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The compositional and configurational heterogeneity of matrix habitats shape woodland carabid communities in wooded-agricultural landscapes.

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Abstract

Context

Landscape heterogeneity (the composition and configuration of matrix habitats) plays a major role in shaping species communities in wooded-agricultural landscapes. However, few studies consider the influence of different types of semi-natural and linear habitats in the matrix, despite their known ecological value for biodiversity.

Objectives

To investigate the importance of the composition and configuration of matrix habitats for woodland carabid communities and identify whether specific landscape features can help to maintain long-term populations in wooded-agricultural environments.

Methods

Carabids were sampled from woodlands in 36 tetrads of 4 km2 across southern Britain. Landscape heterogeneity including an innovative representation of linear habitats was quantified for each tetrad. Carabid community response was analysed using ordination methods combined with variation partitioning and additional response trait analyses.

Results

Woodland carabid community response was trait-specific and better explained by simultaneously considering the composition and configuration of matrix habitats. Semi-natural

and linear features provided significant refuge habitat and functional connectivity. Mature hedgerows were essential for slow-dispersing carabids in fragmented landscapes. Species commonly associated with heathland were correlated with inland water and woodland patches despite widespread heathland conversion to agricultural land, suggesting that species may persist for some decades when elements representative of the original habitat are retained following landscape modification.

Conclusions

Semi-natural and linear habitats have high biodiversity value. Landowners should identify features that can provide additional resources or functional connectivity for species relative to other habitat types in the landscape matrix. Agri-environment options should consider landscape heterogeneity to identify the most efficacious changes for biodiversity.

Keywords

Agriculture; carabid communities; landscape heterogeneity; life-history traits; linear features; matrix habitats; semi-natural habitat; variation partitioning; woodland

Introduction

Changes to European woodland-agricultural environments have occurred over thousands of years; however the post-Second World War period saw an unprecedented rate of landscape modification (Aviron *et al.,* 2005; Hendrickx *et al.,* 2007). Landscape features such as woodlands, hedgerows and natural grasslands were destroyed to develop larger, intensively managed agricultural fields, or converted to non-native commercial coniferous woodland (Firbank *et al.,* 2007; Mason, 2007). These changes have driven significant biodiversity declines in agricultural and semi-natural habitats (Aviron *et al.,* 2005; Devictor and Jiguet, 2007; Radford and Bennett, 2007; Piqueray *et al.*, 2011). Land-use demands are projected to increase (Lawton *et al.,* 2010) and guidance on how to sustain biodiversity with minimal impact on economic productivity is urgently needed (Haslem and Bennett, 2008; Fahrig *et al.,* 2011; Duflot *et al.*, 2014). With increasing awareness of the value of integrated landscape scale action which can meet the needs of biodiversity and people, understanding how landscape factors influence species communities has consequently become a key topic in conservation biology.

A fundamental concept in macroecology is that landscape heterogeneity influences species richness, abundance and the overall composition of species communities in a landscape (Purtauf *et al*., 2005; Mayfield *et al*., 2010; Duflot *et al*., 2014). Landscape heterogeneity is defined by two

components; landscape composition (the number and proportions of different landcover types) and landscape configuration (the spatial arrangement of different landcover types) (Barbaro *et al*., 2007; Fahrig *et al*., 2011). Variations in both these components influence ecological processes such as environmental filtering and competitive exclusion and facilitation which play key roles in determining the composition and community structure of species assemblages in a landscape (Schweiger *et al*., 2005; Mayfield *et al*., 2010).

Scientists have adopted complementary approaches for determining the importance of landscape heterogeneity for biodiversity. Particular attention has been directed towards the spatial landscape patterning of focal habitat types; considering the extent and configuration of a focal habitat, and quantifying the effects of habitat loss, isolation and fragmentation on taxa of interest (e.g. Fahrig, 2003; Cushman and McGarigal, 2003; Öckinger and Smith, 2006). Other studies have considered the biodiversity benefits provided by 'countryside elements' such as gardens, hedgerows and field margins, but often these have been focussed at the local scale without incorporating all the interactions from the wider landscape (Green *et al.,* 1994; Daily *et al.,* 2001; Mayfield and Daily, 2005; Gardiner, 2007). Recently, it has been recognised that methods encompassing both the spatial landscape pattern and the composition of the surrounding matrix provide a more detailed understanding of how species respond in wooded-agricultural mosaics (e.g. Heikkinen *et al.,* 2004; Barbaro *et al.,* 2007; Hendrickx *et al.,* 2007; Fahrig *et al.,* 2011). This shift away from the traditional habitat-matrix paradigm (Fahrig *et al*., 2011), recognises that the matrix plays an important role in shaping community assemblages by influencing species responses such as dispersal, movement, breeding and feeding behaviour and predation risks (Schweiger *et al.,* 2005; Haslem and Bennett, 2008). Adopting a 'whole landscape mosaic' approach therefore helps ascertain the value of different landscape features for biodiversity, while also considering how the different components interact to affect species distributions and community structure (Bennett *et al.,* 2006; Haslem and Bennett, 2008).

