Evidence for the use of connecting features by birds is mostly indirect (Hinsley & Bellamy, 2000; Newmark et al., 2017) or anecdotal (Bailey, 2007), but studies of both birds and ground beetles do suggest that restoring habitat between fragments or providing alternative connecting features in the landscape boosts local populations (Neumann et al., 2016b; Newmark et al., 2017). It can be difficult to determine whether putative 'connecting' features actually facilitate dispersal or simply provide additional habitat (Angold et al., 2006); for example, 'woodland' birds and ground beetles may find suitable habitat in dense mature hedgerows (Green et al., 1994; Millán de la Peña et al., 2003).

### 1.2.3. Landscape Mosaics

In more heterogeneous landscapes, patch size and isolation effects become obscured by matrix effects (Debinski et al., 2001; Cook et al., 2002; Bender & Fahrig, 2005). The surrounding matrix modifies diversity and species composition within a patch (Pryke et al., 2013; Martínez et al., 2015; Yekwayo et al., 2016) and in some cases spillover of species from neighbouring patches may be a more important driver of community composition than connectivity (Schneider et al., 2016; Duflot et al., 2018). Recognising the importance of mosaic heterogeneity for determining the biodiversity of semi-natural habitat fragments in agricultural landscapes, landscape studies increasingly examine a patch-mosaic, rather than patch-matrix paradigm (Bennett et al., 2006; Radford & Bennett, 2007; Neumann et al., 2016a, 2016b). A 'landscape-centred' approach may be the most beneficial (Mimet et al., 2014), especially where landscape is the unit of replication for both response and explanatory variables, i.e., biodiversity data are drawn from the whole landscape mosaic (e.g., Millán de la Peña et al., 2003; Weibull & Östman, 2003; Radford et al., 2005; Bennett et al., 2006; Duflot et al., 2017). Studies of this kind are not particularly common, perhaps because of the logistic difficulties of sampling multiple taxonomic groups or habitat types. Three chapters in this thesis will focus on using whole mosaic data, whilst two trial less intensive forms of 'landscape-centric' sampling.

### 1.3. Landscape Change, Extinction Debt

Landscape change may result in conditions becoming unsuitable for a species, resulting in local extinction. This may be due to the landscape no longer being able to support metapopulations (Hanski & Ovaskainen, 2000b). Local populations in patches will persist after the event, leading to an 'excess' of species doomed to extinction; in other words, they are in 'extinction debt' (Tilman et al., 1994; Hanski & Ovaskainen, 2002). The time in repayment, that is, the time between the initial change and stabilisation at a new equilibrium, is generally termed the relaxation time. Other

mechanisms besides metapopulation capacity can lead to an apparent extinction debt or time lags (Hylander & Ehrlén, 2013; Essl et al., 2015)—for example, where individuals persist in a resilient life-cycle stage beyond the habitat's ability to support reproduction, or the non-immediate occurrence of stochastic extinctions (Hylander & Ehrlén, 2013). Extinction debt's twin is colonisation credit, where a patch or landscape mosaic changes to a state where it is able to support populations but recolonisation from the regional species pool is not immediate (Naaf & Kolk, 2015; Kolk et al., 2017; Waldén et al., 2017; Fuller et al., 2018). Time lag in colonisation obviously depends on mobility, e.g., ground beetles occupy new patches more slowly than spiders (Oxbrough et al., 2010).

Theoretically, time lags may extend many hundreds of years; for example, Gilbert & Levine (2013) estimated that the time to extinction in native plants following the arrival of invasive species may be in the hundreds of years, while Otto et al. (2017) predicted that habitat loss after the arrival of humans in the Canary Islands will still result in future extinctions. The majority of time lag time estimates based on field data are for plants in semi-natural grassland fragments, with periods ranging from several decades (Lindborg, 2007; Koyanagi et al., 2009; Krauss et al., 2010; Bagaria et al., 2018) to one or two centuries (Gustavsson et al., 2007; Rédei et al., 2014).

For insect groups, time lag estimates depend on the mobility of the taxonomic group in question, landscape context and perhaps historical landscape data availability. Cusser et al. (2015) found indirect evidence for an extinction debt of 23 years for pollinators in exurban landscapes, while Bommarco et al. (2014) found no extinction debt for bees after 45 years, suggesting that at least some pollinating insects respond rapidly to change, though Aguirre-Gutiérrez et al. (2015) found that recent changes in pollinator populations were conditioned by landscape patterns 100 years ago. Bommarco et al. (2014) identified an extinction debt in generalist butterfly species, as did Sang et al. (2010) for specialist butterflies (correlated with habitat area 75 years previously), whilst Ibbe et al. (2011) found that butterfly richness was highest in clear-cut patches that had previously (70–90 years ago) been meadows than those that had previously been conifer forest. However, Krauss et al. (2010) found no evidence of extinction debt in specialist butterflies, looking at a comparable time period (40 years). Extinction debts on the order of 50–80 years have also been identified for woodland ground beetles, linked to changes in landscape configuration (Neumann et al., 2017) and changes in the area of broadleaved woodland (Yamanaka et al., 2015).

In general, regional context and species' life histories appear to be important drivers of the magnitude of extinction debts, with no one study system providing a consistent proxy for others. Extinction debt may not be identified for scarce species simply because it has already been 'paid' (Kolk et al., 2017; Koyanagi et al., 2017). Incorporating the likely existence of extinction debts into conservation strategies is a significant challenge (Dullinger et al., 2013; Essl et al., 2015; Semlitsch

et al., 2017), and the way in which both extinction debt and colonisation credit dynamically modify the current species pool needs to be understood in order to interpret monitoring data (Piqueray et al., 2011; Yamanaka et al., 2015).

## 1.4. Beetles as Indicators in Landscape Ecology

Insects are fundamentally important for understanding the biodiversity crisis, with widespread declines in abundance, species richness and biomass across taxa (Conrad et al., 2006; Hayhow et al., 2016; Pozsgai et al., 2016; Hallmann et al., 2017), driven by a complex combination of habitat loss or degradation (Fahrig, 2003; Brouwers & Newton, 2009), urbanisation (Fattorini, 2011), road traffic (Koivula & Vermeulen, 2005a; Dunn & Danoff-Burg, 2007; Graham et al., 2018), artificial light (Macgregor et al., 2017) and pesticides (Ewald et al., 2015; Stenoien et al., 2016; Woodcock et al., 2017). However, non-uniform (Ewald et al., 2015; Hayhow et al., 2016) and context specific or spatially variable trends (Burel et al., 2004; Woodcock et al., 2017) highlight the need for further research. Landscape processes will clearly operate on insects at many spatial and temporal scales, considering their range of life history strategies—long-distance migratory butterflies, relatively long-lived flightless predatory carabids and short-lived and minute residents of ephemeral patch habitats, to name a few examples.

There is probably no ideal indicator group that provides a proxy for all insects (though see possibly parasitic wasps (Mazón, 2016)). However, the sheer diversity of beetles, both in terms of the number of identified species and life history strategies, may provide an appropriately broad focus (Hutcheson, 1990), though it is not feasible to sample across the order within a single study (Gerlach et al., 2013). Thanks to the wide availability of identification resources, the study of beetles is also relatively accessible compared to, e.g., parasitic Hymenoptera. Three groups of beetles are commonly the focus of ecological research. Dung beetles are good indicators for landscape studies (Gerlach et al., 2013) as they are sensitive to changes in anthropogenic landscapes (Bicknell et al., 2014; Filgueiras et al., 2015). They are also commonly used as indicators for change in tropical forests (Korasaki et al., 2013) and to examine ecosystem services in livestock farming systems (Nichols et al., 2008; Manning et al., 2016), but rarely considered in urban or suburban landscapes (Ramírez-Restrepo & Halffter, 2016). Carabids are easy to catch and identify and so are often used in multi-species assessments (Eyre et al., 2004); they have proved useful for examining landscape heterogeneity or land use change (Petit & Burel, 1998b; Neumann et al., 2016b; Cajaiba et al., 2018) as well as assessments of site quality or local environmental change (Luff et al., 1992; Luff, 1996; Koivula & Vermeulen, 2005b; Neumann et al., 2015), but results based on carabids should be interpreted with caution, based on an understanding of how they interact with other groups (Rainio & Niemelä, 2003). Finally, saproxylic beetles are used as indicators for biodiversity associated with deadwood or with forest habitats generally (Lachat et al.,

2012; Sverdrup-Thygeson et al., 2014; Parisi et al., 2016), but perhaps rarely considered in conjunction with other species groups.

Other beetle groups may be suitable for directly studying ecosystem function or within-group trait-driven responses, such as carrion beetles (Wolf & Gibbs, 2004; Magura et al., 2013) and rove beetles (Magura et al., 2013). Rove beetles are the most diverse beetle family and may be excellent indicators for the response of biodiversity to environmental change; however, they are not studied nearly as often as the groups mentioned above (Bohac, 1999; Irmler & Gürlich, 2007; Da Silva et al., 2009; Vásquez-Vélez et al., 2010; Cajaiba et al., 2017).

This thesis will build on the large body of research concerning ground beetles in the first experimental chapter, considering whether the magnitude of extinction debt in woodland ground beetles may be greater than currently recognised. The second experimental chapter considers the response of all flower-visiting beetles to mesoscale landscape heterogeneity, with a follow-up chapter treating a single genus of beetles (*Anaspis*) from a family (Scraptiidae) that is very rarely studied in a landscape context apart from within saproxylic beetles (in a loose sense). The fourth experimental chapter considers beetles attracted to dung on an urban gradient, including rove beetles and other coprophilous families as well as true dung beetles.

## 1.5. Thesis Aims

The main aim of this thesis is to expand our knowledge of how beetle communities are distributed in spatially and temporally heterogeneous agricultural–urban mosaic landscapes. It will make a novel contribution in two main ways.

The first distinctive approach of this thesis is its comprehensive use of the available contemporary and historical land use and remote sensing data. Chapter 2 uses recently completed maps of Historic Landscape Character, not previously used for ecological research, to further investigate extinction debt in woodland ground beetles and ask whether time lags between environmental change and changes in species composition exceed those observed by Neumann, Holloway, Hoodless, & Griffiths (2017). Chapter 3 considers the response of flower-visiting beetles to mesoscale landscape mosaics, categorised using aerial imagery with non-woodland trees and other semi-natural linear features that are manually digitised. Linear features not captured in conventional land cover data are often ecologically important and improve models of landscape heterogeneity (Decleer et al., 2015; Jahnová et al., 2016; Neumann et al., 2016a; Sullivan et al., 2017).

Chapter 4 is developed from observations made in Chapter 3, especially of the genus *Anaspis* (Scraptiidae), the ecology of which is poorly known. LiDAR data are used to investigate the local

response of these beetles to habitat heterogeneity in more detail, demonstrating potential uses for a category of remote sensing data that has recently become much more widely available.

The second distinctive approach concerns sampling methods. Field data for Chapters 3 and 4 are obtained by using abundant spring and summer flowers as effective ready-made 'traps' for beetles. Chapter 5 uses a simplified version of dung-baited traps to sample in highly disturbed urban sites. In each case the community of beetles assembled around these baits is drawn from different elements of the surrounding landscape mosaic, rather than focussing entirely on the species of woodland or semi-natural grassland, for example.

Altogether, this thesis will explore the use of landscape data to identify the extent to which patterns in beetle community composition are driven by landscape heterogeneity. It will consider three communities of beetles, of which two are much less well known in a landscape ecology context than well-studied groups such as ground beetles. It also examines a range of spatial scales and different approaches to constructing variables that describe landscape composition and configuration.

## 1.6. Sampling Methods

Any sampling method potentially introduces bias. All three methods used in the following thesis measure the activity density of beetles rather than the true density. This has been well understood for some time, particularly with respect to pitfall traps (Luff, 1975; Lovei & Sunderland, 1996; Moretti et al., 2002), which are only 'partially successful' for determining relative abundance according to Topping & Sunderland (1992). More active or mobile species are likely to be trapped more often (Greenslade, 1964; Topping & Sunderland, 1992) and catches tend to be biased toward larger species (Spence, 1994); Hancock & Legg (2012) showed that the majority of variation in bias can be explained by body mass. Habitat heterogeneity modifies beetle activity (Melbourne, 1999) and can impact the species composition of catches (Ward et al., 2001); again, the catch rate for species with differing traits might be expected to vary differentially with habitat. Sampling intervals also influence catching rates, with some species attracted to traps that already contain invertebrates (Holland & Reynolds, 2005; Schirmel et al., 2015). In general, while pitfall trapping is a useful method (Luff et al., 1992) results should be interpreted with care.

In this study, traps are set at > 25 m separation to avoid depleting the catch of rarer species (Ward et al., 2001) and to increase the species richness of the samples versus what would be achieved with traps at a closer separation, which is sometimes recommended (Digweed et al., 1995; Weaver, 1995). A cover is used to make traps more robust to longer sampling windows and maximise the probability that traps will be open during a period of high ground beetle activity; covers do not modify the efficacy of traps and reduce vertebrate bycatch (Buchholz & Hannig, 2009).

Flower-visiting insects are sampled in Chapters 3 and 4. Although the abundance of flower-visitors is frequently used in research, particularly with respect to pollinator conservation, fewer studies have examined the bias inherent in the various sampling methods for flower-visiting insects. Studies generally employ standardised transects or plots of flowers and make multiple visits to each to reduce seasonal and weather-related effects; these include other studies of flower-visiting beetles (e.g. Diekötter et al. (2007); Sjödin et al. (2008); Bommarco et al. (2014); Horak (2014); Cusser et al. (2015)). A similar protocol is used in this thesis. Adult beetles on flowers are usually present to feed on nectar rather than for oviposition, with breeding sites elsewhere, but are often observed in copulation (especially Cantharidae and Cerambycidae). In this thesis it is assumed that a higher abundance of a species at a site indicates closer proximity of breeding sites, since the flowering plants used for survey are near ubiquitous in the landscapes studied and unlikely to limit the distribution of beetles themselves. Dung-baited traps are used frequently in studies of true dung beetles (Hanski & Cambefort, 1991; Hutton & Giller, 2003) though usually for longer time windows than used in Chapter 5. To account for the potential bias introduced by a short time window, site visits were randomised and two visits were made to each site only in appropriate conditions in which dung feeding beetles are usually actively searching.

All three methods are consistently applied across sites in randomised sampling protocols, which should reduce the possibility of an artefact of sampling (e.g. weather, seasonality or other drivers of activity) being introduced into the species community data. Although all data obtained necessarily reflect the activity density of species and not always the true relative abundance at a site, this should amount to noise in the data rather than any systematic bias, which increases the possibility of a type I error.

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## 2. Two Centuries of Extinction Debt: Landscape Heterogeneity in the 18th and 19th Centuries Influences Contemporary Woodland Ground Beetle Distribution

### 2.1. Introduction

There is a pressing need to quantify estimates of extinction risk to inform conservation strategies, especially for invertebrates, for which current population estimates are often poor (Kuussaari et al., 2009; Cardoso et al., 2011; Dullinger et al., 2013). Habitat loss is recognised as a major driver of local extinctions, through direct effects or landscape fragmentation, which impacts populations by reducing size and connectivity of habitat patches (Kruess & Tscharntke, 1994; Yekwayo et al., 2016) or decreasing the permeability of surrounding matrix habitats (Kappes et al., 2009; Neumann et al., 2016b). In highly fragmented landscapes, the metapopulation structure may be eroded, especially for species with limited dispersal ability (Hanski & Ovaskainen, 2000). As a result, relict populations can persist in landscapes that no longer contain suitable habitat cover or connectivity; these are effectively in extinction debt (Tilman et al., 1994; Pimm & Askins, 1995; Hanski & Ovaskainen, 2002). Likewise, depending on their size and connectivity, newly established habitat patches may take several centuries to establish a full complement of specialist species such that they carry a colonisation credit (Assmann, 1999; Irmler et al., 2010; Naaf & Kolk, 2015). Extinction debts may also arise from changes in habitat quality impacting the productivity of individuals or loss of habitat, increasing extinction risk in single populations (Jackson & Sax, 2010; Hylander & Ehrlén, 2013).

Though the importance of matrix habitats for reducing extinction thresholds in fragmented landscapes is increasingly well recognised (Bender & Fahrig, 2005; Neumann, Griffiths, Foster, & Holloway, 2016; Neumann, Griffiths, Hoodless et al., 2016), studies addressing extinction debt that use whole-mosaic land use data for past landscapes (Gustavsson et al., 2007; Aguirre-Gutiérrez et al., 2015; Cusser et al., 2015; Neumann et al., 2017) are less well represented in the literature than those working within a patch-matrix paradigm. This is perhaps due to a lack of available historic land use data (though see Skanes & Bunce, 1997; Cui et al., 2014; Auffret et al., 2017), especially for time periods prior to the 20th century. A study of grassland plants in Sweden that used digitised historical maps from as far back as 1712 is among the longest time-depths examined (Gustavsson et al., 2007). In the United Kingdom, many local governments have completed Historic Landscape Character maps (English Heritage, 2018), which, for a given patch of landscape, indicate current and past land use, with the most recently identifiable land-use changes generally being around the late 18th century. These are yet to be exploited for biodiversity research.

Using data from the Dudley Stamp Land Utilisation survey (Clark, 2011; Hooftman & Bullock, 2012), a detailed land cover map produced by fieldworkers in the 1930s, Neumann et al. (2017) found that the contemporary distribution of ground beetles (Coleoptera: Carabidae) in woodlands was better explained by the configuration of landscape elements 80 years ago than by present-day landscape configuration, suggesting an extinction debt. Given that estimates of extinction debt for both plants and lichens in woodland range from 100 to 180 years (Berglund & Jonsson, 2005; Paltto et al., 2006; Ellis & Coppins, 2007; Ranius et al., 2008; Kolk & Naaf, 2015), we might assume that habitat specialist invertebrate species also respond to change with a similar time lag, in excess of 80 years, but few studies of extinction debt consider insects (see Sang et al., 2010; Bommarco et al., 2014; Cusser et al., 2015).

In this study we assess the potential utility of Historic Landscape Character (HLC) mapping for exploring the problem of extinction debt. Specifically, we address the question of the extinction debt identified by Neumann et al. (2017) in woodland carabids, a well-studied group of invertebrates that are sensitive to environmental change and land-use patterns (Burel et al., 1998; Niemelä, 2001; Vanbergen et al., 2005). Using HLC maps, we reconstruct land use data for two further 80-year steps before the Dudley Stamp survey of the 1930s. Target years for reconstruction were 1770, when land use patterns in our study region were largely unplanned and reflected the structure of the ancient countryside, and 1850, after the completion of most parliamentary enclosures in the area saw ancient field patterns replaced by planned farmland divided by newly planted hedges (Rackham, 1986; Berkshire Record Office, 2018).

By comparing the correlation of woodland carabid communities to these two land use reconstructions, land use in the 1930s (data from Dudley Stamp) and in 2015 (contemporary land cover), we seek to answer the following questions:

1)  Can we identify an extinction debt for woodland carabids as per Neumann et al. (2017)?
2)  Are there ecologically meaningful correlations between the land use data derived from Historic Landscape Character maps and contemporary carabid communities?
3)  Is it possible to more precisely determine the nature and relaxation time of extinction debt in woodland carabids by i) identifying significant landscape composition and configuration variables for each time period and ii) using variation partitioning to determine their relative contributions?

## 2.2. Methods

### 2.2.1 Study Region

The study was carried out across an urban–rural mosaic landscape centred on the town of Reading in southern England (Figure 1). This lowland area is bisected by the River Thames and major tributaries, along the valleys of which the landscape is dominated by improved grassland and larger urban settlements including Reading and Wokingham. Arable farming is most dominant in the Chiltern Hills to the north of the Thames, which are also well-wooded. Small remnant patches of semi-natural calcareous grassland can be found on the chalk escarpment to the north and west of the study area and fragments of lowland heath to the south. Larger patches of grassland or heath that existed in the 18th and 19th centuries have gradually been converted to agricultural land or secondary woodland. Elevation ranges from 20 metres above sea level in the Thames valley to just over 200 m in the Chiltern Hills. The climate is temperate, with a mean annual maximum temperature in Reading of 14.5 °C and annual precipitation of 635 mm (Met Office, 2017).

### 2.2.2. Study Design

Sample sites were selected by starting with all woodland patches within 20 km of the centre of Reading, UK. Patches not categorised as ancient woodland (Natural England, 2013) or otherwise continuously wooded since the late 18th century were excluded, as were predominately coniferous patches and woodlands managed for gamebird shooting (Oxbrough et al., 2010; Neumann et al., 2015). Sample points within woodland were then selected randomly, within the constraints of evenly distributing sites on a broad urban-rural gradient assessed using data from Landcover Map 2007 (Morton et al., 2014). Points in the final selection were at least 1 km apart and in separate woodland patches, defined as >20 m separation (Brouwers & Newton, 2009; Neumann et al., 2016b, 2017) or where bisected by roads which present a significant barrier to carabid dispersal (Koivula & Vermeulen, 2005; Neumann et al., 2016b). Selected sampling points were not necessarily in the patch centre but were all in woodland interior (>20 m from any edge). Study landscapes were defined as 1 km radius circular buffers around each sampling point (Figure 1).

### 2.2.3. Carabid Sampling

Carabid communities at each sampling point were surveyed using pitfall traps. Traps consisted of two nested plastic cups: an outer cup with small holes in the bottom for drainage and an inner cup with the top 1 cm removed so that it fitted snugly inside the outer. Cups were 100 mm deep and 70 mm wide at the opening. The trap was dug in so that the rim of the outer cup was completely flush with the ground. A 140 mm wide Petri dish was placed over the top, raised on wooden skewers stuck vertically in the ground, to prevent the trap from flooding. Traps were filled with 50 mL of 50% dilute ethylene glycol antifreeze. Three traps were set at each site, evenly spaced on the

perimeter of a 20 m radius circle around the pre-determined sampling location (see Section 2.2 above) such that all traps were separated by > 20 m (Digweed et al., 1995; Ward et al., 2001). Traps were set for a continuous period of 14 days on start dates between 6th May 2013 and 13th May 2013 with the site order randomised. Traps were then reset for another 14-day period with start dates between 15th June and 25th June 2013, following a different random order. Data from the three traps and two sampling periods were combined for each site and specimens stored in 70% ethanol prior to identification. All carabids were identified to species following Luff (2007) using a binocular microscope; species trait information was taken from Luff (2007) and Duff (2012). We used double blind identification for quality control.
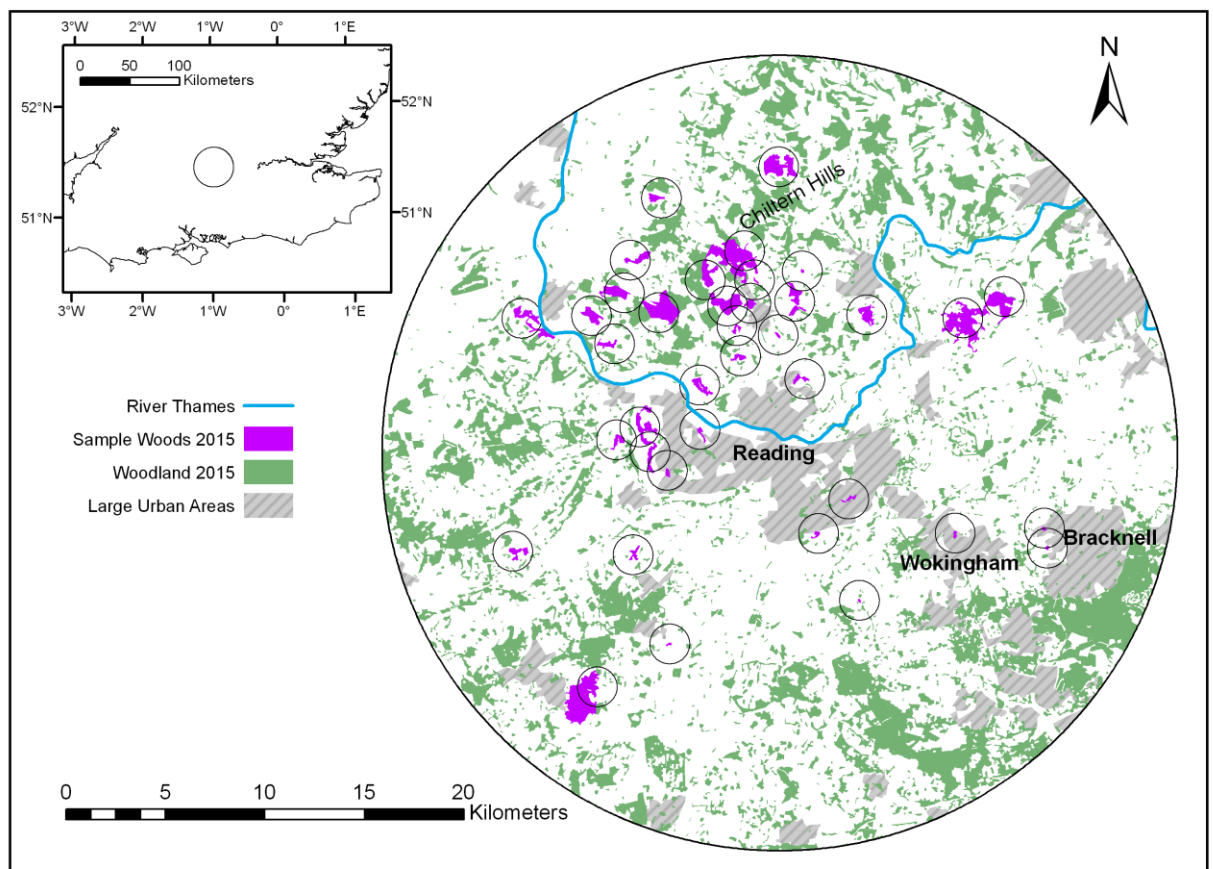


**Figure 1**. The distribution of 36 study woodland patches around Reading and the location of the study area within the UK (inset). 1-km buffers were used to define study landscapes and are illustrated with black open circles. Larger urban areas are labelled on the main map. Woodland data are derived from CEH Land Cover Map 2015 (Rowland et al., 2017), large urban areas and rivers from OS Strategi (Ordnance Survey, 2016). Contains Ordnance Survey data © Crown copyright and database right 2018.

### 2.2.4. Contemporary Land Use Data

Contemporary land use was classified using data from Landcover Map 2015 (LCM2015) (Rowland et al., 2017) reducing the available land use types in the raw data to six categories for closer equivalence with earlier data sources (Table 1). Classification of grassland habitat was improved using data from the Natural England Priority Habitat Inventory (Natural England, 2015).

### 2.2.5. Historic Land Use Data

*Historic land use data (1930s)*

Land use data for the 1930s was based on the Dudley Stamp Land Utilisation Survey maps, originally printed at one-inch-to-one-mile (1:63,360) between 1933 and 1949 from survey data originating in the early 1930s (Southall et al., 2007). The paper maps were digitised in 2011 (Clark, 2011). The categories mapped in the original survey were reclassified into six broad land use classes (Table 1).

*Historic land use data (c. 1770 and c. 1850)*

Historic Landscape Character (HLC) data are supplied as a single layer of polygons with corresponding information for each about current and past land use, estimates of start and end dates for each land use type, and references to data sources. As the precise date of a land use change or original data sources were not available in every case, our land use data for these two time slots should be considered a reconstruction rather than a map of what was actually present in the target year.

Where the appropriate classification was not clear in the HLC data, the primary data sources were consulted directly: the Rocque map of Berkshire (Rocque, 1761), parish enclosure maps (Berkshire Record Office, 2018) and Ordnance Survey county series maps 1st edition (Ordnance Survey, 2015). Classification of woodlands for 1770 was confirmed using Ancient Woodland data from Natural England (Natural England, 2013) with any contemporary woodland patches classified as Ancient Woodland assumed to have been wooded in 1770.

Finally, polygons were reclassified to a reduced set of land use classes adhering as closely as possible to the six categories used for the 1930s Dudley Stamp survey (Table 1). It was not possible to ascertain the exact past use of some ancient or enclosed field patterns; they were therefore classified as permanent farmland and not separated into arable or grassland. However, polygons

were classified as permanent grassland if past use indicated that they were never cropped (e.g., 'pasture' or 'downland'). These differ from the agricultural land use categories derived from Dudley Stamp and LCM2015, in which it is possible to split arable, improved grassland and semi-natural grassland. An example classification for one study landscape is given in Figure 2. All GIS processing was carried out in ArcMap 10.4 (ESRI, 2016).

**Table 1.** Summary of the reclassification of two historic and one contemporary data sources into broad land use categories.

| Classification | HLC character types | Dudley Stamp maps | Land Cover 2015 |
|---|---|---|---|
| Permanent Farmland (c. 1770, c. 1850) Arable (1930s, 2015) | Open fields (various), Enclosures and Assarts (various), Nurseries, Horticulture, Allotments | Arable land | Arable and Horticulture |
| Improved Grassland | n/a | n/a | Improved Grassland |
| Permanent Grassland (c. 1770, c. 1850) Semi-natural Grassland (1930s, 2015) | Pasture, River valley floor, Downland, Meadows, Parkland | Meadowland, Permanent grasslands | Acid grassland, Calcareous grassland, Neutral grassland |
| Heath & Scrub | Common, Heathland, Scrub/Scattered trees, Unenclosed rough ground | Heath, Moorland | Heather, Heather Grassland |
| Urban | Settlement (various), Industrial (various) | Urban core, Suburban | Suburban, Urban |
| Water or Marsh | Lake, Marsh, Pond, River | Water | Freshwater |
| Woodland | Ancient woodland, Woodland plantation, Secondary woodland, Orchard | Forest, Woodland | Broadleaf woodland, Coniferous woodland |

## 2.2.6. Landscape Configuration

Landscape configuration was represented by the mean area and number of patches for woodland and grassland, which were identified as significant elements by Neumann et al. (2017), with the addition of urban patch size since this changed markedly over the course of the study (Table 2). We also included patch size for the woodland patch sampled and the total length of woodland edges as measures of woodland habitat amount and integrity.
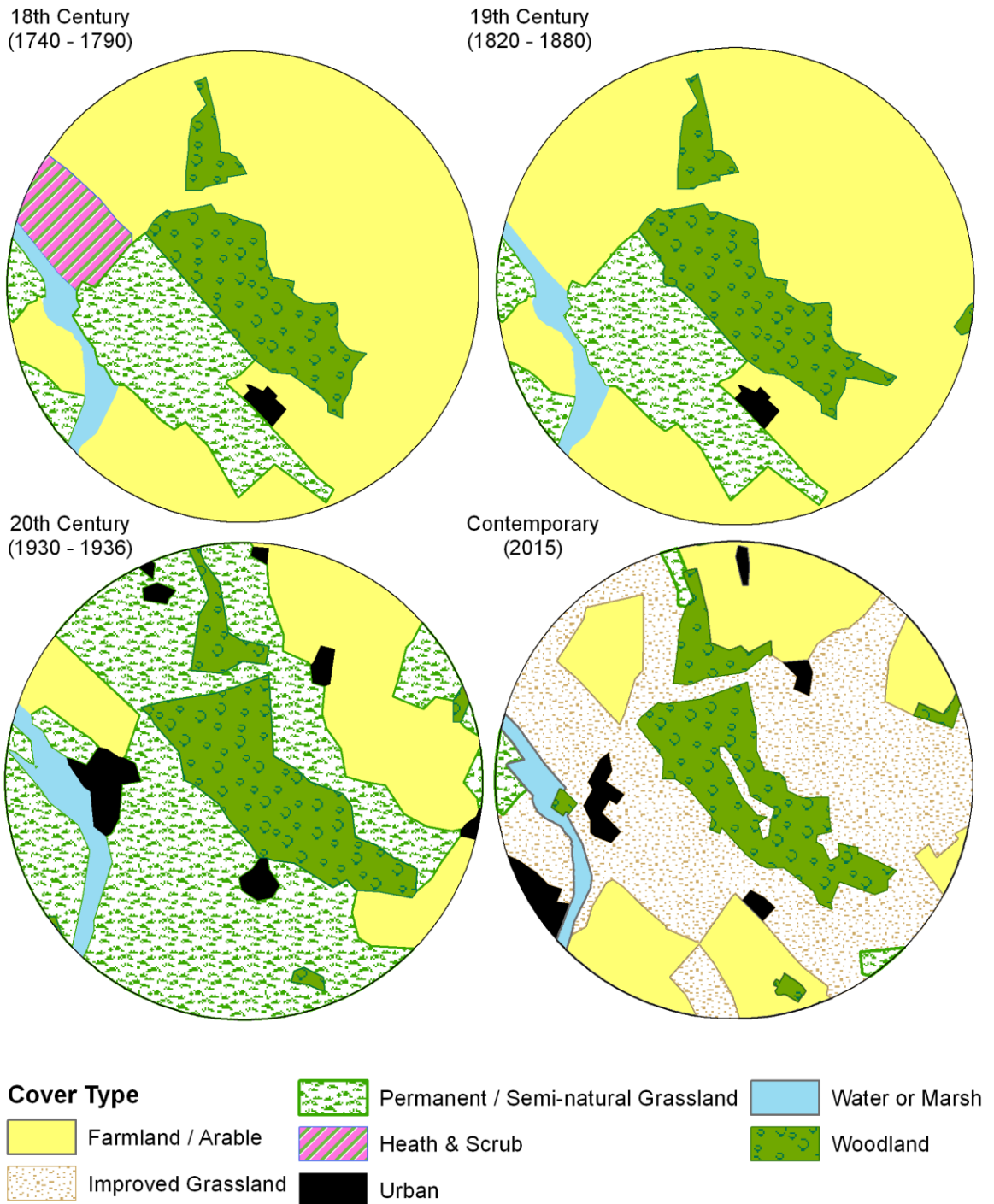
**Figure 2.** Example land use classification of a 1-km radius study landscape for four time periods.

