

Mapping biodiversity in a modified landscape

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Abstract

The majority of the world's biodiversity exists outside protected areas, in landscapes heavily modified by anthropogenic activity. It is therefore necessary to gain a better understanding of the role that modified landscapes play in the maintenance of biodiversity. The application of methods used to assess and prioritise areas for conservation at the landscape scale is limited by the availability of adequate species distribution data, a problem that is commonly solved by combining available data with remotely sensed landcover variables in order to extrapolate estimates of species richness across the region of interest. However, the concepts of complementarity and irreplaceability have highlighted the need for an additional measure describing the level of compositional dissimilarity, or beta diversity, between locations. This study aims to investigate whether patterns of compositional dissimilarity can be modelled across a region in a similar fashion to existing models of species richness.

The response of carabid beetles (Coleoptera: Carabidae) to the effects of habitat modification, in the form of forest fragmentation and resulting edge effects, was investigated in a modified landscape in Berkshire, England. Results showed no significant difference in carabid species diversity between habitat types but a significant increase in carabid diversity and abundance with increasing fragment area. Edge effects had a significant impact on carabid abundance and community evenness. It was found that carabids formed definable assemblages that differed by habitat type and could be reliably predicted using remotely sensed landcover data. Generalized dissimilarity modelling (GDM) was used to model and predict patterns of carabid compositional dissimilarity at the landscape scale, which were then presented visually as a map.

1. Introduction

1.1 Conservation in modified landscapes

Anthropogenic impacts on the environment are a major contributing factor to the global loss of biodiversity (Vanbergen *et al.* 2005). The most significant of these impacts is landscape modification caused by increasing urban development and the conversion of natural habitats to agriculture (Sala *et al.* 2000, Wessels *et al.* 2000). Already, over 36% of the earth's surface has been converted to agriculture and intact ecosystems are being converted at rates of over 1% per year (Meir *et al.* 2004). At the same time, urbanisation is increasing worldwide. Urban sprawl is expanding the extent of urban boundaries, and urban populations are becoming more densely populated at such a rate that it is predicted that the global urban population will have doubled by 2025 (Alarukka *et al.* 2002).

Whilst the global system of protected areas may safeguard key sites from anthropogenic modification, the proportion of the earth's surface under such protection is estimated at just 12% (CBD 2007). The majority of the world's biodiversity must therefore co-exist with human activity. Consequently, it is necessary to progress past the 'protection paradigm' and gain a better understanding of the roles played by modified landscapes in the maintenance of native biodiversity. These are likely to be significant. The nature of the 'matrix' of modified land surrounding protected areas greatly affects their effectiveness and connectivity (Franklin 1993). The matrix itself provides important habitat and ecosystem services (Meir *et al.* 2004), whilst man-made sites and urban green-areas can act as analogues of natural habitats and provide refugia for many species, particularly invertebrates (Eversham *et al.* 1996, Eyre *et al.* 2003).

1.2 Mapping biodiversity at the landscape scale

Methods for the assessment and prioritization of areas for conservation have progressed rapidly, such that there is now a huge range of site-selection algorithms and decision support software available for conservation managers and urban planners

(Margules & Pressey 2000). However, the application of these tools is limited by the availability of adequate species distribution data (Rodrigues & Brooks 2007), which is sparse at best, even for well-known taxa such as birds and mammals (Sarkar *et al.* 2006). It is usually infeasible to remedy the situation by conducting detailed field surveys, since they are expensive, time-consuming and bear high opportunity costs, given that any resources spent on identifying priority areas cannot be used for active conservation management (Ewers *et al.* 2005).

A common alternative strategy is to make use of biodiversity ‘surrogates’, or ‘indicators’. These are entities whose distribution is known and likely to correlate well with spatial patterns of biodiversity as a whole (Margules & Pressey 2000). Recent advances in remote sensing and geographical information systems (GIS) have led to the wide availability of detailed landcover maps at the fine spatial scales necessary for regional conservation planning (Cowley *et al.* 2000, Turner *et al.* 2003). It is therefore easy to sample landscape variables, such as vegetation type or climate, that may act as good surrogates (Ferrier *et al.* 2007). Studies have established strong correlations between landscape diversity and the diversity of plants, invertebrates and birds (Ewers *et al.* 2005). It is then possible to model species presence, or abundance, as a function of landscape variables, and to extrapolate species distributions across the region of interest. This provides geographically complete information for conservation planning and other environmental applications (Guisan & Zimmermann 2000).

Modelling individual species distributions is expensive and time-consuming and is only possible for well-studied species with sufficient distributional data (Ferrier 2002). For these reasons, it is more often the collective, or emergent properties of biodiversity that are modeled, such as species richness (Ferrier *et al.* 2007). Models of species richness have been applied at the global scale to identify biodiversity ‘hotspots’ rich in total species or rare species (Grenyer *et al.* 2006, Fa & Funk 2007, Myers *et al.* 2000, Olson & Dinerstein 2002). Whilst species richness provides an important measure of alpha diversity, it is of limited value to conservation planning at finer spatial scales. The concepts of complementarity and irreplaceability have highlighted the need for an additional measure describing the level of compositional dissimilarity, or beta diversity, between locations (Margules & Pressey 2000, Ferrier

et al. 2007). Decisions about where to focus conservation effort are therefore based on the relative, rather than the absolute, biodiversity value of locations.

1.3 Project aims and objectives

This study will assess the degree to which remotely sensed data can be used in combination with biological survey data in order to identify priority areas for conservation. It aims to:

- 1) Investigate whether patterns of beta diversity can be modelled across a region in a similar fashion to existing models of species richness;
- 2) Investigate the influence of anthropogenic habitat modification on local biodiversity;
- 3) Assess the conservation value of a modified landscape.

The study will sample the ground beetle fauna (Coleoptera: Carabidae) of a modified landscape in Berkshire, England. The main objectives are:

- 1) To identify and characterize patterns of carabid diversity at the landscape scale;
- 2) To investigate the effects of forest fragmentation on carabid diversity;
- 3) To investigate the spatial pattern of carabid diversity along an environmental gradient between forest and grassland habitats;
- 4) To produce a map of ground beetle beta diversity for the region.

2. Background

2.1 Beta diversity

The simplest measure of diversity is species richness, or the number of species present in a community. Species richness can be further split into three main components of diversity, which are described as alpha, or inventory diversity (α), beta, or differentiation diversity (β) and gamma, or regional diversity (γ).

Beta diversity represents the spatial turnover of species, and measures the number of species not shared between two or more locations (Koleff *et al.* 2003, Lande 1996). For a landscape with a given gamma diversity, as beta diversity increases, individual locations become more different to each other and so represent a smaller proportion of the region's total species diversity. Beta diversity therefore represents the spatial pattern of species turnover in the landscape.

The principles behind most approaches to conservation planning, such as complementarity and irreplaceability, are driven by beta diversity (Margules & Pressey 2000). Beta-diversity is determined by complex interactions between species traits and characteristics of the physical landscape and, as a result, captures not only the variation in species diversity between locations but also the corresponding variation in landscape diversity, as well as the underlying ecological and evolutionary processes causing this variation (McKnight *et al.* 2007). The incorporation of measures of beta diversity into the site-selection algorithms used for regional conservation planning therefore results in the improved representation of biodiversity as a whole.

Numerous measures of beta diversity have been proposed and applied to a range of conservation issues, in particular the measurement of changes in species composition along spatial or environmental gradients, and the quantification of site dissimilarity (Koleff *et al.* 2003). At the landscape scale, beta diversity is perhaps best expressed as a measure of compositional dissimilarity between pairs of sites, based on presence/absence or abundance data (Ferrier *et al.* 2002, Legendre *et al.* 2005). The technique of generalized dissimilarity modelling (GDM) analyses and predicts

patterns of compositional dissimilarity, based on environmental variables derived from remotely sensed landcover data (Ferrier & Guisan 2006, Ferrier *et al.* 2007). GDM is an extension of matrix regression, where both the response and explanatory variables are expressed as matrices of dissimilarity (Ferrier *et al.* 2007). The response matrix therefore describes the compositional dissimilarity between sites, whilst the explanatory matrices describe the dissimilarity in the corresponding environmental variables. GDM is based on the hypothesis that species distributions are dependent upon measurable environmental variables, such that sites with similar environmental conditions will also have similar species compositions (Steinitz *et al.* 2005). The resulting output is a map of beta diversity for the study region, which can be used to visualize spatial patterns in community composition, perform constrained environmental classification, extrapolate species distributions, direct future survey effort and, potentially, assess the impacts of climate change (Ferrier *et al.* 2007).

2.2 Characteristics of modified landscapes

Anthropogenically modified landscapes can be highly heterogeneous, consisting of fragments of original habitat surrounded by a matrix of often sharply contrasting landcover types (Cook *et al.* 2002). At the interface between fragments and the matrix surrounding them is an edge representing a transition zone between the two adjacent habitat types (Ewers & Didham 2006, Lovei *et al.* 2006). Changes in the abiotic and biotic conditions at habitat edges, such as wind, humidity, radiation, predation, parasitism and species interactions, are termed edge effects and lead to the creation of unique edge habitats (Fagan *et al.* 1999, Magura *et al.* 2001, Murcia 1995). The extent to which edge effects penetrate a fragment depends on the type and intensity of land use in the surrounding matrix (Ewers & Didham 2006).

The theory of island biogeography (MacArthur & Wilson 1967) provides a basic conceptual model for the study of fragmented terrestrial habitats, such that the species diversity of a fragment is expected to be a function of its area and the distance to the nearest patch of continuous, un-fragmented habitat (Cook *et al.* 2002). However, beyond these broad generalisations, the relevance of the theory is limited (Laurance 2008). For example, the matrix surrounding terrestrial fragments presents a more permeable isolation barrier than the water separating oceanic islands and can either

impede or assist species dispersal, depending on the nature and intensity of surrounding land-use and the degree of similarity between fragment and matrix habitats (Cook *et al.* 2002). It has been suggested that low-intensity agricultural land provides a more easily penetrable matrix than urban land uses (Dunford & Freemark 2004). The degree of fragment isolation therefore depends not only on the Euclidean distance between fragments but also the nature of the matrix (Ricketts 2001).

As well as providing a medium to connect remnant habitat fragments, the matrix itself often has intrinsic conservation value, supporting its own set of species and providing resources to supplement, or replace, those either present or lacking in habitat fragments (Ewers & Didham 2006, Kupfer *et al.* 2006). As a result, there is often overlap between the species present in forest fragments and in the surrounding matrix, particularly at habitat edges (Cook *et al.* 2002, Niemelä *et al.* 2007). Edges may also contain specialist species that require the particular environmental conditions of edge habitat and are not found in either of the adjacent habitats (Magura 2002, Ries & Sisk 2004). This often leads to the observed trend of an increase in species richness from the fragment's core to its edge (Ewers & Didham 2006, Ewers *et al.* 2007, Niemelä *et al.* 2007). However, there are exceptions to this trend, with some studies reporting no edge effect on species richness (Davies & Margules 1998) or decreased richness at fragment edges (Bieringer & Zulka 2003). Very small forest fragments often show no edge effects because the proportion of edge habitat is so high that they lack the typical conditions required by forest-dwelling species, and are consequently dominated throughout by matrix species (Ewers *et al.* 2007).

Edges also alter the structure of communities, such that there is often a substantial change in species composition from fragment edge to interior (Ewers & Didham 2006, Ries & Sisk 2004). Species respond differently to habitat fragmentation depending on individual traits such as trophic level, dispersal ability and degree of habitat specialization (Fagan *et al.* 1999). Fragment edges generally have a negative impact on core-dwelling species, many of which actively avoid edge habitat (Heliola *et al.* 2001, Magura *et al.* 2001) and may become locally extinct if fragments become too small (Ewers & Didham 2007, Tschardtke *et al.* 2002).

The role of urbanized land in the maintenance of biodiversity in modified landscapes has been less well documented. Whilst the process of urbanization destroys habitats and threatens the survival of many native species, undeveloped urban ‘green space’ can alleviate the detrimental effects of urbanization by preserving and creating habitat (Gaston *et al.* 2005). Domestic gardens are a major component of urban green space, comprising 19 – 27% of the entire urban matrix of major UK cities, and are thought to play a critical role in the maintenance of urban biodiversity (Gaston *et al.* 2005). In addition, the wide spectrum of human activities in the urban landscape creates a huge variety of man-made habitats, some natural and others highly modified, which can act as analogues of natural habitats and often harbour a great variety of species, especially invertebrates (Eversham *et al.* 1996, Eyre *et al.* 2003, Niemelä 1999).