Consistently, semi-natural habitats and 'green-veining' (Schweiger *et al.,* 2005) have been found to be of significant importance for a variety of taxa (Vanbergen *et al.,* 2005; Hendrickx *et al.,* 2007; Billeter *et al.,* 2008). Despite often contributing to a relatively small proportion of the total landcover, semi-natural and linear features can provide functional connectivity, i.e., perceived connectedness by organisms which have different ecological requirements (McGarigal and Ene, 2012), and alternative useable habitat for species in modified landscapes (Hinsley and Bellamy, 2000; Devictor and Jiguet, 2007; Gardiner, 2007). Many semi-natural habitats and linear features are also directly amenable to landscape management modification and thus are of practical

conservation interest (Haslem and Bennett, 2008; Oliver *et al.,* 2010). The ecological functions provided by such features are known to vary greatly depending on their composition, e.g., an orchard compared with a mature hedgerow or larger expanse of scrubland; but also their spatial configuration within the matrix, e.g., hedgerows adjacent to different types of landcover provide varying benefits for different species groups (see Hinsley and Bellamy, 2000; Larcher and Baudry, 2013). There are a few studies that have successfully identified the individual contributions of different semi-natural habitats for their taxa of interest, thus providing a better insight for targeting conservation efforts (see Barbaro *et al*., 2007; Devictor and Jiguet, 2007; Haslem and Bennett, 2008). However, the value of different linear features and the interactive role they play within the matrix has not been explored within a whole landscape mosaic context. This is likely to be because accurate spatial data detailing linear features are not readily available and are time-consuming to create. The importance of features such as hedgerows, ditches, field margins and conservation headlands is formally recognised in European policy through agri-environment schemes (Billeter *et al*., 2008; Davey *et al*., 2010); yet landscape scale interpretation largely relies on evidence extrapolated from local scale studies (e.g. Green *et al*., 1994; Hinsley and Bellamy, 2000; Gardiner, 2007). In a few cases where linear habitats have been incorporated at the wider landscape scale, consideration of their interactions within the matrix and importance for biodiversity has been limited. This is because the different types of linear feature have been aggregated and analysed together as one variable, and often in combination with other types of semi-natural habitat (e.g. Schweiger *et al*., 2005; Hendrickx *et al*., 2007; Billeter *et al*., 2008; Duflot *et al*., 2014).

This paper addresses these knowledge gaps and explores how the composition and configuration of whole landscape mosaics, including a detailed representation of semi-natural and linear features, affects woodland invertebrate communities (Coleoptera; Carabidae) in 36 2 x 2 km study tetrads across southern Britain (Figure 1). Carabids have been extensively studied within woodland and agricultural ecosystems and are considered to be highly sensitive to landscape modification making them useful bio-indicators of landscape change (Taboada *et al.,* 2004; Vanbergen *et al.,* 2005; Barbaro *et al*., 2007; Kang *et al*., 2012). It is generally accepted that carabid life-history traits that have resulted from evolutionary adaptation to environmental conditions over time will govern how individuals respond to landscape heterogeneity; specifically traits related to carabid movement, dispersal, phenology and habitat specialism functions (Lavorel *et al*., 1997; Ribera *et al*., 2001; Lindborg and Eriksson, 2004; Schweiger *et al*., 2005; Gibb *et al*., 2006; Barbaro and van Halder, 2009; Oliver *et al*., 2010; Piqueray *et al*., 2011; Duflot *et al*., 2014). Adopting a trait approach provides greater insight into the mechanisms that

determine how landscape factors govern community composition and ultimately, a more accurate indication of long-term population stability in the face of ongoing landscape change (Brouwers and Newton, 2009a; Oliver *et al.,* 2010).

This study addresses four key questions: i) how do woodland carabid communities respond to the composition (the number and proportions of different landcover types) and configuration (the spatial arrangement of different landcover types) of whole landscape mosaics in wooded-agricultural environments? Specifically, ii) do semi-natural habitats and linear features retain their importance for biodiversity as has been indicated in previous studies, when they are considered as individual components and not grouped and analysed together (e.g. Schweiger *et al*., 2005; Vanbergen *et al.,* 2005; Hendrickx *et al.,* 2007; Billeter *et al.,* 2008)? iii) What is the relative importance of landscape composition and landscape configuration for shaping woodland carabid communities, and can greater understanding be achieved by considering both these components of landscape heterogeneity together? Finally iv) can carabid community response to landscape heterogeneity be determined by five carabid life-history and ecological traits? It is hypothesized that smaller-bodied species will respond to different landscape features in comparison with larger carabids. There is generally a positive correlation between body-size and movement rate/dispersal power, however it also expected that interactions with other traits such as flight capability and habitat specialization will be of importance (Kotze and O'Hara, 2003; Schweiger *et al*., 2005; Barbaro and van Halder, 2009). Specifically, it is proposed that larger, flightless species typical of woodland habitats will be negatively affected by the presence of transport routes (main roads and railways) that pose a barrier to movement (Koivula, 2005), but positively associated with woodland patches and mature hedgerows which, as ecologically stable environments, facilitate movement (Aviron *et al*., 2005; Jopp and Reuter, 2005). Conversely, smaller species and generalists within the woodland community will be associated with ephemeral habitats including road verges and woodland edges.