### 2.2.7 Statistical Analysis

The effects of landscape composition, landscape configuration and spatial autocorrelation on carabid community composition were assessed using redundancy analysis (RDA), carried out in R 3.4 (R Core Team, 2017) with the package 'vegan' (Oksanen et al., 2016). Eight models were run,

one each for landscape composition and landscape configuration variables for all data sources: contemporary (2015), Dudley Stamp (1930s) and HLC (c. 1850 & c. 1770). Spatial autocorrelation (where neighbouring sample points may possess similar communities) was also assessed with RDA by using principal coordinates of neighbourhood matrices (PCNM) as predictors of beetle community composition (Borcard & Legendre, 2002).

Following a significant global permutation test (at $p < 0.05$), a forward selection procedure was used to obtain a more parsimonious set of explanatory variables that explained a significant proportion of carabid community variation. Forward selection was carried out using the 'vegan' function *OrdiR2step*, which at each step admits the variable estimated to contribute the largest increase to total variation explained providing a) they are statistically significant and b) their addition does not take the adjusted $R^2$ beyond that achieved by the global model; this avoids overfitting of explanatory variables (Blanchet et al., 2008). Monte Carlo simulations with 9999 permutations were used to estimate probability values for the global permutation tests and the variables included in the reduced models.

Landscape composition variables were transformed by log ($x$+1) to ensure ecologically important land cover types with small coverage gained appropriate weighting within the models (Cleveland, 1993; Neumann et al., 2016a, 2017) Multicollinearity was controlled by inspecting variance inflation factors; terms with high VIF were removed sequentially until all VIF were < 5.0. Carabid community data were $\log_{10}$ transformed (where $x > 0$) (Anderson et al., 2006) in order to downweight the influence of abundant species on the ordination (Vanbergen et al., 2005; Neumann et al., 2017). Variation partitioning was used to explore the total overall variation explained by significant terms from the reduced models as well as what proportion of variation could be uniquely attributed to each time period (Borcard, Legendre, & Drapeau, 1992; Legendre, 2008; Peres-Neto, Legendre, Dray, & Borcard, 2006).

## 2.3. Results

### 2.3.1. Land Use Change

Table 2 summarises the land use data for each time period. The Heath & Scrub category declined at each step, from an initial 12. % in the 18th century to 2% in the contemporary landscape. Woodland cover increased by 32% but this coincided with an increase in the number of woodland patches throughout; the mean woodland patch size in the contemporary data was smaller than for any of the historical time periods. Sample patch size was also lower in the contemporary landscape than in all but the 18[th]century data so, overall, whilst more woodland habitat was available across the

contemporary landscape, it was also more fragmented. Much of the loss of sample patch area was due to fragmentation by roads. The amount of urban land use increased tenfold between the 18th century and the present day, with a similarly large increase in the mean area of urban patches (2–24 ha). It is not possible to make a direct comparison for farmland and grassland between the time periods categorised using HLC (c. 1770, c. 1850) and the later ones (1930s, 2015) since the classifications used were slightly different (Table 1). However, the large increase in grassland coverage between 1850 (permanent grassland) and the 1930s (semi-natural grassland) from 11% to 43% may also reflect the genuine decline in arable acreage in the United Kingdom that gradually followed the repeal of the corn laws in 1846. For example, census data suggest that the proportion of arable farmland in 1869 was at least 60% for all parts of our study area; by 1931 arable ranged from 32% to a maximum of 59% of farmland (University of Portsmouth, 2017).

Thirty percent of permanent grassland was lost between c. 1770 and c. 1850, almost all to enclosed farmland. Most semi-natural grassland in the 1930s data was lost by 2015, with only 3% cover remaining in the landscape. This was mainly due to agricultural improvement, with 48% converted to improved grassland and 21% to arable. A further 20% was developed as new urban areas, whilst 8% became plantation or secondary woodland.

**Table 2.** Mean values for variables used to describe landscape heterogeneity in four time periods across 36 1km radius circular study landscapes.

| | c.1770 | c.1850 | 1930s | 2015 | |
|---|---|---|---|---|---|
| **Composition Variables** (c. 1770, c. 1850) | % cover | % cover | % cover | % cover | **Composition Variables** (1930s, 2015) |
| Permanent Farmland | 62.6 | 66.6 | 20.9 | 21.6 | Arable |
| Permanent Grassland | 12.8 | 10.6 | 42.6 | 2.7 | Semi-natural Grassland |
| Heath & Scrub | 12.2 | 6.0 | 3.5 | 2.0 | Heath & Scrub |
| Urban | 2.3 | 2.8 | 10.8 | 20.5 | Urban |
| Water or Marsh | 1.3 | 1.2 | 1.0 | 1.6 | Water or Marsh |
| Woodland | 18.0 | 20.5 | 23.0 | 23.7 | Woodland |
| | | | | 33.5 | Improved Grassland |
| | | | | | |
| **Configuration Variables** | | | | | |
| Area of sample patch (ha) | 50.2 | 56.2 | 83.5 | 51.5 | |
| Woodland edge (km) | 8.2 | 9.7 | 10.4 | 10.9 | |
| Number of woodland patches | 6 | 8 | 9 | 9 | |
| Mean area woodland patches (ha) | 10.8 | 10.1 | 10.9 | 9.3 | |
| Number of grassland patches | 3 | 3 | 9 | 1 | |
| Mean area grassland patches (ha) | 6.5 | 7.0 | 19.7 | 1.7 | |
| Number of urban patches | 4 | 6 | 10 | 6 | |
| Mean area urban patches | 1.7 | 1.8 | 4.4 | 24.3 | |

### 2.3.2. Carabid Community

Pitfall trapping obtained 4003 beetles from 40 species. Almost 90% of these were from the widespread and abundant species *Nebria brevicollis* (38.2%), *Abax parallelepipedus* (31.3%) and *Pterostichus madidus* (18.7%). All three were ubiquitous, with *N. brevicollis* and *P. madidus* recorded at every site and *A. parallelepipedus* only missing from one. No other species made up more than 3% of the total catch, though several were widespread. *Notiophilus biguttatus* and *Loricera pilicornis*, which are both eurytopic species, and the woodland species *Carabus violaceus, Carabus problematicus* and *Calathus rotundicollis* were all captured on at least 10 out of 38 sites, as was *Leistus rufomarginatus*, which was first recorded in the UK in 1942 (Crowson, 1942), later than the earliest three time periods under consideration here. A full illustrated species list is given in Appendix 1.1.

### 2.3.3. Spatial Autocorrelation

Testing for spatial autocorrelation using PCNM revealed that neighbouring carabid communities were not more similar to each other ($F = 1.2056$, $p = 0.434$).

### 2.3.4. Effect of Land Use Heterogeneity on Carabid Community Composition

A summary of the results for all time periods is provided in Table 3.

**Table 3.** Redundancy analysis results for the effects of landscape composition and configuration in four time periods on the composition of contemporary woodland carabid communities. Global models (left) give the combined effect of all composition or configuration variables, reduced models (right) contain only those key explanatory variables identified by a forward selection procedure.

| Global Models | | | | | Reduced Models | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | F | *p* | % var | $R^2$-adj | Variable | F | *p* | % var | $R^2$-adj |
| **Landscape Composition** | | | | | | | | | |
| 2015 | 1.450 | 0.018 | 25.3% | 7.8% | Arable | 2.721 | 0.016 | 7.0% | 4.4% |
| 1930s | 1.136 | 0.038 | 20.8% | 5.5% | Urban | 2.545 | 0.006 | 7.5% | 4.0% |
| c.1850 | 1.449 | 0.020 | 21.9% | 6.8% | n/a | | | | |
| c.1770 | 1.703 | 0.002 | 24.8% | 10.2% | n/a | | | | |
| **Landscape Configuration** | | | | | | | | | |
| 2015 | 1.246 | 0.078 | 28.6% | 5.6% | Mean urban patch | 3.209 | 0.003 | 8.2% | 5.6% |
| 1930s | 0.971 | 0.549 | 26.3% | 0.0% | | | | | |
| c.1850 | 1.362 | 0.024 | 30.4% | 8.1% | Sample patch area | 2.061 | 0.035 | 6.3% | 7.4% |
| | | | | | N grass. patches | 2.021 | 0.028 | 6.1% | |
| c.1770 | 1.430 | 0.008 | 31.2% | 10.0% | N grass. patches | 3.589 | < 0.001 | 9.1% | 6.5% |

Landscape composition c. 1770 explained 24.8% of variation in the modern carabid community ($F = 1.703$, $p = 0.002$). Although the global model was significant, no terms were included in a reduced model by the forward selection process. Landscape configuration c. 1770 explained 31.2% of variation ($F = 1.430$, $p = 0.008$), with the number of grassland patches the only term included in the reduced model ($F = 3.589$, $p < 0.001$), explaining 9.1% of variation (Figure 3). The large-bodied, flightless woodland species *C. violaceus*, *C. problematicus* and *A. parallelepipedus* were all associated with landscapes with few patches of permanent grassland c. 1770, as was the large-bodied but flight-able woodland species *Pterostichus niger*. *N. biguttatus* and *Pterostichus strenuus* (both eurytopic) and *Poecilus cupreus* (a grassland species) were all associated with landscapes containing more patches of permanent grassland c. 1770.
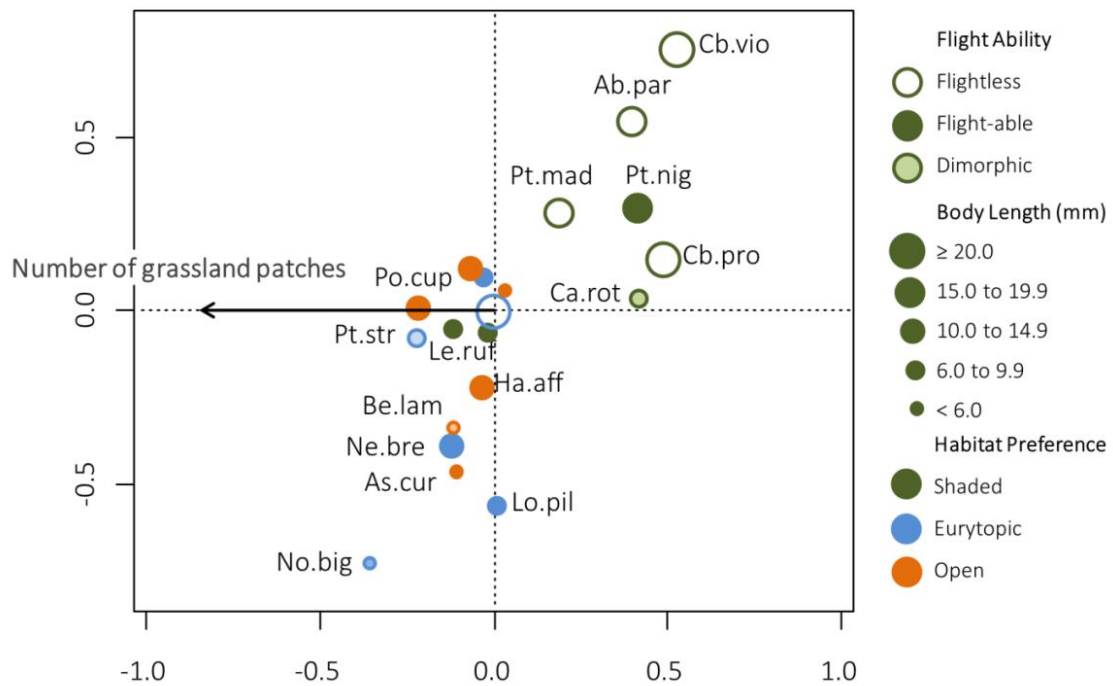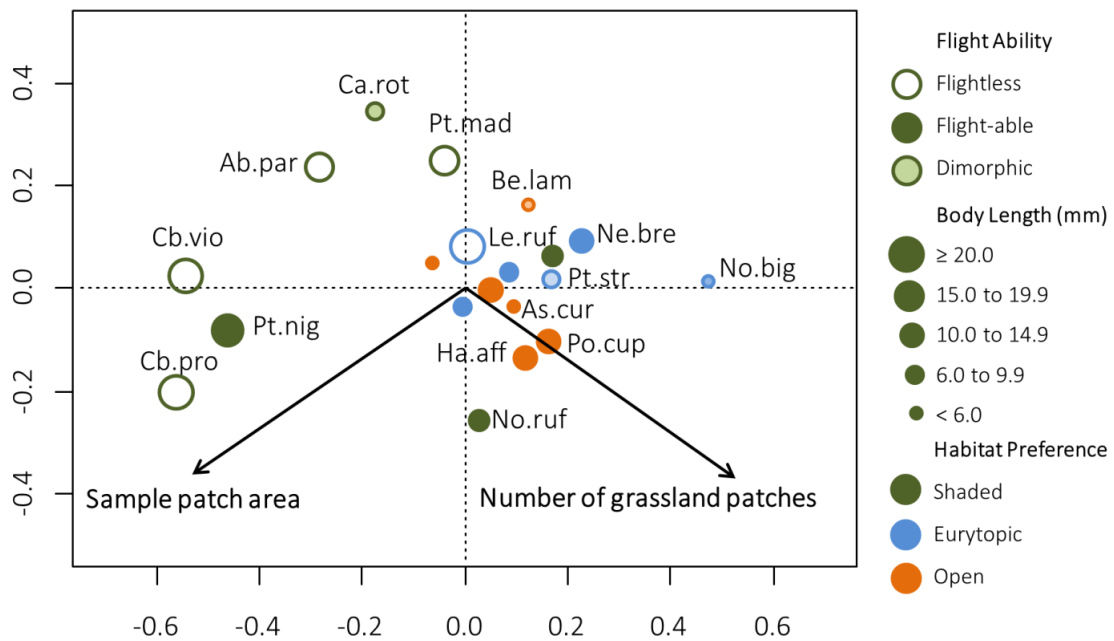


**Figure 3.** Redundancy analysis (RDA) biplot for the response of carabid communities to key c.1770 landscape configuration variables identified by forward selection. Only the first ordination axis is constrained, explaining 9.1% of variation. All species are displayed; for clarity those with low scores on both axes or not otherwise mentioned in the text are unlabelled. Refer to Table S1 in supporting information for full species names.

*HLC data c. 1850*

Landscape composition c. 1850 explained 21.9% of variation in the carabid community ($F = 1.449$, $p = 0.020$). No terms were included in a reduced model by the forward selection process.

Landscape configuration c. 1850 explained 30.4% of variation in the carabid community ($F$ = 1.362, $p$ = 0.024). Sample patch area ($F$ = 2.061, $p$ = 0.035) and the number of grassland patches ($F$ = 2.021, $p$ = 0.028) were included in the reduced model. The two constrained biplot axes explained a total of 12.4% variation in the carabid community, with 9.3% attributable to RDA1 and 3.1% to RDA2 (Figure 4). Species exhibiting the strongest response to either axis were generally the same as those responding in the c. 1770 model. Of the woodland species, *C. violaceus, C. problematicus, P. niger* and *Notiophilus rufipes* were positively correlated with sample patch size c. 1850. The three ubiquitous species showed either a weak positive relationship with sample patch size (*A. parallelepipedus*) or a negative relationship (*P. madidus* and *N. brevicollis*).



**Figure 4.** Redundancy analysis (RDA) biplot for the response of carabid communities to key c.1850 landscape configuration variables identified by forward selection. The two constrained axes together explain 12.4% of variation. All species are displayed; for clarity those with low scores on both axes or not otherwise mentioned in the text are unlabelled. Refer to Table S1 for full species names.

### *Dudley Stamp Land Utilisation 1930s*

Landscape composition in the 1930s explained 20.8% of variation in the carabid community ($F$ = 1.136, $p$ = 0.038). Urban area was the only term included in the reduced model ($F$ = 2.545, $p$ = 0.006), explaining 7.5% of the variation (Figure 5).

Woodland species that were strongly linked with low numbers of grassland patches c. 1770 and c. 1850 were also linked to low urban land use in the 1930s. Species exhibiting the strongest response

were *C. violaceus* and *C. problematicus*, both large-bodied flightless species. *L. pilicornis* and *N. biguttatus*, two eurytopic species frequently found in shady habitats including woodland but also gardens and parks, were positively correlated with urban land use in the 1930s. Landscape configuration variables for the 1930s explained 26.3% of the variation but the global model was non-significant ($F = 0.971$, $p = 0.549$).
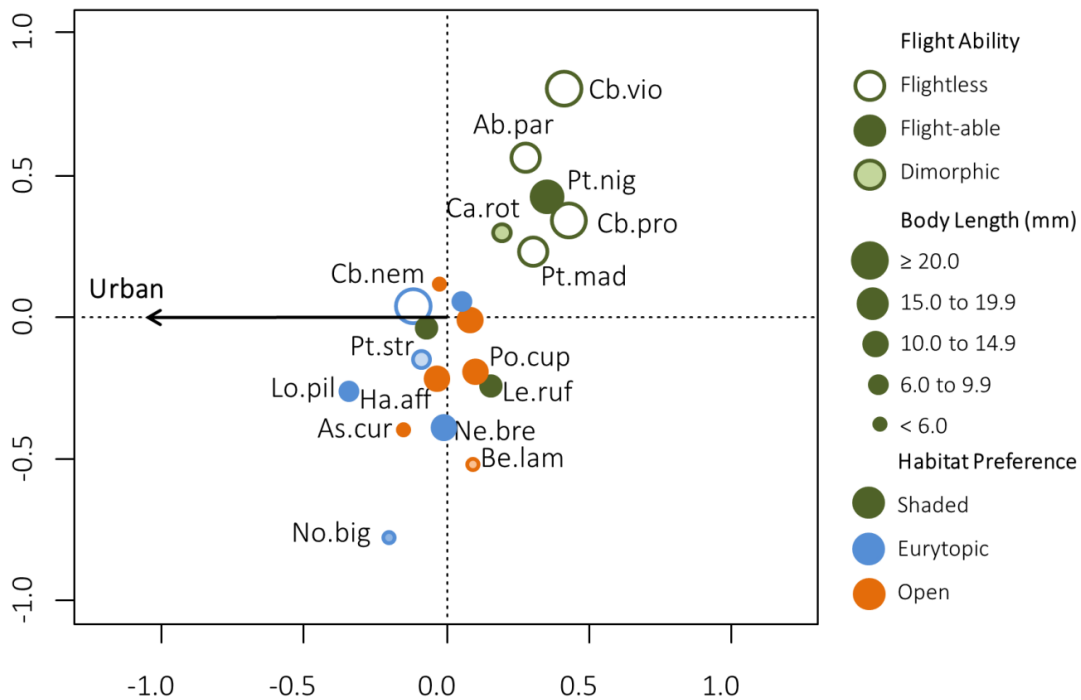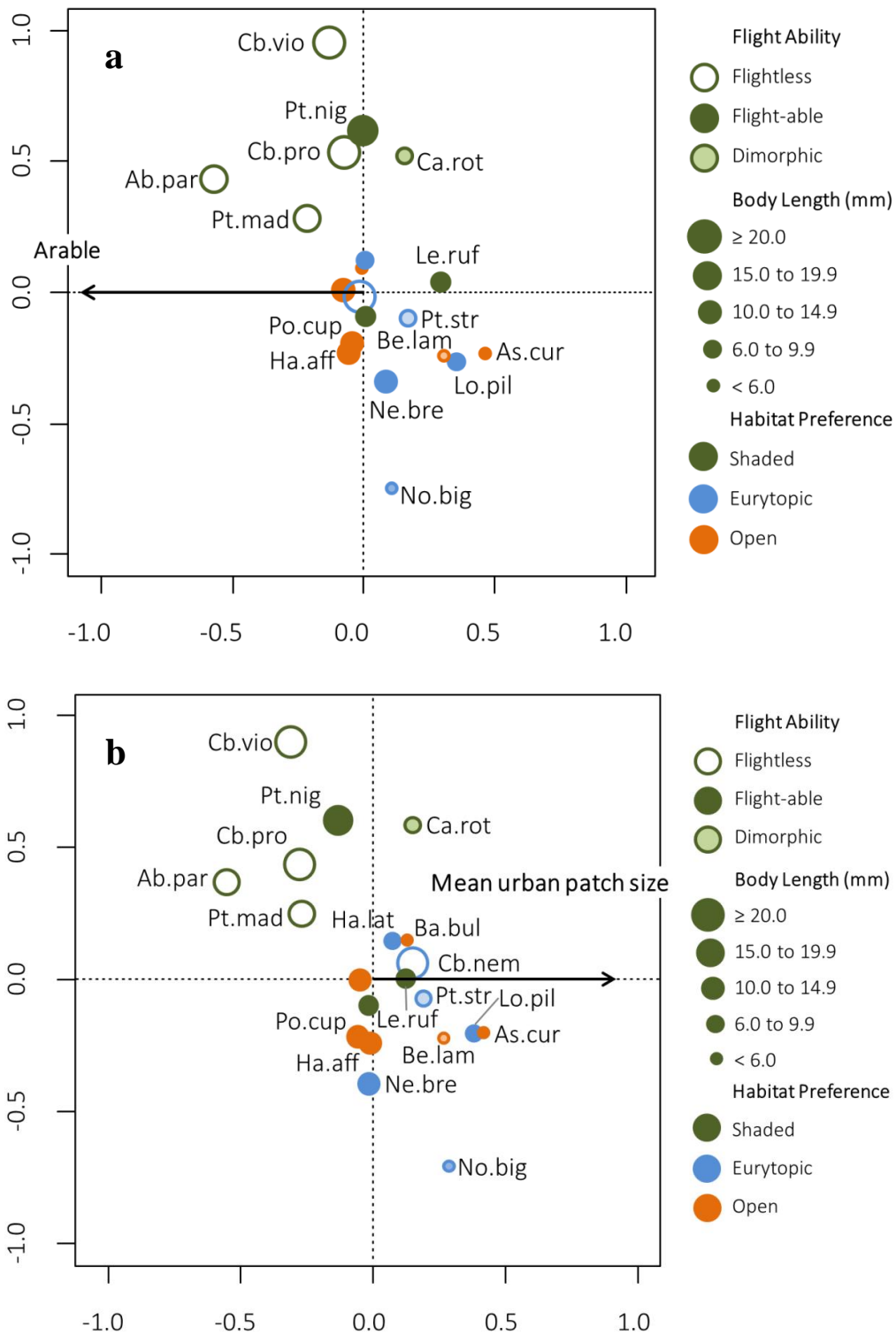


**Figure 5.** Redundancy analysis (RDA) biplot for the response of carabid communities to key 1930s landscape composition variables identified by forward selection. Only the first ordination axis is constrained, explaining 7.5% of variation. All species are displayed; for clarity those with low scores on both axes or not otherwise mentioned in the text are unlabelled. Refer to Table S1 for full species names.

*Land Cover Map 2015*

Landscape composition in 2015 explained 25.3% of the variation in the carabid community ($F = 1.450$, $p = 0.018$). Extent of arable land was included in the reduced model ($F = 2.721$, $p = 0.016$), explaining 7.0% of variation (Figure 6a). Landscape configuration in the 21st century explained 28.6% of the variation ($F = 1.246$, $p = 0.078$), with mean urban patch area (UPA) included in the final model ($F = 3.209$, $p = 0.003$), explaining 8.2% of the variation (Figure 6b). Although the global model for landscape configuration was not significant at $p > 0.05$, inspection of the biplots (Figure 6) shows that a similar environmental gradient is explained by both landscape composition and configuration. *A. parallelepipedus* and *P. madidus* are positively related to area of arable and negatively related to mean urban patch size. Large-bodied woodland species *C. violaceus, C. problematicus* and *P. niger* show a weak positive relationship with arable land use and a stronger

negative relationship with mean urban patch size. *N. biguttatus, L. pilicornis, Asaphidion curtum* and *Bembidion lampros,* all smaller-bodied eurytopic or open habitat species, are positively related to mean urban patch size and negatively related to area of arable.



**Figure 6.** Redundancy analysis (RDA) biplot for the response of carabid communities to key contemporary landscape composition variables (**a**) and configuration variables (**b**) identified by forward selection. Only the first ordination axis is constrained, explaining 7.0% of variation. All

species are displayed; for clarity those with low scores on both axes or not otherwise mentioned in the text are unlabelled. Refer to Table S1 for full species names.

### 2.3.5. Model Comparison & Variation Partitioning

Examining adjusted-$R^2$ to account for the larger number of variables included in the LCM2015 composition model, the HLC model for c. 1770 performed best in terms of variation explained by the global model for both landscape composition and landscape configuration. In both cases the Dudley Stamp 1930s data explained the smallest amount of variation (Table 3). Prior to variation partitioning of variables from all four time periods, the significant variables from LCM2015 data (composition variable Arable and configuration variable mean urban patch size) were partitioned to confirm that they represent the same gradient in the carabid data. Neither significantly explained a unique proportion of variation ($p = 0.146$, $p = 0.325$) and so mean urban patch size was taken forward for final variation partitioning as it explained slightly more variation (8.2% vs. 7.0%).

Variation partitioning showed that the significant variables from the four time periods together explained 14.7% of the variation in the carabid community data (Figure 7). Of this, 5.2% was explained by mean urban patch size from the LCM2015 data, i.e., contemporary landscape, whilst 9.7% was explained by combined effects of variables from the historic data sources. 2.6% was shared between contemporary and historic variables. Unique fractions for the 1930s (2.4%, $F = 1.867$, $p = 0.031$) and 2015 (5.2%, $F = 3.042$, $p < 0.001$) were significant. Unique fractions explained by the 18th (0.9%, $F = 1.493$, $p = 0.106$) and 19th centuries (2.0%, $F = 1.408$, $p = 0.085$) were not significant but the total fraction uniquely explained by the 18th- and 19th-century variables together, i.e., all those constructed using the Historic Landscape Character data, was significant (5.8%, $F = 1.798$, $p = 0.003$).
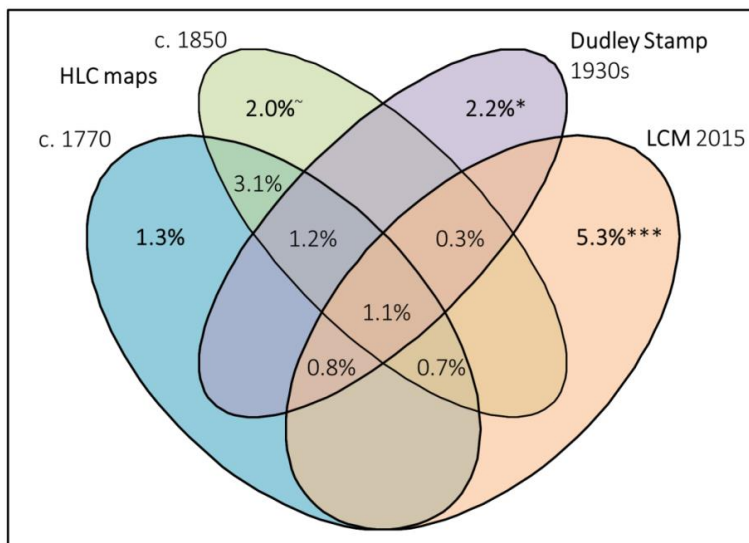


**Figure 8.** Variation partitioning for carabid community composition in terms of the variation uniquely explained by key variables from each time-period. Fractions in overlapping parts of the Venn diagram are shared variation that cannot be uniquely attributed to any particular time period. Proportions of variation explained are expressed in terms of $R^2$-adj. Significance of fractions determined by Monte-Carlo tests with 9999 permutations: no symbol $p > 0.01$, ~$p < 0.01$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

## 2.4. Discussion

### 2.4.1. Extinction Debt

There was a significant relationship between carabid community composition and landscape composition for each of the four time periods. Landscape configuration was significantly correlated with carabid communities for all but the 1930s. Although the land use data for 1770 and 1850 are reconstructed from a number of sources, rather than mapping features that were definitely present in the landscape (as for the 1930s data based on DSLU field surveys, or contemporary data based on remote sensing), the response of carabids to landscape heterogeneity in the HLC data is ecologically plausible. This can be seen by the groupings of species with similar traits in the biplots (Figures 3–7); it is also notable that variation partitioning showed that each of the data sources made a unique contribution to the total variation.

For both landscape composition and configuration, land use for c. 1770 best predicted the distribution of woodland carabids. Though no significant variables were identified by forward selection, the relatively good performance of the global model for c. 1770 composition suggests that by some mechanism land use patterns in the late 18th century continue to shape woodland carabid communities (Gustavsson et al., 2007; Rédei et al., 2014). Landscape configuration for c. 1850 contributed the most variation to the reduced models. Though variation partitioning showed that contemporary landscape elements made the largest unique contribution of any single time point, the historic data sources taken together explain a greater proportion of carabid community composition. Like Neumann et al. (2017) we consider this consistent with an extinction debt (Lindborg & Eriksson, 2004; Helm et al., 2006) and confirm the suggestion that extinction debt in woodland carabids may extend well beyond 80 years. Given the relative unimportance of the 1930s data in our study compared to land use in the late 18th and mid-19th centuries, we conclude that the time lag for woodland carabids in this landscape is on the order of 160 to 240 years. This is consistent with or in excess of the relaxation times previously found in woodlands for plants (Paltto et al., 2006; Kolk & Naaf, 2015) and lichens (Berglund & Jonsson, 2005; Ellis & Coppins, 2007; Ranius et al., 2008).

### 2.4.2. Carabid Communities Through Time

The species showing the strongest response to each of the models (Figures 3–7) were large-bodied, flightless carabids that are either woodland specialists or generalist species that can reach high population levels in woodlands (*C. violaceus, C. problematicus, P. niger, A. parallelepipedus, P.*

*madidus*). Species exhibiting the opposite preferences to this group were generally smaller-bodied, flight-able species that are generalists or affiliated most greatly with non-woodland habitats. This corresponds with Duflot et al. (2014) who showed that species distribution patterns in fragmented landscapes are mediated by traits, with dispersal-limited species the most sensitive to landscape heterogeneity (Lindborg, 2007; Koyanagi et al., 2012). In Neumann et al (2017) the same group of large-bodied, flightless carabids only responded to conditions in the historic landscape; here there is some indication of a continuing effect of landscape fragmentation from the contemporary data since most of these species were at low levels or absent in woodlands adjacent to large urban areas. A time lag in the distribution of *A. parallelepipedus* responding to changes in functional connectivity was observed by Petit & Burel (1998). In our data *A. parallelepipedus* was still present in all but one of the woodlands surveyed, so in this specific case extinction debt may best be described as an expected loss of a proportion of the population rather than a decline in species richness (Hylander & Ehrlén, 2013; Semlitsch et al., 2017).

Scarce species were absent from the community in this study, including specialists of large mature woodlands reported by Neumann et al. (2017) such as *Bembidion mannerheimii* and *Calodromius spilotus.* Our sampling was not comprehensive enough to rule out their presence in the study area but it is also possible that they were never present in even the larger woodland patches sampled here, though woodland cover increased at each time step to 23.7% in 2015, which exceeds most estimates of regional extinction threshold (Andrén, 1994; Betts et al., 2007; Cousins & Vanhoenacker, 2011). However, the absence of rare habitat specialists is consistent with an extinction debt that has already been paid at a local level, possibly due to a decline in habitat quality in the proximity of large-scale urbanisation (Hylander & Ehrlén, 2013) as well as direct loss of habitat (Cousins, 2009).

### 2.4.3. Sample Patch Size

The two largest-bodied species, *C. problematicus and C. violaceus,* were both strongly associated with large sample patch size in the 19th century, as was *P. niger*, another large-bodied species associated with damp woodland. *A. parallelepipedus*, which is found in similar habitats to *P. niger*, showed no association with patch size despite being similarly large-bodied and also flightless. Whilst both species may be impacted by connectivity (both respond to features in the matrix) other factors clearly determine suitable patch size thresholds and the overall community in woodlands does not respond linearly to patch size (Fahrig, 2013; Lindgren & Cousins, 2017). *N. rufipes* was also correlated with larger 19th-century sample woods. As a smaller, winged species it is unlikely to be severely impacted by fragmentation, so this may reflect better habitat quality for the species in larger patches at least c. 150 years old. *N. rufipes* was not strongly correlated with any other

variable but was consistently well separated on the biplots from its more widespread congener *N. biguttatus*. There was no indication of a link between carabid distribution and sample patch size in the 1930s despite an increase between 1850 and the 1930s from 56 to 84 ha, as well as an increase in overall woodland cover and mean woodland patch size. This could reflect an increasingly heterogeneous landscape matrix reducing the influence of patch size and isolation (Bender & Fahrig, 2005), slow colonisation by woodland species of new habitat that may not be of sufficient quality (Fuller et al., 2018) and the potential decrease in connectivity introduced by roads through the 20th century (Koivula & Vermeulen, 2005).

### 2.4.4. Historical Landscape Matrix Features

Permanent grassland in the 18th and 19th centuries was the most important historical landscape component. The number of grassland patches in each period was positively correlated with later urbanisation and negatively with contemporary arable, but the fact that significant landscape configuration variables from c. 1770 and c. 1850 made a unique contribution to the observed carabid variation suggests that there is a real effect of historical grassland or that it predicts the distribution of an aspect of woodland habitat type not measured here.