2.3 Carabids as a bioindicator

This study used carabid beetles (Coleoptera: Carabidae) as a bioindicator. A bioindicator can be defined as ‘a species or a species group that reflects the abiotic or biotic state of the environment, represents the impact of environmental change on a habitat, community or ecosystem, or indicates the diversity of other species’ (Rainio & Niemelä 2003). Carabids are considered good bioindicators because (1) their taxonomy and ecology are well known (Lovei & Sunderland 1996); (2) they are abundant and widely distributed, inhabiting all major habitats except deserts (Rainio & Niemelä 2003); (3) they form definable assemblages (Vanbergen *et al.* 2005); (4) the relationship between carabid assemblages and satellite-derived landcover types has been well explored (Eyre *et al.* 2001, Eyre *et al.* 2003, Eyre & Luff 2004, Judas *et al.* 2002); (5) they are sensitive to environmental change and so respond rapidly to habitat modification (Niemelä *et al.* 2000); (6) they are easy and cost-effective to survey using pitfall traps (Niemelä *et al.* 2000, Rainio & Niemelä 2003).

Carabids have been used successfully as bioindicators in a wide range of studies, which most frequently concentrate on their response to changing environmental conditions or management practices (Magura *et al.* 2004, Niemelä *et al.* 2000, Niemelä *et al.* 2002, Rainio & Niemelä 2003). Carabids are therefore well suited as a study organism for use in the assessment of the impact of anthropogenic activity at the landscape scale.

2.4 Carabids in modified landscapes

Within fragmented landscapes, the survival of carabid species depends critically upon their habitat preference, dispersal abilities and the distance between fragments (Sadler *et al.* 2006, Niemelä *et al.* 2007). Carabids therefore show a variety of responses to fragmentation. The trend of higher species richness at habitat edges has been observed in carabids (Magura 2002, Magura *et al.* 2001, Heliola *et al.* 2001) but this trend is not without exceptions (Davies & Margules 1998). General patterns of species richness in forest fragments have described a decrease in richness with reduced fragment size (Fujita *et al.* 2008), no change with reduced fragment size (Margules & Davies 1998) and increased richness with reduced fragment size (Niemelä *et al.* 2007). As fragment size is reduced, the proportion of edge habitat to interior habitat increases and so forest species with habitat requirements typical of the forest interior decline until the fragment becomes so small that it is dominated by edge effects, their requirements are no longer met and, unless they are able to disperse, they become locally extinct (Niemelä *et al.* 2007). This reduction in fragment species richness can be offset by the invasion of generalist species from the surrounding matrix. The extent to which these species can penetrate the fragment depends on its size and shape, the proportion of edge to total habitat and individual species traits (Ewers & Didham 2007, Fagan *et al.* 1999, Niemelä *et al.* 2007). Consequently, as fragment area decreases, the number of generalist species within fragments increases, while the number of forest-preferring species decreases (Fournier & Loreau 2001, Magura *et al.* 2001, Niemelä *et al.* 2007).

Forest fragmentation therefore changes the species composition of carabid assemblages (Margules & Davies 1998, Fujita *et al.* 2008). Within a forest fragment of a certain size, it is the distance to the nearest edge and the strength of edge effects that determine patterns of carabid community composition (Ewers *et al.* 2007). Carabid communities at the forest edge are generally more similar to those of the forest interior than to those of the surrounding matrix (Magura *et al.* 2001). The number of edge-specialists present increases with the proportion of edge to total habitat (Lovei *et al.* 2006) and depends on edge type; edge specialist carabids are rarely found in abrupt, man-made forest edges, such as those created by logging, but have been documented in natural forest edges showing a more gradual transition between habitat types (Heliola *et al.* 2001). Whilst edges do not act as barriers to the

dispersal of generalist species, they do prevent the dispersal of specialist species; forest-preferring carabids do not frequently enter the matrix, and open-habitat carabids rarely enter the forest and if they do, they do not penetrate further than tens of metres (Niemelä *et al.* 2007). In particular, many larger bodied, slow-growing forest species, such as *Carabus* spp., are completely absent from the surrounding matrix (Vanbergen *et al.* 2005).

The response of carabid communities to urbanization has recently been investigated as part of a global initiative to assess the impacts of anthropogenic land-use change on biodiversity (Niemelä *et al.* 2000). Again, results for species richness have been mixed, with some studies reporting no change in species richness across urban-rural gradients (Alaruikka *et al.* 2002, Magura *et al.* 2003), whilst others report a decrease (Ishitani *et al.* 2003, Venn *et al.* 2003) or an increase in species richness in urban areas (Magura *et al.* 2004). Urban forest fragments were characterized by winged generalist species with good dispersal abilities and contained fewer forest specialist species than rural forest fragments (Alaruikka *et al.* 2002, Magura *et al.* 2003, Venn *et al.* 2003).

2.5 The study site

The study site is located in Berkshire, in the southeast of England (Figure 1). The landscape of the United Kingdom is particularly heavily modified and in England, intensive land uses affect nearly three quarters of the country (Fuller *et al.* 2000). The remaining semi-natural land consists of equal parts woodland, both broad-leaved and coniferous, and grassland (Fuller *et al.* 2000). Figure 1 shows the landcover of the study site.

The study site covers an area of approximately 70km², centred on Imperial College's Silwood Park campus (51°24'31"N, 0°38'28"W). The study site is characteristic of a typical anthropogenically modified landscape and consists of a patchwork of forest fragments, agricultural land, which is predominantly a pastoral, and urban development. The site also includes part of Windsor Great Park, a 5000-acre deer park managed by the Crown Estate.

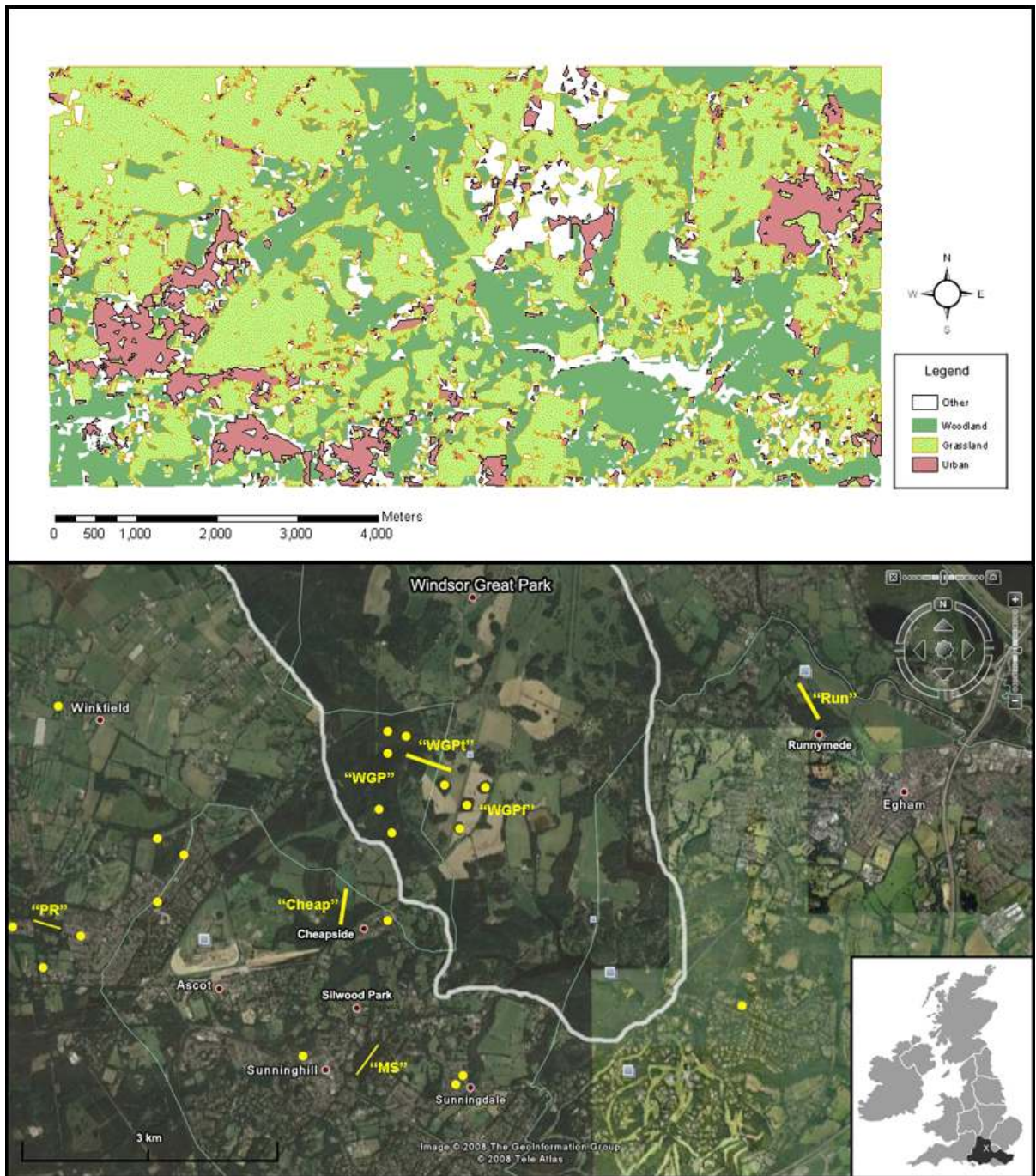


Figure 1: The study site. Top – landcover map showing the three major habitat types: woodland, grassland and urban. Source: Landcover Map of Great Britain 1990, produced by the Centre for Ecology and Hydrology. Bottom – satellite image showing the location of sampling sites within the study area. Yellow lines represent transects, yellow circles represent individual sampling points. Sampling sites are labelled with their site codes. Source: Google Earth.

3. Methods

3.1 Selection of sampling sites

Sampling sites within the study site were selected in order to represent the three major habitat types in the landscape: woodland, grassland and urban. The locations of the sampling sites are shown on Figure 1, whilst Table 1 details the site codes used throughout the study.

Table 1: Sampling site codes used in the study

Site Code	Location	Type
Cheap	Cheapside	Edge transect
Run	Runnymede	Edge transect
WGPt	Windsor Great Park	Edge transect
MS	Marist Schools, Sunninghill	Woodland transect
PR	Ascot Priory	Woodland transect
WGP	Windsor Great Park	Woodland points
WGPf	Windsor Great Park	Woodland points

Three edge transects measured the change in carabid community composition between woodland and grassland habitats. These transects were 500 m long, with the central sampling point sited at the edge between habitat types. The transects therefore extended from a point 250 m into the woodland, through the edge and 250 m into the grassland. Sampling points were spaced at 50m intervals, with two extra sampling points at 25 m either side of the edge. Sampling points at 0 m and 25 m were classed as ‘edge’ habitat. Heliola *et al.* (2001) suggested that for carabids, most edge effects are dampened at a distance of 60 m from the edge, whilst Magura (2002) studied a carabid edge zone of 40 m. Spacing sampling points at 25 m and 50 m intervals should therefore reliably capture any edge effects, whilst extending the transects 250 m into each habitat type should adequately represent core habitat. Grassland at the WGP transect was un-grazed, whilst the grassland at the Cheapside and Runnymede transects was grazed by cattle.

In order to investigate the effect of fragment size on carabid diversity, additional woodland fragments ranging in area from 0.7 ha to 270 ha were sampled. The number of sampling points in each fragment varied with fragment size, with the smallest fragments having a single sampling point and the largest having a transect of eleven. Sampling points on transect lines were always spaced at 50 m intervals.

Twelve urban sites were sampled. These consisted of seven domestic gardens and five churchyards. Each urban site had a single sampling point.

3.2 Field sampling

Beetles were sampled using un-baited pitfall traps, as this is thought to be the most efficient way to gather data on carabid diversity over a short period (Eversham *et al.* 1996; Luff, 1975). Pitfall trapping is a cheap and relatively quick survey method and has been shown to reliably reflect variation in carabid species composition (Niemelä *et al.* 2000). However, it is important to note that pitfall trapping is associated with several disadvantages. Most importantly, pitfall capture rate is a function of both species abundance and activity and so varies with carabid species and is often higher for large-bodied species than smaller species (Halsal & Wratten 2008, Spence & Niemelä 1994). As such, pitfall catches do not represent the true abundance of species within the study area (Southwood & Henderson 2000). Capture rate may also differ with the density of surrounding vegetation, which impedes carabid movement (Greenslade 1964). Pitfall traps are, however, generally suitable for comparative studies (Greenslade 1964).

Pitfall traps consisted of plastic cups, of diameter 7cm and depth 8cm, filled with water and a small amount of detergent to a depth of at least 3cm. The detergent acted to reduce surface tension and prevent smaller beetles escaping. Traps were sunk into the ground so that the rim was level with, or slightly lower than, the ground surface. At each sampling point, traps were arranged in a standard three by three grid of nine traps positioned at two-metre intervals (Simon Leather, personal communication). A GPS unit was used to record the exact position of each sampling point. Each trapping grid was also marked with a high-visibility plastic tag to aid relocation.

Based on the results of pilot studies run in the grounds of Silwood Park, which yielded ten carabids per trapping grid per day, traps were left out for four days then collected and the beetles identified to species level using a standard key (Luff 2007). All sites were sampled between 12th May and 8th July 2008.

3.3 Environmental variables

Landcover variables were obtained from the Land Cover Map of Great Britain (1990) produced by the Centre for Ecology and Hydrology (CEH). The map is based on a 25 by 25 metre grid and was produced using Landsat Thematic Mapper data. The following variables were determined for each sampling point: habitat type (either woodland, grassland or urban; other habitat types were not sampled and so were classed as Other); patch area (m²); distance to the nearest edge (m); habitat type of the nearest edge (either woodland, grassland or urban); and the proportion of each habitat type surrounding each sampling point in buffers of 250 m, 500 m and 750 m radius.

3.4 Statistical analysis

All analysis was carried out using R version 2.6.2 (R Development Core Team 2004) and ArcGIS 9.0. The additional R package “Vegan” was used for ordination, cluster analysis and the calculation of diversity indices and the Bray-Curtis dissimilarity index. The package “Maptools” was used to transfer data between ArcGIS and R. The R code for fitting generalized dissimilarity models (GDM) is available at <http://www.biomaps.net.au/gdm/>.

3.4.1 Diversity indices

Carabid species diversity was calculated using Simpson’s reciprocal index (1/D),

where
$$D = \sum_{i=1}^S \frac{n_i(n_i - 1)}{N(N - 1)}$$
, n_i is the number of individuals in the i th species and N is the total number of individuals in the sample.

Community evenness was calculated using Pielou's evenness (E), where $E = \frac{H'}{H_{\max}}$

and $H' = -\sum_{i=1}^S p_i \log_2 p_i$, p_i is the proportion of the i th species and H'_{\max} is the maximum value of the Shannon-Weiner index, or $\log(n)$, where n is the number of species in the sample.

The abundance, diversity and evenness of carabid communities in each habitat type and sampling site were compared using an ANOVA with normal error structure. The abundance of each carabid species in each habitat type was also investigated using an ANOVA. The data used in this analysis was corrected for sampling effort based on the number of sampling points in each habitat type (37 woodland, 9 edge, 12 grass and 12 urban). Species found to be significantly more abundant in a particular habitat type were classed as preferring that habitat.

3.4.2 Fragmentation and edge effects

Carabid response to fragmentation was investigated by pooling the data collected from woodland sample points and analysing it as a function of fragment area. Species diversity and evenness were analysed using ANOVAs, whilst abundance data was analysed using a generalised linear model (glm) specifying the error family 'poisson' and corresponding log link function.

Transect data was pooled and diversity indices were analysed as a function of distance from the edge. All sampling points from the Runnymede transect were included. One sampling point was omitted from the Windsor Great Park transect, as it was located in a forest clearing and therefore did not represent core forest habitat. The Cheapside transect suffered trap losses in the grassland due to trampling by cattle.

Consequently, sampling points only existed at 25 m, 50 m and 100 m in the grassland. In addition, traps at 25 m into the woodland were not included because the ground was extremely boggy, whilst the sampling point at 250 m was omitted because it was also located in a forest clearing and did not represent core habitat. The Cheapside transect therefore only contributed 8 sampling points, rather than the full quota of 13.

3.4.3 Carabid species assemblages

Ordination (Detrended Correspondance Analysis) and cluster analysis were used in order to determine whether carabids formed definable assemblages in each of the three sampled habitat types.

3.4.4 Modelling carabid diversity at the landscape scale

Carabid species diversity, expressed as Simpson's reciprocal index, was modelled using multiple linear regression. The variables used in the model were derived from GIS analysis of the landcover data. In order to avoid over parameterization, separate preliminary models were run in order to determine which, if any, quadratic and interaction terms were significant. Only the significant terms were included in the final model. The resulting minimum adequate model for species diversity was used to predict values for un-sampled points in the study site using ArcGIS. Since the CEH landcover map covered an area far larger than the study site, GIS layers were clipped so that diversity was only modelled and mapped for those pixels falling inside the study site.

Carabid community dissimilarity was modelled using generalized dissimilarity modelling (GDM). The model calculated the compositional dissimilarity between pairs of sampling points using the Bray-Curtis index, based on species presence/absence data. Community dissimilarity was then modelled as a function of the environmental variables at each sampling point. A separate GDM model was produced for each of the three landscape buffers. The models were then used to predict dissimilarity for un-sampled points in the landscape. Dissimilarity values for each point were expressed as a value between 0 and 1, with 0 indicating no dissimilarity (i.e. sites are similar) and 1 including complete dissimilarity. Each pixel within the study site was compared with a typical woodland pixel, and so community dissimilarity was expressed as dissimilarity to a typical woodland carabid community. The GDM model output was a vector of predicted dissimilarity values for each pixel in the landscape, which was converted to an ASCII file and imported into the GIS to be displayed as a map. Again, GIS layers were clipped so that dissimilarity was only modelled and mapped for those pixels falling inside the study site.

4 Results

A total of 2,351 carabid beetles, representing 48 species and 23 genera, were captured over the eight-week trapping period. For a full list, see the Appendix.

4.1 Abundance

The most abundant species are listed in Table 2. Six species were represented by a single individual and were considered rare; *Amara communis*, *A. eurynota*, *A. tibialis*, *Cychrus caraboides*, *Ocys harpaloides*, *Pogonus chalceus* and *Pterostichus nigrita*. Three species showed a clear habitat preference, particularly *Harpalus rufipes*, which preferred edge habitats above all others (Table 2, Figure 2). Analysis of data collected from the three edge transects showed that two species exhibited a strong preference for woodland over edge and grassland habitats (Table 2, Figure 2). However, this preference was not significant when the total data, corrected for sampling effort, was analysed.

Table 2: The most abundant carabid species trapped during the study. Species marked with an asterisk were significantly more abundant in a particular habitat (*W = woodland, *E = edge), as determined by a one-way ANOVA. Resulting F- and P-values are provided, together with the dataset used in the analysis.

Species	No. individuals	% total catch	ANOVA Abundance~Habitat
<i>Nebria brevicollis</i> * ^W	653	28	F ₂ = 24.98, P < 0.001, transect data
<i>Pterostichus madidus</i>	588	25	-
<i>Abax parallelepipedus</i> * ^W	301	13	F ₂ = 6.18, P < 0.05, transect data
<i>Notiophilus biguttatus</i>	158	7	-
<i>Bembidion lampros</i>	147	6	-
<i>Harpalus rufipes</i> * ^E	101	4	F ₃ = 10.36, P < 0.001, total data
<i>Agonum muelleri</i>	54	2	-
<i>Carabus violaceus</i>	47	2	-
<i>Amara familiaris</i>	45	2	-
<i>Pterostichus aethiops</i>	30	1	-
<i>Carabus problematicus</i> * ^W	21	1	F ₂ = 4.34, P < 0.05, transect data
Totals	2145	91	

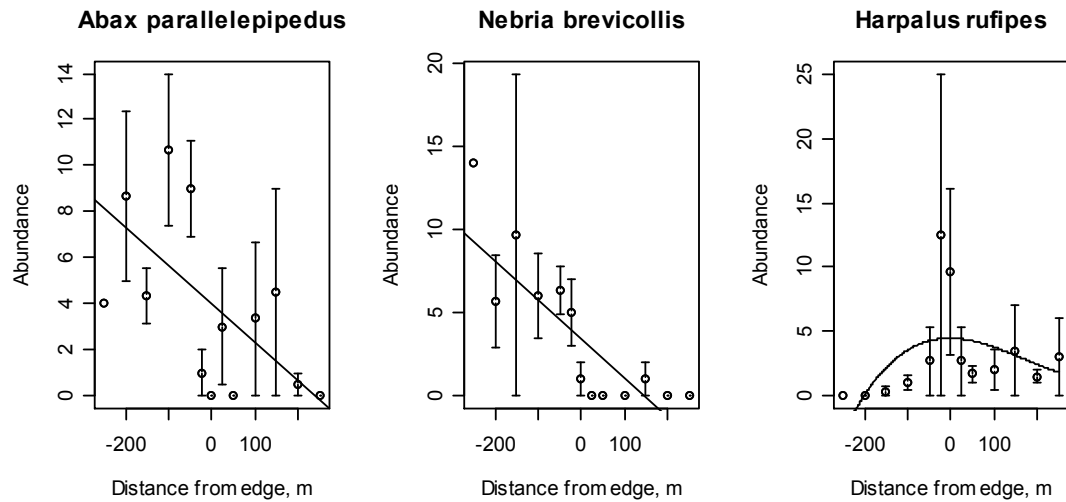


Figure 2: Abundance across edge transects for three species showing significant habitat preferences. Error bars represent one standard error above and below the mean. Negative distances represent woodland, positive distances represent grassland.

Mean carabid abundance did not differ significantly between habitat types ($F = 1.10$, $P = 0.35$) or between sampling sites ($F = 1.63$, $P = 0.17$), (Figure 3).

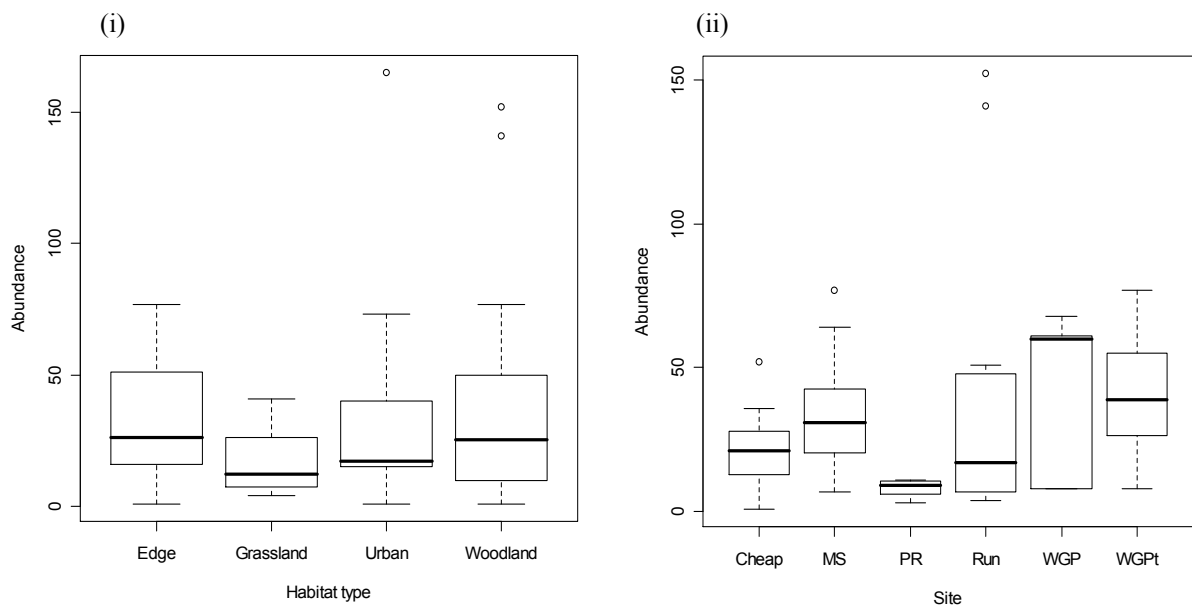


Figure 3: Carabid abundance per habitat type (i) and per sampling site (ii). The box represents the interquartile range and is divided at the median value. Whiskers extend to the largest and smallest values within 1.5 interquartile ranges. Outliers are represented by open circles.

4.2 Diversity and evenness

Mean carabid diversity did not differ significantly between habitat types ($F_3 = 2.06$, $P = 0.11$), (Figure 4(i)). Mean carabid diversity did vary significantly between sampling sites ($F_5 = 9.82$, $P < 0.001$), (Figure 4(ii)). Mean evenness of carabid communities did not differ significantly with habitat type ($F_3 = 1.82$, $P = 0.15$), (Figure 4(iii)) but did differ significantly between sampling sites ($F_5 = 4.13$, $P < 0.001$) (Figure 4(iv)).