Species that were positively correlated with the number of historic grassland patches do include some species associated with grassland or other open habitats such as *Poecilus cupreus*, *Harpalus affinis* and *B. lampros*. Scarcer grassland specialists were not detected, unlike in the results of Neumann et al. (2017), who sampled at woodland edges in landscapes that on average have retained more semi-natural grassland patches in the contemporary landscape (5 vs. 1) and slightly higher overall cover (3.6% vs. 2.7%). Nonetheless, it does appear that the composition of semi-natural matrix habitats is reflected in woodland species communities (Debinski et al., 2001; Koyanagi et al., 2009; Neumann et al., 2016a) and that in woodland carabids this signal persists for a long period after most of those additional habitats have been lost.

Species affiliated with shaded habitats were negatively associated with grassland patches, with the strongest correlations seen for the largest-bodied species. It is possible that landscapes with many grassland patches historically were less permeable to large-bodied carabids, which reach higher population levels in patches connected by woody linear features (Jopp & Reuter, 2005; Neumann et al., 2016b). In the 18th and 19th century permanent grassland—mostly comprising downland or floodplain meadows—would have been unhedged and potentially a poor environment for dispersal of carabids that disperse more slowly through grass than cereal crops (Frampton et al., 1995).

### 2.4.5. Urbanisation

The long-term increase in urban cover in this landscape (Table 2) is detectable in carabid communities with a unique portion of variation attributable to 1930s urban area. The response of carabids to urbanisation in this study broadly follows that observed elsewhere, with larger-bodied and flightless species declining with urbanisation (Sadler et al., 2006) and a transition in the species community from woodland specialists to generalists (Magura et al., 2008, 2013). Even two woodland species still widespread in the contemporary landscape, *P. madidus* and *Calathus rotundicollis*, were negatively associated with 1930s urban cover, and the former also responded negatively to urban patch size in the contemporary landscape. Urbanisation may reduce the probability of species occurrence through increased disturbance and reduction in habitat quality, especially in small habitat patches (Gibb & Hochuli, 2002), though urbanisation is not always found to impact beetle communities beyond the effects of habitat fragmentation (Wolf & Gibbs, 2004).

### 2.4.6. Conservation implications

The extinction debt identified here for woodland carabids shows the legacy of dynamic landscape change, with species communities shaped by each of the time intervals examined. The overall community response is comparable to that observed by Neumann et al. (2017), but the different set of landscape features identified as most influential underlines the importance of considering regional context. The long time lag, in the region of two centuries, suggests that there is much to gain from further use of historical land use data in biodiversity research. This should enable a better understanding of species distributions in the current landscape and how they may respond to further landscape change. Some of the patterns observed may ultimately retain a signal of pre-human habitat distribution, as suggested by Otto et al. (2017) for the Canary Islands.

Extinction debt suggests that in a static landscape scenario further loss of biodiversity in the future is inevitable. Restoring or creating connections between existing habitat patches may reduce extinction risk by restoring metapopulation structures, especially for poor-dispersing species (Hanski & Ovaskainen, 2000). Our study also further underlines the importance of retaining large patches of woodland that are at least in the region of 200 years old. Large urban developments in close proximity to existing ancient woodland should be avoided where possible.

Further studies of colonisation credit (e.g., Naaf & Kolk, 2015; Brin et al., 2016; Fuller et al., 2018) will improve the targeted creation of new habitats and connecting features, as would consideration of a wide range of taxonomic groups since their responses to spatial and temporal scale are not always consistent (Dullinger et al., 2013; Bommarco et al., 2014; Gonthier et al., 2014). Finally, we

stress that consideration of historical land use will improve the targeting and delivery of agri-environment schemes by allowing time as well as space to be considered in their design (Donald & Evans, 2006; Neumann et al., 2017).

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# 3. Linking Mesoscale Landscape Heterogeneity and Biodiversity: Gardens and Tree Cover Significantly Modify Flower-Visiting Beetle Communities

## 3.1. Introduction

The need for landscapes to maintain or even exceed current levels of biodiversity is well-recognised, with both governmental and non-governmental conservation strategies increasingly adopting landscape-scale approaches (Lawton et al., 2010). This is a significant challenge in lowland mosaic landscapes where urban development and agricultural intensification have fragmented habitats over long timescales, with variable but often negative impacts on biodiversity (Andrén, 1994; Haila, 2002; Fahrig, 2003; Kappes et al., 2009; Fletcher Jr et al., 2018). Successful management of landscapes for wildlife requires an understanding of how landscape heterogeneity determines patterns of species distribution and modifies community composition.

Landscape heterogeneity can be considered a function of both landscape composition—the amounts of different habitat cover types within the landscape—and landscape configuration, i.e., the heterogeneity of their spatial arrangement (Fahrig et al., 2011). Landscape heterogeneity is recognised as a key driver of species distributions in lowland agricultural landscapes for many taxonomic groups including birds (Fuller et al., 1997; Virkkala et al., 2013; Neumann et al., 2016a), bees and wasps (Fabian et al., 2013; Steckel et al., 2014), mammals (Bender & Fahrig, 2005; Mortelliti et al., 2011) and plants (Jules & Shahani, 2003). However, whilst landscape conservation or landscape planning tends to consider landscape from an anthropogenic point of view, perhaps at a kilometres-wide scale, there is no single 'landscape scale' relevant to all species since responses to landscape heterogeneity vary both between and within taxonomic groups (Schweiger et al., 2005; Ekroos et al., 2013; Fuentes-Montemayor et al., 2017).

Highly mobile species groups such as birds or Orthoptera respond to landscape composition even when examined at fairly broad scales, e.g., cricket species richness in 10-km squares (Cherrill, 2015) or bird community composition in 2-km tetrads (Neumann et al., 2016a). For invertebrates with more limited dispersal, landscape heterogeneity within a radius of hundreds of metres is important, as seen for ground beetles (Carabidae) at a 400-m radius (Barbaro et al., 2007; Barbaro & van Halder, 2009) and Lepidoptera, hoverflies and bees at 600 m (Sjödin et al., 2008). This spatial scale is comparable to the size of common units of land management, with for example many new housing developments in the United Kingdom in the range of 5–20 ha.

Links between mesoscale landscape heterogeneity and biodiversity might therefore be successfully applied to the planning of new habitat networks as mitigation for single housing developments, or to the spatial optimisation of agri-environment schemes at a farm scale. These processes would ideally take account of whole landscape biodiversity, but whilst the synergistic effect of whole

landscape mosaics has been shown to impact community composition, species communities of the whole mosaic are less often considered (Bennett et al., 2006; Neumann et al., 2016b; Duflot et al., 2017), perhaps due to the challenge of gathering data from multiple habitats and taxonomic groups. Methods which rapidly capture a 'snapshot' of landscape biodiversity by sampling a single species community would facilitate this.

Flower-visiting beetles cover a range of habitat affiliations within a single well-studied order, but few studies consider the effect of landscape heterogeneity on their distributions (Sjödin et al., 2008; Horak, 2014). Among the Coleoptera, frequent flower visitors include Cerambycidae, which are mostly saproxylic (feeding on dead wood), and Cantharidae, which are associated with more open habitats. By focussing on flower-visiting beetles, this study aims to provide a window into how mesoscale landscape heterogeneity (calculated for a 200-m buffer around transects) influences the distribution of insect communities across the wider lowland agricultural mosaic.

Sampling used linear patches of flowering plants in the Apiaceaea (e.g. cow parsley, *Anthriscus sylvestris*, and hogweed, *Heracleum sphondylium*), which are very abundant in a range of lowland habitats across Northern Europe. Apiaceaea attract a diverse variety of insect visitors (Willis & Burkill, 1892; Zych, 2007) and are key plant species in some ecological networks (Zych et al., 2007; Pocock et al., 2012). Their tendency to grow in dense stands alongside public roads and footpaths facilitates access to ready-made sampling transects. Since the dispersal distances of many flower-visiting beetles are poorly known this study compares the response of beetle communities to local habitat composition and mesoscale landscape heterogeneity, using variation partitioning to explore whether there is a unique contribution of mesoscale landscape apart from as a predictor of the immediate presence of suitable habitat.

We address the following key questions: (i) What proportions of the variation in beetle community can be explained by local habitat composition and mesoscale landscape heterogeneity? (ii) Which local habitat types and mesoscale landscape variables are the most important drivers of community composition? (iii) Do both the local and mesoscale explain a *unique* portion of variation in beetle communities or is mesoscale landscape simply a proxy for local habitat patterns?

## 3.2. Methods

### 3.2.1. Study Site Selection

The study area boundary was defined by a 6 km$^2$ grid, located in the northern part of the country of Hampshire, southern England (Figure 1). From Land Cover Map 2015 (Rowland et al., 2017) the study area represents a heterogeneous mosaic of agricultural land (48% improved grassland, 26% arable), semi-natural habitats (woodland 23%) and small urban settlements (3%). The study area is

low-lying (between 49 and 86 m above sea level) and has a temperate climate, with mean annual maximum temperature in Reading (10 km away) of 14.5 °C and annual precipitation of 635 mm (Met Office, 2017).

Within each of the resulting 36 1-km$^2$ grids, a 200-metre sampling transect was established. Transects were situated along a road or public footpath, which as well as facilitating access also tended to be bordered by linear habitat strips containing dense stands of flowering Apiaceae. They were placed as close as possible to the centre of each 1-km square to maximise the distance between transects and reduce both spatial autocorrelation between samples and overlap in mesoscale landscape units. Precise locations of the transects (Figure 1) were determined by the presence of flowering Apiaceae during the initial visit in May (predominately cow parsley, *A. sylvestris*) as well as the vegetative presence of later flowering species (e.g. hogweed, *H. sphondylium*) to ensure continued usability of the transect through time. For the one case where no suitable transect was present within the square a suitable location within the adjacent square was selected, maintaining the maximum possible separation with neighbouring transects.

### 3.2.2. Beetle Sampling

Each transect was surveyed three times. The first visit was made between 16th May and 10th June 2013, the second between 26th June and 8th July 2013 and the third between the 10th and 26th July 2013. Sampling was carried out between 10 a.m. and 6 p.m. in dry and non-windy conditions only. Transects were walked slowly in a single direction for 30 minutes. Flower heads were searched by eye and any beetles present captured in a plastic collecting tube (90 mm length x 25 mm diameter). Large aggregations of beetles were captured by shaking the flower head over a plastic funnel inserted into the mouth of the collecting tube, taking advantage of the fact that beetles tend to drop off vegetation when disturbed. Members of the family Nitidulidae were not sampled as they are often present in very large numbers, associated with nearby flowering crops (e.g., *Meligethes aeneus*, a common pest of oilseed rape), potentially obscuring the presence of other beetle species.

All beetles were identified to family following keys in Duff (2012a) and nomenclature in the checklist of British beetles (Duff, 2012b). All individuals besides members of the family Nitidulidae were subsequently identified to species (see Appendix 2.1 for a full table of references). Records from all three visits were pooled for each transect to give a final count of individuals and species. Voucher specimens for this study are held in the Centre for Wildlife Assessment & Conservation at the University of Reading.

The identity of all flowering Apiaceae species was recorded during each visit along with an estimate of the number of flowering plants within 5 metres of the transect. To account for seasonal variability and variation in flower density and (nectar richness) plant count data were transformed

into an index where the maximum count for each survey period was 100. Weather data were recorded in the field (cloud cover in oktas) and from an automatic weather station 10 km away (rainfall on the previous day: yes/no) (University of Reading, 2013). Start time was recorded to the nearest 5 minutes and later converted into three categories (Morning = 10:00 –11:55, Noon = 12:00 – 13:55, Afternoon = later than 14:00) Transects were excluded from the final analysis where no beetles were recorded during two or more visits.

### 3.2.3. Landscape Data

*Local and mesoscale buffers*

Few studies address the local movement and dispersal of multiple beetle species. However Irmler et al. (2010) provide a useful summary of the distances some saproxylic beetle species (many of them nectivorous) fly away from patches of woodland habitat. The smallest dispersal category for species in Irmler et al. (2010) was 0–30 m. Using this figure as a guide, local habitat is defined here as anything up to 30 metres away from the transect, with the assumption that flowers on the sampling transect are within a single flight range from this zone, even for species that only disperse short distances. The maximum flight distance found by Irmler et al. (2010) was >80 metres but for the majority of species dispersal was limited to <80 m. In this study mesoscale landscapes are defined as 200-metre buffers from the sampling transect, assuming that this is outside the average dispersal flight distance for flower-visiting beetles and represents a scale at which spatial processes may operate on the beetle community. Dispersal flight distances for beetles reported elsewhere generally fall within 200 metres (Schallhart et al., 2009; Torres-Vila et al., 2017; Rodwell et al., 2018).

*Landscape composition (200-m buffer)*

Landscape composition, the area of different habitat cover types, was digitized for a 200-m buffer around each transect in ArcMap 10.4 (ESRI, 2016), following the classification in Table 1. The delineation of patches and classification was based primarily on OS Mastermap (Ordnance Survey, 2015). Where MasterMap categorised a patch as 'General Surface,' classifications were based on a combination of underlying broad land cover types from Land Cover Map 2007 (Morton et al., 2014) and visual inspection of aerial imagery (Getmapping Plc, 2015).
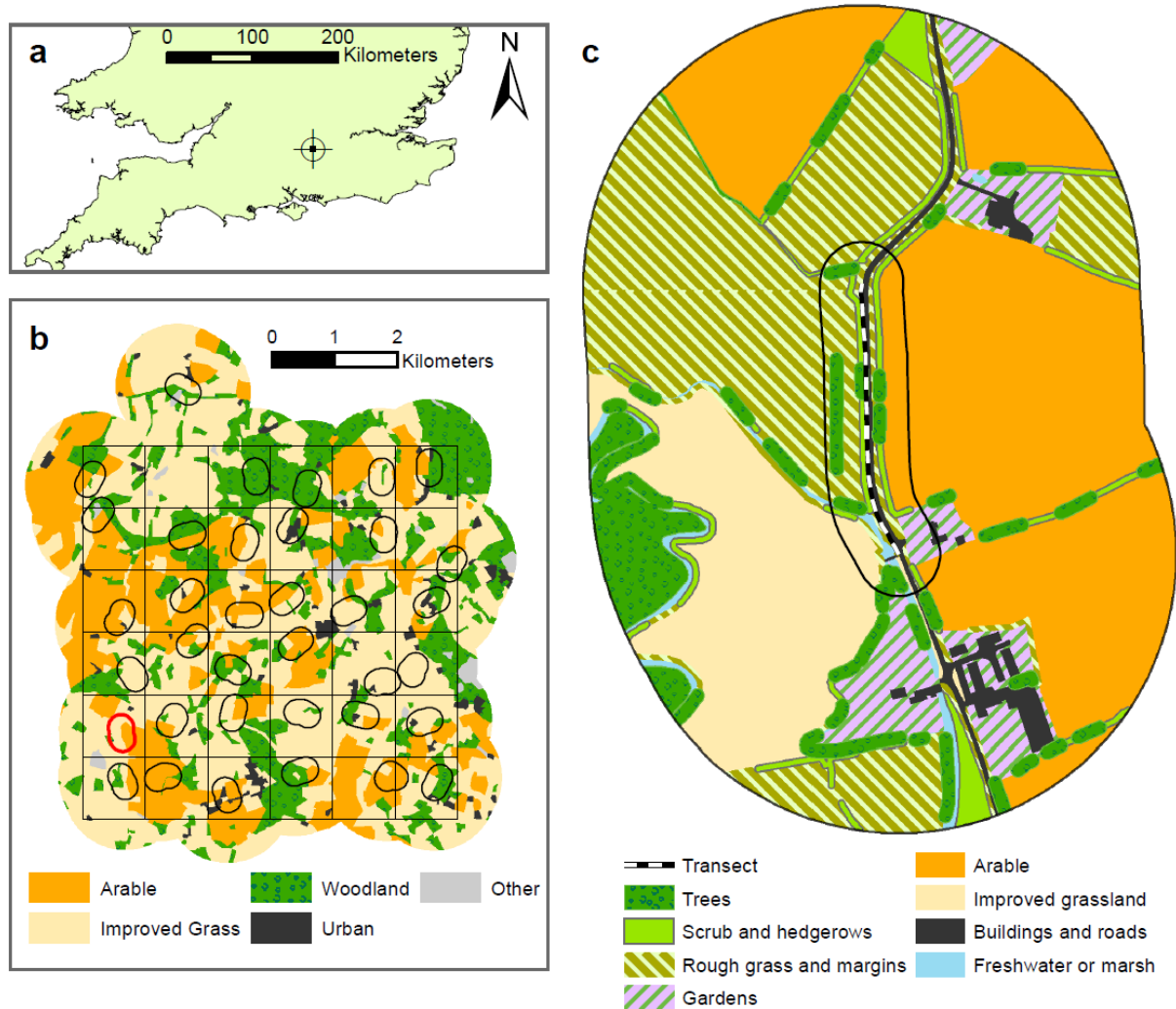
**Figure 1a.** Location of the 6-km$^2$ grid used for selecting transect locations within southeast England. **1b** Broad land cover from CEH Landcover Map 2015 (Rowland et al., 2017), shown for a 1-km buffer around the transects. **1c** Example habitat classification of a 200-m buffer around a transect (outlined in red on **1b**), based on OS Mastermap polygons (© Crown copyright 2018 Ordnance Survey).

### *Linear elements (composition)*

Incorporating linear elements improves models of species and community distribution (Neumann et al., 2016b; Sullivan et al., 2017). Linear features not represented as patches in Mastermap were digitized as polylines following patch boundaries. These were classed as 'Line of Trees' (non-woodland trees where feature width was > 5 metres), 'Hedges' (linear woody elements < 5 m wide) or 'Margin' (strips of non-woody vegetation along patch boundaries appearing more texturally complex in aerial imagery than adjacent habitats, for example road verges or field margins). Areas were assigned to linear elements based on the mean width of features measured with reference to aerial imagery in ArcMap. Forty measurements were taken for each linear feature type; the standard error was < 0.5 m for each feature type.

'Line of Trees' was combined with patches of Woodland cover to create the variable TREES. Many tree-dwelling beetles visit flowers as adults and utilise arboreal habitats outside of woodland, with for example open-grown oaks harbouring higher species richness of saproxylic beetles than those in denser woodland (Widerberg et al., 2012; Parmain & Bouget, 2018). 'Hedges' were further categorised as either Garden or Rural by selecting those which intersected with a patch of the Garden cover type for > 50% of their length. Rural Hedges were added to the Scrub cover type to form the variable SCRUB as they offer comparable insect habitat with a similar species mix of woody shrub species and small trees. Garden hedges were not incorporated into the composition data as they predominately overlapped with patches already categorised as gardens, representing a diverse mix of lawns, small trees, shrubs and hedges. Margins were incorporated into the composition variable ROUGH. An example of final landscape composition classification for a transect, including linear elements, is given in Figure 1c.

*Landscape configuration (200-metre buffer)*

Landscape configuration describes the spatial arrangement and geometry of the various landscape components and was represented here by the edge length and mean patch size of important cover types and two diversity metrics. Shannon's Diversity Index and Contagion Index were calculated for each buffer in Fragstats 4.1 (McGarigal & Ene, 2012) and included as measures of landscape heterogeneity.

Edge habitats potentially provide a beneficial combination of larval habitats such as dead wood or herbaceous vegetation and abundant flowering plants frequented by adult beetles. Lengths of woodland edge (WOOD EDGE) and scrub edge (SCRUB EDGE) were therefore included as landscape configuration variables, calculated from the perimeters of the TREES and SCRUB composition variables, which for SCRUB EDGE included the lengths of rural hedges. Lengths of margin identified in the linear feature analysis were combined with the edge length of land cover type MARGIN to create the variable MARGIN LENGTH, representing road verges and field margins that may serve as connecting features and host flowering Apiaceae. Potential patch area effects were assessed by including the mean patch size of three cover types, forming the variables TREE PATCH, SCRUB PATCH, and ROUGH PATCH.

Finally, the length of GARDEN HEDGE, weighted by total Garden Area, was included as a measure of potential habitat quality in urban areas. Areas of garden rich in hedges are likely to be different in character to those bordered by wooden fences or laid extensively to lawn with few boundary features.

*Local habitat (30-metre buffer)*

Local habitat composition was obtained by clipping the landscape composition data to a 30-metre buffer, representing the combination of habitats immediately adjacent to the sampling transect. A summary of all variables used for analysis and their mean values is provided in Table 1.

### 3.2.4. Data Analysis

All analysis was conducted in R 3.4.1 (R Core Team, 2017) using package vegan 2.4-4 (Oksanen et al., 2016). Beetle data were examined as both the full community data incorporating abundance (full community) and species presence–absence. This follows Blanchet et al. (2014) who suggested that relevant information about less frequently encountered species can be obscured in ordination results driven by very common species. Species were included in the analysis if they occurred on three or more transects.

To address questions (i) and (ii), the effects of local landscape composition (30 m composition), mesoscale landscape composition (200 m composition) and landscape configuration (200 m configuration) were determined using direct ordination methods. Presence–absence data were analysed using redundancy analysis (RDA). Preliminary analysis revealed a significant effect of survey time during the second visit (TIME2) on the full community data; this was entered as a control in partial Redundancy Analysis (pRDA) (Borcard et al., 1992) to identify the true proportion of community variation attributable to either local habitat or landscape variables. Both the full community and presence–absence data were transformed using the Hellinger distance (Rao, 1995; Legendre & Gallagher, 2001) in order to reduce the weight of rarely encountered species (which may not be truly biologically rare, merely undersampled). All habitat and landscape variables measured in $m^2$ were $Log_{10}(x+1)$ transformed so that the effect of potentially important semi-natural cover types was not obscured by variation in dominant cover types such as arable or improved grassland (Neumann et al., 2016a).

Following a significant ($p < 0.05$) global permutation test on the combined effect of all variables, a reduced model providing the most parsimonious explanation for beetle community composition was identified using the Vegan function *OrdiR2step*. Variables were added to the final model if they were significant ($p < 0.05$) *and* increased the adj-$R^2$ of the model; provided this value did not exceed the adj-$R^2$ of the global model (Blanchet et al., 2008), this reduces the incidence of Type I errors and overestimation of explained variation.

**Table 1.** Summary of variables used to describe local habitat composition (30-metre buffer around transects), landscape composition and landscape configuration (200-metre buffer).

| Variable | Description | 30-metre buffer (m$^2$) | | | 200-metre buffer (ha) | | |
|---|---|---|---|---|---|---|---|
| | | Min | Mean | Max | Min | Mean | Max |
| *Landscape Composition* | | | | | | | |
| ARABLE | Arable & Horticulture | 0 | 3742 | 12566 | 0.0 | 6.1 | 16.7 |
| GARDEN | Suburban gardens | 0 | 961 | 4234 | 0.0 | 1.0 | 5.0 |
| IMPGRASS | Improved Grassland | 0 | 2898 | 11332 | 0.0 | 8.3 | 18.6 |
| MANMADE | Buildings, Roads, Paths | 0 | 1657 | 4031 | 0.0 | 1.1 | 6.7 |
| ROUGH | Road and field margins, semi-natural grassland | 21 | 2227 | 7348 | 0.0 | 1.7 | 9.0 |
| TREES | Areas of tree cover (woodland, lines of trees) | 663 | 4543 | 10550 | 0.2 | 1.6 | 10.9 |
| SCRUB | Areas of woody vegetation without mature trees (scrub and hedgerows) | 0 | 198 | 679 | 0.1 | 1.0 | 4.6 |
| WET | Freshwater and marsh | 0 | 144 | 1463 | 0.0 | 0.7 | 4.5 |
| | **Area of 200-m buffer:** | | | | 20.1 | 20.7 | 21.9 |
| *Landscape Configuration* | | | | | | | |
| WOODEDGE | Length of woodland edge and lines of trees (m) | 0 | 279 | 973 | 595 | 2821 | 6098 |
| SCRUBEDGE | Length of scrub edge and hedgerows (m) | 0 | 35 | 255 | 0 | 483 | 1748 |
| MARGIN | Length of road verge and field margin (m) | 0 | 348 | 657 | 92 | 1204 | 3011 |
| GARHEDGE | Length of hedges per m$^2$ of garden (m/m$^2$) | 0 | 5 | 68 | 0.0 | 7.5 | 58.2 |
| ROUGHPATCH | Mean patch size in ROUGH composition variable (m$^2$, ha) | 11 | 675 | 3070 | 0.0 | 0.3 | 2.7 |
| TRPATCH | Mean patch size in TREES composition variable (m$^2$, ha) | 166 | 1208 | 6503 | 0.0 | 0.3 | 1.4 |
| SCPATCH | Mean patch size in SCRUB composition variable (m$^2$, ha) | 0 | 40 | 226 | 0.0 | 0.1 | 0.3 |
| SHDI | Shannon's Diversity Index | | n/a | | 0.3 | 1.2 | 1.8 |
| CONTAGION | Contagion Index | | n/a | | 51.2 | 65.5 | 87.8 |

Probability values for the global model, each variable retained in the reduced model and the constrained ordination axes were estimated using Monte Carlo tests with 9999 permutations. Multicollinearity between explanatory variables was controlled using variance inflation factors

(VIF, Neter et al., 1996); terms with the highest VIF were removed sequentially from the initial model until all VIF were < 3.0. Sites close to each other may have similar species communities, leading to spatial autocorrelation. This was assessed using Principle Coordinates of Neighbourhood Matrices (PCNM) based on the XY coordinate of the transect midpoints (Borcard & Legendre, 2002). All PCNM were entered into a redundancy analysis as predictors of beetle community composition.

Variables from the reduced 200 m composition and 200 m configuration analyses were combined into final 200 m landscape models. Any collinear (redundant) terms were discarded at this stage by inspecting VIF for the combined model. To address question (iii), variation partitioning using a simplified version of redundancy analysis (RDA) (function *varpart)* was used to unpick any unique explanatory contributions of 30 m habitat composition and the 200 metre landscape variables (Borcard et al., 1992; Peres-Neto et al., 2006), expressed in terms of adjusted-$R^2$.

### 3.3. Results

### 3.3.1. Beetle Community

Excluding Nitidulidae, 2662 beetles of 69 species from 18 families were collected across the three sampling visits. The lowest total species richness recorded at any one transect was five; the highest was 18, with a mean of $11.0 \pm 0.7$. The best represented families were Cantharidae (11 species), Cerambycidae (10 species), Scraptiidae (nine species) and Elateridae (seven species). All of these contain known flower-visiting species. The most widespread species were *Anaspis pulicaria and Anaspis maculata* (Scraptiidae), *Anthrenus verbasci* (Dermestidae), *Agriotes pallidulus* (Elateridae) and *Rhagonycha fulva* (Cantharidae). *Anaspis* species are frequently found on *Apiaceae* and *Crateagus* spp. flowers in spring and early summer (Levey, 2009), both *maculata* and *pulicaria* were ubiquitous in this study, appearing on 31 and 27, respectively, of the 36 transects. *A. verbasci* is a synanthropic species often found in homes, where the larvae feed on keratinaceous material, e.g., hair and skin (Peacock 1993). The adults are widespread on flowers in spring and summer but not usually found in numbers far from buildings (Woodroffe & Southgate, 1954). Of the 20 most widespread species recorded, roughly equal numbers are broadly associated with trees and with open habitats (Table 2). A full illustrated species list is given in Appendix 2.2. Transects that were close to each other did not have more similar beetle communities, with no significant relationship between PCNM and full community composition ($F = 1.045$, $p = 0.305$) or species presence–absence ($F = 1.185$, $p = 0.113$).

**Table 2.** Summary of the 20 most widespread species (recorded in six or more transects) and their broad habitat associations.

| Family | Species | Bi-plot Code | Transects (n = 35) | Total | Broad Habitat |
|---|---|---|---|---|---|
| Scraptiidae | *Anaspis maculata* | As.ma | 31 | 410 | Trees |
| Scraptiidae | *Anaspis pulicaria* | As.pu | 27 | 475 | Open Habitats |
| Dermestidae | *Anthrenus verbasci* | At.ve | 22 | 439 | Synanthropic |
| Elateridae | *Agriotes pallidulus* | Ag.pa | 21 | 74 | Open Habitats |
| Cantharidae | *Rhagonycha fulva* | Rh.fu | 18 | 126 | Open Habitats |
| Cerambydicae | *Grammoptera ruficornis* | Gr.ru | 17 | 59 | Trees |
| Scraptiidae | *Anaspis humeralis* | As.hu | 17 | 58 | Trees |
| Byturidae | *Byturus tomentosus* | By.to | 15 | 60 | Open Habitats |
| Elateridae | *Athous haemorrhoidalis* | Ah.ha | 14 | 22 | Open Habitats |
| Scraptiidae | *Anaspis frontalis* | As.fr | 14 | 15 | Trees |
| Scraptiidae | *Anaspis costai* | As.co | 13 | 79 | Trees |
| Oedemeridae | *Oedemera nobilis* | Oe.no | 11 | 43 | Open Habitats |
| Cerambydicae | *Rutpela maculata* | Ru.ma | 10 | 19 | Trees |
| Coccinellidae | *Propylea quatuordecimpunctata* | Pr.qu | 10 | 12 | All Habitats |
| Dermestidae | *Anthrenus fuscus* | At.fu | 9 | 14 | Trees, Synanthropic |
| Scraptiidae | *Anaspis garneysi* | As.ga | 8 | 13 | Trees |
| Byturidae | *Byturus ochraeus* | By.oc | 7 | 18 | Open Habitats |
| Chrysomelidae | *Bruchus rufimanus* | Br.ru | 7 | 7 | Open Habitats |
| Coccinellidae | *Coccinella septempunctata* | Co.se | 6 | 50 | All Habitats |

### 3.3.2. 30 metre local habitat

Results for all ordination analyses are summarised in Table 3. 28.8% of variation in the full community ($F = 1.412$, $p = 0.01$) and 29.0% of presence–absence ($F = 1.327$, $p = 0.002$) was explained by the combined effect of the 30 metre habitat composition variables. After forward selection the reduced landscape composition model for full community explained 12.8% of variation. GARDEN ($p = 0.006$) and TREES ($p = 0.006$) were identified as significant predictors of community composition. The bi-plot (Figure 2a) shows that the first constrained axis (RDA1, 8.0% variation explained, $p < 0.001$) represents a gradient from transects with high tree cover to ones with a relatively high proportion of garden cover. The second axis (RDA2, 4.8%, $p = 0.023$) represents a gradient from transects with large amounts of both gardens and trees to those with a more open rural character with low garden and tree cover. Species response was dominated by the most abundant species recorded. More species showed a moderate to strong positive association with trees than a negative one; those responding negatively include *A. pulicaria*, which is thought to breed in more open habitats than other members of *Anaspis* (Levey, 2009). More species responded negatively to gardens than positively. However, *A. verbasci* was very strongly associated with gardens and a few other species also showed weakly positive correlations with garden cover including *Byturus tomentosus*, which is known as a pest of cultivated raspberries.

GARDEN ($p = 0.003$), TREES ($p = 0.001$) and ROUGH ($p = 0.04$) were significant predictors of species presence–absence, together explaining 14.8% of variation. The first constrained axes (RDA1, 6.8%, $p < 0.001$) is a gradient from transects with low tree cover and higher proportion of rough vegetation and gardens to transects with high tree cover (Figure 2b). The second constrained axis (RDA 2 5.1%, $p = 0.014$) is a gradient from transects with high garden cover and less rough vegetation to those with fewer gardens in the vicinity. Very abundant species that responded strongly in the full community analysis show a similar direction of response on the presence–absence bi-plot but are less dominant on each axis compared to other species. A stronger association with gardens is revealed for some species such as *Anthrenus fuscus* and *Oedemera nobilis* (Oedemeridae). *Anaspis humeralis, Anaspis frontalis* and *Cantharis nigricans* were more likely to be found on transects with high rough vegetation cover.

Habitat configuration variables explained (23.7%) of the full community data ($F = 1.275, p = 0.074$) and 23.1% of the species presence–absence ($F = 1.156, p = 0.072$), the global model for configuration was not significant in either case.

**Table 3.** Summary of redundancy analysis (RDA, presence–absence models) and partial redundancy analysis (pRDA, full community models) results. Global model shows the combined effect of all variables; reduced models are determined via forward selection to identify key explanatory variables.

| | Global Model | | | Reduced Model | | | |
|---|---|---|---|---|---|---|---|
| | *F* | *p* | Explained | Variable | *F* | *p* | Explained |
| 30 metres | 1.412 | 0.010 | 28.8% | GARDEN | 2.311 | 0.006 | 6.4% |
| | | | | TREES | 2.248 | 0.006 | 6.4% |
| 30 metres | 1.327 | 0.002 | 29.0% | GARDEN | 1.776 | 0.003 | 4.9% |
| | | | | TREES | 2.071 | < 0.001 | 5.8% |
| | | | | ROUGH | 1.466 | 0.040 | 4.1% |
| 200 metres | 1.412 | 0.009 | 29.2% | GARDEN | 2.311 | 0.004 | 7.0% |
| | | | | TREES | 2.248 | 0.003 | 7.0% |
| 200 metres | 1.247 | < 0.001 | 27.0% | TRPATCH | 2.198 | < 0.001 | 6.2% |

### 3.3.3. 200 metre landscape

Mesoscale landscape composition explained 29.2% of variation in the full community data ($F = 1.412, p = 0.009$) and 29.0% of presence–absence ($F = 1.327, p = 0.023$). Forward selection again identified GARDEN ($p = 0.004$) and TREES ($p = 0.003$) as significant predictors of full community composition, explaining 13.9% of total variation. Only TREES ($p < 0.001$) was retained in the reduced model for species presence–absence, explaining 5.9% of variation.

Landscape configuration variables explained 26.0% of variation in the full community composition ($F = 1.453$, $p = 0.012$) and 27.0% of species presence–absence ($F = 1.247$, $p < 0.001$), with TRPATCH the only variable retained in the reduced model in both cases (both $p < 0.001$).