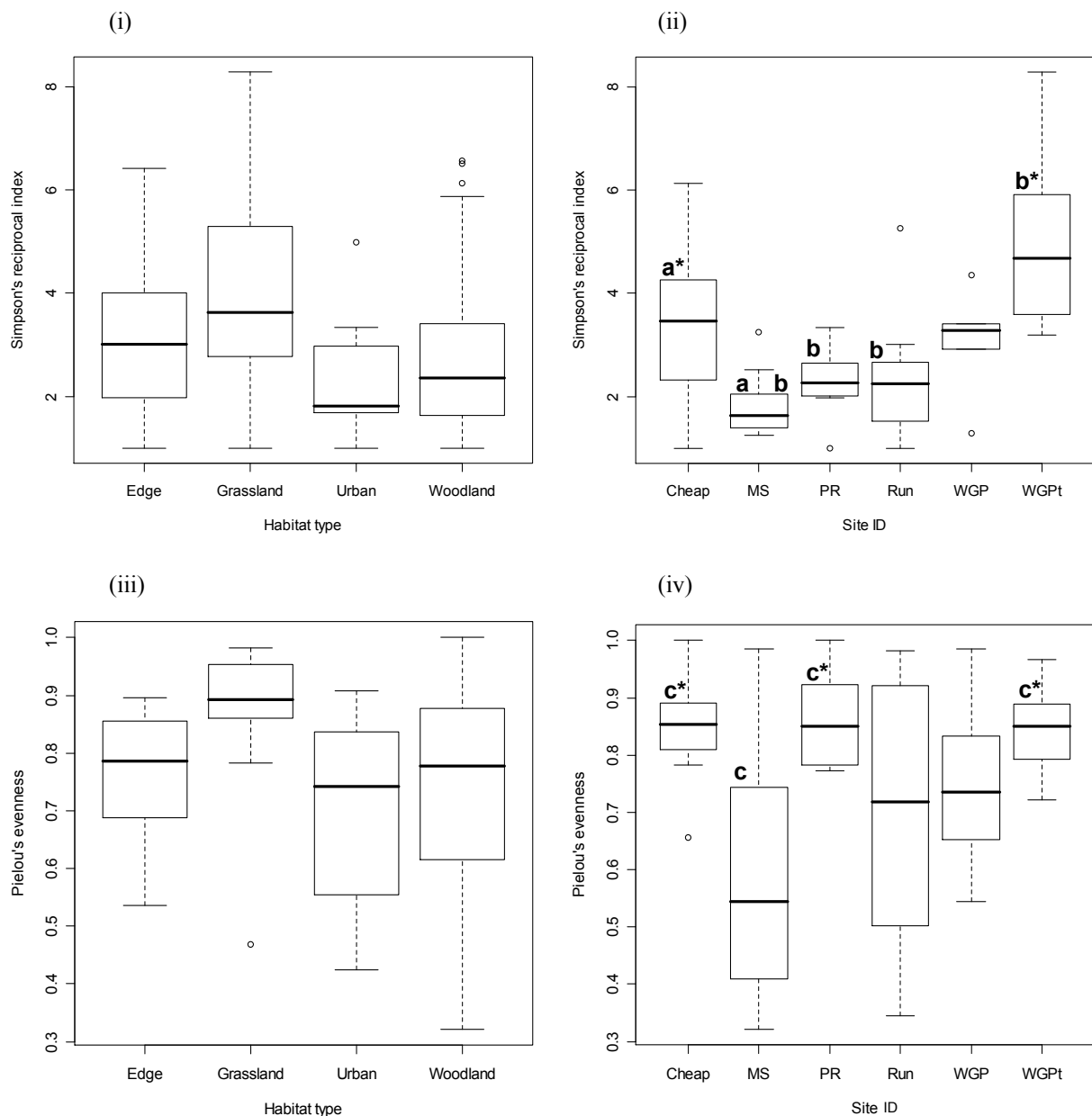


Figure 4: Carabid species diversity per habitat type (i) and per sampling site (ii); evenness of carabid communities per habitat type (iii) and per sampling site (iv). Significantly different sites ($P < 0.05$) are marked with a letter: n^* is significantly higher than all sites marked n .

4.3 Fragmentation effects

The slope of the species area curve (Figure 5) gave a z value of 0.31. Carabid species diversity showed a significant increase with forest fragment area ($F_1 = 4.53$, $p < 0.05$), (Figure 6 (i)), as did abundance (Log area = 0.38, $t_{43} = 10.75$, $P < 0.001$), (Figure 6 (ii)). Evenness did not vary significantly with fragment area ($F_1 = 2.59$, $P = 0.12$).

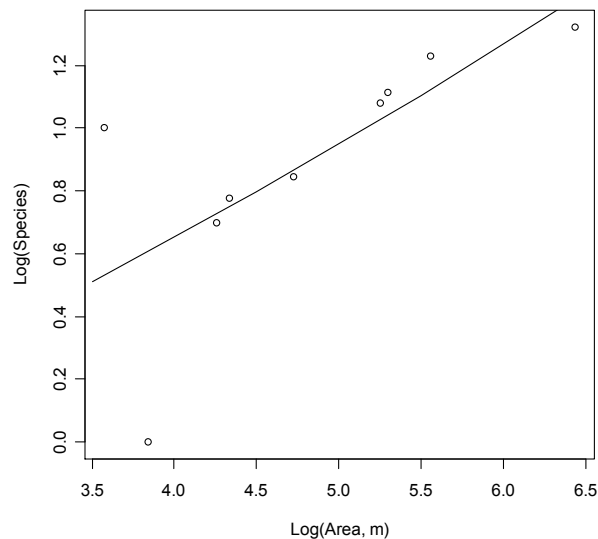


Figure 5: Carabid species area curve ($S = cAz$) plotted using woodland data.

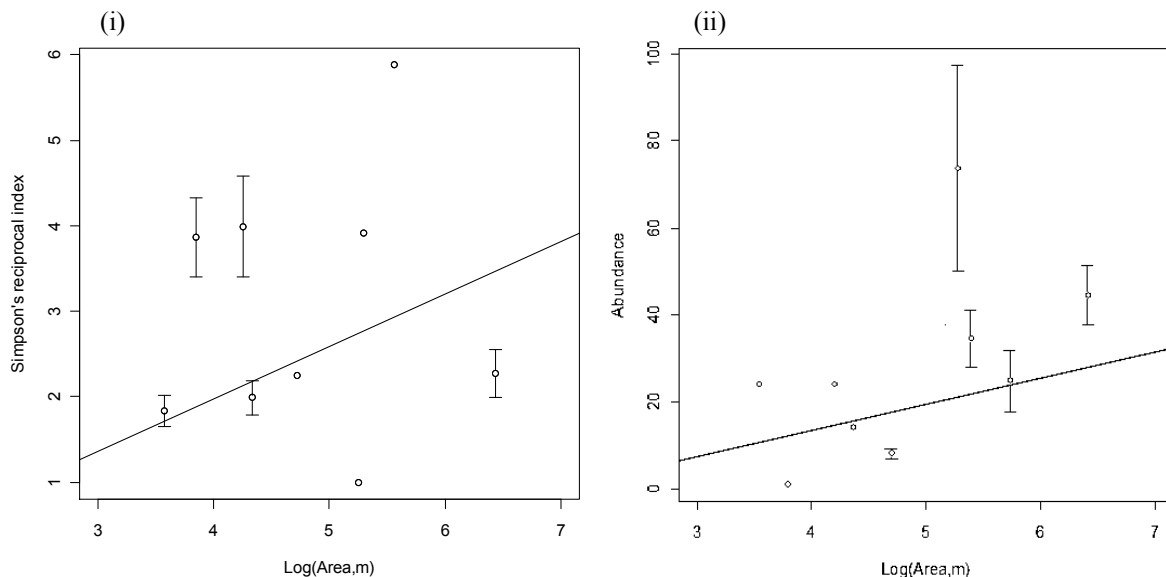


Figure 6: Carabid diversity (i) and abundance (ii) as a function of area. Error bars represent one standard error above and below the mean

4.4 Edge effects across transects

The mean diversity, abundance and evenness of woodland and grassland habitats were compared with t-tests using data from the sampling points furthest from the edge (250 m, 200 m and 150 m). There was no significant difference in mean abundance ($t_{10} = 1.83$, $P = 0.09$), mean diversity ($t_6 = -1.55$, $P = 0.18$) or mean evenness ($t = -1.73$, $P = 0.12$) between habitat types. However, when the Runnymede transect was analysed individually, the mean evenness of grassland was significantly higher than that of woodland ($t_3 = -12.23$, $p = 0.001$).

Diversity showed a weak tendency to increase across transects from woodland to grassland (Figure 7 (i)), but this effect was not statistically significant ($F = 1.67$, $P = 0.21$). Carabid abundance differed significantly across transects (Distance = -0.0026 , $z_{31} = -11.52$, $P < 0.001$) and peaked at the edge (Figure 7 (ii)).

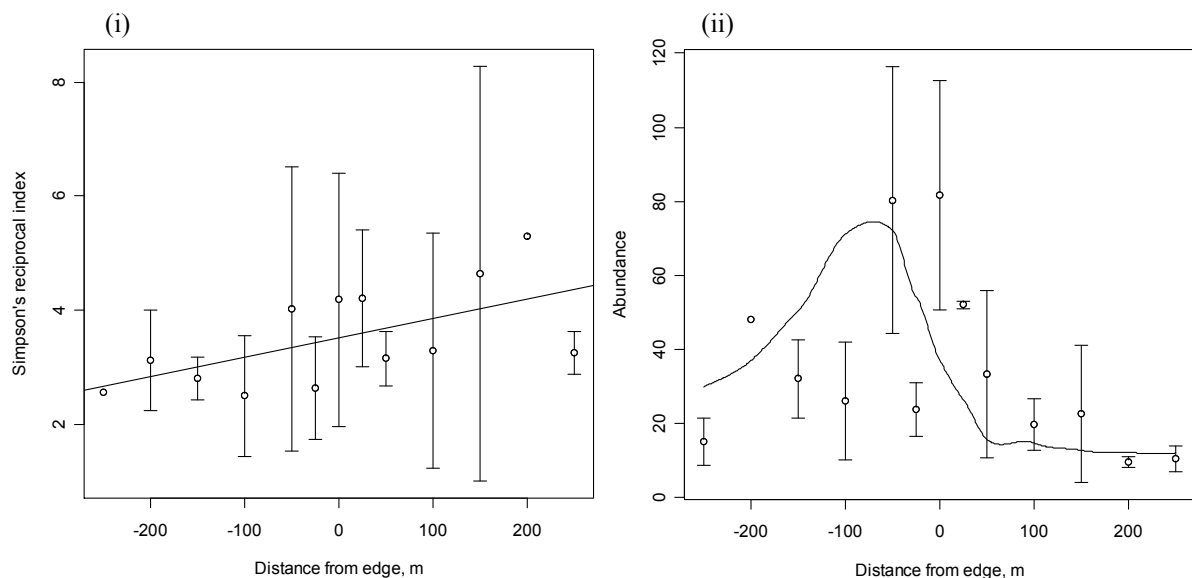


Figure 7: Carabid species diversity (i) and abundance (ii) across a woodland/grassland edge. Error bars represent one standard error above and below the mean. Negative distances represent woodland, positive distances represent grassland.

Evenness showed two separate patterns (Figure 9). For the Runnymede and WGP transects combined, evenness increased significantly from the woodland into the grassland ($F_1 = 6.42$, $P < 0.05$), (Figure 9 (i)). Visual inspection of the data showed four points that appeared to be outliers, so the analysis was repeated after removing

them. Removal of the outliers strengthened the relationship ($F_1 = 40.26$, $P < 0.001$), (Figure 9 (ii)). The Cheapside transect showed an opposite relationship, with evenness higher in the woodland than the grassland (Figure 9 (iii)). but this trend was not statistically significant ($F_1 = 5.61$, $P = 0.064$). The difference in trends between transects was tested with an ANCOVA and was not significant ($F_2 = 2.8862$, $P = 0.075$).

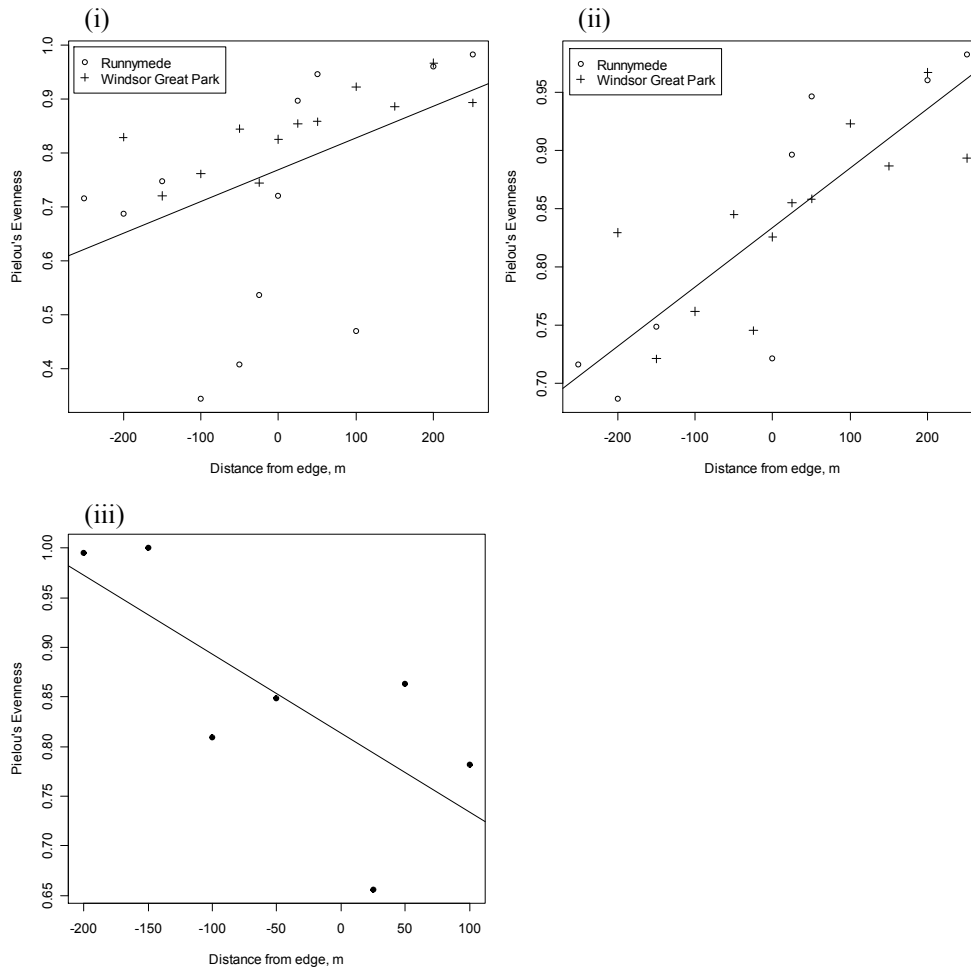


Figure 9: Carabid community evenness across a woodland/grassland edge (i) Runnymede and Windsor Great Park transects, circled points are outliers; (ii) Runnymede and Windsor Great Park transects, outliers removed; (iii) Cheapside transect. Edge = 0, negative values represent woodland and positive values represent grassland.