GARDEN and TREES were retained in a combined composition/configuration model for full community data. TRPATCH was removed as it was collinear with TREES and the model explained more variation with TREES included rather than TRPATCH. The bi-plot (Figure 2c) is similar to that for local habitat composition but with some changes in the strength of association for individual species. *R. fulva* was negatively associated with tree cover on the local habitat bi-plot but showed a weak positive association at the mesoscale landscape level. *Anthrenus fuscus* was positively associated with gardens at local habitat scale but showed a weak preference for mesoscale landscapes with lower garden cover. The top-middle section of the bi-plot is empty, showing that no species had a strong negative association with both trees and gardens.

In the combined model for presence–absence, TREES and TRPATCH were collinear. TRPATCH was retained as it explained a larger proportion of variation (6.2%, $p < 0.001$). The one constrained axis explained 6.2% of the variation and described a gradient from landscapes with on average larger tree patch size to those with smaller patches of trees (Figure 2d).

### 3.3.4. Variation Partitioning

Variation partitioning for the full community showed that the reduced models for 30 metre local habitat, 200 metre landscape and the conditional variable TIME2 together explained 16.1% of variation in the full community data (Figure 3a). The part of this attributable uniquely to local habitat was 2.4% ($p = 0.004$). 200 m landscape explained 3.7% ($p = 0.007$) and 5.7% was shared variation, not attributable to local habitat or landscape alone. The condition TIME2 explained 3.6% of variation and 1.2% was shared between all three elements. For the presence–absence data, the total variation explained was 6.9% (Figure 3b). Of this, 3.5% was uniquely attributable to 30 m habitat composition ($p = 0.010$) and 0.4% to 200 m landscape; this portion was non-significant ($p = 0.272$). 3.0% was shared.
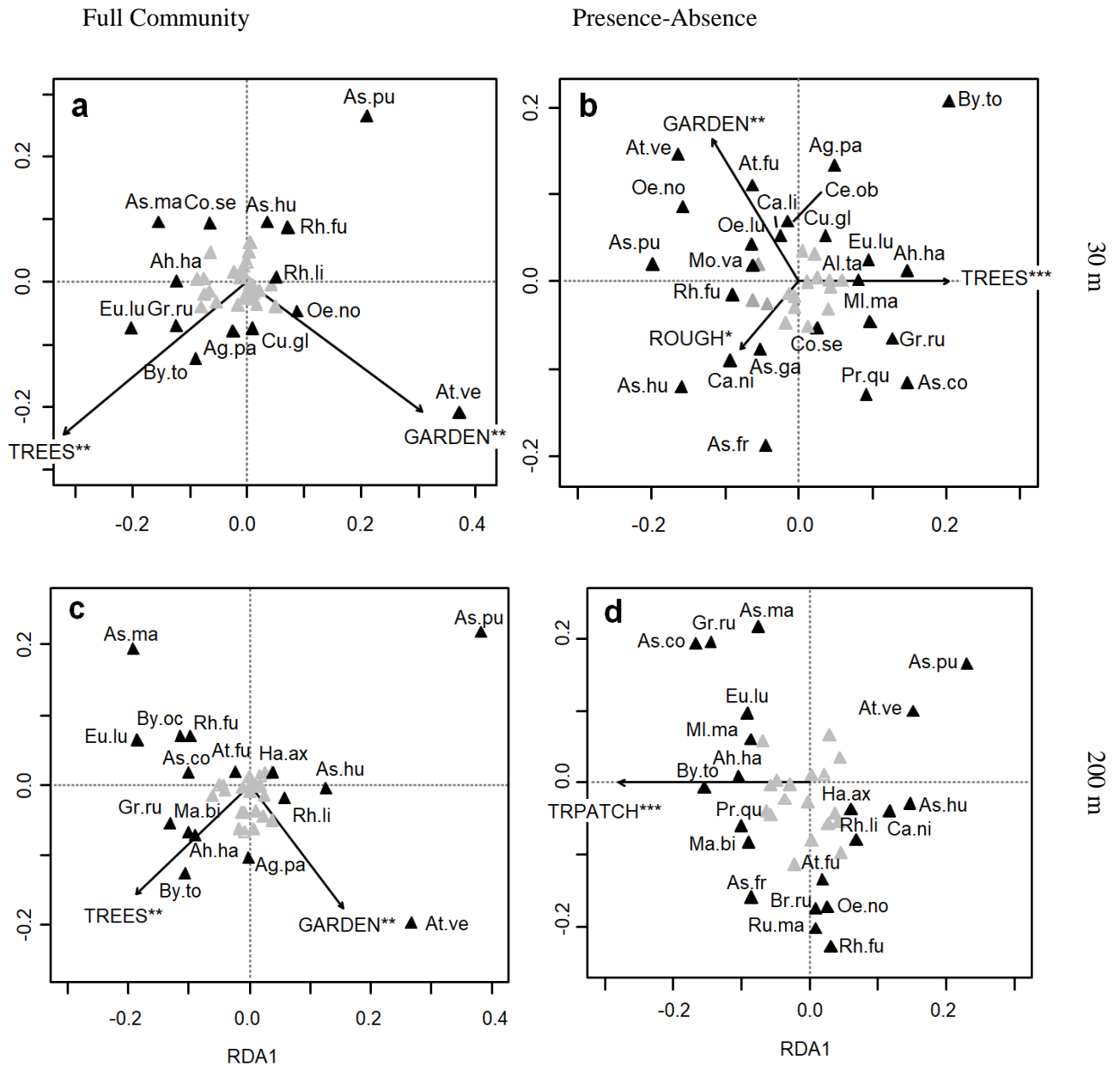
**Figure 2.** Redundancy analysis bi-plots showing the key 30 m habitat composition (**a** + **b**) and 200 m mesoscale landscape (**c** + **d**) variables that explain flower-visiting beetle community composition. **a** + **c** shows analysis for full community data, **b** + **d** for presence–absence only. The length of arrows indicates the strength of correlation between the variables and the constrained axes. Significance of variables *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Species can be projected perpendicularly onto the arrows to infer the strength of the correlation between individual species and predictor variables. The highest scoring species on either axis or those otherwise mentioned in the text are labelled. Codes for frequently encountered species are listed in Table 2; additional species labelled are *Alosterna tabacicolor* (Al.ta), *Cantharis livida* (Ca.li), *Cantharis nigricans* (Ca.ni), *Ceutorynchus obstrictus* (Ce.ob), *Curculio glandium* (Cu.gl), *Eusphalerum luteum* (Eu.lu), *Harmonia axyridis* (Ha.ax), *Malachus bipustulatus* (Ma.bi), *Malthodes marginatus* (Ml.ma), *Mordellochroa variegata* (Mo.va), *Oedemera lurida* (Oe.lu) and *Rhagonycha limbata* (Rh.li).
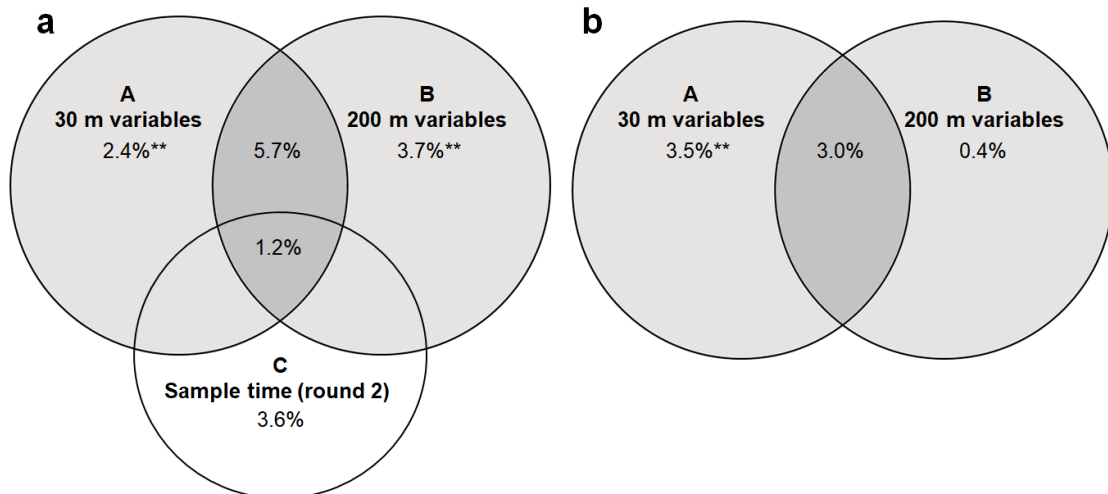
**Figure 3.** Variation partitioning for full community (**a**) and presence–absence only (**b**) data. Proportions of variation explained are expressed in terms of $R^2$-adj; A + B indicate the unique effect of the reduced model in each case; C is the joint effect. Significance of fractions: no symbol $p > 0.05$, *$p < 0.05$, **$p < 0.01$.

### 3.4. Discussion

#### 3.4.1. Flower-Visiting Beetle Community

The total number of species recorded in this study and mean site richness were higher than achieved in previous studies of flower-visiting beetle communities, though others did not target sampling exclusively at beetles (Sjödin et al., 2008; Horak, 2014; Baldock et al., 2015). The consistent capture of a few common species but otherwise high turnover of species between sites in the present study suggests that the community sampled here provides a useful metric for rapidly comparing insect species communities at this scale. Since other insects are also abundant on flowering Apiaceae, especially flies (Diptera), we propose that the sampling strategy used in this study could prove a useful standardised method of monitoring insect populations across taxonomic groups.

#### 3.4.2. Local Habitat

At the local (30-m buffer) level a few species were most abundant on transects bordered by large amounts of their habitat. *G. ruficornis* and *Malachius bipustulatus* breed in decaying trunks or branches and under bark respectively and were both more abundant on tree-rich transects, though presence–absence for *M. bipustulatus* was not impacted by tree cover locally. *A. verbasci* was never found far from buildings by Woodroffe and Southgate (1954) and was strongly correlated with garden extent here. *Anaspis pulicaria* has been described as 'more of an open habitat species' (Levey, 2009), the present study confirms this observation as the species was negatively correlated with tree cover.

In the presence–absence analysis many species were correlated strongly with more than one explanatory variable, suggesting finer niche selection at the local scale associated with nearby oviposition sites or a preference for certain flower situations. Preferences for sunny sites (Kadej et al., 2018) and shady or sheltered ones (Dover et al., 1997) have both been observed in insects; the response of beetles and other insect communities to small-scale habitat complexity varies widely (Lassau et al., 2005; Pak et al., 2015; Ford et al., 2017).

Large amounts of rough vegetation, which in the present study refers mainly to rank vegetation dominated by a mix of Apiaceae and other herbaceous vegetation alongside long grass, increased the chances that some species would be present on the transect. This may indicate preferences for large expanses of flowering Apiaceae for nectaring, though flower-head density was directly measured during sampling and not found to be a significant driver of community composition. Several species that were positively correlated with rough vegetation are predators of other insects (*Cantharis nigricans, R. fulva, Harmonia axyridis, M. bipustulatus*), perhaps indicating that large extents of this cover type can support diverse insect communities, as seen in arable field margins (Thomas & Marshall, 1999; Birkhofer et al., 2014).

### 3.4.3. Mesoscale Landscape Composition

Variation partitioning showed that the unique contribution of landscape at a 200-m radius to full beetle community variation was larger than that for local habitat composition. For the presence–absence analysis the reverse was true and the landscape element non-significant. This suggests that the local abundance of some flower-visiting beetles is enhanced by landscape at this scale (contrary to Sjödin et al. (2008)), but not species richness. Previous studies of other beetle communities at similar spatial scales have also obtained variable results; with landscape composition within a 400-m radius the main driver of Carabid communities in Barbaro et al. (2007) but unimportant (at any scale between 200 m and 2000 m radius) in Philpott et al. (2014). Landscape composition within a few hundreds of metres radius has also been linked to species richness in solitary bees and wasps (Steckel et al., 2014; Hardman et al., 2016).

Mean tree patch size explained a significant portion of variation in the presence–absence data, confirming expectations for saproxylic beetles (Irmler et al., 2010) but not a previous study of flower-visitors (Horak, 2014). However, patch size did not uniquely explain any variation once partitioned with local habitat, suggesting that this variable is a proxy for patch size or habitat amount adjacent to the transect. Indeed, no landscape configuration variables (including diversity and contagion) were important, concurrent with the suggestion of Barbaro et al. (2007) that, at the mesoscale, spatial heterogeneity is a proxy for composition.

### 3.4.4. Woodland and Non-Woodland Trees

This study underlines the importance of trees—both inside and outside woodland—as habitat for a diverse community of beetles. Thirty-one of the species recorded are associated with trees. Higher tree cover at local and mesoscale levels boosted both the presence and abundance of a number of species; where these are saproxylic (breeding on deadwood), this could be a proxy for deadwood availability (Götmark et al., 2011; Jacobsen et al., 2015). Species positively correlated with trees for which the main larval habitat is indeed arboreal included *Grammoptera ruficornis* (Cerambycidae), *Malachus bipustulatus* (Malachiidae) and *Malthodes marginatus* (Cantharidae), while others such as *Eusphalerum luteum* (Staphylinidae) and *Byturus tomentosus* are not associated with trees in terms of larval habitat but could have a preference for shady conditions when feeding on flowers as adults.

Forest cover in the surrounding landscape has also been identified as the most significant driver of community composition in bees on wildflower strips (Fabian et al., 2013) (Fabian et al. 2013) and hoverflies in flower-rich grasslands (Sjödin et al., 2008). Whilst some saproxylic beetles are known to be dispersal-limited (Irmler et al., 2010; Brin et al., 2016), this study found no evidence that landscape configuration variables—i.e., measures of connectivity—influenced community composition.

Although one-third of the species recorded was associated with decaying wood, most that were detected on enough transects to be included in the analysis are associated with short-lived habitats (e.g., *Anaspis* spp. in dead twigs and small branches) and so are likely to disperse relatively well (Southwood, 1977; Nordén et al., 2014). During fieldwork individuals of *Anaspis* were observed to fly readily, if not strongly, and being small bodied (2.5–4.5 mm) could potentially travel some distance beyond the local dispersal flights away from habitat patches reported by (Irmler et al., 2010), especially in convective conditions. No measure of habitat quality was included here and much of the unexplained variation in the community data, especially that pertaining to tree-associated species, is likely to be related to the finer-scale distribution of habitat resources and conditions within the broad cover type 'Trees'.

### 3.4.5. Gardens

In the case of *A. verbasci*, a positive correlation with gardens is likely to be a proxy for buildings, though the fact that gardens explained more variation in the overall beetle community suggests that the modifying impact of urban areas on biodiversity overall is more complex than a straightforward loss of habitat and thus biodiversity to impervious surfaces (McIntyre et al., 2001; Wolf & Gibbs, 2004; Plascencia & Philpott, 2017). More species were negatively correlated with gardens in the 30-m buffers than positively, but at 200 m slightly more species responded positively to gardens. Negative impacts of urbanisation might be assumed and a large-scale study in France found that flower-visiting insect communities are functionally more homogenous in urban areas (Deguines et

al., 2016). However, gardens with high canopy cover or diverse planting support more diverse arthropod communities (Lowenstein et al., 2014; Otoshi et al., 2015; Salisbury et al., 2015), and Baldock et al. (2015) found bee species richness and abundance were higher in urban gardens than in nearby farmland or nature reserves. Small rural villages and farmsteads have been identified as important reservoirs of bird diversity in agricultural landscapes (Rosin et al., 2016). It is possible that small settlements similarly act as modifiers and in some cases enhancers of insect communities, given that gardens were one of only two landscape components identified as significant in the current study despite only covering an average 5% of the landscape buffers.

### 3.4.6. Implications for Landscape Conservation

These results show that for flower-visiting beetles, local habitat and mesoscale landscape composition explain a significant proportion of community composition. A strong component of species abundance at a site stemmed from habitat cover in the surrounding 200 m. That landscape configuration was not important suggests that the community sampled is not dispersal-limited, though community analysis of this type is not able to investigate the response of rare species in any detail. Our results do suggest that at any particular point insect abundance may be enhanced by the provision of additional habitat within 200 metres. Habitat availability remains the key indicator for presence of a species, so whilst spatial planning of habitat networks is not crucial for this community at this scale, habitat creation at a relatively small 'landscape' scale is demonstrated here to have a potentially wider impact.

The variable Trees included non-woodland trees and improved variation explained when compared to models that only included woodland patches (Henry et al., 2017; Sullivan et al., 2017), underlining the importance of non-woodland trees for biodiversity in heterogeneous landscapes. Tree cover should be retained in the landscape wherever possible, balanced with the need to provide a diverse mix of semi-natural habitats that supports the maximum possible number of species, including those affiliated with open habitats. The community-modifying impact of gardens suggests that, given appropriate management, both within gardens and spatially across urban areas, gardens could make a significant contribution to maintaining biodiversity in agricultural mosaic landscapes (Hunter & Hunter, 2008; Goddard et al., 2010; Plascencia & Philpott, 2017).

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**4. Seeing the Trees for the Wood: LiDAR-Derived Vegetation Height Describes the Distribution and Sex Ratios of *Anaspis* spp. (Coleoptera: Scraptiidae) across Three Lowland Agricultural Landscapes**

**4.1. Introduction**

Detailed knowledge of insect life histories is vital for forming conservation strategies (Thomas et al., 2009; Kadej et al., 2018) and managing ecosystem services (Prather & Laws, 2018). However, the basic ecology of the vast majority of insect species remains poorly understood or even completely unknown, including their spatial distributions and habitat associations (Cotterill & Foissner, 2009; Cardoso et al., 2011). Studies of how whole insect communities are influenced by spatial and temporal habitat heterogeneity are increasing (e.g., Neumann et al., 2016b, 2017; Delgado de la Flor et al., 2017; Reynolds et al., 2018) but species-level information may fall behind what is needed considering the apparent challenges facing insect conservation (Conrad et al., 2006; Hallmann et al., 2017); this is the 'scientific shortfall', as outlined by Cardoso et al. (2011).

The requirements of well-studied species may be used to make predictions for data-poor ones (Boieiro et al., 2010; Broughton et al., 2013) or inform habitat management that may benefit other species (Elmes & Thomas, 1992). Studies of whole-community response to landscape heterogeneity do not necessarily provide robust evidence for single species but provide useful information on the overall response of taxonomic groups or species with similar traits (Duflot et al., 2014; Neumann et al., 2016b). Widely available land cover mapping or raw remote sensing imagery can then be used to predict species distributions (Eyre et al., 2004; Shirley et al., 2013) and plan conservation spatially across landscapes (Holloway et al., 2003b).

Environmental data obtained from LiDAR can perform equally well and in some cases better than ground-based data (Davies & Asner, 2014), for example in predicting spider distributions (Vierling et al., 2011) or species composition in forest beetles (Müller & Brandl, 2009), whilst vertical canopy structure estimated at ground level has also been suggested as a proxy for canopy beetle communities (Jukes et al., 2002). LiDAR data are increasingly accessible: for example, accurate elevation data are now available freely under an Open Government Licence at 1 m resolution for >70% of England (Environment Agency, 2017). This opens up the possibility of more accurately predicting insect biodiversity across large areas by incorporating measures of vertical habitat structure as well as habitat cover of landscape composition (Jukes et al., 2002; Barbaro et al., 2005).

Towards this end, a potentially useful phenomenon of insect ecology is that dispersal behaviour often differs between sexes, with male-mediated dispersal in some species meaning males are found more widely across the landscape (Holloway et al., 2003a; Rodwell et al., 2018), while the proportion of females in a population may be higher closer to breeding sites (Holloway &

McCaffery, 1990). *Anaspis* (Coleoptera: Scraptiidae) is a common and widespread genus of beetles that can be readily sexed using external sexual characteristics, which facilitates the examination of sex ratios at a large number of sites. *Anaspis* are frequently encountered on flowers in the spring and summer, where several species can be encountered together (Levey, 2009), but despite their apparent abundance the distribution and ecology of most *Anaspis* species are poorly known. Most species are associated with deadwood or leaf litter, where the larvae may be predatory (Webb et al., 2018), whilst some are affiliated with more open habitats. This study aims to quantify the habitat associations of some *Anaspis* by examining the abundance and sex ratio of beetles collected on transects of umbellifer inflorescences using a simple survey methodology. The cover of four key habitat types around the transects is estimated using maps classified from aerial photography, whilst LiDAR-derived maximum vegetation height is used as a measure of vertical habitat structure. Habitat variables are related to the occurrence patterns of male and female *Anaspis* in three lowland agricultural landscapes, in order to address the following key questions:

1.  Do males and females of *Anaspis spp.* in a community respond similarly to key habitat variables, or are there any differences that might help identify habitat associations?
2.  Where the sex ratio of an *Anaspis* species is heterogeneous across the landscape, do key habitat variables explain a significant proportion of the variation in abundance and sex ratio between sites?
3.  How does maximum vegetation height perform as an indicator of abundance and sex ratio in *Anaspis spp.*, relative to the mapped extent of tree cover?

## 4.2. Methods

### 4.2.1. Study Areas

Samples of *Anaspis* were taken in three study areas, each defined by a 6-km$^2$ grid. All three grids were located in southern England, two in the county of Hampshire with origins at 51.299 N, 1.012 W (N.Ham) and 50.914 N, 1.283 W (S.Ham) and one in Gloucestershire (Gloc) with origin at 51.986 N, 2.220 W (Figure 1). Within each of the resulting 108-km squares, a sampling transect was established by locating suitable 200-m stretches of road or footpath bordered by flowering Apiaceae, an especially abundant and widespread family of plants that is a key nectar source in agricultural landscapes (Zych, 2007; Pocock et al., 2012). Placement was guided by the presence of flowering cow parsley *Anthriscus sylvestris* during the first visit in May as well as the vegetative presence of later-flowering species, especially Hogweed *Heracleum sphondylium*, aiming for a transect that would be usable throughout the study. Transects were located as close as possible to the centre of 1-km squares to maximise their independence. In one case where no suitable transect was present, a suitable selection was made in an adjacent 1-km square, outside the original 6-km$^2$ grid. For the purposes of analysis only, transects for which LiDAR data were available were used

(see Section 2.3 below), resulting in a final sample of 89 transects (Figure 1): 26 in the NHam study area, 32 in SHam and 31 in Gloc.
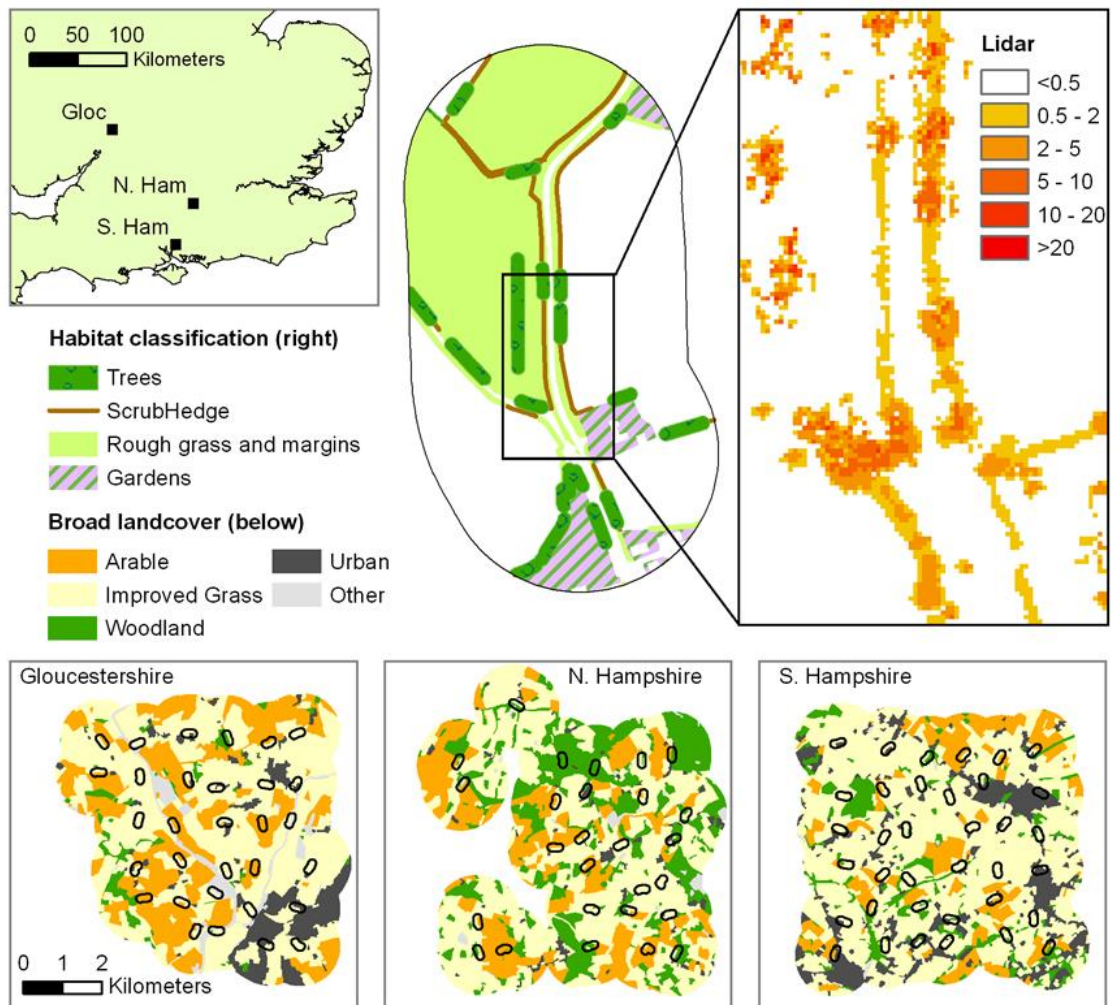


**Figure 1.** Location of the three study areas in southern England. Panels for each study area show the broad landcover for 1 km around the transects for which LiDAR data was available. Transect map (top middle) shows the distribution of four key habitat covers for the 100-m buffer around a single transect, pull out box (top right) shows LiDAR-derived vegetation height.

### 4.2.2. Beetle Sampling

Transects were surveyed three times each in 2013, in the intervals 16 May–10 June, 26 June–8 July and 10–26 July. Sampling was carried out between 10 a.m. and 6 p.m. in dry, calm conditions. Transects were walked slowly for 30 minutes in a single direction. Flowers were searched by eye and any beetles present captured in a plastic collecting tube (90 mm length x 25 mm diameter). Dense clusters of individuals were captured by shaking the flowers into a plastic funnel inserted into the mouth of the collecting tube. Specimens of *Anaspis* were returned to the laboratory and stored in 70% ethanol prior to identification. Specimens were then sexed and identified to species

following Levey (2009). For the purposes of analysis, data from the three visits were pooled for each transect.

### 4.2.3. Habitat Variables

Habitat cover was digitized for a 100-m buffer around each transect in ArcMap 10.4 (ESRI, 2016). This is just outside the single dispersal flight distance for *Anaspis spp.* leaving woodland patches reported by Irmler et al. (2010), so any *Anaspis* recorded on the transects were assumed to have emerged from a breeding site within the 100-m buffer and not outside it. A study of the response of flower-visiting beetle communities to landscape heterogeneity (see Chapter 3) determined that the extent of trees, gardens and 'rough vegetation' (including semi-improved or semi-natural grassland, road verges and field margins) significantly influenced community composition in all flower-visiting beetles, including *Anaspis* spp. These habitats are therefore included as the variables 'Trees', 'Gardens' and 'Rough' in the current study. They describe the gradient from availability of tree-dominated (shaded) to grass- or herb-dominated (open) semi-natural habitats as well as the mixture of habitats provided in suburban or rural gardens. Delineation of habitat patches was based on OS Mastermap (Ordnance Survey, 2015) and categorised using information directly from Mastermap and with reference to (aerial imagery. Isolated trees and lines of trees not captured by Mastermap were added manually by creating line features, assumed to have a canopy width of 10 m for combining with the rest of the tree extent data ('Trees'). Deciduous and coniferous trees were not separated as the majority of 100-m transect buffers contained no coniferous tree cover.

Although not a key variable for modifying the full beetle community in Chapter 3, the length of hedges (outside of gardens) and scrub edge are also included here as the variable 'Scrub-Hedge'. These habitats may harbour breeding sites for some *Anaspis* either in dead twigs or woody herbaceous vegetation retained in the vicinity of hedges; hedgerows provide habitat for a wide variety of invertebrates (Maudsley, 2000). The presence of hedgerows may also be a proxy for the abundance of Apiaceae across the wider landscape since these plants often flower in dense stands along linear features and edge habitats. Scrub edge was calculated from the perimeter of Mastermap patches classified as scrub. Hedgerows were traced along Mastermap patch boundaries with reference to aerial imagery.

Vegetation height data were derived from 1 m resolution LiDAR digital terrain (DTM) and digital surface models (DSM) (Environment Agency, 2017) The height of all objects was calculated by subtracting DTM values for each cell from the DSM. The resulting raster data were masked with the outline of buildings and other manmade structures from OS Mastermap (Ordnance Survey, 2015) and all remaining LiDAR height data in the raster was then assumed to pertain to vegetation. Comparing the resulting data to satellite imagery suggested that solitary trees, lines of trees, taller trees within woodland stands and woodland edges were all well captured by the 1 m resolution

LiDAR but that the interior of even-age woodlands often returned no signal. Maximum vegetation height (Max-Height) was therefore used as a variable in the analyses rather than average vegetation height, indicating the presence of large mature trees, whether they were solitary trees or part of a large stand. A summary of all five habitat variables and their values in each study area is provided in Table 1.

**Table 1.** Summary of habitat variables across the three study landscapes.

|  |  | Gloc | Nham | SHam |
|---|---|---|---|---|
| **Garden (ha)** | Min | 0.00 | 0.00 | 0.00 |
| Extent of gardens | Median | 0.02 | 0.10 | 0.48 |
|  | Max | 2.39 | 2.37 | 3.32 |
| **Rough (ha)** | Min | 0.00 | 0.09 | 0.00 |
| Extent of rough grassland, | Median | 0.27 | 0.47 | 0.30 |
| road verges, field margins | Max | 3.35 | 2.67 | 2.75 |
| **Trees (ha)** | Min | 0.02 | 0.17 | 0.02 |
| Extent of tree cover including | Median | 0.29 | 1.47 | 0.85 |
| woodland and lines of trees | Max | 4.39 | 5.73 | 3.07 |
| **Scrub-Hedge (km)** | Min | 0.11 | 0.00 | 0.13 |
| Length of scrub edge and all | Median | 0.67 | 0.43 | 0.68 |
| non-garden hedgerows | Max | 2.17 | 1.12 | 2.08 |
| **Max-Height (m)** | Min | 5.70 | 10.23 | 9.74 |
| Maximum vegetation height | Median | 15.11 | 21.08 | 20.92 |
| recorded by Lidar | Max | 24.29 | 32.82 | 34.57 |

### 2.4. Statistical Analysis

To explore question 1, the effect of all habitat variables on *Anaspis* community composition was assessed using partial redundancy analysis (pRDA), with study area included as a conditional variable to remove the effect of regional differences in the abundance of *Anaspis* species. Males and females of each species were entered into the analysis separately in order to illustrate any sex-determined response to habitat variables, with only males or females of each species recorded from at least five sites included to avoid unduly influencing the analysis with data-poor species. All species data were transformed using the Hellinger distance (Rao, 1995; Legendre & Gallagher, 2001), which further reduces the weight of species that may be under sampled rather than truly biologically rare. Autocorrelation between explanatory variables was assessed by referring to Variance Inflation Factors (Neter et al., 1996) and correlation coefficients. Variables with VIF > 3 were removed from the model sequentially until all VIF were < 3 (Zuur et al., 2010). Where two

variables had correlation coefficients >0.6 the model was run twice, excluding one of the variables each time and retaining one of them in the model based on the maximum amount of variation constrained. Probability values for the combined effect of all terms and for each constrained axis in the ordination were estimated using Monte Carlo tests with 9999 permutations.

The widespread species *Anaspis maculata* and *Anaspis pulicaria* were well distributed across all study areas (Table 2) and collected at enough sites (79 and 73 out of the 89) to analyse in greater detail. To address question 2, uncorrected log likelihood ratio tests of independence (G Tests) (Sokal & Rohlf, 1969; Pickup & Barrett, 2013) were performed to determine whether sex ratio in *A. maculata* or *A. pulicaria* was heterogeneous between sites. The contribution of habitat variables to variation in the abundance of *A. maculata* and *A. pulicaria* and their sex ratios were then estimated using generalised linear models (GLM). One model for the abundance of each species was fitted using a negative binomial error distribution with log-link function (O'Hara & Kotze, 2010). A binomial GLM was fitted for sex ratio in each species using the proportion of females (= f / (f + m)) as the response, weighted by the total number (f + m) such that sites for which the true proportion of females could be estimated with greater confidence were given greater weight in fitting the model. Checks that model assumptions were met were made by visually inspecting the output from model plotting functions in R.

Five habitat variables were entered as predictors: Trees, Gardens, Rough, Scrub-Hedge and Max-Height. Study Area was also included as a fixed factor in any of the four models where an effect of study area was judged to be important based on a significant Kruskal–Wallis test ($p < 0.05$). Bonferroni-corrected post hoc Dunn tests were used to determine the relationships between pairs of study areas and therefore select the appropriate factor reference level. Multicollinearity between predictors was examined using VIF; terms with VIF >3 were removed sequentially from the model until all VIF were <3.

A reduced model containing only key explanatory variables was obtained using a forward selection procedure. Beginning with only a blank intercept, variables were added to the model sequentially based on their estimated contribution to improving model fit as determined by Akaike's Information Criterion (AIC), stopping when no term was predicted to make a further improvement. Where adding or removing further terms resulted in an alternative model structure within 2 AIC of the model obtained by forward selection ($\Delta < 2$), coefficient estimates for these terms are also presented in the results (Burnham & Anderson, 1998; Richards, 2005). Predicted values and 95% confidence intervals were plotted for each variable other than study area, scaled to the original response variable.

All analyses were carried out in R 3.4 (R Core Team, 2017) using the packages 'vegan' (Oksanen et al., 2016) for redundancy analysis, 'DescTools' (Signorell, 2018) for G tests, 'MASS' (Venables

& Ripley, 2002) and 'car' (Fox & Weisberg, 2011) for binomial GLMs, 'dunn.test' (Dinno, 2017) for Kruskal-Wallis and Dunn tests and 'visreg' (Breheny & Burchett, 2017) for plotting predicted values from GLM results.

**Table 2.** Summary of *Anaspis* spp. recorded in three parts of southern England, with number of transects and total number of individuals for those sites used in the analysis. * denotes presence on a transect in the region that was not used for analysis in the current study.

| Species | N. Ham. (26) | S. Ham. (32) | Gloc. (31) |
|---|---|---|---|
| | Sites (Individuals) | | |
| *A. costai* | 11 (54) | | * |
| *A. frontalis* | 8 (8) | 3 (3) | 3 (4) |
| *A. garneysi* | 7 (12) | 6 (8) | 4 (13) |
| *A. humeralis* | 14 (42) | 4 (6) | 5 (6) |
| *A. lurida* | 1 (1) | 1 (2) | |
| *A. maculata* | 23 (325) | 27 (292) | 29 (770) |
| *A. pulicaria* | 19 (347) | 29 (1241) | 25 (710) |
| *A. regimbarti* | 1 (1) | 5 (12) | 6 (8) |
| *A. rufilabris* | 3 (8) | * | |
| **Species** | 9 | 7 | 6 |
| **Individuals** | 798 | 1564 | 1511 |

## 3. Results

### 3.1. *Anaspis* Community in Three Study Areas

A total of 3873 *Anaspis* were captured, with representatives of nine species (Table 2). Only two of the *Anaspis* spp. on the British list (Duff, 2012) were not found during this study. Of the missing two, *A. bohemica* is restricted to Caledonian pine forest in the Scottish Highlands (Levey, 2009) whilst *A. thoracica* is considered a rare species in the UK, associated with deadwood habitats (Levey, 2009). *Anaspis maculata* and *A. pulicaria* were very widespread, captured at >70% of sites in all three study areas (Table 2). No other species was captured at >20% of sites in Gloucestershire or South Hampshire, whereas the *Anaspis* community in North Hampshire was more diverse, with *A. humeralis*, *A. costai*, *A. frontalis* and *A. garneysi* all widespread. Total transect species numbers differed between study areas (Kruskal–Wallis $\chi^2_2$ =11.91, $p < 0.001$), with species richness in North Hampshire higher than in Gloucestershire ($z = -3.09$, $p = 0.001$) or South Hampshire ($z = 2.98$, $p = 0.001$). The abundance of all *Anaspis* together did not differ significantly between study areas (Kruskal–Wallis $\chi^2_2 = 1.947$, $p = 0.38$) and was actually lower in N. Hants. (Table 2), suggesting that the observed higher diversity of species here was not necessarily due to larger samples leading to a higher probability of detection.

### 3.2. *Anaspis* Community Composition

Due to small sample size (recorded from <5% of sites) *Anaspis lurida*, *Anaspis rufilabris* and males of *A. humeralis* were excluded from the redundancy analysis. There was a significant effect of landscape variables on the remaining *Anaspis* community (F = 3.837, $p < 0.001$). The conditional variable Study Area explained 12.3% of the variation. Max-Height and Trees were collinear (correlation coefficient 0.65) and explained the same gradient in the ordination; the model explained slightly more variation when Max-Height was included in place of Trees (13.8% vs. 13.3%). Of the 13.8% total variation explained, Max-Height contributed 4.7% (F = 5.555, $p = 0.003$), Gardens 4.7% (5.612, $p = 0.002$) and Rough 3.3% (F = 3.885, $p = 0.012$). Scrub-Hedge explained 1.2% and was not significant (F = 1.422, $p = 0.202$). The first bi-plot axis (Figure 2) explained almost all of the constrained variation (12.8%, F = 14.156, $p < 0.001$). It describes a gradient from sites with high maximum vegetation height (i.e., mature trees) and greater extent of rough vegetation to sites with greater extent of gardens and a weak correlation with scrub edge and hedgerows. Well-recorded species *A. maculata* and *A. pulicaria* dominate the bi-plot (Figure 2a), with *A. maculata* males especially strongly associated with Max-Height and both sexes strongly associated with Rough. *A. pulicaria* is negatively correlated with Max-Height. Responses are weaker for all other species; however, there was a clear separation between the sexes in *A. costai* and *A. frontalis* (Figure 2b). In both cases, females were correlated with Max-Height; males of *costai* were correlated with Rough, while *frontalis* was correlated with Gardens.
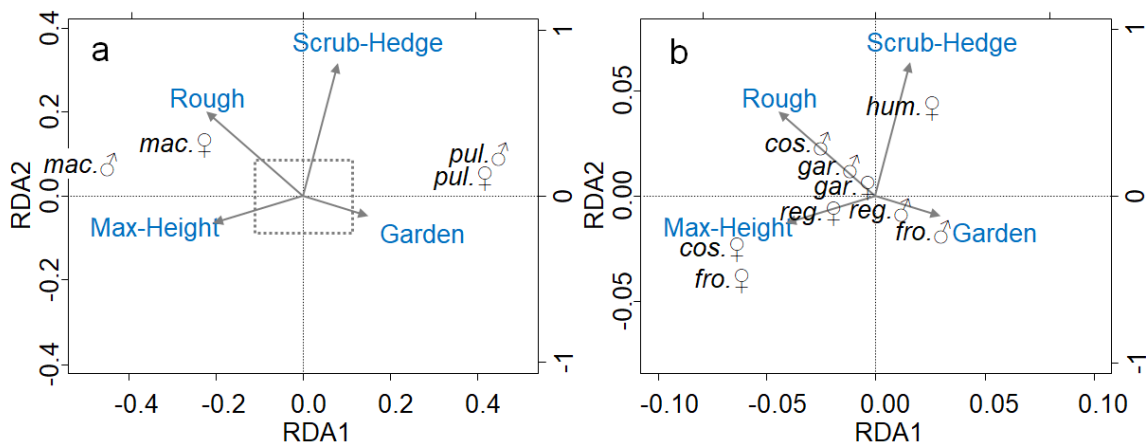


**Figure 2.** Redundancy analysis bi-plot for males and females of *Anaspis* in response to habitat variables. (**a**) displays dominant species only; (**b**) displays centre of the plot (area marked by dotted line on (**a**) to illustrate the response of less well described species. The strength of correlations between species/sex and habitat variables can be inferred by projecting perpendicularly onto the arrows. Abbreviations: *mac.* = *A. maculata*, *pul.* = *A. pulicaria*, *cos.* = *A. costai*, *fro.* = *A. frontalis*, *gar.* = *A. garneysi*, *hum.* = *A. humeralis*, *reg.* = *A. regimbarti*.

### 3.3. Sex Ratio in *Anaspis pulicaria* and *Anaspis maculata*

The overall proportion of females in *Anaspis pulicaria* recorded at all sites was $0.430 \pm 0.024$, which is significantly male-biased (G = 54.131, $\chi^2$ df = 1, $p < 0.001$). The sex ratio was significantly heterogeneous among sites (G = 114.56, $\chi^2$ df = 72, $p = 0.001$). The overall proportion of females in *Anaspis maculata* was $0.606 \pm 0.026$, which is significantly female-biased (G = 5.212, $\chi^2$ df = 1, $p = 0.022$) and also significantly heterogeneous among sites (G = 190.2, $\chi^2$ d.f. = 78, $p < 0.001$).

### 3.4. Generalised Linear Models for Abundance and Sex Ratio in *Anaspis pulicaria* and *Anaspis maculata*

*A. maculata* was significantly less common in both of the Hampshire study areas than in Gloucestershire ($\chi^2_2 = 14.986$, $p < 0.001$; N.Ham z = 3.470, $p < 0.001$; S.Ham z = 3.218, $p < 0.002$), and the proportion of females in the population was significantly higher in North Hampshire than in South Hampshire ($\chi^2_2 = 7.594$, $p = 0.020$; S.Ham z = 2.641, $p = 0.024$; Gloc z = $-2.115$, $p < 0.052$). Study area was therefore included as a variable in the *A. maculata* abundance GLM with Gloucestershire as reference level and in the GLM for *A. maculata* proportion female with North Hampshire as reference level. *Anaspis pulicaria* was more abundant in South Hampshire than in the other two areas ($\chi^2_2 = 8.685$, $p = 0.010$; Gloc z = $-1.723$, $p = 0.127$; N.Ham z = $-2.922$, $p = 0.005$), so study area was included as a variable in the GLM for *A. pulicaria* abundance with South Hampshire as the reference level. There was no significant different in the proportion female in *A. pulicaria* between study regions ($\chi^2_2 = 4.516$, $p = 0.100$).

The abundance of *A. maculata* increased with maximum vegetation height and was lower at sites surrounded by a greater extent of gardens (Table 3, Figure 3b, 3a). A positive effect of rough vegetation extent was included in an alternative model with $\Delta < 2$ (Table 3).

The proportion of females in the population increased with longer total lengths of scrub edge and hedgerow (Table 3, Figure 3f) and greater extent of gardens (Figure 3d). Proportion female decreased with maximum vegetation height (Table 3, Figure 3e) and area of rough vegetation (Figure 3c), though confidence in the latter term was low and models excluding Rough were not significantly different from the best-fitting model ($\Delta < 2$) (Table 3).

The abundance of *Anaspis pulicaria* increased with greater lengths of scrub edge and hedgerow (Table 3, Figure 4b) and decreased with greater area of rough vegetation (Table 3, Figure 4a). It was also negatively associated with area of trees and maximum vegetation height; these terms were not included in the best fitting model (Table 3). The proportion of females decreased where maximum vegetation height was high (Table 3), with the population predicted to be 60–70% male
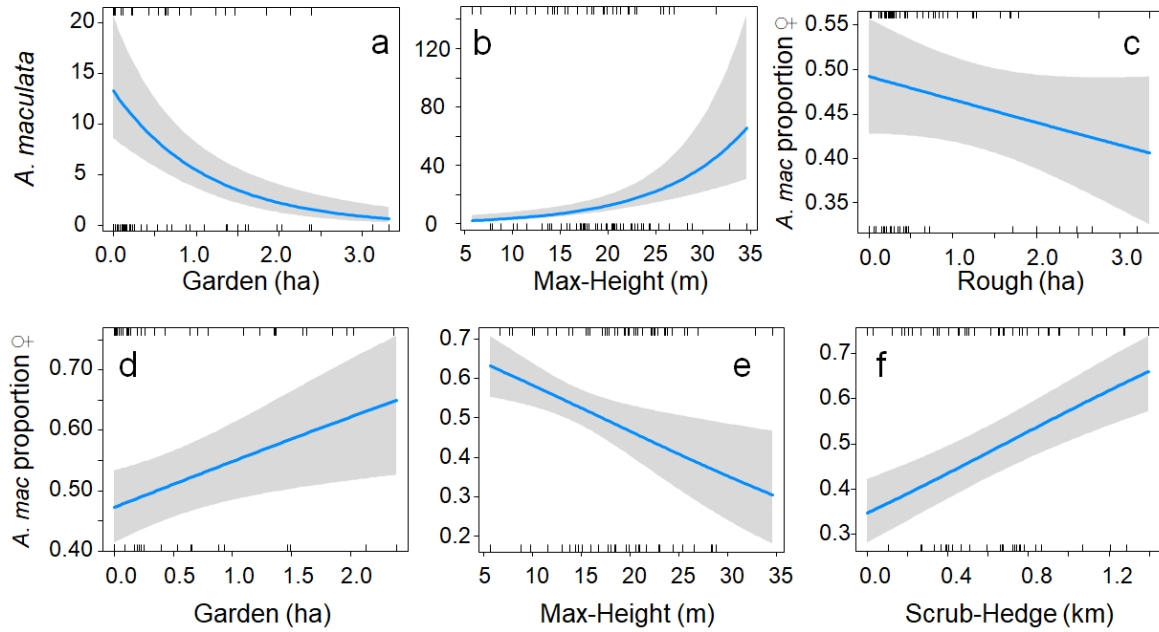
where trees over 20 metres were present in the nearby landscape (Figure 4c). An alternative model with Δ < 2 included a small negative effect of hedgerow and scrub edge (Table 3).

Overall, the GLMs predicted the distribution and sex ratio of *Anaspis maculata* relatively well, with Pseudo-$R^2$ of 0.370 and 0.509, respectively. The abundance and proportion female of *Anaspis pulicaria* were less well described, with a Pseudo-$R^2$ of 0.182 for the abundance model and 0.085 for proportion female.

**Table 3**. Results of Generalised Linear Models for the effects of habitat variables on abundance and sex ratio (proportion female) of *Anaspis maculata* and *Anaspis pulicaria*, after forward selection. Values for terms are the estimated regression coefficient ± standard error. Coefficient estimates in italics indicate that the term is included in an alternative model within 2 AIC (not significantly different from the best fitting model). REFERENCE denotes reference level used for the Study Area factor. Codes for *p* values: *** < 0.001 < ** < 0.01 < * < 0.05.

| | *Anaspis maculata* | | *Anaspis pulicaria* | |
| --- | --- | --- | --- | --- |
| | Abundance | Proportion female | Abundance | Proportion female |
| Pseudo $R^2$ | 0.371 | 0.509 | 0.182 | 0.085 |
| AIC | 603.4 | 273.54 | 705.96 | 301.77 |
| Garden | −0.886 ± 0.165*** | 0.303 ± 0.120* | | |
| Rough | *0.215 (0.142)* | −0.104 ± 0.071 | −0.552 ± 0.194** | |
| Trees | | *−0.043 ± 0.066* | *−0.132 ± 0.143* | |
| Max-Height | 0.112 ± 0.023*** | −0.047 ± 0.017** | *−0.028 ± 0.295* | −0.026 ± 0.009** |
| Scrub-Hedge | | 0.927 ± 0.186*** | 1.115 ± 0.466* | *−0.159 ± 0.141* |
| Gloc. | REFERENCE | −1.225 ± 0.232*** | −0.6933 ± 0.348* | |
| N. Ham. | −1.945 ± 0.319*** | REFERENCE | −0.962 ± 0.368** | |
| S. Ham. | −1.524 ± 0.300*** | −1.183 ± 0.158*** | REFERENCE | |
| Alternative models Δ < 2 AIC. | 603.47 (+Rough) | 273.68 (−Rough)<br>275.36 (+Trees)<br>275.26 (+Tr, -Ro) | 707.2 (+TreesHa)<br>707.49 (+MAX) | 302.49<br>(+ScrubHedge) |

**Figure 3**. Predicted values from generalised linear models for abundance (a–b) and proportion female (c–f) of *Anaspis maculata* in response to habitat variables. Values are scaled to the original response variable. Shaded area shows 95% confidence intervals.
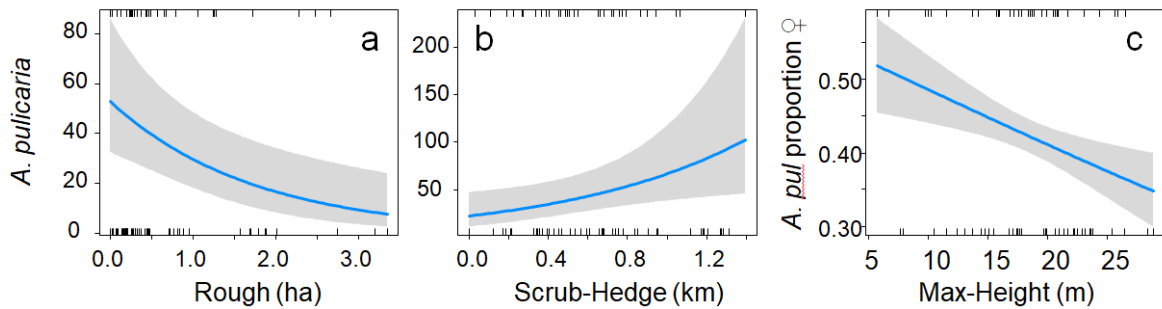


**Figure 4.** Predicted values from generalised linear models for abundance (**a–b**) and proportion female (**c**) of *Anaspis pulicaria* in response to habitat variables. Values are scaled to the original response variable. Shaded area shows 95% confidence intervals.

## 4. Discussion

### 4.1. Community of *Anaspis* Species

Most *Anaspis* species in the UK and more widely are associated with trees in some way, including species that are listed as scarce or threatened in a variety of European countries (Levey, 2009; Tingstad et al., 2017). Of the three study areas, North Hampshire was the most extensively covered by trees and also hosted the most diverse community of *Anaspis.* Species more widespread in North Hampshire included *A. costai* and *A. frontalis*. This difference is more likely due to habitat availability rather than regional differences since *frontalis* is widespread throughout the UK, with records north to the Highlands of Scotland (NBN Atlas, 2018), whilst *costai* is well-scattered

throughout southern England and Wales, with one occurrence in the Gloucestershire study area during this study (on a transect for which LiDAR was not available). Økland et al. (1996) found *A. frontalis* to be absent in Norwegian spruce forest where deadwood density in the surrounding 4 km$^2$ fell below a threshold. This suggests that habitat amount within the broader landscape may be an important driver of *Anaspis* distribution, more so than dispersal limitation, as indicated for *Anaspis ruficollis* by Schauer et al. (2018). Other studies confirm the importance of deadwood availability for species richness in saproxylic beetles, at scales from local to landscape (Müller & Bussler, 2008; Götmark et al., 2011; Lachat et al., 2012; Jacobsen et al., 2015). In the current study, females of deadwood associated species *A. costai* and *A. frontalis* were more strongly correlated with maximum vegetation height than males, which were weakly or even negatively correlated with vegetation height. This potentially suggests that vegetation height is a useful proxy for deadwood availability. In reality, the relationship is unlikely to be strictly linear given that open-grown trees, particularly oaks, may obtain lower heights than trees in closed-canopy forest but are associated with the highest species richness of saproxylic beetles, including some *Anaspis* (Franc & Götmark, 2008; Widerberg et al., 2012; Bouget et al., 2013; Parmain & Bouget, 2018). In the case of the LiDAR 1 m resolution data used in this study, there may well be a genuine relationship between maximum vegetation height and the presence of large open-grown mature trees, since its performance at resolving tree height appeared to be better where these were lone trees in hedgerows or on woodland edges.

## 4.2. Habitat Associations of *Anaspis pulicaria* and *Anaspis maculata*

In the single-species analyses, the abundance of *Anaspis maculata* increased strongly with maximum vegetation height, though with lower certainty for large height values. *A. maculata* was one of the most common species captured by Stork et al. (2001) in an oak canopy fogging experiment in the UK and was also obtained in canopy traps in France by Bouget et al. (2008), suggesting that it does indeed have an association with the canopies of large trees. Recently, Müller et al. (2018) found higher arthropod abundance associated with greater tree height in beech woodland.

*A. maculata* was also more abundant in the wider countryside away from gardens. The proportion of females decreased with tree height and increased with garden extent, such that where abundance of the species was high, the proportion of females in the population decreased. This could potentially be explained by wide dispersal of males through the landscape (Rodwell et al., 2018), with high numbers of *A. maculata* being recorded in particularly attractive sites for nectaring adults that are not necessarily associated with breeding sites, perhaps displaying a preference for Apiaceae in shaded situations. Alternatively, if male–female dispersal in *A. maculata* follows the pattern observed in a bark beetle (Scolytidae) by Doležal et al. (2016), then the proportion female would be

expected to increase slightly within 100 m of emergence points before falling away. If this were the case, since habitat variables in this study were measured within a 100-m buffer, a more female-biased sex ratio would in fact indicate transects that were more distant from breeding sites. Female dispersal distances also exceed those of males in the butterfly *Melitaea cinxia* (Kuussaari et al., 1996).

Rough vegetation extent, associated with potentially flower-rich grassland and road verges, also had a small positive effect on the abundance of *A. maculata* and a negative effect on the proportion of females. The strong increase in proportion female with the length of scrub edge and hedgerow may indicate the presence of breeding sites; that this species was so widespread across all three study areas suggests that suitable habitat is present in all kinds of woody vegetation besides large mature trees, perhaps in dead twigs. It has, for example, been recorded as one of the most common insect species on juniper, *Juniperis communis*, in southern England (Ward, 1977).

*Anaspia pulicaria* displayed a similar inverse pattern of abundance and sex ratio as *maculata*, with higher abundance but fewer females in the population with longer lengths of hedgerow and scrub edge. However, both the proportion of females and possibly overall abundance decreased with maximum vegetation height. This suggest that *pulicaria* is indeed more of an open habitat species compared to other *Anaspis* (Levey, 2009). That it was more abundant in southern Hampshire, where the landscape was more open, than in the north of the county might confirm this, though it was negatively associated across all study regions with open rough vegetation and less abundant than *maculata* in Gloucestershire, the study area with the lowest tree cover. Its larval ecology is apparently unknown; if a higher proportion of females does in fact indicate the proximity of breeding sites for *pulicaria* then all that can be said here is that these are likely to be in more open, unshaded situations, potentially in woody herbaceous vegetation or low hedgerows. Models for *pulicaria* were less successful than for *maculata*. Vierling et al. (2011) also found in a woodland spider community that LiDAR variables performed better for shade-affiliated species. Again, assuming that a high proportion of females equates to breeding site proximity, the female-biased sex ratio across all *maculata* collected compared to a male-biased sex ratio in *pulicaria* may indicate that the transects were systematically closer to *maculata* breeding sites, guided by the locations in which suitably dense patches of Apiaceae for sampling are located.

### 4.3. Performance of LiDAR Data and Further Applications

LiDAR-derived maximum vegetation height was retained as a significant explanatory variable in the redundancy analysis and three of the GLMs. In all but one case, it explained the same variation as tree cover but was a better fit with the beetle data. For the proportion female in *A. maculata* there was possibly an additional negative effect of tree cover in addition to that identified for vegetation height. Both variables appear to be good proxies for wooded habitats, describing a

transition from open habitats with lower hedges, scrub and young trees to ones with mature trees. The slightly better performance of vegetation height suggests that for beetles the presence of mature trees is more important than the extent of woodland cover per se, again this is as expected if beetle species richness is associated with more open wooded habitats (Franc & Götmark, 2008; Widerberg et al., 2012). However, given that there is a scale-dependent link between habitat amount in the surrounding landscape and the distribution of some insects as well as other taxonomic groups such as birds (Barbaro et al., 2007; Haslem et al., 2008; Brouwers & Newton, 2009; Bergman et al., 2012; Neumann et al., 2016a), better indicators of arboreal habitats may combine measures of horizontal extent and vertical structure (Davies & Asner, 2014; Müller et al., 2018; Schulte to Bühne & Pettorelli, 2018).

Preparing the height data required only a few automated steps in ArcGIS, whereas accurately incorporating non-woodland trees into OS Mastermap required more manual classification and digitisation. In this respect it is a more useful variable in terms of processing time for covering large areas as well as more accurately predicting the distribution of beetle communities. A nationwide LiDAR-derived model of woody linear features for the UK has been shown to improve predictions of bird and butterfly abundance (Sullivan et al., 2017) but average accuracy in identifying features of 60% may not be sufficient at more local scales and the published data do not contain height information (Scholefield et al., 2016). Nonetheless, as higher-resolution LiDAR becomes more accessible and measures of vertical habitat structure improve (Davies & Asner, 2014; Schulte to Bühne et al., 2018) , there is great potential to achieve a better understanding of how biodiversity is linked to both landscape and habitat heterogeneity and how these interact (e.g., Barbaro et al., 2005; Kosicki et al., 2015).

In the UK, large-scale studies of Lepidoptera, Orthoptera and ladybirds (Coleoptera: Coccinellidae) have all drawn on citizen science data (Roy et al., 2012; Cherrill, 2015; Oliver et al., 2017) which can be used to accurately predict species habitat associations (Redhead et al., 2015), but for most insect groups insufficient data are available to unpick habitat associations in any detail. For example, although there are 5850 verified records of *Anaspis* in the national biodiversity atlas for the UK (NBN Atlas, 2018) only half record location to within 100 m, one-fifth contain estimates of abundance, and fewer than 100 records indicate the sex of individuals encountered. This highlights the continuing value of intensive programmes of fieldwork with insect specimens retained for later examination, as in the present study.

**4.4. Conclusions**

The combination of habitat variables derived from aerial imagery and LiDAR gave a useful insight into the distribution of *Anaspis* species, a little studied genus of beetles, across three study landscapes. To answer the first two key questions, differences in the distribution of males and

females in *Anaspis* were identified and the most successful model in terms of variation explained was for the sex ratio in *Anaspis maculata*. To our knowledge, few studies of insect distributions across the wider landscape incorporate potential differences in movement and dispersal between sexes; we suggest this is a useful technique for investigating the spatial ecology and habitat affiliations of other poorly known insects. Maximum tree height is potentially a good indicator of habitat type or availability for beetles within the scale measured (100-metre landscape buffers) and is widely available from 1 m LiDAR in the UK. Higher-resolution data or a combination of LiDAR and habitat cover maps could provide a better picture of the spatial distribution of insect biodiversity than habitat cover alone.

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## 5. Crap Towns? Response to Urbanisation and Landscape Heterogeneity Mediated by Family, Feeding Guild and Body Size among Beetles at Dung-Baited Traps

### 5.1. Introduction

Urbanisation is among the foremost threats to biodiversity, with an increasing proportion of the global human population living in cities (United Nations, 2014). Yet it is this high population density that makes urban green spaces a key point of interaction between humans and wildlife, driving the need to understand biodiversity and ecosystem function in urban areas (Niemelä, 1999). Historically, much urban biodiversity research concerned birds, which undergo significant community homogenisation and restructuring along gradients of urbanisation (Baker et al., 2010; Gagné & Fahrig, 2011). An increasing number of studies address invertebrates in urban areas (Jones & Leather, 2012) and show that the response to urbanisation is far from uniform, varying both within and between taxonomic groups (McIntyre et al., 2001; Gibb & Hochuli, 2002; Angold et al., 2006; Egerer et al., 2017) and mediated by factors such as body size (Magura et al., 2006), feeding guild (Hochuli et al., 2004; Magura et al., 2013), degree of specialism (Gaublomme et al., 2008) and mobility (Angold et al., 2006; Snep et al., 2006; Delgado de la Flor et al., 2017).

These non-uniformly negative impacts mean that urban greenspaces can host a diverse range of species (Angold et al., 2006), and ecosystem function is not necessarily impaired by urbanisation beyond its fragmentation of habitats (Wolf & Gibbs, 2004). Bee diversity can be particularly high in urban green spaces (Lowenstein et al., 2014; Baldock et al., 2015; Banaszak-Cibicka et al., 2018), suggesting that urban areas may contribute to maintaining pollination services across the wider landscape (Theodorou et al., 2017). This highlights that urban areas are an important part of the contemporary landscape mosaic and their 'spillover' effect into agricultural landscape or neighbouring semi-natural habitats, whether positive or negative, needs to be addressed.

Some argue that by hosting novel ecosystems (Hobbs et al., 2009; Kowarik, 2011) urban areas actually boost overall biodiversity at a broad landscape scale, e.g., regional or national (Sattler et al., 2011). Species communities in a habitat patch may even be modified by the presence of urban areas in the surrounding landscape (Neumann et al., 2016a), with a positive effect on the occurrence of some species observed in Chapter 3. To assess the full effect of landscape heterogeneity on biodiversity, including how urban areas interact with other land cover types, ideally a measure of gamma diversity would be obtained, i.e., the species diversity of the whole landscape. However, studies that address this are not particularly common (Duflot et al., 2014, 2017). Though not a complete substitute, sampling insects on ecotones using a common attractant, such as baited traps or flowers, may provide a snapshot of landscape biodiversity that can be assessed at a large number of sites relatively easily (Chapter 3). Such a method can be carried out in urban sites as well as rural, where a habitat-focussed experimental design is not always feasible.

It may also facilitate focussing on a particular functional group, which may be a more meaningful measure for assessing the value of urban greenspaces than the more random assemblages of species collected by passive trapping methods (Gagic et al., 2015; Pinho et al., 2016).

Scarabaeoidea (henceforth 'dung beetles') are a well-studied group that are important ecosystem-service providers in pastoral agricultural systems (Nichols et al., 2008; Manning et al., 2016) and often used as indicators in tropical ecosystems (Nichols et al., 2007), where they are threatened by habitat fragmentation including urbanisation (Korasaki et al., 2013). They are usually sampled using a variety of dung-baited trapping techniques or by direct searching of dung. In general, very few studies consider dung beetles in an urban context (Ramírez-Restrepo & Halffter, 2016). However, not all dung-feeding Scarabaeoidea are obligate dung feeders (Gittings & Giller, 1997) and some will feed on dog dung, even preferentially so for species that prefer omnivore to herbivore dung (Cave, 2004; Carpaneto et al., 2005). As such, a stable community of dung beetles might persist in urban green spaces that either provide a ready supply of dung or other sources of rotting organic material for species with broadly saprophagous larvae. In addition, other beetles besides Scarabs are coprophilous, attracted to dung either as a direct food source or to predate on the eggs and larvae of other insects (Hanski & Cambefort, 1991). Many of these species belong to the Staphylinidae, which despite potentially being a good indicator group (Bohac, 1999; Vásquez-Vélez et al., 2010) are less often the focus of urban or landscape studies (though see Delgado de la Flor et al., 2017; Magura et al., 2013; Vergnes, Pellissier, Lemperiere, Rollard, & Clergeau, 2014).

In this study, we use simple baited traps to sample the coprophilous beetle community in 48 habitat patches close to a large urban area in southern England. By stratifying the sites into three urban distance bands, we investigated the effect of proximity to urban land cover on beetle abundance, richness and community composition. We examined how the effect of urbanisation varies between members of different feeding guilds, and on beetles of different body size. We ask whether coprophagous species (including saprophagous beetles that are not obligate dung feeders) are more abundant and speciose at rural sites, where we would anticipate greater herbivore dung availability from livestock and wild mammals and potentially greater availability of other rotting vegetation in less 'tidy' habitats. In addition, we explored the effect of landscape on the distribution of dung-attracted beetles in more detail using an ordination analysis, identifying the key elements of landscape heterogeneity and the spatial scales at which they most strongly influence community composition in coprophilous beetles.

## 5.2. Methods

### 5.2.1. Study Design

Forty-eight study sites were selected on woodland edges or the perimeters of partly wooded urban green spaces (edges >50 m in length). Study sites were selected in three groups based on their distance from the large urban centre of Reading in southern England (51.45, –0.97). A circular area with a 15 km radius originating at the town centre was divided into eight sections following compass intervals, e.g., the area between bearings north and northwest. In each of the eight sections six sites were selected. Two of the six were 'Urban' sites, defined as being less than 200 m from the main Reading conurbation, as mapped in Land Cover 2007 (Morton et al., 2014). Two were 'Fringe' sites, between 200 m and 1000 m away from either the Reading conurbation or other urban areas >10 ha in extent. Finally, two 'Rural' sites were selected, all of which were >1000 m away from any urban area >10 ha. Urban, Fringe and Rural are henceforth referred to as urban distance bands. All selected sites were at least 1 km from their nearest neighbour to maximise independence between beetle populations. During fieldwork, site locations occasionally had to be changed to find a suitable place to set traps. Sites were subsequently recategorised after fieldwork was complete, again according to the distance bands above but using the precise field survey locations and updated urban land cover data from Land Cover 2015 (Rowland et al., 2017). This resulted in a final sample of 15 'Urban' sites, 16 'Fringe' sites and 17 'Rural' sites (Figure 1).

## 5.2.2. Beetle Sampling

Due to the high likelihood of trap disturbance in the urban sites, we assessed the dung-attracted beetle community using simple baited traps deployed for a short time period. Traps consisted of a 140 mm wide, 20 mm deep petri-dish filled to the brim with horse dung, which is attractive to a wide variety of species (Mroczyński & Komosiński, 2014). Dung was collected early in the morning from an enclosed stable in order to reduce the potential for colonisation by beetles ahead of its use for sampling (Krell, 2007). Between collection and use for trapping, the dung was kept inside in a covered bucket to keep it moist and exclude insects. Blends of dung collected on three different days were used to fill the traps in order to reduce variability in the age and consistency of dung provided between sampling sites. Any dung older than three days was discarded and not used for sampling since dry dung is less attractive to dung beetles (Aschenborn et al., 1989; Hanski & Cambefort, 1991) and possibly other coprophilous beetles.