4.5 Carabid species assemblages

The results of Detrended Correspondance Analysis of species abundance data showed that woodland and grassland sites were well separated from each other along the first axis, whilst within-habitat variation was expressed on the second axis (Figure 10).

First axis scores were plotted against distance from the edge and showed a significant increase with distance from woodland to grassland ($F_1 = 24.81$, $P < 0.0001$), (Figure 11).

Cluster analysis of Bray-Curtis dissimilarity values confirmed that woodland and grassland carabid assemblages could be differentiated, and that edges were more similar to grassland than to woodland (Figure 12). Urban sites were split, with one half showing greater similarity to woodland and the other half to grassland (Figure 12).

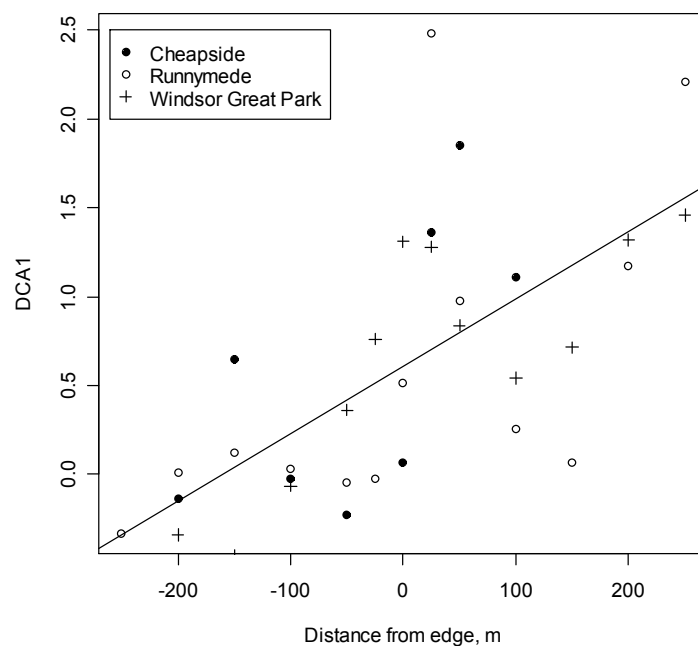


Figure 11: First axis scores from Detrended Correspondance analysis of species abundance data, plotted against distance in metres from the edge for three edge transects. Negative values represent woodland and positive values represent grassland.

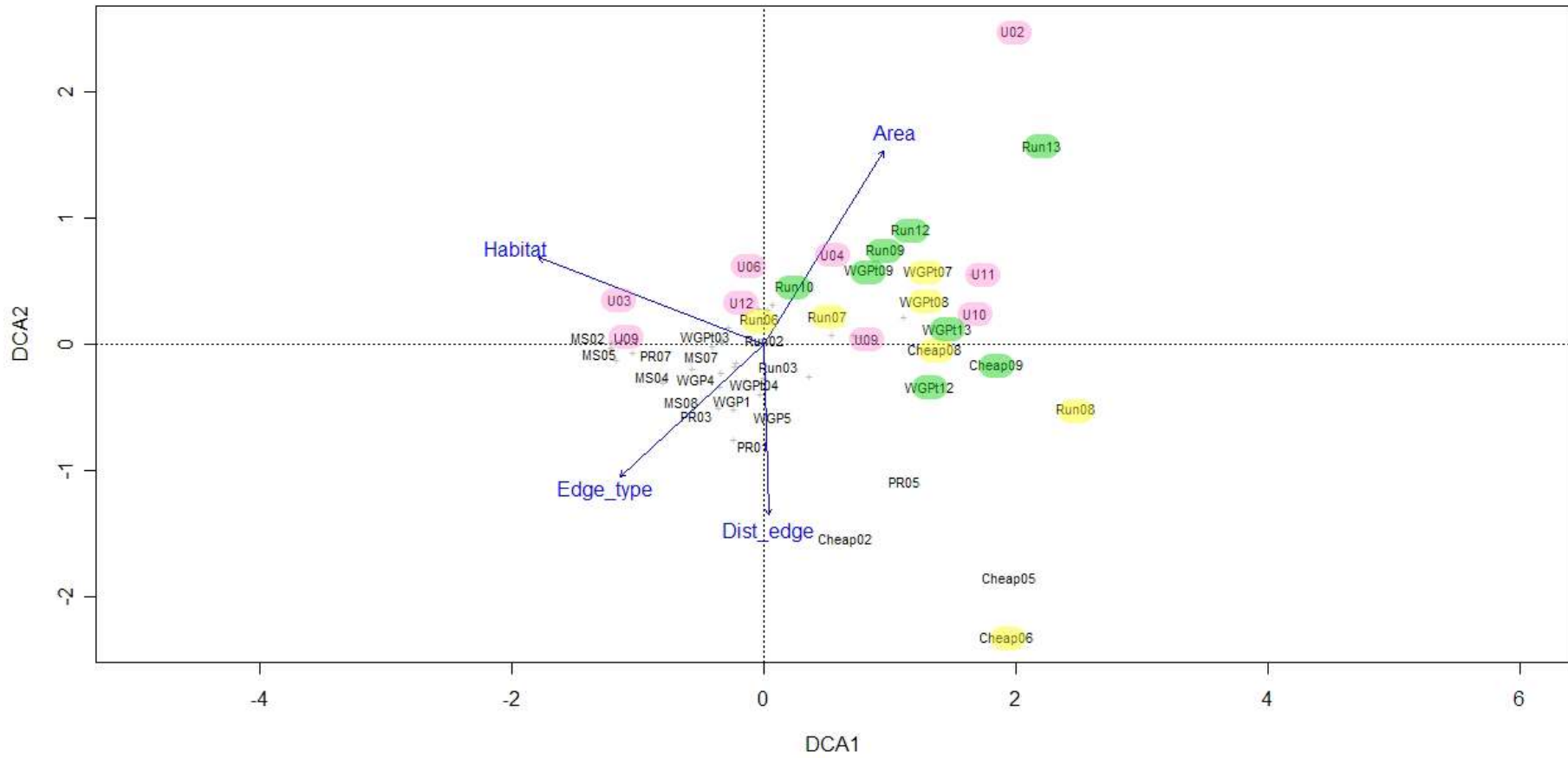


Figure 10: Detrended Correspondence Analysis of species abundance data. Site labels correspond to individual sampling points. Points are colour-coded by habitat type: green = grassland, yellow = edge, pink = urban, uncoloured = woodland.

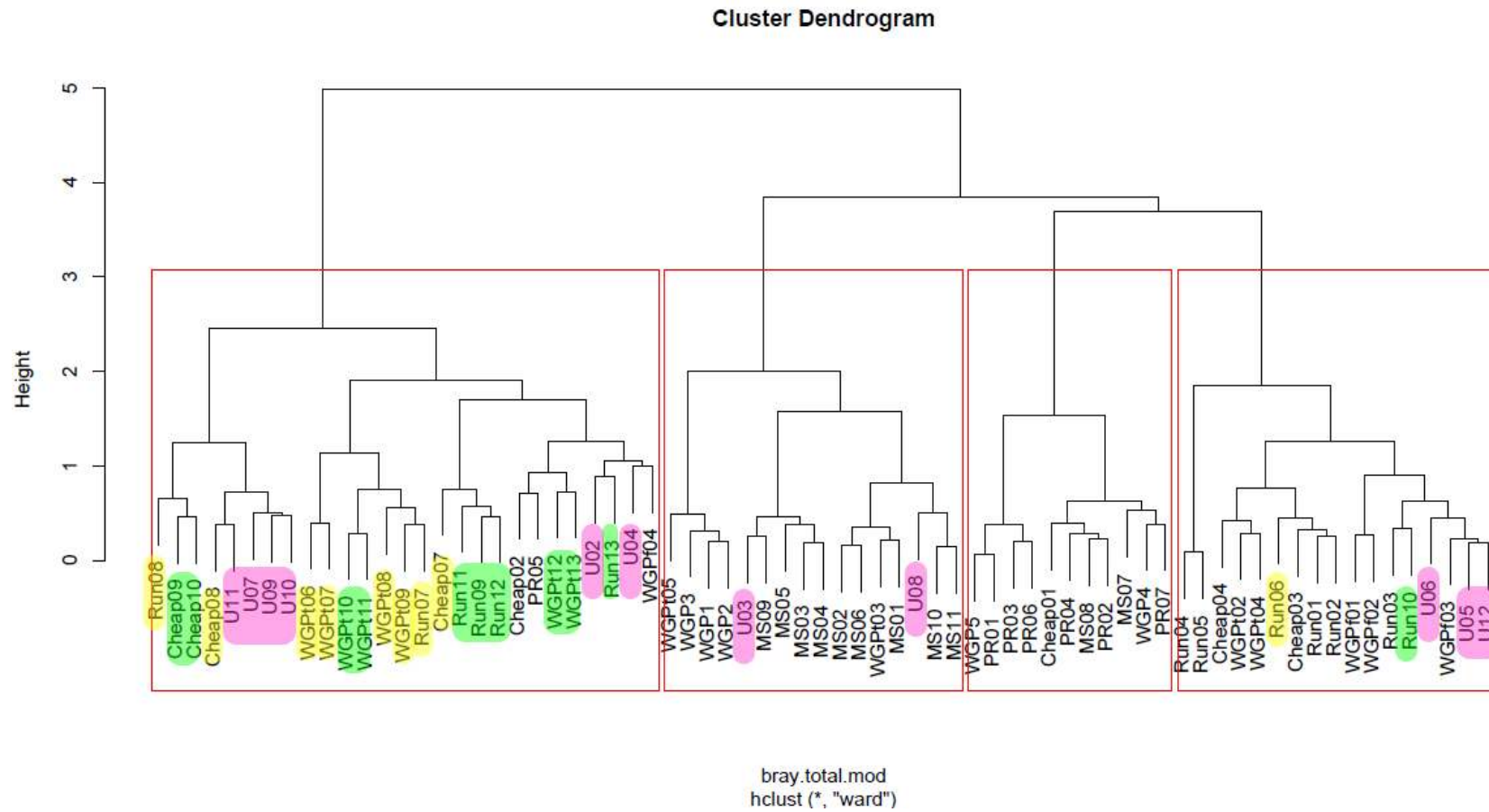


Figure 12: Cluster analysis of site dissimilarity for carabid assemblages in a modified landscape. Site labels correspond to individual sampling points. Points are colour-coded by habitat type: green = grassland, yellow = edge, pink = urban, uncoloured = woodland. Red boxes signify the four main site clusters.

4.6 Predicted species diversity

Figure 13 shows the predicted species diversity of the study area, expressed as Simpson's reciprocal index. The minimum adequate model used to create Figure 13 is presented in Table 3 below.

Table 3: Minimum adequate model for carabid species diversity, expressed as Simpson's reciprocal index. P indicates $P < 0.01$.**

Coefficients:				
	Estimate	Std. Error	t₇₁	P
(Intercept)	5.98456	1.89111	3.165	0.00229 **
Log_area	-2.0612	0.69471	-2.967	0.00410 **
I(Log_area^2)	0.20684	0.06254	3.308	0.00148 **

4.7 Predicted beta diversity – Generalized Dissimilarity Modelling

Figure 14 shows the predicted compositional dissimilarity of each pixel in the study area, expressed as the dissimilarity to a typical woodland community.

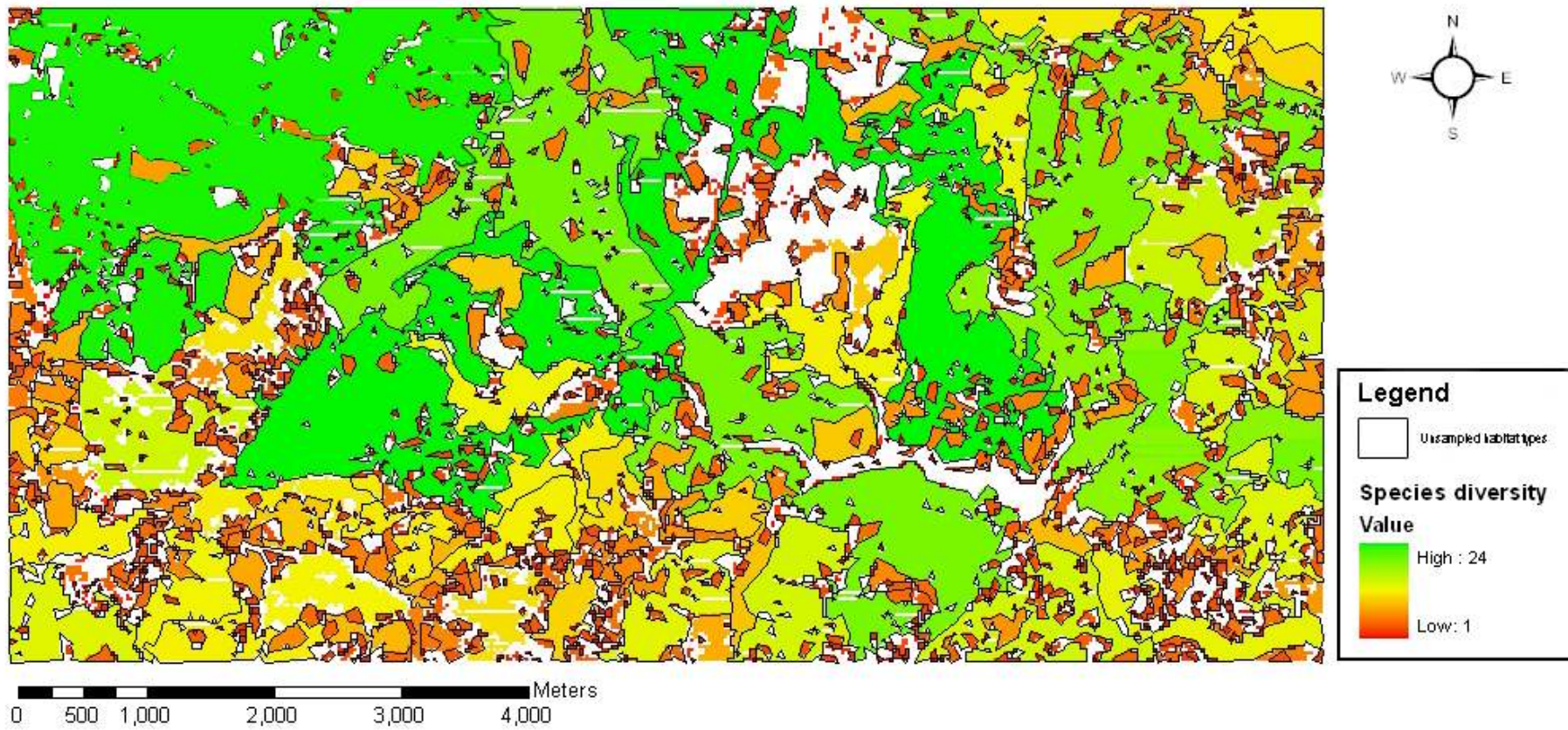


Figure 13: Predicted species diversity (Simpson's reciprocal index)

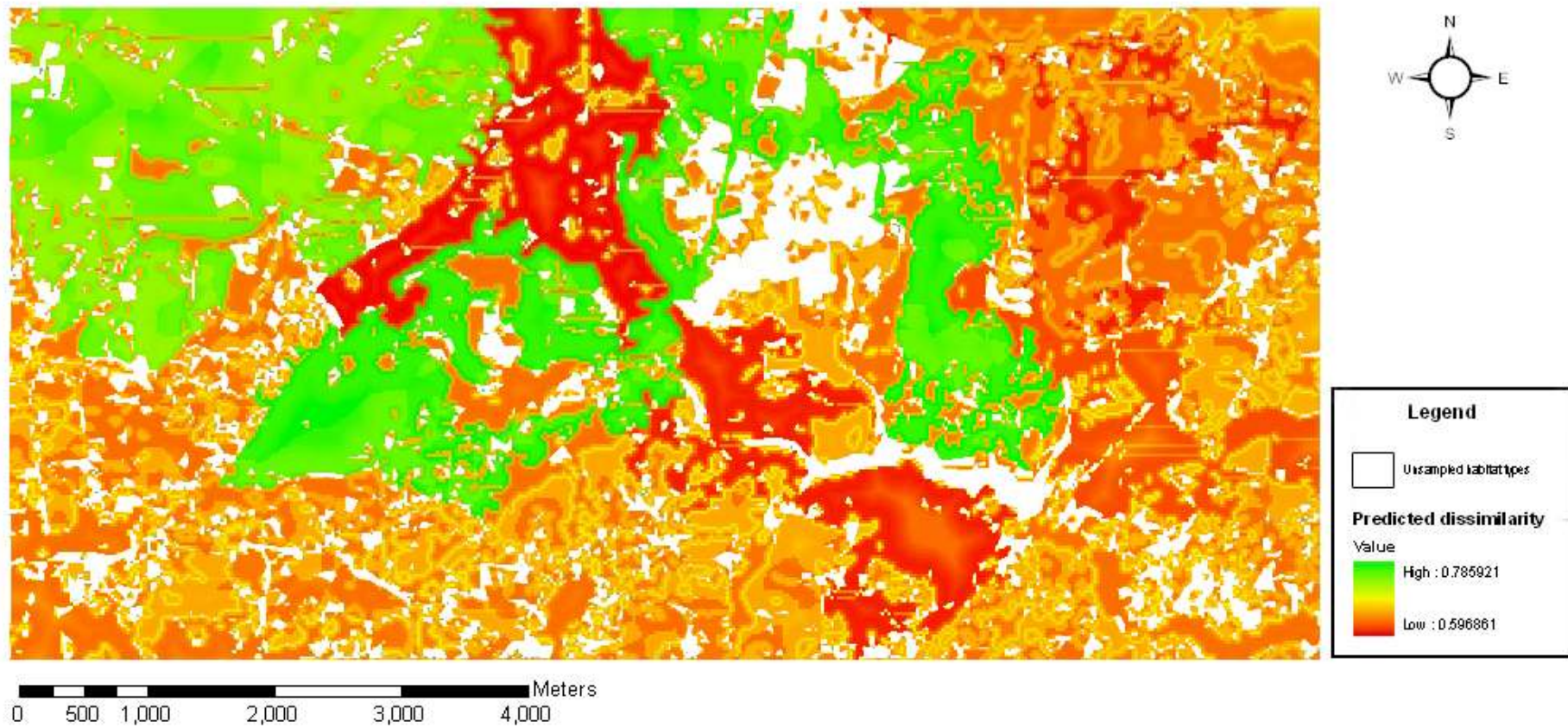


Figure 14: Predicted Bray-Curtis dissimilarity, expressed as dissimilarity to woodland carabid community.

5. Discussion

5.1 Carabid species diversity, evenness and abundance

Species diversity and evenness did not vary significantly with habitat type but did show significant variation between sampling sites (Figure 4). Simpson's reciprocal index quantifies both the number of species present and the relative abundance of each species in the community, such that higher values can signify either greater species richness or higher evenness. The graphs of carabid diversity and evenness in Figure 5 are therefore linked. For example, the WGP transect was significantly more diverse than the PR sampling site, yet both sites had equal evenness, suggesting that the WGP transect was more diverse due to a higher species richness. This is to be expected, since the WGP transect sampled both woodland and grassland habitats, whereas the PR site sampled just woodland. Interestingly, the WGP sampling site, which sampled the largest intact woodland fragment in the study area, was not significantly more diverse than the MS or PR sampling sites, which were smaller, isolated urban woodland fragments. This suggests that small woodland fragments can provide important habitat for carabids.

Within the landscape, abundance did not vary significantly between habitat types or sampling sites. However, carabid abundance and diversity did vary within habitat types, showing an increase with increased woodland fragment area (Figure 6). Since there was no change in evenness with fragment area, these increases must be caused by increased species richness. Larger woodland fragments have a larger proportion of forest interior to forest edge, and so can support a greater diversity of forest-interior species (Magura *et al.* 2001, Niemelä *et al.* 2007). The smallest woodland fragment sampled had an area of 0.7 ha but still supported typical woodland species, including *Carabus problematicus* and *Abax parallelepipedus*, and was grouped in the cluster dendrogram with core woodland habitat (Figure 13), suggesting that even very small fragments are still perceived by carabids as woodland. However, this fragment also supported a greater variety of carabid species than the other, larger fragments, suggesting that it may have been more easily penetrated and colonised by matrix species.

5.2 Edge effects

There was no significant difference in carabid diversity between habitat types, although diversity showed a weak increase from woodland to grassland (Figure 7). Since sampling effort in the grassland was reduced by trap losses, this relationship might be strengthened with the addition of more grassland sampling points to the dataset. The expected trend of increased species diversity at habitat edges was not observed, which implies that woodland and grassland species did not overlap completely at the edge. Habitat edges clustered in the same group as grassland sampling points (Figure 12), suggesting that conditions at the edge were more similar to grassland than woodland. Consequently, woodland-preferring species, including *A. parallelepipedus* and *N. brevicollis*, may actively avoid the edge (Figure 2). Species diversity of woodland carabids at the edge is therefore reduced but this reduction may be offset by the presence of grassland carabids. Rather than peaking at the edge, species diversity may therefore remain at a similar level.

Evenness showed a significant increase across the WGP and Runnymede transects (Figure 9) and so it is likely that the slight increase in species diversity across transects signifies more even communities in the grassland, rather than greater species richness. Woodland sampling points were generally dominated by several species (*A. parallelepipedus*, *N. brevicollis*, *Notiophilus biggutatus* and *Pterostichus madidus*), whereas grassland sampling points yielded a more varied catch with lower abundance per species. The outliers removed from Figure 10 were all sampling points from the Runnymede transect and had a very low evenness value due to the high abundance of *P. madidus*, which constituted 75-90% of the total catch at each of the omitted sampling points. *P. madidus* is a ubiquitous British species and is often extremely abundant (Luff 2007).

Evenness across the Cheapside transect showed an opposite trend and decreased from woodland to grassland, although this trend was not significant (Figure 9). Beginning at the woodland interior and working towards the edge, there were initially only a few woodland species present in equal numbers (*A. parallelepipedus*, *N. brevicollis* and *Carabus violaceus*) and so evenness was initially high. From -100 m, several additional species were present but in low numbers, such that the community was dominated by the woodland species. The extremely low evenness value at +25 m was

due to the high abundance of *Bembidion lampros* and *A. parallelepipedus*, accounting for 58% and 31% of the total catch respectively. Again, *B. lampros* is a common species and is often very abundant (Luff 2007). Differences in evenness may also have been due to the grazing regime at Cheapside, which was more intensive than at Runnymede because fencing restricted the cattle to a smaller area. Disturbance at Cheapside was therefore higher and could have caused reduced community evenness (Townsend & Scarsbrook 1997).

Abundance differed significantly across transects, displaying a peak at the edge (Figure 7). Differences in the structural complexity of vegetation at the forest edge result in increased solar radiation and higher temperatures, which may lead to increased carabid activity and so increased capture rate (Halsall & Wratten 2008, Magura *et al.* 2001). The presence of edge-preferring species, such as *Harpalus rufipes*, could also account for increased carabid abundance. Alternatively, carabids may aggregate at the edge if prey species are present at high numbers (Magura *et al.* 2001).

5.3 Carabid species assemblages

Ordination and cluster analysis showed a clear separation of woodland and grassland carabid communities (Figures 10 and 12). Sampling points at the edge generally clustered with grassland points, with the exception of 'Run6', which was dominated by *P. madidus*, representing 75% of the total catch. One grassland sampling point, 'Run10', also clustered with the woodland points, and was again dominated by *P. madidus*, representing 90% of the total catch. Three woodland sampling points, each with three or fewer species and showing high evenness, were clustered with grassland points. Woodland communities therefore tend to be less even and dominated by a few abundant species, whereas grassland communities have greater species diversity.

Urban points were split, with half clustering with woodland and half with grassland points. 'Woodland'- and 'grassland'-urban points did not differ significantly in mean diversity, evenness or abundance but did differ in general patterns of community composition. 'Woodland'-urban points were typically dominated by several

woodland species (*A. parallelepipedus*, *N. brevicollis*, *N. biguttatus* and *P. madidus*), whereas 'grassland'-urban points contained a greater variety of species and were more even. However, neither 'woodland'- nor 'grassland'-urban points contained large-bodied *Carabus* species. Based on the data from landcover buffers, 'grassland'-urban points were generally surrounded by urban habitat type, whereas 'woodland'-urban points were surrounded predominantly by grassland and could be classed more accurately as suburban or rural rather than urban. Urban sites can therefore sustain some forest species but the extent to which they provide suitable habitat depends on the greater landscape context.

The fact that carabids form distinct assemblages implies that each of the three major habitat types present in the study site has conservation value for the maintenance of carabid biodiversity. However, studies have shown that most generalist carabid species in the UK that are able to persist in a variety of habitat types have maintained or increased their distribution and abundance, whilst habitat specialists dependent on ancestral habitat fragments are in decline (Eversham *et al.* 1996). Conservation attention should therefore focus on the specialist species, which in this case are associated with woodland fragments. As such, large woodland fragments containing true interior habitat should be given highest priority within the landscape.

5.4 Predicted species diversity

The only significant term in the minimum adequate model of carabid species diversity was patch area. The model did not distinguish between habitat types but this was to be expected, considering there was no significant difference in carabid diversity with habitat type. It therefore follows that edge type and distance to edge will also be insignificant, since the neighbouring habitat type is irrelevant. As such, the species diversity model is of limited use to conservation, as it simply predicts an increase in diversity with increasing patch area.