Sampling sites were visited twice each between 19th May 2015 and 25th July 2015 in dry, calm conditions. Two sites in each urban distance band were visited on each day of fieldwork to eliminate collinearity between weather or date and urban distance. Within bands, sites were visited in a random order. Four traps were set out in a line at each sampling location, following a woodland edge or other semi-natural habitat boundary. Traps were placed on the ground at least 10 m apart. Presence/absence of livestock at the sampling location was also recorded during sampling

as dung availability is known to modify the efficacy of dung-baited traps (Finn et al., 1998). After one hour, traps were sealed using the petri dish lid and returned to the laboratory.
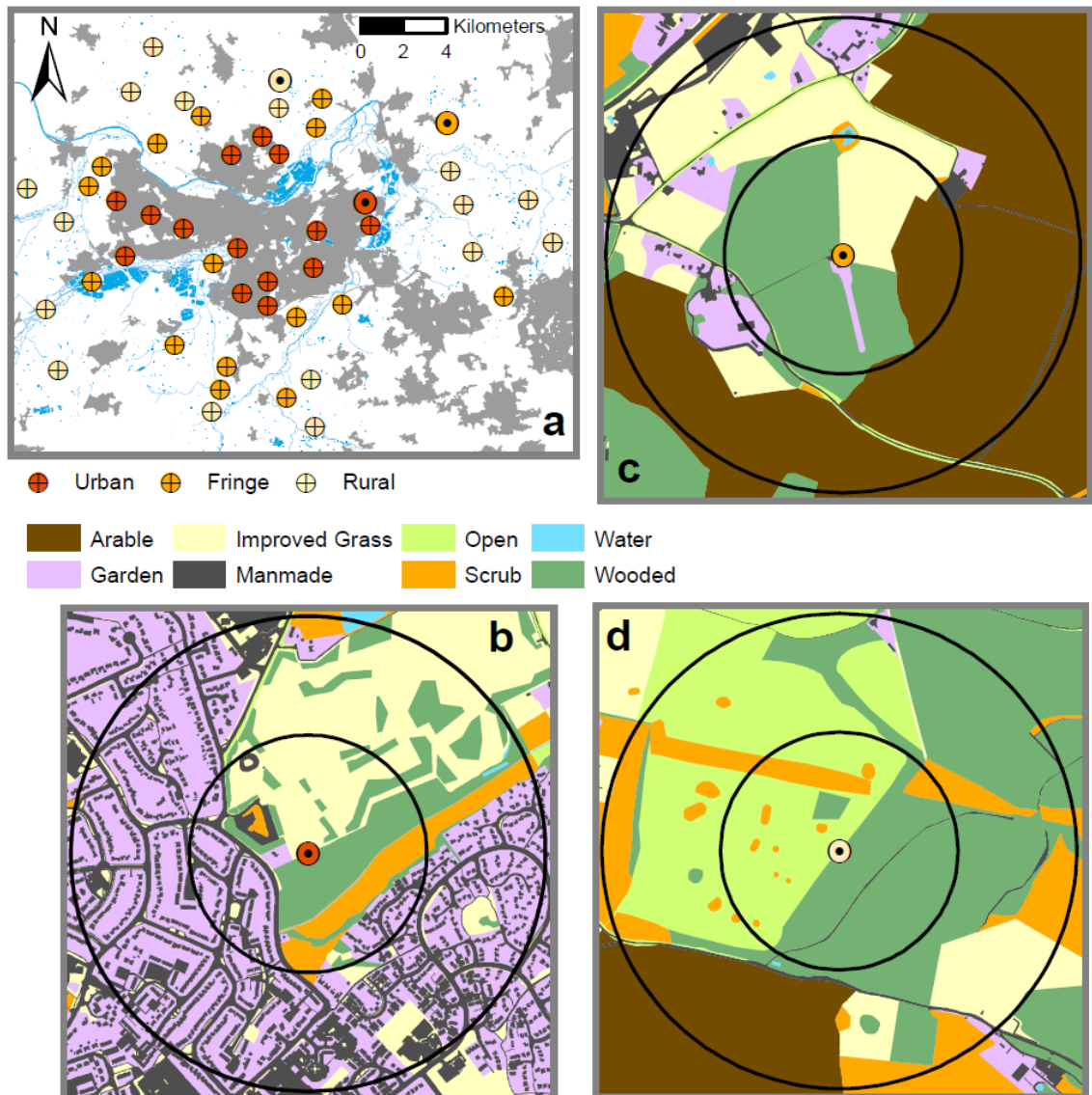


**Figure 1.** (**a**) The location of 48 sampling sites in the vicinity of Reading, UK, separated into three types according to their distance from urban areas >10 ha. Urban areas in grey shading, blue shading denotes rivers and other bodies of freshwater. Landscape composition for a 250 m and 500 m radius around the sites (black circles) is shown for (**b**) an urban site, (**c**) a 'fringe' (peri-urban) site and (**d**) a rural site.

Trap contents were emptied into a bucket of water to float out any adult beetles present, which were removed using a small sieve. Beetles were stored in 70% ethanol prior to identification. Beetles were identified to species following the relevant identification literature (Lott, 2009; Lott & Anderson, 2011; Duff, 2012; Dung Beetle UK Mapping Project, 2018). Members of the family

Ptilidae and subfamily Staphylinidae: Aleocharinae were counted a maximum of once each towards the species total for each site but not identified to species for use in community analysis. We used double-blind identification for quality control. Where necessary, specimens were dissected to confirm identification and compared to reference material. (Specimens for this study are held in the Centre for Wildlife Assessment and Conservation at the University of Reading and available to view on reasonable request.) Species were split into larval feeding guilds based on expert information contained in the PANTHEON database (Webb et al., 2018). The majority fell into one of two groups, either saprophagous (feeding on rotting organic material including dung) or predatory. They were also assigned an average body length from information provided in the identification resources for each family.

### 5.2.3. Landscape Data for Ordination Analysis

*Spatial scale, landscape variables*

Dung beetles in pasture habitat generally remain within the field in which they emerged (Roslin, 2000), though dispersal of individuals is leptokurtic, with some 1% of marked beetles observed by Roslin (2000) found 1 km away. If the appropriate spatial scale at which to examine the effects of landscape heterogeneity can be drawn from recorded dispersal flight distances, evidence from other beetle families is mixed. Irmler, Arp, & Nötzold (2010) reported very few saproxylic beetle species in flight intercept traps >80 m from woodland, whereas Doležal, Okrouhlík, & Davídková (2016) observed a maximum movement in a bark beetle of over 1 km. The harlequin ladybird *Harlequin axyridis* may be capable of regular dispersal flights >18 km (Jeffries et al., 2013), so clearly some beetles are unlikely to be impacted by habitat fragmentation. Most flight-able rove beetles are probably highly mobile, potentially dispersing long distances assisted by weather patterns. To account for this uncertainty, landscape variables were extracted for three different scales. These were 250-m, 500-m and 1-km buffers around the centre of the sampling sites. Landscape variables are split into two conceptual categories: landscape composition, which is the amount of different land cover types, and landscape configuration, which describes the spatial arrangement of those types, i.e., heterogeneity and fragmentation.

*Landscape composition*

The topography of land cover patches for landscape variables was taken from OS Mastermap (Ordnance Survey, 2015) and analysed in ArcGIS 10.4 (ESRI, 2016). All patches intersecting 2000-m buffers around the sampling points were classified into one of eight landscape composition variables, in total comprising a complete landscape mosaic analysis. All buildings, structures, paved roads and unsurfaced tracks were classified as MANMADE. Patches listed in Mastermap as 'Make = Multiple' (a mixture of manmade and natural surfaces) were classified as GARDEN.

Semi-natural habitat patches were classified as either WOODED (nonconiferous trees, coniferous trees, coppice), SCRUB (scrub, scattered coniferous trees, scattered non coniferous trees, orchard) or OPEN (freshwater marsh, heath, heather grassland, neutral grassland, acid grassland and calcareous grassland). Linear patches of habitat alongside railway lines were classified as OPEN. Linear patches alongside roads were also classified as OPEN unless the underlying land cover type in LCM2015 (Rowland et al., 2017) was urban, in which case they were classified as improved or amenity grassland (IMPGRASS). Freshwater types including rivers, lakes, streams and ditches were classified as WATER. Remaining unclassified polygons with no attributes listed in OS Mastermap were assigned to a category with reference to Natural England priority habitats data (Natural England, 2018) and Land Cover Map 2015 (Rowland et al., 2017), categorising agricultural land as either improved grassland (IMPGRASS) or arable/horticulture (ARABLE).

*Landscape configuration*

A variable estimating the availability of livestock dung (DUNGAV) in the surrounding landscape (Webb, Beaumont, Nager, & McCracken, 2010) was created by multiplying the area of each grassland patch (improved and semi-natural) by a 'livestock index'. The index was derived from livestock headage data (DEFRA, 2010) at a 5 $km^2$ grid cell resolution. Vales for each cell were rescaled to 0 – 1 where 0 = no livestock in the corresponding 5-$km^2$ grid cell and 1 = the maximum value for any cell intersecting with the study area.

To calculate mean patch size for the semi-natural habitat categories WOOD, SCRUB and OPEN, any patches closer than 20 metres were functionally considered to represent a single patch (Neumann et al., 2016b) and aggregated into one. Most beetles attracted to dung-baited traps are likely to arrive by flying, so gaps of this size are unlikely to present a significant barrier to dispersal. The mean size of aggregated patches that intersected the landscape buffers was then used to create the variables WOPATCH, SCPATCH and OPPATCH. Road verges were not included in the patch size calculation for OPPATCH, so this variable refers only to more extensive semi-natural grassland. As a further measure of habitat fragmentation, the mean distance to each of the three semi-natural habitats within landscape buffers was calculated, forming the variables WOODDIS, SCRUBDIS and OPENDIS. These were based on the original non-aggregated habitat patches, again excluding road verges for OPENDIS.

Finally, mean garden size (GARSIZE) was included as an alternative measure of urbanisation. Garden size tends to be smaller in core urban areas and larger in suburbs (Smith et al., 2009). Larger gardens may be more likely to contain a diverse mix of habitats, with a range of sources of decaying vegetation such as compost heaps that may provide habitat for saprophagous beetles that are also attracted to dung. A summary of all landscape composition and configuration variables and their mean values in each urban distance band is given in Table 1.

**Table 1.** Summary of landscape variables determined for three spatial scales, showing the median values for sites at three distances from large urban areas. Numbers in bold are significantly different between urban distance bands (Kruskal–Wallis tests); superscript letters denote post hoc groupings.

| | | 250 m | | | 500 m | | | 1 km | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Urban | Fringe | Rural | Urban | Fringe | Rural | Urban | Fringe | Rural |
| Composition (ha) | MANMADE (ha) | **3.4$^a$** | **0.5$^b$** | **0.5$^b$** | **18.7$^a$** | **3.3$^b$** | **2.2$^b$** | **85.8$^a$** | **25.2$^b$** | **10.4$^b$** |
| | GARDEN (ha) | **3.0$^a$** | **0.4$^b$** | **0.0$^b$** | **20.8$^a$** | **1.5$^b$** | **1.2$^b$** | **99.8$^a$** | **13.6$^b$** | **9.9$^b$** |
| | WOODED (ha) | 2.7 | 5.3 | 5.0 | **5.5$^a$** | **9.9$^{ab}$** | **16.7$^b$** | **20.9$^a$** | **35.7$^a$** | **60.7$^b$** |
| | SCRUB (ha) | 2.3 | 0.5 | 1.6 | 4.1 | 4.1 | 5.9 | 12.2 | 13.0 | 23.3 |
| | OPEN (ha) | 0.4 | 0.2 | 0.3 | 0.8 | 2.0 | 1.5 | 5.0 | 7.1 | 6.6 |
| | WATER (m$^2$/ha) | 433 | 347 | 86 | 0.2 | 0.3 | 0.4 | 2.6 | 1.9 | 1.2 |
| | IMPGRASS (ha) | 4.6 | 5.0 | 3.6 | 11.1 | 21.2 | 13.8 | **54.0$^a$** | **106.7$^b$** | **82.7$^b$** |
| | ARABLE (ha) | **0.0$^a$** | **1.7$^b$** | **0.1$^{ab}$** | **0.0$^a$** | **18.6$^b$** | **9.3$^b$** | **0.0$^a$** | **74.5$^b$** | **73.8$^b$** |
| | DUNGAV | 0.7 | 3.5 | 2.5 | **3.0$^a$** | **15.1$^b$** | **12.1$^b$** | **15.0$^a$** | **66.5$^b$** | **54.7$^b$** |
| Configuration | WOPATCH (ha) | 0.7 | 15.8 | 16.3 | **2.8$^b$** | **3.6$^b$** | **19.9$^a$** | **2.9$^b$** | **4.8$^b$** | **14.6$^a$** |
| | SCPATCH (ha) | 0.6 | 0.3 | 0.8 | 0.9 | 1.4 | 2.2 | 2.0 | 1.5 | 2.1 |
| | OPPATCH (m$^2$/ha) | 126 | 0 | 0 | 126 | 0.4 | 0.3 | 1.5 | 11.0 | 1.1 |
| | WOODDIS (m) | 59 | 36 | 48 | **97$^a$** | **82$^{ab}$** | **63$^b$** | **146$^a$** | **113$^{ab}$** | **75$^b$** |
| | SCRUBDIS (m) | 76 | 99 | 83 | 114 | 128 | 125 | 155 | 156 | 143 |
| | OPENDIS (m) | 274 | 288 | 383 | 386 | 338 | 353 | 665 | 466 | 352 |
| | GARSIZE (m$^2$) | 147 | 332 | 0 | **168$^a$** | **1062$^b$** | **1440$^b$** | **187$^a$** | **538$^b$** | **1425$^c$** |

## 5.2.4. Statistical Analysis

All analysis was carried out in R 3.4 (R Core Team, 2017). Data from the two visits were considered separately when testing for differences in abundance and species number. For species richness estimates and all community analyses, data from the two visits were pooled into a single value for each site.

### *Landscape variables, abundance, species richness and mean body length*

Differences in the values of i) landscape variables, ii) beetle abundance, iii) species number and iv) mean body length between urban distance bands were assessed using Kruskal–Wallis tests (adjusted for ties), followed by Dunn's test for multiple comparisons with Bonferroni corrected $p$ values. These were carried out using the R package 'dunn.test'.

For abundance and species richness, 12 initial Kruskal–Wallis tests were performed, examining the abundance and species richness in visit 1 and 2 of i) all beetles ii) those with saprophagous larvae and iii) those with predatory larvae. As numbers of dung beetles appeared to strongly influence the results for saprophagous species, the abundance of these species alone during each visit were examined in two further tests.

Estimated species richness for each distance band was calculated using the function 'Specpool' in the R package 'Vegan' (Oksanen et al., 2016), examining predicted species richness ± standard

error using the Jacknife, and Bootstrap methods (Smith & van Belle, 1984; Palmer, 1990). Estimates were made for all beetles and for those with saprophagous larvae only.

*Community analysis: distance categories*

All community analyses were carried out using the R package Vegan (Oksanen et al., 2016). Permutational analysis of variance was performed using the function *Adonis* (with 999 permutations) in order to assess whether beetle communities differed between urban distance bands. Beetle community data were standardised using the alternative Gower measure (Anderson et al., 2006) and log base 2 transformed such that a doubling in abundance was weighted the same as a change in composition (we were equally interested in both potential modifications of the species community ). Analysis of multivariate homogeneity of group dispersions using the function *Betadisper* was used to check whether any observed difference in community structure between distance bands might in fact be attributable to within group variation. Tests were carried out for all beetles and for each of the main feeding guilds (saprophagous or predatory) only.

*Community analysis: landscape heterogeneity*

Only species occurring in four or more sites were included in the community data used for ordination analyses. The community data matrix was log transformed ($\log_2(x) + 1$ for $x > 0$) (Anderson et al., 2006). Key landscape composition and configuration variables were identified via canonical correspondence analysis (CCA), followed by a forward selection procedure. Landscape composition variables were log transformed to reduce multicollinearity between predictors and ensure the influence of small but potentially important components of the landscape was not overlooked (Neumann et al., 2016a).

Six initial models were run in total, one for all landscape composition and one for all landscape configuration variables at each of the spatial scales (250 m, 500 m and 1000 m buffers). Collinearity between predictors was tested using Variance Inflation Factors (VIF) (Neter et al., 1996) and correlation coefficients. Terms with high VIF were removed sequentially until all terms in the global model had VIF <5.0 and correlation coefficients were all <0.6 (Radford & Bennett, 2007; Neumann et al., 2016b).

Forward selection to obtain a reduced model for composition or configuration at the three scales was carried out only after a significant global test of all variables ($p < 0.05$). Terms were added sequentially to the model based on their predicted contribution to adjusted-$R^2$ (Peres-Neto et al., 2006), and retained only if significant at $p < 0.05$ (Blanchet et al., 2008). Model building stopped before the adjusted-$R^2$ of the reduced model exceeded that of the global model to avoid over-fitting of explanatory variables (Blanchet et al., 2008). Probability values for the global model and

individual terms retained in the reduced model were estimated using Monte Carlo tests with 9999 permutation via the function *Anova.cca*.

A final model for each of the three spatial scales was obtained by adding all significant composition and configuration variables as predictors and removing any that were collinear by referring again to VIF and correlation coefficients. If any terms in the resulting model were still non-significant, they were considered likely to be explaining the same environmental gradient and a further forward selection procedure (without the adjusted $R^2$ stopping rule) was carried out to obtain a more parsimonious model. Finally, this procedure was repeated with the best fitting variables from each scale entered into a single model to obtain a final set of landscape variables that best described the beetle community composition.

### *Spatial and temporal autocorrelation, variation partitioning*

The effects of temporal autocorrelation and livestock presence at a site were also assessed using CCA following the model selection steps above. Dates of the first and second round of sampling were entered as two continuous variables; this will capture peaks in species activity as CCA assumes a unimodal, not linear relationship. Livestock presence was a factor with two levels indicating simple presence/absence.

We tested for spatial autocorrelation by calculating Principle Coordinates of Neighbourhood Matrices based on the XY coordinates of the sampling sites. All PCNM were used as predictors in a CCA followed by a further forward selection procedure to identify significant gradients of spatial autocorrelation. The interaction between space (represented by significant PCNM), landscape (key landscape variables) and date/livestock presence was then explored using variation partitioning. This finds the unique fraction of variation explained by each set of constraints, based on their contribution to adjusted-$R^2$ (estimated for CCA by permutation following Peres-Neto et al., 2006). Probability values for the unique effects of space, landscape or time/dung were estimated by using partial canonical correspondence analysis to partition out the other two sets of variables, followed by Monte Carlo tests with 9999 permutations.

### 5.3. Results

### 5.3.1. Beetle Sampling

A total of 2636 individual beetles were collected from the 48 sites, with representatives of 34 species and a further two groups not identified to species (Staphylinidae: Aleocharinae, Ptilidae). The 19 species recorded from four or more sites are listed in Table 2. Of these, seven belonged to the saprophagous larval guild (of which some also feed on dung as adults); the rest all had predatory larvae and *Heleophorus brevipalpus* are also predators as adults. Five of the top 10 most

abundant species, including the two most frequently recorded, belonged to the subfamily Oxytelinae (Staphylinidae), which are often among the most abundant rove beetles in dung (Caballero & León-Cortés, 2012; Mroczyński & Komosiński, 2014; Yamamoto et al., 2014). Eight species of dung beetle were recorded, with four among the most widespread species. The most common, *Volinus sticticus,* is widespread in woodland and scrub habitats (Dung Beetle UK Mapping Project, 2018).

**Table 2.** Species captured in dung-baited traps at four or more sites. Species in shaded rows have saprophagous larvae; the rest are predatory (Webb et al., 2018).

| Family | Biplot | Species | Sites | Total | May 19th – 15th June | | | | 17th June – 25th July | | | |
| | | | | | Urban | Fringe | Rural | Total | Urban | Fringe | Rural | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Staphylinidae | An.scu | *Anotylus sculpturatus* | 43 | 704 | 9 | 11 | 13 | 527 | 9 | 13 | 11 | 177 |
| Staphylinidae | An.tet | *Anotylus tetracarinatus* | 40 | 1230 | 6 | 4 | 6 | 52 | 13 | 13 | 11 | 1178 |
| Scarabaeidae | Vi.sti | *Volinus sticticus* | 29 | 218 | 4 | 10 | 13 | 197 | 0 | 3 | 6 | 21 |
| Staphylinidae: | Ox.laq | *Oxytelus laqueatus* | 22 | 50 | 6 | 5 | 7 | 37 | 4 | 3 | 2 | 13 |
| Staphylinidae: | Pl.are | *Platystethus arenarius* | 17 | 32 | 0 | 2 | 3 | 7 | 8 | 2 | 2 | 25 |
| Hydrophilidae | Ce.hae | *Cercyon haemorrhoidalis* | 12 | 39 | 0 | 2 | 5 | 34 | 3 | 0 | 2 | 5 |
| Hydrophilidae | Ce.mel | *Cercyon melanocephalus* | 11 | 30 | 1 | 1 | 3 | 20 | 1 | 2 | 4 | 10 |
| Staphylinidae | Me.pro | *Megarthrus prosseni* | 10 | 20 | 4 | 2 | 1 | 9 | 2 | 1 | 1 | 11 |
| Staphylininae | Bi.fim | *Bisnius fimetarius* | 9 | 28 | 1 | 3 | 4 | 26 | 0 | 1 | 1 | 2 |
| Staphylinidae | An.nit | *Anotylus nitidulus* | 9 | 17 | 0 | 0 | 0 | 0 | 3 | 6 | 0 | 17 |
| Scarabaeidae | Me.pro | *Melinopterus prodromus* | 8 | 16 | 1 | 3 | 4 | 16 | 0 | 0 | 0 | 0 |
| Staphylininae | Ph.var | *Philonthus varians* | 7 | 15 | 0 | 0 | 1 | 1 | 3 | 0 | 3 | 14 |
| Scarabaeidae | On.sim | *Onthophagus similis* | 6 | 20 | 0 | 0 | 4 | 12 | 0 | 1 | 1 | 8 |
| Staphylinidae | An.inu | *Anotylus inustus* | 5 | 11 | 1 | 2 | 1 | 7 | 1 | 1 | 0 | 4 |
| Scarabaeidae | On.coe | *Onthophagus coenobita* | 5 | 7 | 1 | 1 | 3 | 7 | 0 | 0 | 0 | 0 |
| Helophoridae | He.bre | *Heleophorus brevipalpus* | 5 | 5 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 4 |
| Staphylininae | Ph.mar | *Philonthus marginatus* | 5 | 5 | 0 | 2 | 2 | 4 | 0 | 0 | 1 | 1 |
| Staphylininae | Ga.pil | *Gabrius piliger* | 4 | 5 | 0 | 1 | 0 | 2 | 2 | 0 | 1 | 3 |
| Hydrophilidae | Ce.pyg | *Cercyon pygmaeus* | 4 | 4 | 1 | 1 | 1 | 3 | 1 | 0 | 0 | 1 |

### 5.3.2. Abundance

There was a significant difference between distance bands in visit 1 for all species with saprophagous larvae (K–W $\chi^2 = 11.660$, $p < 0.01$) but not for all beetles together (K–W $\chi^2 = 5.074$, $p = 0.08$). For saprophagous species, numbers at Urban sites were significantly lower than at Rural sites ($z = 3.414$, $p = 0.001$) but the difference between Fringe and Urban sites was not significant ($z$

= 1.718, $p$ = 0.130;) (Figure 2a). There was no difference in the abundance of predators between distance bands (K–W $\chi^2$ = 3.21, $p$ = 0.20) (Figure 2c).

During the second visit, overall beetle abundance did not differ between urban bands (K–W $\chi^2$ = 1.808, $p$ = 0.40), neither did the abundance of saprophagous species (Figure 2b; K–W $\chi^2$ = 2.713, $p$ = 0.26) or predators (Figure 2d; K–W $\chi^2$ = 0.862, $p$ = 0.65). When data for dung beetles only were examined, there was a significant difference between Rural and Urban sites, with no dung beetles at all recorded at Urban sites during the second visit (K–W $\chi^2$ = 7.819, $p$ = 0.02; z = 2.760, $p$ = 0.009; Table 2).

### 5.3.3. Species Richness

Neither the overall species richness (K–W $\chi^2$ = 3.638, $p$ = 0.16) nor the richness of saprophagous species (Figure 2e; K–W $\chi^2$ = 4.939, $p$ = 0.08) was significantly different between urban bands during the first visit, though the number of dung beetle species was (K–W $\chi^2$ = 8.513, $p$ = 0.01). More dung beetle species were recorded at Rural sites than Urban ones (z = 2.906, $p$ = 0.006). There was no difference in the species richness of predators (Figure 2g; K–W $\chi^2$ = 1.652, $p$ = 0.44). The same pattern occurred during the second visit, with no difference between bands for total species number (K–W $\chi^2$ = 1.475, $p$ = 0.48), saprophagous species (Figure 2f; K–W $\chi^2$ = 1.605, $p$ = 0.45) or predators (K–W $\chi^2$ = 0.862, $p$ = 0.65). Between the first and second visit patterns of species richness in predators reversed, with the highest values in Rural sites in visit 1 (Figure 2g) and Urban sites in visit 2 (Figure 2h).

Both estimates of species richness for urban bands predicted that Rural sites are the most species rich overall, higher than Fringe, with Urban the most species poor (Table 3), though the standard error ranges overlapped in each case. The same predicted pattern of species richness occurred for saprophagous species. The bootstrap estimate predicted that Rural sites host 50% more saprophagous species than Urban sites, with no overlap in standard error range between Rural and Urban sites. Conversely, Rural sites are predicted to have the lowest richness of predatory species with the highest richness in Fringe sites (Table 3).

### 5.3.4. Mean Body Length

There was a significant difference in mean body length between distance bands in the first visit (K–W $\chi^2$ = 6.033, $p$ = 0.05). Beetles at Rural sites averaged larger than those at Urban sites (Figure 3a, z = 2.393, $p$ = 0.025). In the second visit, there was no difference in average body length between distance bands (K–W $\chi^2$ = 1.826, $p$ = 0.40), driven by greater variability at Fringe and Rural sites (Figure 3b).
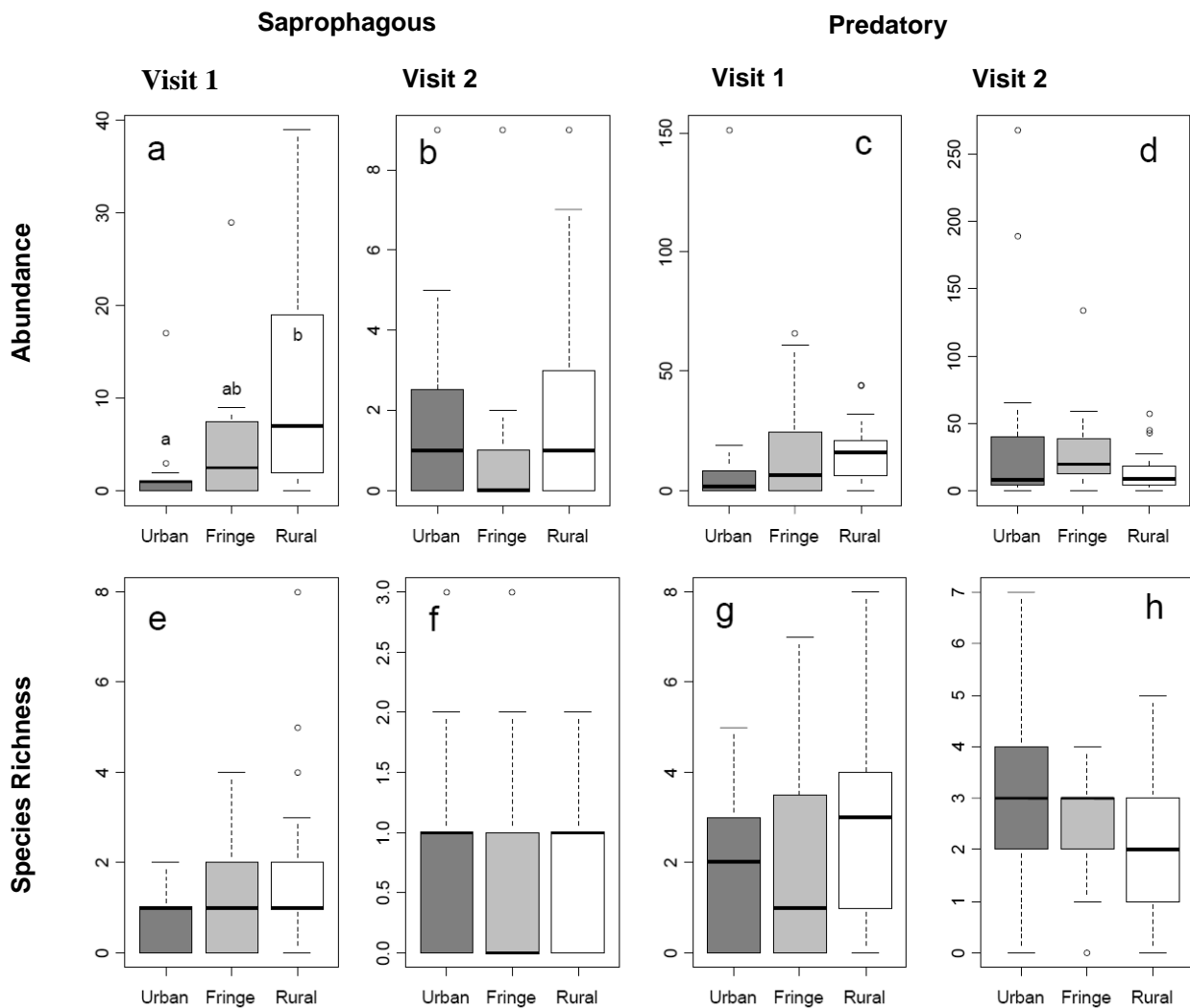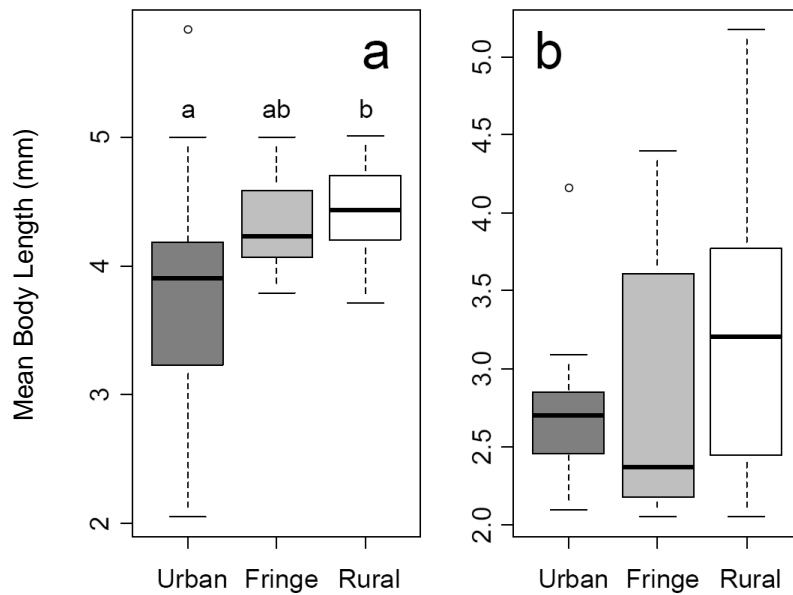
**Figure 2.** Median (black bars) and inter-quartile range (shaded boxes) of (**a**) the abundance of saprophagous beetles during the first sampling visit, (**b**) abundance or saprophagous beetles during the second sampling visit, (**c**) abundance of predatory beetles during the first visit, (**d**) abundance of predatory beetles during the second visit, (**e**) species richness of saprophagous beetles during the first visit, (**f**) richness of saprophagous beetles during the second visit, (**g**) richness of predatory beetles during the first visit, (**h**) richness of predatory beetles during the second visit. Values shown for three sets of sites grouped according to their distance from urban areas >10 ha.

**Table 3.** Species richness estimates. Highest estimates for each group are in bold text.

|  |  | Urban | Fringe | Rural |
|---|---|---|---|---|
| All Species | Jacknife | 34.29 ± 3.51 | 36.38 ± 3.27 | **38.41 ± 3.55** |
|  | Bootstrap | 29.13 ± 2.03 | 31.32 ± 2.07 | **33.02 ± 1.89** |
| Saprophagous | Jacknife | 10.64 ± 1.81 | 11.69 ± 1.84 | **14.73 ± 2.31** |
|  | Bootstrap | 8.40 ± 0.87 | 9.56 ± 1.00 | **12.54 ± 1.24** |
| Predatory | Jacknife | 19.64 ± 2.08 | **22.56 ± 2.83** | 18.71 ± 2.10 |
|  | Bootstrap | 17.33 ± 1.52 | **18.92 ± 1.72** | 15.87 ± 1.05 |

**Figure 3.** Median (black bars) and inter-quartile range (shaded boxes) for mean body length (mm) of coprophilous beetles (mean length per beetle captured, assuming average values for the species) at Urban, Fringe and Rural sites in (**a**) the first sampling visit and (**b**) the second visit.
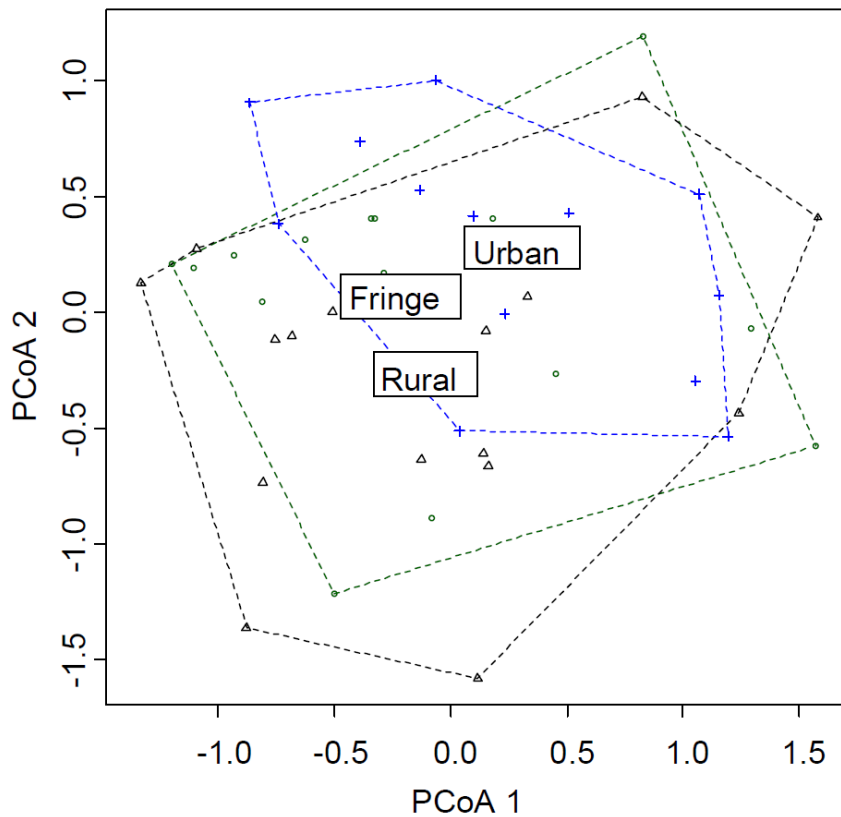
### 5.3.5. Community Dissimilarity

In the permutational analysis of variance, communities were significantly dissimilar between urban band (F = 1.931, $p$ = 0.032), which explained 8.7% of the dissimilarity between sites. There was no significant difference in within band homogeneity (F = 0.539, $p$ = 0.587). When Fringe sites were excluded, the difference between Urban and Rural sites alone explained slightly more variation (9.1%; F = 2.889, $p$ = 0.009).