5.5 Predicted beta diversity

The generalized dissimilarity model (GDM) did differentiate between habitat types, since site dissimilarity was expressed as the dissimilarity to a typical woodland carabid community. Large woodland fragments are clearly displayed in red, whilst large expanses of grassland are bright green (Figure 14). Clearings in the northernmost woodland fragment are visible in orange. It is also possible to distinguish core woodland habitat within fragments, which is displayed as a deep orange. The model could therefore be used to identify forest fragments of sufficient size to contain core habitat necessary for the survival of forest specialist species. Core woodland is most clearly visible in the most southerly red woodland fragment, which is more uniform in shape than the other large woodland fragments and is relatively intact, with few clearings. This provides evidence for the importance of fragment shape in determining the proportion of true interior habitat present (Ewers & Didham 2007).

Based on the values predicted by the model, the edge transect in Windsor Great Park should show the greatest contrast in community composition between habitat types, since the transect passes from red to green, whilst the Runnymede transect should show the least contrast as it passes from orange to yellow. The Cheapside transect is predicted to show an intermediate contrast, passing from orange to green. However, such differences in contrast were not detected, as evidenced by Figure 11, which shows that all three transects displayed the same trend across the woodland/grassland edge.

Urban areas appear on Figure 14 as a mixture of orange and yellow. Yellow pixels with the greatest dissimilarity values represent small patches of grassland within the urban matrix. Smaller urban woodland fragments are hard to distinguish but are generally a deep orange, with the smallest fragments surrounded by a yellow border. Small woodland fragments are therefore more similar to woodland than they are to grassland and can be expected to sustain typical woodland species not found in the surrounding urban matrix, as evidenced by the presence of *Carabus* species at the MS sampling site. However, the smallest woodland fragments have a much greater proportion of edge to interior habitat, such that several are comprised mainly of yellow pixels highly dissimilar to woodland habitat. These fragments may be too

dominated by edge effects to provide enough, if any, true interior forest habitat necessary for the persistence of species requiring such conditions.

Interestingly, the urban centres are represented by the same shade of orange as small woodland fragments, suggesting that urban sites are generally more similar to woodland than grassland. This may be linked to the fact that woodland communities tend to be characterized by high dominance, and that dominance is more prevalent in more disturbed habitats (Townsend & Scarsbrook 1997). Urban areas are often highly disturbed, depending on the level of human activity, and urban woodlands in particular are more likely to be disturbed by recreational use (Ishitani *et al.* 2003, Magura *et al.* 2004, Sadler *et al.* 2006). Urban carabid communities may therefore appear more similar to woodland communities on the basis of dominance, rather than the similarity of species present.

The influence of the surrounding landscape on the composition of carabid communities at urban sampling points was discussed in section 5.3. However, the explanatory power of the GDM did not increase with the inclusion of data from the landcover buffers and so the model used to create Figure 14 did not include these data. Had a significant predictor of landscape context been included in the model, it may have been possible to distinguish between urban and suburban carabid communities.

GDM modelling can account for patterns of spatial autocorrelation in species composition by including the geographic distance between points as a predictor of dissimilarity. This may contribute to the predictive power of GDM models, since sites located close together are expected to share more species than sites located further from each other (Legendre 1993, Koenig 1999). It was possible to create a GDM incorporating geographic distance but it was not possible to use this model to predict values of dissimilarity, since it would have been necessary to calculate the latitude and longitude of every pixel within the landscape for which a prediction was to be made. The resulting map of predicted dissimilarity therefore does not take into account patterns of spatial autocorrelation and could be improved by including a measure of geographical distance.

Whilst the GDM model used to create the predicted dissimilarity map of the study site could be improved, the resulting map still conveys a significant amount of useful information about the spatial pattern of carabid diversity at the landscape scale. The survey data used to construct this model could be considered sparse, as only 70 pixels out of over 8,000 were actually sampled, equating to less than 1% of the study site. As such, the GDM model provides evidence that biological survey data can be combined with detailed landcover data to produce realistic predictions in the form of a useful and easily interpreted visual output. The degree to which maps of carabid community dissimilarity can provide information useful for the conservation of other taxa, however, remains untested. If data had been collected for an additional taxa, whether an invertebrate or a higher taxa, it would have been possible to assess the degree of congruence between predicted dissimilarity values. Carabids have not been widely used as indicators of species diversity and existing studies report little or no correlation with other taxa (Rainio & Niemelä 2003). However, a recent investigation into the degree of congruence in compositional dissimilarity between different taxa found a significant correlation between birds and land snails, to such an extent that snail dissimilarity was a better predictor of bird dissimilarity than models incorporating measures of environmental and geographical distance (Steinitz *et al.* 2005). The use of indicator taxa may therefore be more justified in studies using measures of beta, rather than alpha diversity.

In conclusion, this study has shown that it is possible to model and map patterns of beta diversity at the landscape level, producing data useful for conservation and urban planning. Anthropogenic habitat modification has had a significant impact on native carabid diversity but the resulting modified landscape still supports a varied carabid fauna. Whilst the matrix supports carabid communities that differ significantly from those in woodland fragments, it also provides habitat suitable for the survival of some woodland species. However, the maintenance of large, intact fragments of ancestral woodland habitat is necessary in order to maximise carabid diversity at the landscape scale. Conservation focus should therefore remain on the preservation of fragments of original habitat in modified landscapes but the conservation value of the surrounding matrix should not be underestimated.

6. References

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8, 750 words.

8. Appendix

Table 4: Carabid species caught during the study

Species ID	Genus	Species	Species ID	Genus	Species
Aaen	<i>Amara</i>	<i>aenea</i>	Hrub	<i>Harpalus</i>	<i>rubripes</i>
Acomm	<i>Amara</i>	<i>communis</i>	Hruf	<i>Harpalus</i>	<i>rufipes</i>
Acon	<i>Amara</i>	<i>convexior</i>	Lfulvi	<i>Leistus</i>	<i>fulvibarbis</i>
Aeury	<i>Amara</i>	<i>eurynota</i>	Lpil	<i>Loricera</i>	<i>pilicornis</i>
Afame	<i>Amara</i>	<i>famelica</i>	Lrufo	<i>Leistus</i>	<i>rufomarginatus</i>
Afami	<i>Amara</i>	<i>familiaris</i>	Lspin	<i>Leistus</i>	<i>spinibarbis</i>
Aflav	<i>Asaphidion</i>	<i>flavipes</i>	Mmin	<i>Microlestes</i>	<i>minutulus</i>
Amuel	<i>Agonum</i>	<i>muelleri</i>	Nbig	<i>Notiophilus</i>	<i>biguttatus</i>
Anit	<i>Amara</i>	<i>nitida</i>	Nbrev	<i>Nebria</i>	<i>brevicollis</i>
Apara	<i>Abax</i>	<i>parallelepipedus</i>	Nsal	<i>Nebria</i>	<i>salina</i>
Aprae	<i>Amara</i>	<i>praetermissa</i>	Oharp	<i>Ocys</i>	<i>harpaloides</i>
Atib	<i>Amara</i>	<i>tibialis</i>	Paet	<i>Pterostichus</i>	<i>aethiops</i>
Bden	<i>Bembidion</i>	<i>dentellum</i>	Palb	<i>Paranchus</i>	<i>albipes</i>
Blun	<i>Bembidion</i>	<i>lunulatum</i>	Pass	<i>Platynus</i>	<i>assimilis</i>
Blamp	<i>Bembidion</i>	<i>lampros</i>	Patro	<i>Patrobus</i>	<i>atorrufus</i>
Buni	<i>Badister</i>	<i>unipustulatus</i>	Pchal	<i>Pogonum</i>	<i>chalceus</i>
Ccara	<i>Cychrus</i>	<i>caraboides</i>	Pcup	<i>Poecilus</i>	<i>cupreus</i>
Cmic	<i>Calathus</i>	<i>micropterus</i>	Plong	<i>Pterostichus</i>	<i>longicollis</i>
Cnem	<i>Carabus</i>	<i>nemoralis</i>	Pmace	<i>Pterostichus</i>	<i>macer</i>
Cprob	<i>Carabus</i>	<i>problematicus</i>	Pmad	<i>Pterostichus</i>	<i>madidus</i>
Crot	<i>Calathus</i>	<i>rotundicollis</i>	Pnig	<i>Pterostichus</i>	<i>nigrita</i>
Cvio	<i>Carabus</i>	<i>violaceus</i>	Pquad	<i>Pterostichus</i>	<i>quadrifoveolatus</i>
Ecup	<i>Elaphrus</i>	<i>cupreus</i>	Pstren	<i>Pterostichus</i>	<i>strenuus</i>
Haffi	<i>Harpalus</i>	<i>affinis</i>	Pver	<i>Poecilus</i>	<i>versicolor</i>

Table 5: Site data. Edge type, Buffer_250, Buffer_500 and Buffer_750: 1 = woodland, 3 = grassland, 4 = urban.

Site	Habitat	Lat	Long	Area/m ²	Dist edge/m	Edge-type	Buffer 250	Buffer 500	Buffer 750	Abundance	Diversity	Evenness
Cheap1	Woodland	51.41739	0.65292	362488	250	3	1	1	1	13	2.96	0.995
Cheap2	Woodland	51.41790	0.65263	362488	200	3	1	1	1	4	2.00	1.000
Cheap3	Woodland	51.41825	0.65181	362488	100	3	1	1	1	52	4.91	0.809
Cheap4	Woodland	51.41875	0.65214	362488	150	3	1	1	1	36	3.93	0.848
Cheap5	Woodland	51.41831	0.65108	362488	90	3	1	1	3	28	6.13	0.890
Cheap6	Woodland	51.41853	0.65064	362488	50	3	1	1	3	16	4.00	0.854
Cheap7	Edge	51.41900	0.65094	362488	0	3	1	1	3	1	1.00	NaN
Cheap8	Grassland	51.41956	0.65169	6883422	25	1	1	1	3	26	2.32	0.656
Cheap9	Grassland	51.41981	0.65158	6883422	50	1	3	3	3	15	4.25	0.863
Cheap10	Grassland	51.42022	0.65147	6883422	100	1	3	3	3	26	2.99	0.782
MS1	Woodland	51.40417	0.64521	178647	70	3	1	1	3	40	1.82	0.577
MS2	Woodland	51.40387	0.64606	178647	135	4	1	1	3	38	1.24	0.322
MS3	Woodland	51.40356	0.64690	178647	106	4	1	1	3	31	2.51	0.688
MS4	Woodland	51.40306	0.64722	178647	112	3	1	1	3	23	2.12	0.798
MS5	Woodland	51.40278	0.64778	178647	125	3	1	1	4	27	1.60	0.544
MS6	Woodland	51.40250	0.64833	178647	103	3	1	1	4	45	1.44	0.432
MS7	Woodland	51.40222	0.64889	178647	75	3	1	4	4	9	3.24	0.918
MS8	Woodland	51.40167	0.64917	178647	56	3	1	4	4	7	1.96	0.985
MS9	Woodland	51.40139	0.64972	178647	25	3	1	4	4	18	1.62	0.521
MS10	Woodland	51.40083	0.65000	178647	35	3	1	4	4	64	1.34	0.388
MS11	Woodland	51.40028	0.64972	178647	25	4	1	4	4	77	1.34	0.374
PR1	Woodland	51.41861	0.70750	53070	25	4	1	1	3	7	1.00	NaN
PR2	Woodland	51.41917	0.70750	53070	25	1	1	1	3	11	2.28	0.834
PR3	Woodland	51.41889	0.70694	53070	80	4	1	1	3	11	2.05	0.783
PR4	Woodland	51.41889	0.70611	53070	100	3	1	1	3	10	3.33	0.923
PR5	Woodland	51.41889	0.70528	53070	100	3	3	1	3	3	3.00	1.000

Table 5 cont. Site data. Edge type, Buffer_250, Buffer_500 and Buffer_750: 1 = woodland, 3 = grassland, 4 = urban.