When only saprophagous species were examined, urban distance band explained 15.0% of variation between sites (F = 3.174, $p$ = 0.013), whereas for predators urban distance band explained only 4.5% of variation between sites and was not significant (F = 1.027, $p$ = 0.397). On the PCA bi-plot for all species (Figure 4), Urban sites scoring above 0.5 on PCA2 were well separated from the Fringe and Rural sites. Fringe and Rural sites were interspersed between each other, much of the overlap between polygons draws from three Fringe and three Rural sites that scored highly on at least one of the axes.

### 5.3.6. Landscape Variables

Cover of manmade surfaces, garden and arable land were significantly different between urban distance bands at all measured spatial scales. Woodland cover, dung availability, woodland patch size, distance between woodland patches and average garden size were all different between distance bands when measured at 500 m or 1 km. Improved grassland was only significantly different at 1 km. The highest woodland cover and patch size was around Rural sites. Manmade

surface and garden cover was much higher in Urban than in Rural or Fringe sites, which were not significantly different from each other. The only variable to completely separate out the three distance bands was average garden size measured at 1 km, for which there was a significant difference between each pair of categories (Table 1).



**Figure 4.** Principal Component Analysis of the dissimilarity in coprophilous beetle communities at 48 sites, using the alternative Gower distance (Anderson et al., 2006). Sites are grouped according to their distance from urban areas. Crosses = Urban sites, circles = Fringe sites, triangles = Rural sites. Dashed lines show the minimum convex polygons for each group.

**5.3.7. Landscape Heterogeneity: Canonical Correspondence Analysis**

There was a significant global effect of landscape composition and landscape configuration variables for each spatial scale (Table 4). Landscape variables measured at 500 m performed best in explaining variation in beetle community composition. At 250 m only semi-natural habitats (the size of woodland and open habitat patches) and water were identified as key variables. At 500 m the only semi-natural habitat variable retained was the size of scrub patches, otherwise manmade surfaces, arable and improved/amenity grassland best described the landscape in terms of beetle community response. At the 1000 m radius manmade surfaces were highly collinear with other variables. After MANMADE was removed from the model the extent and average size of gardens described the urban gradient whilst the extent of scrub or scattered trees was also important at this scale.

All of the variables from 500 m were retained in the final model, strongly suggesting that this is the best scale at which to assess the response of this beetle community to landscape heterogeneity. Area of water in the surrounding 250 m was the only other variable retained. On the CCA bi-plot (Figure 5), the first axis (CCA1, F = 5.269, p < 0.001 ) explained 10.2% of the variation and described a gradient away from more urban landscapes (as measured by manmade surface coverage) and those with greater extent of improved or amenity grassland. The second axis (CCA2, F = 3.271, $p = 0.019$) explained 6.3% of the variation and described a gradient from landscapes with large patches of scrub or scattered trees and larger amounts of water nearby, to drier landscapes with greater arable cover.

Beetle community composition was significantly spatially autocorrelated (F = 1.560, $p < 0.001$) with six PCNM retained in a reduced model explaining 26.6% of beetle community composition. There was also a significant effect of sampling date and dung presence (F = 1.980, $p = < 0.001$) with Day1 (F = 2.053, $p = 0.013$), Day 2 (F = 2.669, $p = 0.002$) and Stock (F = 1.848, $p = 0.03$) together explaining 13.6% of beetle community composition.
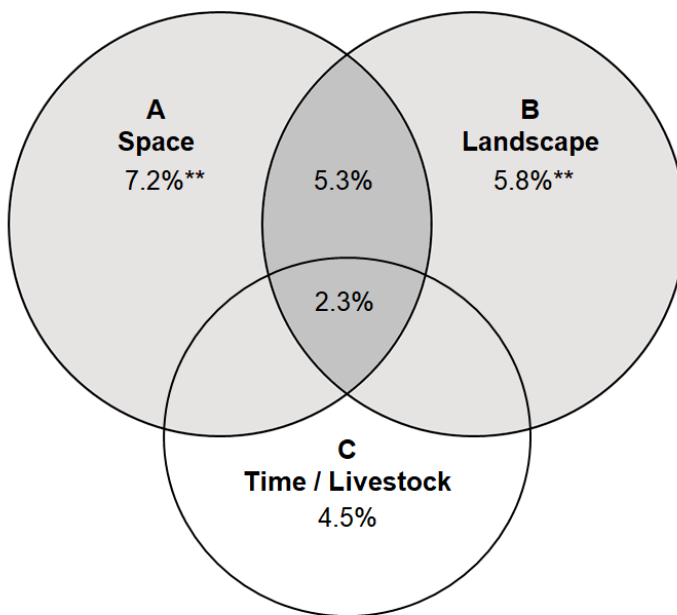
In the variation partitioning, the contribution to adjusted-$R^2$ of space (significant PCNM), landscape (final model for landscape heterogeneity) and time / stock presence was 7.2%, 5.8% and 4.5%, respectively (Figure 6). 5.3% of the variation was shared between landscape and space, and 2.3% shared between all three fractions. Overall variation explained was estimated at 25.8%. All individual fractions were significant after the other two were partitioned out (Space: F = 1.5985, $p = 0.005$; Landscape: F = 1.553, $p = 0.005$; Date/Stock: F = 1.674, $p = 0.012$).

**Table 4.** Summary of canonical correspondence analysis for the effects of landscape composition and configuration at three spatial scales on coprophilous beetle communities.

| Model / Variable | F | *p* | Explained |
|---|---|---|---|
| **Final Model** | **2.430** | **< 0.001** | **23.3%** |
| Water 250 | 1.906 | 0.049 | 3.5% |
| Manmade 500 | 3.961 | < 0.001 | 7.3% |
| Arable 500 | 2.257 | 0.008 | 4.2% |
| ImpGrass 500 | 2.034 | 0.018 | 3.8% |
| ScrubPatch 500 | 2.415 | 0.025 | 4.5% |
| Composition (250, all terms) | 1.735 | < 0.001 | 24.2% |
| Configuration (250, all terms) | 1.485 | 0.011 | 24.3% |
| **Composition + Configuration 250** (* = retained in combined model) Wooded 250 | **2.390** | **0.003** | **14.6%** |
| Water 250* | 2.243 | 0.031 | |
| WoodPatch 250* | 2.420 | 0.020 | |
| OpenPatch 250* | 2.278 | 0.024 | |
| Composition (500, all terms) | 1.926 | < 0.001 | 26.2% |
| Configuration (500, all terms) | 1.554 | 0.003 | 25.1% |
| **Composition + Configuration 500** (* = retained in combined model) Manmade 500* | **2.983** | **< 0.001** | **19.6%** |
| Manmade 500* | 3.092 | < 0.001 | |
| ImpGrass 500* | 3.017 | 0.001 | |
| Arable 500* | 3.137 | 0.002 | |
| Scrub 500 | | | |
| WoodDis 500 | | | |
| Scrub Patch 500* | 2.481 | 0.022 | |
| Composition (1000, all terms) | 1.626 | 0.002 | 23.0% |
| Configuration (1000, all terms) | 1.534 | 0.006 | 24.9% |
| **Composition + Configuration 1000** (* = retained in combined model) Garden 1000 | **2.700** | **< 0.001** | **11.1%** |
| Scrub 1000* | 2.092 | 0.010 | |
| Water 1000 | | | |
| GardenSize 1000* | 3.410 | < 0.001 | |
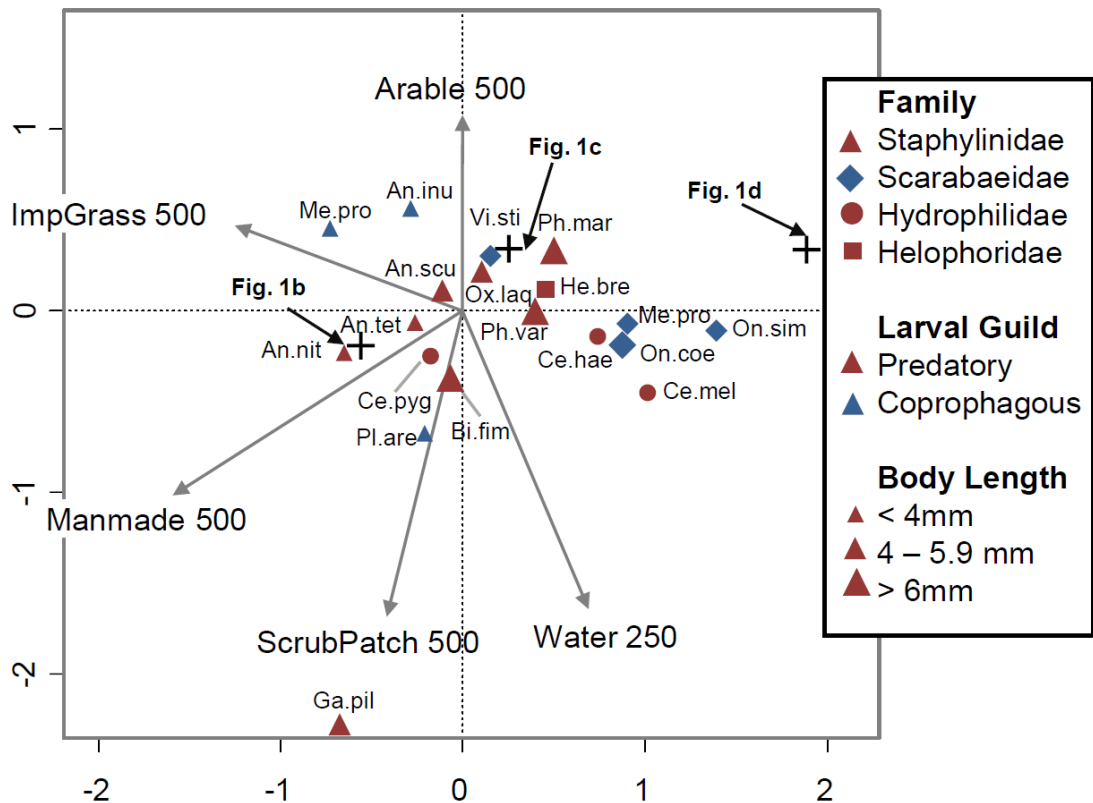
**Figure 5.** Canonical correspondence analysis bi-plot for the effects of landscape variables on coprophilous beetle community composition. Length of arrows indicates the strength of correlation between predictor variables and constrained axes in the ordination. Optimal values of landscape variables for each species can be inferred by projecting the species location on the bi-plot perpendicularly onto the arrows. Abbreviations for species are listed in Table 2.



**Figure 6**. Variation partitioning for the effects of space (PCNM), key landscape variables and survey date/livestock presence on coprophilous beetle community composition. Values are the proportion contributed to overall adjusted-$R^2$ by each fraction.

## 5.4. Discussion

### 5.4.2. Coprophilous Beetle Community

For the whole coprophilous beetle community, urban distance band explained a relatively small proportion of the dissimilarity between sites, even when using a dissimilarity measure that deliberately gave a high weight to changes in abundance. This suggests that in urban areas this community represents a subset of the wider species pool found in surrounding agricultural landscapes and semi-natural habitat patches beyond, rather than a novel assemblage of species (cf. Hobbs et al., 2009; Kowarik, 2011). Several urban sites were similar in species composition to some of the rural or fringe sites, whilst overall abundance and richness was not significantly lower in urban sites. In other words, the 'best' semi-wooded urban green spaces can host a rich diversity of species, sometimes comparable to similar sites further from urban settlements, as observed in other insect communities (Angold et al., 2006; Sadler et al., 2006; Croci et al., 2008).

### 5.4.3. Dung Beetles

Analysing data from the first and second visits separately revealed that patterns of activity in the beetle community were seasonally dependent (Finn et al., 1998). During the first visit, richness and abundance of all saprophagous beetles increased sequentially from urban sites through to rural. In the second visit there was little difference between the urban bands. This can be explained by the active season for dung beetles. These were significantly more abundant at rural sites but only during the first visit in late May and early June, when spring active dung beetles are still abundant (Finn et al., 1998). All of the larger saprophagous species collected were dung beetles belonging to the tribe *Aphodiini* or the genus *Onthophagus*. Dung beetles were recorded at only four urban sites during the study; these were all at sites on the outside edge of the Reading conurbation not completely surrounding by built-up areas. There are two possible reasons for this. Either urban areas present dispersal barriers for larger, slow-flying beetles (Magura et al., 2006; Sadler et al., 2006; Croci et al., 2008) or their populations are limited by lower resource availability in urban habitat patches (Gibb & Hochuli, 2002). Previous casual observations of *Aphodiini* and *Onthophagus* species by the authors in a large urban green space in the study area (not sampled in the current study) possibly suggest that resources rather than dispersal limitations are the key limiting factor for urban dung beetles.

### 5.4.3. Staphylinidae on Dung

Very few studies have examined the community of Staphylinidae on dung. Yamamoto et al. (2014) determined that the Staphylinid fauna on deer dung in Japan was dominated by a saprophagous *Anotylus* species. Three saprophagous Staphylinidae were found in the current study, of which two,

*Platystethus arenarius* (like *Anotylus* in the subfamily Oxytelinae) and *Megarthrus prosseni*, were recorded at more than 10 sites, though none were nearly as abundant as the predatory Staphylinids that dominated the highest beetle counts in this study. *Platystethus* was present in all urban distance bands but was particularly common in urban sites during the second visit, associated with large patches of scrub in moderately wet landscapes. *Megarthrus* was also more frequent at urban sites, but in association with greater improved grassland cover. *M. prosseni* occurs in all kinds of decaying vegetation (Cuccodoro & Löbl, 1997) and has been reported as common in horse dung in the UK (D. Mann, personal communication, August 2018), which was used as the bait for traps in this study, though in a study in Poland it showed no preference for horse dung over cow (Mroczyński & Komosiński, 2014). These species could be more common in the vicinity of urban areas because there tends to be more suitable habitat available, but following a similar experimental design Magura et al. (2013) found that the abundance and species richness of saprophagous Stapylinidae was higher in rural forests than urban ones. Alternatively, they may be experiencing competitive release in the absence of dung beetles or a release from certain predators (MacArthur & Levins, 1964; Atkinson & Shorrocks, 1981; Kruess & Tscharntke, 1994).

### 5.4.5. Predatory Species

The dominant species across all sites were two predatory *Anotylus* species. Considering the short trapping window of one hour, they were extremely abundant at some sites, with four counts of over 100 individuals recorded. Interestingly, all of the 100+ counts were at urban (3) or fringe (1) sites. In terms of species richness, samples taken during the first visit would confirm the idea that predators can be limited by urbanisation (Hochuli et al., 2004; Rocha & Fellowes, 2018), though the effect observed here was small, equating to one fewer active species at urban sites than rural ones. On the second visit there were no clear differences between urban, fringe and rural sites, suggesting that phenology of some coprophilous beetles may vary between rural and urban sites, as observed in butterflies (Dennis et al., 2017). Overall, there is no consistent evidence that urbanisation strongly impacts the abundance or richness of predatory beetles associated with dung and other patchy habitats. There is some evidence for a shift in the type of species that occur, however. Although dissimilarity analysis found no significant difference between distance bands, in the canonical correspondence analysis the smallest predators in each family (*Anotylus* spp., *Cercyon pygmaeus*) were mostly associated with higher manmade surface cover surfaces, while the larger species (*Philonthus spp.*, larger *Cercyon*) tended to be associated with small amounts of manmade surfaces. The larger predators often occurred in association with dung beetles, perhaps because the presence of dung beetles indicates a site rich enough in dung or other patch habitats to support good numbers of all saprophagous insect larvae.

### 5.4.6. Landscape Heterogeneity

The combination of higher numbers of dung beetles, larger predators and higher mean body size in rural areas (at least during the first visit, when the larger Scarabs were more active) suggests a shift along the urban gradient from larger specialist species to smaller generalists. This fits the trend frequently observed in ground beetles (Alaruikka, Kotze, Matveinen, & Niemela, 2002; Gaublomme et al., 2008; Magura et al., 2006; see also Chapter 2), even though, unlike ground beetles, this community of insects is unlikely to be limited by dispersal. The main exceptions to this trend were *Bisnius fimetarius* and *Gabrius piliger*, which favoured manmade surfaces, water and large patches of scrub, *G. piliger* very strongly so. Both are associated with any patch habitat that has a high concentration of insect larvae (Lott & Anderson, 2011) , but little other information is available regarding their ecology. The peri-urban areas of Reading have a good deal of scrub cover, often bordering large water bodies or rivers (Figure 1); suburbs offer a heterogeneous environment that may be associated with high species richness (Blair & Launer, 1997; Blair & Johnson, 2008). This could explain the preference of some species for landscape types that fit this description and the higher predicted richness of predators at Fringe and Urban sites compared to Rural in our study area. Some of the trends observed in the beetle community may also be related to interactions with other coprophilous organisms, such as flies or fungi, which it is not possible to quantify with our data.

When landscape heterogeneity was considered at a 250 m radius, large patches of woodland and semi-natural grassland were identified as drivers of beetle community composition. They were not included in the final model as other landscape variables measured at 500 m better described the same gradient of variation in the beetle data. However, the fact that woodland and grassland patch sizes were not significantly different between urban distance bands suggests that larger patches of semi-natural habitat are valuable regardless of the location of the site on the urban gradient (Wolf & Gibbs, 2004; Sadler et al., 2006); Söderström, Svensson, Vessby, & Glimskär, 2001 also found a positive association between tree cover in the surrounding landscape and some dung beetle species recorded in grasslands. The amount of water within 250 m explained some of the variation on the second axis of the correspondence analysis. This may be linked to the preference of some species for damper soils or be a proxy for habitat quality close to water.

The inclusion of improved grassland in the final model might be expected if this cover type was linked to the presence of grazing livestock. In this case it was positively correlated with manmade surfaces, suggesting that the influential grassland type here was more likely to be amenity grassland, e.g., in parks or golf courses. Dung beetles were in fact associated with landscapes with relatively low improved grassland cover and the dung availability index was not included in any model. In this landscape they appear therefore to be more associated with semi-natural habitats,

suggesting that livestock farming in the area does not support a high abundance of dung beetles (Hutton & Giller, 2003; Webb et al., 2010).

Most of the key landscape variables identified describe landscape composition. The 500 m radius that best explained community composition is comparable to scales used in other landscape studies (Barbaro, Rossi, Vetillard, Nezan, & Jactel, 2007; Sjödin, Bengtsson, & Ekbom, 2008; also see Chapter 3); in most of these cases measures of landscape composition or habitat amount were again more important than landscape, depending on the mobility of the species group. Given the long dispersal distances reported for some dung beetles (Roslin, 2000), the effects of landscape configuration may operate at a larger scale than any measured here or may simply not be important for this community of beetles, especially as none of the species recorded is regarded as particularly specialist (Roslin, 2001; Roslin & Koivunen, 2001).

Landscape composition in this case is likely to be a proxy for the availability of suitable microhabitats, since the species community is formed around a patchy resource. The final proportion of variation explained by key landscape variables was not particularly high, especially after the portion attributable to spatial autocorrelation was removed, suggesting that local factors may be more important (Söderström et al., 2001; Philpott et al., 2014; Otoshi et al., 2015). The most important gradient in the beetle community is correlated with an increase in manmade surfaces, which is difficult to disentangle with the wider effects of distance from urban area. It is therefore not possible to be certain whether urbanisation, measured as an increase in impervious surfaces, is directly responsible for the trends observed in the beetle community or whether other features of the landscape that are correlated with urbanisation are more influential, as for habitat fragmentation and forest carrion beetles (Wolf & Gibbs, 2004). The canonical correspondence analysis in any case usefully illustrates the character of landscapes that host different assemblages of coprophilous beetles, even if all the relationships described are not directly causal.

### 5.4.7. Summary

This is probably the first study to consider the composition of the whole beetle community on dung on an urban gradient. Semi-natural habitats in rural areas appear to support a much greater abundance of true dung beetles than equivalent habitat patches in urban areas. While landscape features are of lesser importance for other species in the coprophilous beetle community, there is some modification of the community by landscape heterogeneity at a 500 m radius that should be taken into account. Fringe sites in the peri-urban zone had a distinct character, though the differences between them and either urban or rural sites were generally small. Both peri-urban and urban sites can support an equivalent diversity of coprophilous beetles as rural sites, given the right local conditions, and some species are perhaps favourably associated with peri-urban sites in the heterogeneous landscape within 1 km of the main built-up area.

The experimental design was deliberately robust to disturbance in urban areas, using traps deployed for short time periods that nonetheless detected a difference between the three urban distance bands. This could provide a useful model for other studies. A potential alternative would be to use private gardens as sampling sites, which has been successful for a number of other insect sampling studies, including in the same study area (Orros et al., 2015; Rocha et al., 2018). An interesting possibility in suitably undisturbed sites would be to directly assess ecosystem function by quantifying the decomposition rates of dung or other rotting vegetation, in parallel with observations of the species composition of the whole functional community of saprophagous insects and associated predators.

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## 6. General Discussion

### 6.1. Importance of Landscape Heterogeneity

A statistically significant effect of landscape heterogeneity on community composition was identified for each of the three groups of beetles considered. In Chapter 2, which used a fairly simple land cover classification for four time periods, 20–25% of variation in ground beetle communities was explained by landscape composition and 26–31% by landscape configuration. This is comparable to the amount of variation in woodland ground beetles explained in Neumann et al. (2017), using a similar land cover classification (23–30% for composition and 32–35% for configuration). In the current study, overall variation explained, estimated in terms of adjusted-$R^2$, was only 15%, but a low figure might be expected since it was obtained using land use data that were necessarily simple to enable comparisons between time periods. The effects of landscape heterogeneity on ground beetle communities appear much more important when the most accurate available contemporary landscape data are used, including the addition of categorised linear features (Neumann et al., 2016b). In Chapter 3, the total amount of variation in flower-visiting beetle community composition explained by landscape heterogeneity, again in terms of adjusted-$R^2$, was 12%. For this more mobile group of beetles, landscape heterogeneity would appear to be less important than it is for ground beetles (Sjödin et al., 2008; Horak, 2014). Likewise, for coprophilous beetles, landscape heterogeneity explained somewhere between 6 and 13%, depending on how much shared variation is attributed to either landscape or spatial autocorrelation. None of the sampling regimes were hugely intensive in terms of effort per site. However, each delivered a dataset comprising some several thousand individuals and between 34 and 69 species. In each case the data were sufficient to identify the major gradients in community composition and link these to environmental gradients.

With a more complete inventory of community composition at each site and an exhaustively detailed capture of landscape patterns, perhaps more variation would have been attributed to landscape, but there is no strong evidence in this thesis to counteract the idea that habitat quality or management is a more important driver of recent biodiversity change in the United Kingdom than changes in habitat extent (Burns et al., 2016). Nonetheless, the weight of previous research continues to suggest that local habitat factors, landscape heterogeneity and their interactions need to be taken into account for most taxonomic groups (Holzschuh et al., 2007; Cousins, 2009; Soga et al., 2015; Fuentes-Montemayor et al., 2017; Helbing et al., 2017; Fusser et al., 2018, etc.).

### 6.2. Community Response to Landscape Heterogeneity

The response of beetle communities to landscape heterogeneity varied, but there were some consistencies between chapters and with other studies. For the two more mobile taxa (comprising winged species only), landscape composition variables generally explained more of the variation in community composition than landscape configuration variables. For flower-visiting beetles (Chapter 3), landscape configuration appeared only to be a proxy for the presence of wooded habitat locally; similarly, for coprophilous beetles (Chapter 5), nearby urban areas appeared to be the major driver of community composition over and above any measure of habitat amount or connectivity.

For ground beetles in Chapter 2, elements of both composition and configuration were important, with significant configuration variables including past size of the woodland patch sampled, number of grassland patches and the size of contemporary urban patches. The effect of historical landscape configuration was greater than that of contemporary configuration, as for Neumann et al. (2017). It is possible the configuration variables identified are good proxies for habitat amount (Fahrig, 2013), but the fact that the ground beetle community was structured according to size and mobility suggests that connectivity, as measured by landscape configuration, has a real effect in this study system.

The influence of historical grassland patches suggests that the spillover effect in ground beetles from adjacent habitats, whether from woodland to grassland or vice versa (Schneider et al., 2016; Duflot et al., 2018), may persist for some time even after most of the original habitat patch has been lost (Neumann et al., 2017). In flower-visiting beetles and coprophilous beetles (both communities drawn from mesoscale mosaics), adjacent habitat was again an important determiner of which species were present in the community, but the effect of wider landscape composition was confirmed in each case by calculating composition variables for more than one spatial scale. This confirms the advantage of using multi-scale analysis to determine the most appropriate scale for management aimed at benefitting a particular species community (Sjödin et al., 2008; Bergman et al., 2012; Bellamy & Altringham, 2015; Delgado de la Flor et al., 2017). For these two communities of patchy, ephemeral resources, the habitat amount hypothesis potentially holds true (Fahrig, 2013), with cover of favourable habitats being influential. However, the significant influence of some cover types that would appear not to represent optimum habitat for most species suggests that the composition of matrix habitats also plays a role in shaping community composition (Ricketts, 2001; Cook et al., 2002; Neumann et al., 2016a; Sánchez-de-Jesús et al., 2016).

In Chapters 2 and 3 a major driver of community composition was the transition from communities dominated by open habitat species to those with species associated with trees or shaded habitats, as

previously observed for ground beetles on a gradient of more open to more wooded landscape mosaics (Vanbergen et al., 2005). The affiliation of coprophilous beetles was less bimodal, with groups of species displaying a unimodal response to combinations of landscape variables.

## 6.3. Body Size and Mobility

In Chapters 2 and 5 the response of beetle communities to landscape heterogeneity was trait mediated, with landscape filtering species depending on body size, feeding guild and flight ability (Driscoll, 2005; Duflot et al., 2014; Neumann et al., 2016b). This was especially evident for woodland ground beetles with similar trends observed as for previous studies: larger flightless species in the largest and oldest woodland habitats and smaller generalists associated with urbanisation (Magura et al., 2006; Sadler et al., 2006; Vergnes et al., 2014; Neumann et al., 2016b, 2017). Trait analysis by Neumann et al. (2016) suggested, perhaps surprisingly, that flight ability is not a significant driver associated with landscape heterogeneity and explains more of the community composition associated with composition than with configuration, in that woodland ground beetle species tend to be flightless. Body size was the most important trait in that study, which fits with the distribution of ground beetle species by body size in Chapter 2. The traits in Neumann et al. (2016) that explained most of the community response to landscape composition were moisture requirement and habitat preference, an intuitive result that fits with the observed response of species in all chapters here. Size also appears to mediate the response of coprophilous beetles (Chapter 5) to landscape, with larger coprophagous species less abundant near towns. None of the species captured can be described as pasture specialists, which are more mobile and form patchy populations across the landscape (Roslin, 2000; Roslin & Koivunen, 2001), though some dung beetles exist in classical metapopulations (Roslin & Koivunen, 2001) that may be disrupted by dispersal barriers provided by urban areas. In both Chapters 2 and 5, one or two larger species appear to 'break the rules', showing that the relationship between body size and response to landscape heterogeneity is not always strictly linear (Barbaro & van Halder, 2009; Bellamy & Altringham, 2015).

## 6.4. Habitat Specialism

With a focus on woodland in Chapter 2 and the use of wooded habitats for sampling in Chapter 5, inevitably beetles of woodland or other tree-rich habitat formed the majority of species recorded overall. However, even in Chapter 3, where sampling was carried out in a range of landscape contexts including quite open ones, trees were disproportionately influential on the species community. Woodland and mature non-woodland trees represent the key semi-natural habitat in the landscapes under consideration, all of which have a relatively low proportion of open semi-natural habitat such as species-rich grassland.

It is worth considering that habitat, especially in the broader sense, is an anthropogenic construct. In selecting habitat, a beetle is 'looking for' a site that meets a set of requirements such as temperature, humidity, substrate type and food availability. As such, landscape composition variables describing 'woodland' and 'grassland' are proxies for the potential presence of a suite of species associated with conditions likely to occur in woodland or grassland. In Chapter 4, LiDAR data were used to determine tree height as a simple measure of habitat quality. Again, this is a proxy for the presence of, e.g., deadwood or for the extent of shady conditions in the ground layer, not a precise measure of habitat availability for any one species. However, focussing on species rather than community response and using this potentially improved habitat proxy did provide a good fit for the distribution of one species, when compared to the response of the whole community to 'trees' in Chapter 3. Determining the true extent of semi-natural grassland from remote sensing data is more challenging. Prority habitat data from Natural England (Natural England, 2018) were used to categorise grassland in Chapter 2 and 5, but probably do not offer a good indication of habitat quality. A truly habitat-focussed study should aim to capture a more precise measure of habitat structure and complexity, which is known to determine the composition of several invertebrate groups (Lassau et al., 2005; Woodcock & Pywell, 2009; Davies & Asner, 2014; Ford et al., 2017; Helbing et al., 2017); this was not deemed practical for the current study as the focus was on landscape mosaics, not a single habitat. Species associated with patch habitats, such as the coprophilous beetles studied in Chapter 5, are most likely less attached to broader habitat and more concerned with the fine-scale availability of resources that are even more impractical to map exactly at a landscape scale except by proxy (e.g., Webb et al. (2010) dung and avermectin index).

True habitat specialist species (i.e., those that are nationally scarce or rare) were not recorded in sufficient numbers to be included in the analysis for any chapter. Sampling may well not have been intensive enough to detect rare species persisting at low population levels, but their absence may also reflect the fact that most of the sampling sites were located in 'ordinary' mosaic landscapes, not associated with scarce habitats managed for species of conservation concern.

## 6.5. The Influence of Urban Land Cover

Urban land cover modified each of the beetle communities examined. Aside from the effects of an urban gradient observed in dung beetles, gardens associated with small urban areas were influential in flower-visiting beetles (Chapter 3) and urban cover, especially larger urban areas, and had an additive modifying effect on beetle communities in the 1930s and recent times. In all three cases, some species were positively associated with more urban landscapes. For ground beetles these were mostly mobile, small-bodied generalist species (as for Sadler et al., 2006; Magura et al., 2008), whilst in flower-visiting beetles some of the beneficiaries were synanthropic species, but others are

otherwise associated with semi-natural habitats, suggesting that garden management such as maintenance of a diverse mix trees and shrubs can support insect biodiversity, especially where heterogeneous native planting is favoured (Helden et al., 2012; Salisbury et al., 2015; Plascencia & Philpott, 2017). Smaller coprophagous beetles and some predators associated with more urban landscapes may not have been benefitting directly from urban land use or gardens but from particular land use or spatial dynamics in the urban fringe, where the intermediate disturbance hypotheses would predict the highest diversity (Blair & Launer, 1997; Kun et al., 2009), as seen for spiders in the Paris suburbs (Vergnes et al., 2014) or perhaps reduced competition from other species (Atkinson & Shorrocks, 1981; Kruess & Tscharntke, 1994).

## 6.6. Conservation Implications

In the first instance, conservation action in agriculture or urban-dominated landscapes will necessarily need to continue focussing on the creation, retention and management of semi-natural habitat fragments (Öckinger & Smith, 2007; Krauss et al., 2010). Beyond that, it is clear that landscape context influences the success of habitat restoration or management (Jorgensen et al., 2014; Rubene et al., 2017) and that maintaining landscape connectivity through space and time is important for some species groups (Lindborg & Eriksson, 2004; Watts et al., 2010; Neumann et al., 2017; Sverdrup-Thygeson et al., 2017), particularly less mobile specialists, though landscape configuration was not found to be particularly important for two of the beetle communities considered in this thesis. This thesis does provide further evidence that the composition of matrix habitats is a driver of species communities in woodland (Chapter 2), and that the composition of landscape mosaics shapes diverse multi-taxa beetle communities (Chapters 3–5), confirming the importance of considering the heterogeneity of whole landscape mosaics (Ricketts, 2001; Bennett et al., 2006; Neumann et al., 2016b). It also underlines the place of history as a key part of landscape context, suggesting that habitat restoration should be targeted in areas where it is likely to mitigate existing extinction debts, or more quickly claim colonisation credit, i.e., support the full range of specialist species (Kuussaari et al., 2009; Nordén et al., 2014; Cliquet & Decleer, 2017).

Chapters 3 and 4 show that the composition of landscape mosaics defined at a fairly small scale (100–200 metre distance) influence the distribution and abundance of a flower-visiting beetle community and some individual species. Using a multi-scale analysis, Chapter 5 was able to show that the response of coprophilous beetles to landscape heterogeneity (mostly mosaic composition) is best assessed within a 500 metre radius. Adding to evidence from other mesoscale studies of insect responses to landscape heterogeneity (Barbaro et al., 2007; Sjödin et al., 2008; Barbaro & van Halder, 2009), this demonstrates that habitat creation or modification at this scale may have an impact beyond the site of intervention.

Evidence from all chapters suggests that gardens and the wider urban area may to varying degrees have a different species mix to rural areas, but are not uniformly negative for beetle communities that are not as clearly restructured along urban gradients as, e.g., birds (Devictor et al., 2007; Baker et al., 2010). Management in gardens and other urban greenspaces should focus on enhancing the benefits for species that can tolerate them, while mitigating negative impacts through the creation of green corridors, which are likely to benefit biodiversity whether or not they actually provide functional connectivity (Angold et al., 2006). Ultimately, the goal would be to fully integrate urban areas into functioning ecological networks at a broad landscape scale, rather than seeing them as 'black holes' for biodiversity.

Finally, each sampling method used was able to detect differences in community composition that could be linked to elements of landscape heterogeneity. Especially for Chapters 3 and 4, this was focussed on landscape as the level of inference, since transects of flowers were not always adjacent to the same type of habitat. A more directly quantifiable assessment of whether flower-visiting insect communities are a useful proxy for landscape level biodiversity (i.e., gamma diversity) would be interesting.

## 6.7. Suggestions for Future Work

Chapter 2 illustrates the value of incorporating multiple time steps in studies of landscape change (Gustavsson et al., 2007; Koyanagi et al., 2009; Cristofoli et al., 2010), providing a more comprehensive picture of the cumulative effects of landscape heterogeneity over time. In the United Kingdom, a recently completed nationwide historic landscape character dataset, available for 50-m grid cells (Locus Consulting, 2017), Ordnance Survey mapping going back to the early 19th century and four relatively recent national land cover assessments (1990, 2000, 2007, 2015) provide a comprehensive set of resources for further assessing the effect of landscape history on biodiversity at a national scale. Studies that utilise record scheme data may be particularly fruitful, especially where sufficient historical species data that are contemporary with some of the earlier landscape data sources are also available. Theoretical modelling of dynamic landscapes offers another interesting approach, as shown in a recent study by Martensen et al. (2017) highlighting the potential connectivity value of ephemeral 'temporal stepping-stone' patches. Empirical studies, as in the current thesis, provide evidence for parameterising models, which in turn can be tested with further field data, testing the extent to which metrics describing landscape heterogeneity usefully describe biodiversity (Walz, 2011). Predictive models are often used to unpick species distributions and range shifts (e.g., Greaves et al., 2006; Rotenberry et al., 2006; Razgour et al., 2011); predictive models for multiple species (e.g., Holzkämper et al., 2006; Broughton et al., 2013) may provide a greater breadth of evidence for landscape planning.

Results of landscape-scale studies may be clearer where study site selection is more tightly controlled by the initial aims or hypotheses. Direct experimental manipulation is very rarely feasible at a landscape scale, but habitat manipulation (e.g., Johansson et al., 2007) or smaller-scale experiments (Rocha & Fellowes, 2018) can be placed within varying landscape contexts to determine optimum strategies for habitat creation (Kouki et al., 2012). In the United Kingdom, the WrEN project used historical landscape data to design a natural experiment examining 160 years of woodland creation and the subsequent effect on woodland biodiversity (Watts et al., 2016). Research output to date is providing evidence to underpin habitat creation strategies at a landscape scale (Fuentes-Montemayor et al., 2017), as well as suggestions for habitat management (Fuller et al., 2018).

Although a diverse range of insect taxa has now been considered in a landscape context, some groups are still underrepresented considering their diversity. Few studies cover any flies beyond hoverflies (see: Sjödin et al., 2008; Fuller et al., 2018), though results for these may be applicable to other groups of flies, e.g., craneflies (Fuller et al., 2018). In a study of population structure in three saproxylic insects, Schauer et al. (2018) found comparable results for two flies and a beetle. In the United Kingdom, flies are more speciose than beetles and probably play a crucial role in all ecosystems. Though few are likely to be dispersal-limited (e.g., hoverflies not affected by fragmenation in Jauker et al., 2009; Fuller et al., 2018), the wide-ranging foraging and dispersal behaviour of some species means landscape heterogeneity is likely to play a role in structuring populations and species communities. Although more beetle species have been described, parasitic hymenoptera may well be the most speciose group of insects globally (Grissell, 1999; Forbes et al., 2018), and have been found to genuinely indicate the richness of other taxa (Anderson et al., 2011; Mazón, 2016). Where species richness is the desired measure of biodiversity response, they are probably an ideal focus for future studies, especially if new resources can overcome significant barriers in identification. However, examining the response of parasitic hymenoptera to a higher taxonomic level than species or using morphospecies might be sufficient (Andersen et al., 2002; Timms et al., 2013).

Hemiptera are also rarely considered in a landscape context. Major et al., 2003 focussed on Miridae, a diverse family of phytophagous insects that must have potential for considering changes in species interactions (cf. Stewart et al., 2015). Helbing et al. (2017) recently found a strong effect of landscape structure on leafhoppers in acidic grasslands. Phytophagous insects in grassland would be an interesting topic for further study in light of the long extinction debts identified in grassland plants by some authors. To truly assess what makes for biodiverse landscapes, mosaic-centred, multi-taxa studies with landscape-level inference of biodiversity are the ideal (Bennett et al., 2006; Mimet et al., 2014; Duflot et al., 2017). Studies of complete ecological networks (e.g. Pocock et al. (2012)) and how these are modified in space and time through factors such as climate

(Gray et al., 2014; Stewart et al., 2015; Thompson & Gonzalez, 2017) would provide the most comprehensive information for future landscape planning but may be challenging to distil into on-the-ground applications.

## 6.8. Concluding Remarks

We know that conservation at a landscape scale can be successful (Ellis et al., 2012; Newmark et al., 2017), but research output from landscape ecology can be complex to interpret. As one NGO scientist put it to me in a phone conversation in the early stages of this project, "a lot of tosh is talked about landscape conservation; you look at a lot of this stuff and think, how do you apply this!?" Very few of the landscape variables used in this thesis are overly technical. This was a deliberate decision to facilitate translating results into evidence that is interesting and preferably useful in the 'real' world. But whether the preceding chapters are simply adding to the 'tosh' or have the potential to make a genuine difference remains to be seen. This is merely the start of a process: restoring and maintaining multi-functional landscapes that are rich in wildlife means conversation, collaboration and large-scale partnerships (Adams et al., 2016). For this to be possible requires landscape ecology to continue to develop as a multifaceted discipline, transforming research into practice. Landscape ecology is a broad field now backed by a vast, one might even say daunting, volume of literature. This thesis makes a further contribution and finishes above with suggestions for future work, but I am tempted to suggest that research is now subordinate to the need to build social and political capital for conservation, unless it feeds directly back into that process. In summary, to build 'beetlescapes' we first need to win more friends for beetles and all the other little things that run the world (Wilson, 1987).

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## Acknowledgements

**Appendix 1.1.** Full list of Carabidae captured in woodland pitfall traps, May–June 2015.

| Species | Authority | Plate | Total | Sites |
|---------|-----------|-------|-------|-------|
| *Abax parallelepipedus* | Piller & Mitterpacher, 1783 | 1 | 1253 | 37 |
| *Agonum emarginatum* | Gyllenhal, 1827 | | 1 | 1 |
| *Amara communis* | Panzer, 1797 | 2 | 1 | 1 |
| *Amara eurynota* | Panzer, 1797 | | 2 | 1 |
| *Amara familiaris* | Duftschmid, 1812 | | 2 | 2 |
| *Amara ovata* | Fabricius, 1792 | | 1 | 1 |
| *Amara similata* | Gyllenhal, 1810 | | 1 | 1 |
| *Asaphidion curtum* | Heyden, 1870 | | 14 | 3 |
| *Badister bullatus* | Schrank, 1798 | 3 | 6 | 4 |
| *Bembidion biguttatum* | Fabricius, 1779 | | 2 | 1 |
| *Bembidion lampros* | Herbst, 1784 | 4 | 39 | 6 |
| *Bembidion lunulatum* | Geoffroy in Fourcroy, 1785 | 5 | 1 | 1 |
| *Calathus fuscipes* | Goeze, 1777 | 6 | 1 | 1 |
| *Calathus rotundicollis* | Dejean, 1828 | | 32 | 14 |
| *Carabus granulatus* | Linnaeus, 1758 | 7 | 1 | 1 |
| *Carabus nemoralis* | Müller, O.F., 1764 | 8 | 5 | 4 |
| *Carabus problematicus* | Herbst, 1786 | 9 | 42 | 12 |
| *Carabus violaceus* | Linnaeus, 1758 | 10 | 49 | 15 |
| *Curtonotus aulicus* | Panzer, 1796 | | 2 | 1 |
| *Cychrus caraboides* | Linnaeus, 1758 | 11 | 2 | 1 |
| *Harpalus affinis* | Schrank, 1781 | 12 | 8 | 6 |
| *Harpalus latus* | Linnaeus, 1758 | | 5 | 5 |
| *Harpalus rufipes* | De Geer, 1774 | | 4 | 3 |
| *Leistus ferrugineus* | Linnaeus, 1758 | 13 | 4 | 2 |
| *Leistus rufomarginatus* | Duftschmid, 1812 | | 15 | 10 |
| *Leistus spinibarbis* | Fabricius, 1775 | | 4 | 2 |
| *Loricera pilicornis* | Fabricius, 1775 | 14 | 23 | 16 |
| *Nebria brevicollis* | Fabricius, 1792 | 15 | 1528 | 38 |
| *Notiophilus biguttatus* | Fabricius, 1779 | 16 | 93 | 28 |
| *Notiophilus rufipes* | Curtis, 1829 | | 17 | 8 |
| *Oxypselaphus obscurus* | Herbst, 1784 | 17 | 3 | 1 |
| *Paranchus albipes* | Fabricius ,1796 | 18 | 1 | 1 |
| *Platynus assimilis* | Paykull, 1790 | | 14 | 2 |
| *Poecilus cupreus* | Linnaeus, 1758 | 19 | 7 | 6 |
| *Pterostichus madidus* | Fabricius, 1775 | 20 | 750 | 38 |
| *Pterostichus melanarius* | Illiger, 1798 | | 36 | 2 |
| *Pterostichus niger* | Schaller, 1783 | | 18 | 7 |
| *Pterostichus oblongopunctatus* | Fabricius, 1787 | | 5 | 2 |
| *Pterostichus strenuus* | Panzer, 1796 | | 10 | 6 |
| *Trechus quadristriatus* | Schrank, 1781 | 21 | 1 | 1 |

**1** **2** **3** **4** **5**

**6** **7** **8** **9** **10**

**11** **12** **13** **14** **15**
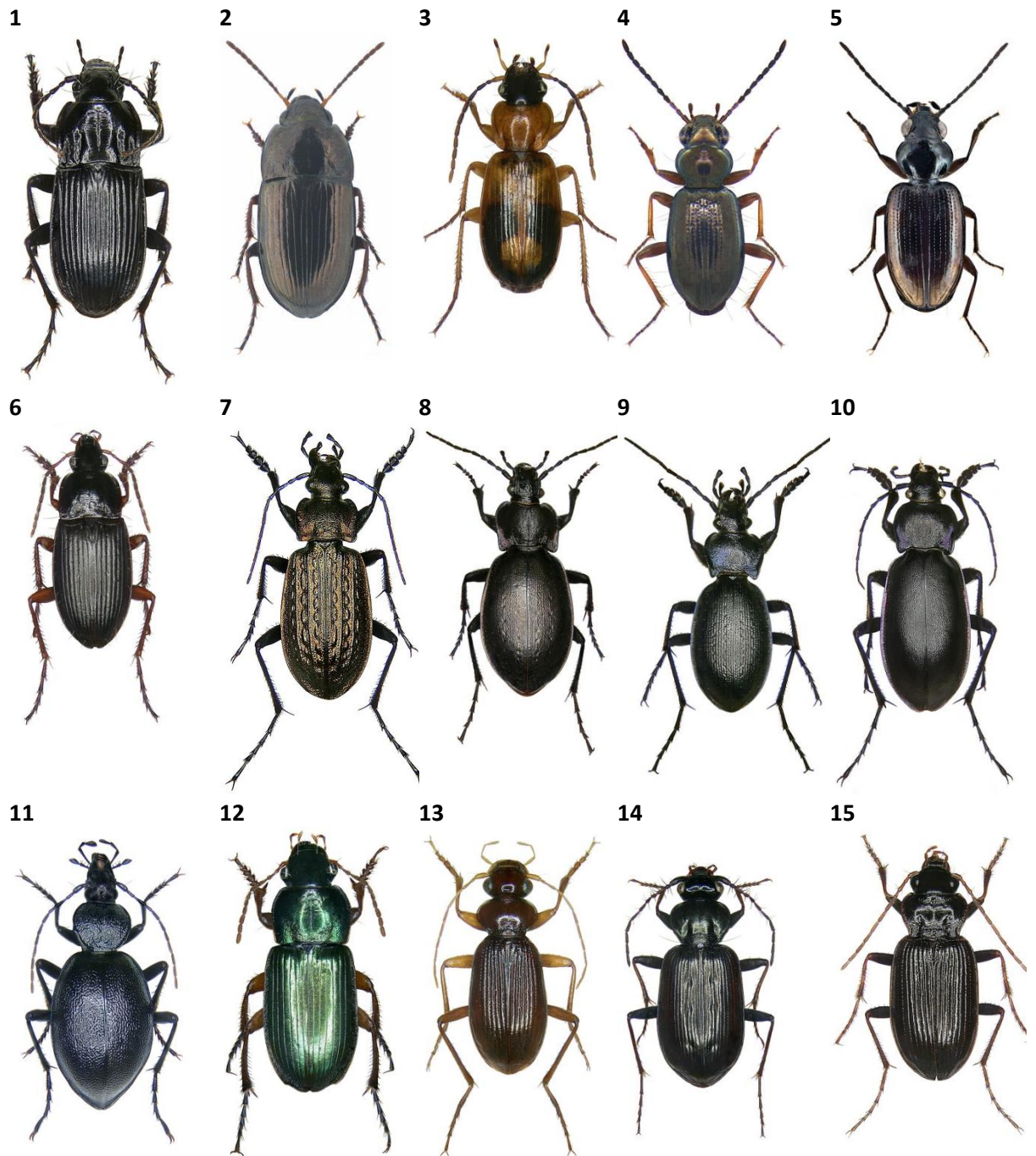
16        17        18        19        20

21

**Appendix 1.2. Plates 22–25.** Images from fieldwork in Oxfordshire, Berkshire and Hampshire woodlands, May to June 2015 (taken by Chris Foster).

**22** Trap set with one covered pitfall and a bottle trap designed to catch flying insects. Flight trap data were not used in this thesis.
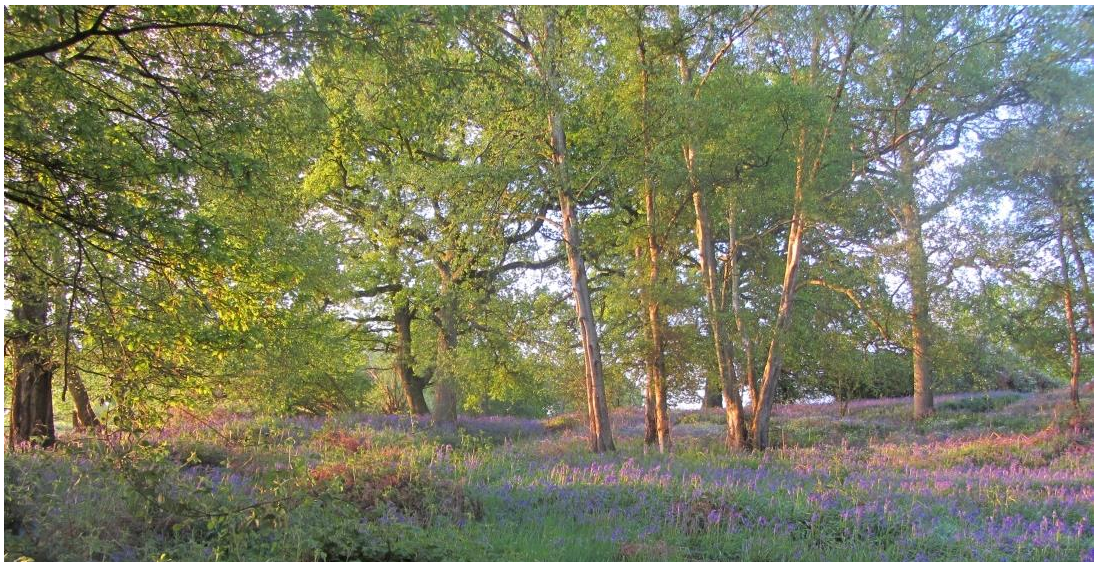
**23** An open woodland habitat.

**24** Looking south from the a woodland edge in the Chiltern hills towards the Thames Valley.



**25** Many of the site visits to retrieve trap contents were made at dawn.

**Appendix 2.1.** Full table of references for the identification flower-visiting beetles captured in North Hampshire.

| Family | Source for Species Identification |
|---|---|
| Apionidae | Duff, 2016 |
| Byturidae | Watford Coleoptera Group, n.d. |
| Cantharidae | Alexander & Harvey, 2010; Fitton & Eversham, 2006; Gurney, 2017 |
| Cerambycidae | Duff, 2016; Duff & Lewington, 2007 |
| Chrysomelidae | Duff, 2016 |
| Curculionidae | Duff, 2016; Gurney, 2018 |
| Coccinellidae | Roy et al., 2013 |
| Cryptophagidae | Hackston, n.d. |
| Dasytidae | Hackston, n.d. |
| Dermestidae | Peacock, 1993 |
| Elateridae | Hackston, n.d. |
| Kateretidae | Watford Coleoptera Group, n.d. |
| Malachiidae | Hackston, n.d. |
| Mordellidae | Hackston, n.d.; Telfer, 2011 |
| Oedemeridae | Hackston, n.d. |
| Pyrochroidae | Hackston, n.d. |
| Scraptiidae | Levey, 2009 |
| Staphylinidae | Lott & Anderson, 2011 |
| Tenebrionidae | Hackston, n.d. |

**Appendix 2.2.** Full list of beetles captured on umbellifers in the North Hampshire study area, May–July 2013.

| Family | Species | Authority | Plates | Total | Sites |
|---|---|---|---|---|---|
| Byturidae | *Byturus ochraceus* | Scriba, 1790 | **1** | 18 | 7 |
| | *Byturus tomentosus* | De Geer, 1774 | **2** | 60 | 15 |
| Cantharidae | *Cantharis decipiens* | Baudi, 1871 | | 5 | 4 |
| | *Cantharis flavilabris* | Fallen, 1807 | | 3 | 2 |
| | *Cantharis fusca* | Linnaeus, 1758 | **3** | 1 | 1 |
| | *Cantharis lateralis* | Linnaeus, 1758 | | 2 | 1 |
| | *Cantharis livida* | Linnaeus, 1758 | | 3 | 3 |
| | *Cantharis nigricans* | Muller, I.F., 1776 | **4** | 5 | 4 |
| | *Cantharis pellucida* | Fabricius, 1792 | | 3 | 3 |
| | *Cantharis rustica* | Fallen, 1807 | | 6 | 4 |
| | *Malthodes marginatus* | Latreille, 1806 | **5** | 8 | 5 |
| | *Rhagonycha fulva* | Scopoli, 1763 | **6, 37** | 126 | 18 |
| | *Rhagonycha limbata* | Thomson, C.G., 1864 | **7** | 7 | 4 |

| | | | | | |
|---|---|---|---|---|---|
| Cerambydicae | *Alosterna tabacicolor* | De Geer, 1775 | **8, 43** | 8 | 3 |
| | *Anaglyptus mysticus* | Linnaeus, 1758 | **9** | 2 | 2 |
| | *Clytus arietis* | Linnaeus, 1758 | **10** | 3 | 3 |
| | *Glaphyra umbellatarum* | von Screber, 1759 | | 3 | 2 |
| | *Grammoptera ruficornis* | Fabricius, 1781 | **11** | 59 | 17 |
| | *Molorchus minor* | Linnaeus, 1758 | **12** | 1 | 1 |
| | *Pachytodes cerambyciformis* | Schrank, 1781 | **13** | 1 | 1 |
| | *Pseudovadonia livida* | Fabricius, 1777 | **14** | 1 | 1 |
| | *Rutpela maculata* | Poda, 1761 | **15, 38** | 19 | 10 |
| | *Stenurella melanura* | Linnaeus, 1758 | **16** | 2 | 2 |
| Chrysomelidae | *Bruchus loti* | Paykull, 1800 | | 1 | 1 |
| | *Bruchus rufimanus* | Boheman, 1833 | | 7 | 7 |
| | *Chrysolina polita* | Linnaeus, 1758 | **17** | 1 | 1 |
| | *Crepidodera aurata* | Marsham, 1802 | **18** | 5 | 2 |
| | *Crepidodera plutus* | Latreille, 1804 | | 1 | 1 |
| Circulionidae | *Archarius pyrrhoceras* | Marsham, 1802 | | 1 | 1 |
| | *Ceutorhynchus obstrictus* | Linnaeus, 1758 | | 4 | 4 |
| | *Curculio glandium* | Marsham, 1802 | **19** | 11 | 4 |
| | *Curculio venosus* | Gravenhorst, 1807 | | 2 | 1 |
| Coccinellidae | *Coccinella septempunctata* | Linnaeus, 1758 | **20** | 50 | 6 |
| | *Harmonia axyridis* | Pallas, 1773 | **21, 36** | 7 | 4 |
| | *Propylea quatuordecimpunctata* | Linnaeus, 1758 | | 12 | 10 |
| | *Subcoccinella vigintiquatuorpunctata* | Linnaeus, 1758 | **22, 39** | 1 | 1 |
| Cryptophagidae | *Antherophagus pallens* | Linnaeus, 1758 | **35** | 1 | 1 |
| Dermestidae | *Anthrenus fuscus* | Olivier, 1789 | | 14 | 9 |
| | *Anthrenus verbasci* | Linnaeus, 1767 | **23, 44** | 439 | 22 |
| Elateridae | *Agriotes acuminatus* | Stephens, 1830 | | 6 | 5 |
| | *Agriotes pallidulus* | Illiger, 1807 | | 74 | 21 |
| | *Agriotes sputator* | Linnaeus, 1758 | | 1 | 1 |
| | *Ampedus elongantulus* | Fabricius, 1787 | | 1 | 1 |
| | *Athous haemorrhoidalis* | Fabricius, 1801 | **24** | 22 | 14 |
| | *Athous vittatus* | Fabricius, 1792 | | 1 | 1 |
| | *Kibunea minuta* | Linnaeus, 1758 | **25** | 3 | 3 |
| Kateretidae | *Brachypterus urticae* | Fabricius, 1792 | **26** | 3 | 3 |
| Malachiidae | *Anthocomus fasciatus* | Linnaeus, 1758 | **27** | 1 | 1 |
| | *Malachus bipustulatus* | Linnaeus, 1758 | | 14 | 6 |
| Mordellidae | *Mordellistena humeralis* | Linnaeus, 1758 | | 1 | 1 |
| | *Mordellistena neuwaldeggiana* | Panzer, 1796 | **28** | 1 | 1 |

| | | | | | |
|---|---|---|---|---|---|
| | *Mordellistena pumila* | Gyllenhal, 1810 | | 1 | 1 |
| | *Mordellistena variegata* | Fabricius, 1798 | | 5 | 5 |
| | *Mordellochroa abdominalis* | Fabricius, 1775 | **29** | 4 | 3 |
| Oedemeridae | *Oedemera lurida* | Marsham, 1802 | | 8 | 5 |
| | *Oedemera nobilis* | Scopoli, 1763 | **30, 45** | 43 | 11 |
| Phalacridae | *Phalacridae sp.* | | | 1 | 1 |
| Scarabaeidae | *Phyllopertha horticola* | Linnaeus, 1758 | **31** | 3 | 2 |
| Scraptiidae | *Anaspis costai* | Emery, 1876 | **40** | 79 | 13 |
| | *Anaspis frontalis* | Linnaeus, 1758 | | 15 | 14 |
| | *Anaspis garneysi* | Fowler, 1889 | | 13 | 8 |
| | *Anaspis fasciata* | Fabricius, 1775 | **34** | 58 | 17 |
| | *Anaspis lurida* | Stephens, 1832 | | 1 | 1 |
| | *Anaspis maculata* | Geoffroy in Fourcroy, 1785 | **32, 41** | 410 | 31 |
| | *Anaspis pulicaria* | Costa, A., 1854 | | 475 | 27 |
| | *Anaspis regimbarti* | Schilsky, 1895 | **42** | 2 | 2 |
| | *Anaspis rufilabris* | Gyllenhal, 1827 | | 8 | 3 |
| Staphylinidae | *Eusphalerum luteum* | Marsham, 1802 | | 504 | 5 |
| Tenebrionidae | *Nalassus laevioctostriatus* | Goeze, 1777 | **33** | 1 | 1 |

**Plates 1–32.** Images by Udo Schmidt, used under Creative Commons License CC BY-SA 2.0. Retrieved from https://www.flickr.com/photos/coleoptera-us/.
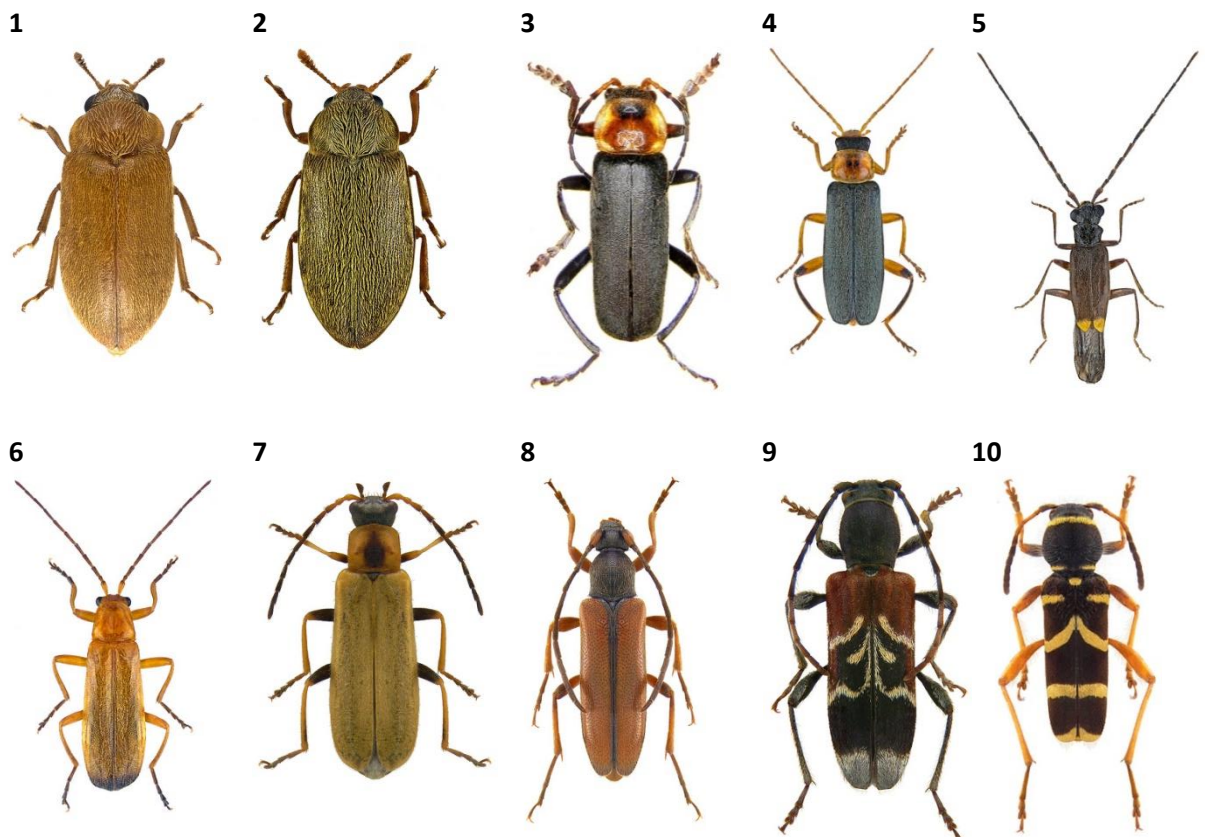
**31**    **32**    **33**

**Plates 34–39.** Images from 2013 field season in North Hampshire (taken by Chris Foster).

**34** Scraptiidae: *Anaspis fasciata*



**35** Cryptophagidae: *Antherophagus pallens*



**36** Cryptophagidae: *Antherophagus pallens*



**37** Cantharidae: *Rhagonycha fulva*

**38** Cerambycidae: *Rutpela maculata*     **39** Coccinellidae: *Subcoccinella 24-punctata*





**Plates 40–45.** Images of species recorded in 2013 and photographed elsewhere (taken by Chris Foster).

**40** *Scraptiidae: Anaspis costai*

**41** Scraptiidae: *Anaspis maculata*



**42** Scraptiidae: *Anaspis regimbarti*



**43** Cerambycidae: *Pseudavadonia livida*



**43** Dermestidae: *Anthrenus verbasci*



**44** Oedemeridae: *Oedmera nobilis*

**References for Appendix 2.1.**

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**Appendix 3.** Full list of beetles captured in dung-baited traps near Reading, UK, May–July 2015.

| Family: Subfamily | Species | Authority | Plates | Total | Sites |
|---|---|---|---|---|---|
| Cantharidae | *Rhagonycha fulva* | Scopoli, 1763 | | 1 | 1 |
| Cerambycidae | *Grammoptera ruficornis* | Fabricius, 1781 | | 1 | 1 |
| Elateridae | *Athous vittatus* | Fabricius, 1792 | | 3 | 3 |
| Helophoridae | *Helophorus brevipalpis* | Bedel, 1881 | **1** | 5 | 5 |
| Hydrophilidae | *Cercyon haemorrhoidalis* | Fabricius, 1775 | **2** | 39 | 12 |
| | *Cercyon melanocephalus* | Linnaeus, 1758 | | 31 | 11 |
| | *Cercyon pygmaeus* | Illiger, 1801 | | 4 | 4 |
| | *Cryptopleurum minutum* | Fabricius, 1775 | **3** | 5 | 3 |
| | *Sphaeridium lunatum* | Fabricius ,1792 | **4** | 2 | 2 |
| | *Sphaeridium marginatum* | Fabricius, 1787 | | 2 | 1 |
| Ptilidae | *Ptiliidae sp.* | | | 15 | 11 |
| Scarabaeidae: Aphodiinae | *Agrilinus ater* | De Geer, 1774 | **5** | 2 | 2 |
| | *Melinopterus prodromus* | Brahm, 1790 | **6** | 16 | 8 |
| | *Melinopterus sphacelatus* | Panzer, 1798 | **7** | 6 | 3 |
| | *Nimbus obliteratus* | Sturm, 1823 | | 3 | 1 |
| | *Volinus sticticus* | Panzer, 1798 | **8** | 259 | 29 |
| Scarabaeidae: Scarabaeinae | *Onthophagus coenobita* | Herbst, 1783 | | 20 | 6 |
| | *Onthophagus joannae* | Goljan, 1953 | | 7 | 5 |
| | *Onthophagus similis* | Scriba, 1790 | **9** | 2 | 1 |
| Staphylinidae: Aleocharinae | *Aleocharinae* | | | 131 | 33 |
| Staphylinidae: Oxytelinae | *Anotylus complanatus* | Erichson, 1839 | | 3 | 2 |
| | *Anotylus inustus* | Gravenhorst, 1806 | | 11 | 5 |
| | *Anotylus nitidulus* | Gravenhorst, 1802 | | 17 | 9 |
| | *Anotylus sculpturatus* | Gravenhorst, 1806 | | 749 | 43 |
| | *Anotylus tetracarinatus* | Block, 1799 | | 1230 | 40 |
| | *Oxytelus laqueatus* | Marsham, 1802 | **10** | 53 | 22 |
| | *Platystethus arenarius* | Fourcroy, 1785 | **11** | 32 | 17 |
| Staphylinidae: Proteininae | *Megarthrus prosseni* | Schatzmayr, 1904 | | 21 | 10 |
| Staphyinidae: Staphylininae | *Bisnius fimetarius* | Gravenhorst, 1802 | | 30 | 9 |
| | *Gabrius piliger* | Mulsant & Rey, 1876 | | 5 | 4 |
| | *Gyrohypnus fracticornis* | Müller, O.F., 1776 | **12** | 2 | 2 |
| | *Philonthus cognatus* | Stephens, 1832 | | 1 | 1 |
| | *Philonthus intermedius* | Lacordaire, 1835 | | 1 | 1 |
| | *Philonthus marginatus* | Müller, O.F., 1764 | | 5 | 5 |
| | *Philonthus varians* | Paykull, 1789 | | 15 | 7 |
| Staphylinidae: Tachyporinae | *Tachinus rufipes* | (Linnaeus, 1758) | | 6 | 3 |