Site	Habitat	Lat	Long	Area/m ²	Dist edge/m	Edge-type	Buffer 250	Buffer 500	Buffer 750	Abundance	Diversity	Evenness
PR6	Woodland	51.41889	0.70472	53070	100	3	3	3	4	9	1.98	0.773
PR7	Woodland	51.41861	0.70389	53070	90	3	3	3	4	5	2.27	0.865
RUN1	Woodland	51.43917	0.56111	198078	250	3	1	3	3	48	2.57	0.716
RUN2	Woodland	51.43972	0.56111	198078	200	3	1	3	3	33	2.24	0.687
RUN3	Woodland	51.44000	0.56194	198078	150	3	1	3	3	17	2.43	0.748
RUN4	Woodland	51.44028	0.56250	198078	100	3	1	3	3	152	1.44	0.345
RUN5	Woodland	51.44083	0.56333	198078	50	3	1	3	3	141	1.52	0.407
RUN6	Woodland	51.44083	0.56389	198078	20	3	1	3	3	51	1.73	0.536
RUN7	Edge	51.44111	0.56472	198078	0	3	1	3	3	22	1.97	0.721
RUN8	Grassland	51.44139	0.56472	301654	25	1	1	3	3	6	3.00	0.896
RUN9	Grassland	51.44167	0.56500	301654	50	1	3	3	3	4	2.67	0.946
RUN10	Grassland	51.44222	0.56472	301654	100	1	3	3	3	10	1.22	0.469
RUN11	Grassland	51.44278	0.56500	301654	150	1	3	3	3	4	1.00	NaN
RUN12	Grassland	51.44306	0.56556	301654	200	1	3	3	3	11	5.26	0.960
RUN13	Grassland	51.44389	0.56528	301654	250	1	3	3	3	7	2.88	0.982
U1	Urban	51.41833	0.64194	11018	10	1	3	4	4	0	0.00	0.000
U2	Urban	51.40278	0.66139	82145	71	1	4	3	3	10	3.33	0.836
U3	Urban	51.39944	0.63056	82145	103	3	4	3	3	14	1.58	0.545
U4	Urban	51.39861	0.65028	11346	50	4	4	1	1	1	1.00	NaN
U5	Urban	51.40706	0.57978	6711	25	3	3	3	3	20	2.47	0.908
U6	Urban	51.44361	0.69944	25623	25	1	1	3	3	17	3.11	0.892
U7	Urban	51.41806	0.71000	189785	100	1	3	3	3	43	1.81	0.554
U8	Urban	51.41417	0.70639	13409	35	4	4	4	4	165	1.65	0.425
U9	Urban	51.42083	0.68417	112485	35	3	1	4	3	37	2.83	0.819
U10	Urban	51.42639	0.68083	692619	25	4	4	4	4	73	4.99	0.799
U11	Urban	51.41722	0.70194	53070	50	3	3	3	4	16	1.71	0.593

Table 5 cont. Site data. Edge type, Buffer_250, Buffer_500 and Buffer_750: 1 = woodland, 3 = grassland, 4 = urban.

Site	Habitat	Lat	Long	Area/m ²	Dist edge/m	Edge-type	Buffer 250	Buffer 500	Buffer 750	Abundance	Diversity	Evenness
U12	Urban	51.42731	0.68528	6383444	75	1	3	3	3	17	1.80	0.685
WGP1	Woodland	51.43778	0.63917	2735195	50	3	1	1	1	68	3.40	0.653
WGP2	Woodland	51.43750	0.64167	2735195	50	3	1	1	1	60	3.28	0.736
WGP3	Woodland	51.43944	0.64306	2735195	75	3	1	1	1	61	4.35	0.834
WGP4	Woodland	51.42889	0.64250	2735195	35	3	1	1	1	8	2.91	0.985
WGP5	Woodland	51.43139	0.64500	2735195	55	3	1	1	1	8	1.28	0.544
WGPf1	Woodland	51.43472	0.62917	3750	25	3	3	3	3	24	5.88	0.866
WGPf2	Woodland	51.43278	0.63250	21563	50	3	3	3	3	14	3.92	0.901
WGPf3	Woodland	51.43083	0.62806	18017	70	3	3	3	3	24	2.25	0.679
WGPf4	Woodland	51.42778	0.63000	6943	25	3	3	3	3	1	1.00	NaN
WGPt1	Woodland	51.43500	0.63917	2735195	250	3	1	1	1	19	6.56	0.917
WGPt2	Woodland	51.43500	0.63861	2735195	200	3	1	1	1	50	4.01	0.829
WGPt3	Woodland	51.43500	0.63778	2735195	150	3	1	1	1	57	3.18	0.721
WGPt4	Woodland	51.43500	0.63722	2735195	100	3	3	3	3	37	3.56	0.761
WGPt5	Woodland	51.43500	0.63639	2735195	50	3	3	3	3	68	6.51	0.845
WGPt6	Woodland	51.43500	0.63611	2735195	25	3	3	3	3	53	3.53	0.745
WGPt7	Edge	51.43500	0.63556	2735195	0	3	3	3	3	77	6.41	0.826
WGPt8	Grassland	51.43500	0.63528	6883422	25	1	3	3	3	27	5.40	0.855
WGPt9	Grassland	51.43528	0.63472	6883422	50	1	3	3	3	26	3.63	0.858
WGPt10	Grassland	51.43500	0.63417	6883422	100	1	3	3	3	35	5.35	0.923
WGPt11	Grassland	51.43500	0.63306	6883422	150	1	3	3	3	41	8.28	0.886
WGPt12	Grassland	51.43500	0.63250	6883422	200	1	3	3	3	8	5.33	0.967
WGPt13	Grassland	51.43500	0.63111	6883422	150	1	3	3	3	14	3.63	0.893

Table 6: Collection data

	<i>Cvio</i>	<i>Cprob</i>	<i>Cnem</i>	<i>Apara</i>	<i>Nbrev</i>	<i>Nbig</i>	<i>Pmad</i>	<i>Pnig</i>	<i>Cmic</i>	<i>Crot</i>	<i>Buni</i>	<i>Pcup</i>	<i>Mmin</i>	<i>Atib</i>	<i>Aaen</i>	<i>Hruf</i>	<i>Afame</i>	<i>Afami</i>	<i>Blamp</i>	<i>Lpil</i>	<i>Nsal</i>	<i>Plong</i>	<i>Patro</i>	<i>Acon</i>	<i>Aprae</i>	<i>Anit</i>	<i>Acomm</i>	
Cheap01	4	0	0	5	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cheap02	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheap03	0	0	0	8	9	1	10	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheap04	2	1	0	9	11	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheap05	0	0	0	3	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cheap06	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheap07	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheap08	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	1	15	0	0	0	0	0	0	0	0	0
Cheap09	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	6	0	0	0	0	0	0	0	0	0
Cheap10	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	1	0	0	8	0	0	0	0	0	0	0	0	0
WGPT01	0	1	0	4	3	3	4	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
WGPT02	0	1	0	16	11	7	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPT03	0	1	0	5	29	4	10	0	0	0	0	0	0	0	1	1	0	0	6	0	0	0	0	0	0	0	0	0
WGPT04	1	0	0	17	4	3	8	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
WGPT05	1	2	3	13	6	18	1	0	2	1	0	0	0	0	0	8	0	0	9	0	0	0	0	0	0	0	0	0
WGPT06	4	0	0	2	3	11	3	0	0	0	0	0	0	0	0	25	0	0	3	0	0	0	0	0	0	0	0	0
WGPT07	11	0	1	0	3	4	2	0	0	0	0	0	0	0	0	22	0	11	11	0	0	0	0	0	0	0	0	0
WGPT08	1	0	1	1	0	0	5	0	0	0	0	4	0	0	0	8	1	1	0	0	0	0	0	0	0	0	0	0
WGPT09	4	0	0	0	0	0	12	0	0	0	0	3	0	0	0	3	0	2	0	0	0	0	0	0	0	0	0	0
WGPT10	4	0	0	10	0	2	8	0	0	0	0	0	0	0	0	5	4	2	0	0	0	0	0	0	0	0	0	0
WGPT11	3	1	1	9	2	1	5	0	0	0	0	0	0	0	0	7	2	3	4	0	0	1	0	0	0	0	0	0
WGPT12	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	1	0	0	0	0	0	0
WGPT13	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	6	3	0	0	0	0	0	0	0	0	0	0	0
WGP1	1	1	1	30	14	16	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
WGP2	2	6	0	30	8	9	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
WGP3	3	5	0	15	15	19	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGP4	0	0	0	2	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGP5	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
U01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U02	0	0	0	0	0	0	0	0	0	0	0	0	5	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0

Table 6 cont. Collection data

	<i>Amuel</i>	<i>Palb</i>	<i>Ecup</i>	<i>Pstren</i>	<i>Lfulvi</i>	<i>Lspin</i>	<i>Ccara</i>	<i>Lrufo</i>	<i>Hrub</i>	<i>Oharp</i>	<i>Aeury</i>	<i>Haffi</i>	<i>Pver</i>	<i>Pquad</i>	<i>Paet</i>	<i>Pchal</i>	<i>Pmace</i>	<i>Aflav</i>	<i>Pass</i>	<i>Bluna</i>	<i>Bden</i>	
Cheap01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheap02	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Cheap03	2	0	0	0	3	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Cheap04	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0
Cheap05	7	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	5	0
Cheap06	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	2
Cheap07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheap08	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cheap09	0	0	0	3	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Cheap10	0	0	0	1	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
WGPt01	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPt02	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPt03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPt04	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPt05	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPt06	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
WGPt07	1	0	0	0	0	0	0	0	6	1	1	3	0	0	0	0	0	0	0	0	0	0
WGPt08	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
WGPt09	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPt10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPt11	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPt12	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPt13	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
WGP1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGP2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGP3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGP4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGP5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U02	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 6 cont. Collection data

	<i>Cvio</i>	<i>Cprob</i>	<i>Cnem</i>	<i>Apara</i>	<i>Nbrev</i>	<i>Nbig</i>	<i>Pmad</i>	<i>Pnig</i>	<i>Cmic</i>	<i>Crot</i>	<i>Buni</i>	<i>Pcup</i>	<i>Mmin</i>	<i>Atib</i>	<i>Aaen</i>	<i>Hruf</i>	<i>Afame</i>	<i>Afami</i>	<i>Blamp</i>	<i>Lpil</i>	<i>Nsal</i>	<i>Plong</i>	<i>Patro</i>	<i>Acon</i>	<i>Aprae</i>	<i>Anit</i>	<i>Acomm</i>	
U03	0	0	0	0	11	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
U04	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U05	0	0	0	4	5	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U06	0	0	0	0	6	0	7	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
U07	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	7	31	0	0	0	1	0	0	0	0	
U08	0	0	0	3	126	5	25	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	
U09	0	0	0	0	12	0	1	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	
U10	0	0	0	0	4	2	4	0	0	0	0	5	2	0	0	0	0	7	19	0	0	0	0	0	0	4	1	
U11	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	12	0	0	0	0	0	0	0	0	
U12	0	0	0	0	4	0	12	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
MS01	0	0	0	3	29	5	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
MS02	0	0	0	0	34	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	
MS03	0	0	0	11	16	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	
MS04	0	0	0	7	14	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
MS05	0	0	0	3	21	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	
MS06	0	0	0	6	37	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
MS07	2	0	0	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
MS08	0	0	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
MS09	0	0	0	1	14	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	
MS10	0	0	0	1	55	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
MS11	0	0	0	2	66	8	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
PR01	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
PR02	0	0	0	4	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
PR03	0	0	0	7	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
PR04	0	0	0	3	4	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
PR05	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
PR06	0	0	0	6	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
PR07	0	0	0	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
WGPf01	0	1	0	2	4	6	6	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
WGPf02	0	0	0	1	4	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Table 6 cont. Collection data

	<i>Amuel</i>	<i>Palb</i>	<i>Ecup</i>	<i>Pstren</i>	<i>Lfulvi</i>	<i>Lspin</i>	<i>Ccara</i>	<i>Lrufo</i>	<i>Hrub</i>	<i>Oharp</i>	<i>Aeury</i>	<i>Haffi</i>	<i>Pver</i>	<i>Pquad</i>	<i>Paet</i>	<i>Pchal</i>	<i>Pmace</i>	<i>Aflav</i>	<i>Pass</i>	<i>Bluna</i>	<i>Bden</i>
U03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U08	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
U09	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U10	24	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
U12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS06	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS08	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MS11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PR01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PR02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PR03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PR04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PR05	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
PR06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PR07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPf01	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
WGPf02	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 6 cont. Collection data

	Cvio	Cprob	Cnem	Apara	Nbrev	Nbig	Pmad	Pnig	Cmic	Crot	Buni	Pcup	Mmin	Atib	Aaen	Hruf	Afame	Afami	Blamp	Lpil	Nsal	Plong	Patro	Acon	Aprae	Anit	Acomm
WGPF03	0	0	0	1	5	2	15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WGPF04	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run01	0	0	0	4	14	3	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run02	0	0	0	5	2	4	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run03	0	0	0	6	0	1	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run04	0	0	0	6	3	0	126	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Run05	0	0	0	6	4	0	113	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run06	1	0	0	0	7	0	38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run07	0	0	0	0	0	0	14	0	0	1	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0
Run08	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Run09	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Run10	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Run11	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run12	2	0	0	0	0	0	3	0	0	0	1	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0
Run13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0

Table 6 cont. Collection data

	Amuel	Palb	Ecup	Pstren	Lfulvi	Lspin	Ccara	Lrufo	Hrub	Oharp	Aeury	Haffi	Pver	Pquad	Paet	Pchal	Pmace	Aflav	Pass	Bluna	Bden		
WGPF03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
WGPF04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run01	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run02	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run03	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run04	2	0	0	0	0	0	0	0	1	0	0	0	0	0	12	0	0	0	0	0	0	0	0
Run05	0	0	0	0	0	0	0	1	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
Run06	3	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run08	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Run09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Run10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Run12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Run13	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	3	0	0	0	0	0	0