Methods

Study region

The study was undertaken in central southern England (Figure 1), a region of intensive arable and improved grassland land-use, interspersed with woodland patches varying in size, shape, and isolation. The climate is temperate, with a mean annual temperature of 10.2°C and precipitation averaging 850 mm. Topography is low lying with an average elevation of 140 m above sea level. The principal soils are clay enriched brown earths and calcareous lithomorphic substrate.
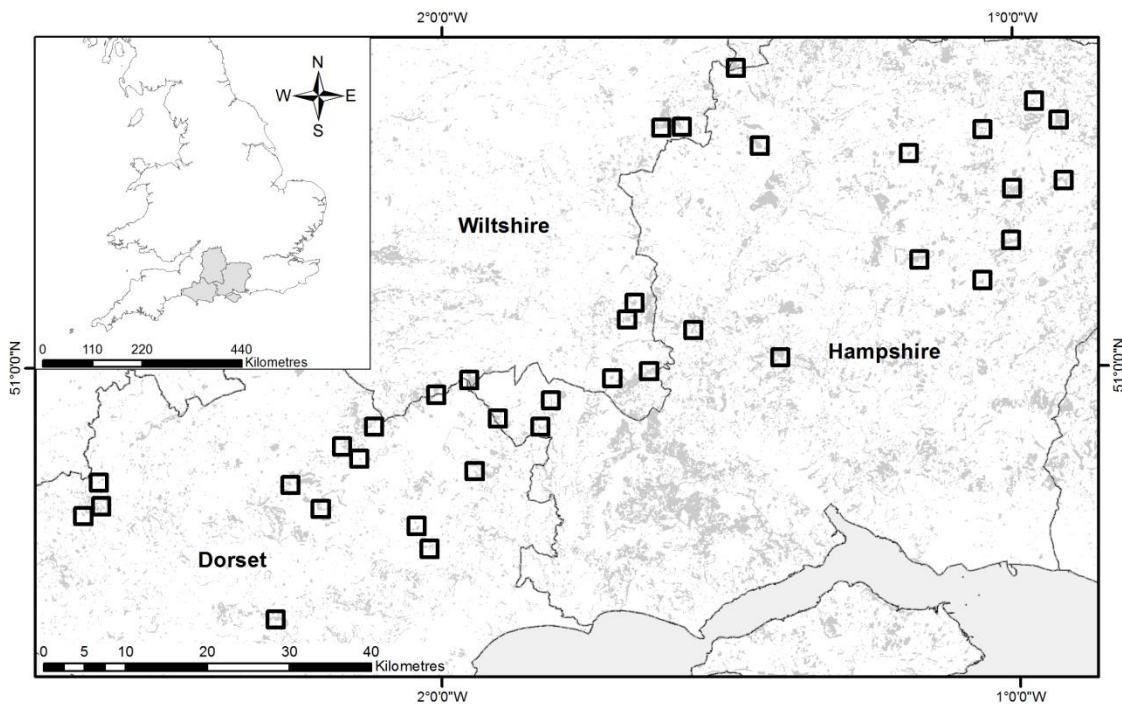
Figure 1: Location of the study region and 36 2 x 2 km study tetrads in central southern Britain. Grey shading indicates native broadleaved and mixed woodland cover derived from CEH Landcover 2000 (Fuller *et al*., 2002).

Study design

Thirty-six sample woodlands representing a range of sizes, shapes and densities (configuration) in the landscape were identified. All were classified as broadleaved although some larger woods also contained areas of conifers mixed with deciduous trees (Forestry Commission, 2011). Each sample woodland was located at the centre of a 2 x 2 km study tetrad from which landscape variables were measured (Table 1). 2 x 2 km was deemed large enough to incorporate variation in landscape heterogeneity, while also small enough to allow replication across the study region and be relatable to farm scale management options (Haslem and Bennett, 2008). Tetrads avoided large urban areas, floodplains, lowland heath and coastal regions. It was also ensured that variations in slope, elevation and aspect (derived from a Digital Terrain Model (Ordnance Survey, 2012)) were statistically comparable between all study tetrads. Finally, tetrads did not overlap to ensure there was no duplication in the landscapes sampled (Radford and Bennett, 2007).

Carabid sampling

Carabid beetles were collected from the interior and edge habitat of each sample woodland using pitfall traps (diameter 60 mm, depth 80 mm). Two traps were set at the woodland centre,

with further pairs also placed at the most Northerly, Southerly, Easterly and Westerly-facing woodland edge adjacent to non-woodland habitat, providing 10 traps in total per tetrad. This provided a systematic sampling method and ensured interior woodland specialists and edge-sensitive species with different life-history traits were recorded. The decision to use 10 traps was based on similar studies conducting carabid sampling at landscape scales (Aviron et al., 2005; Purtauf et al., 2005). In each tetrad, traps were set for a 14 day period between early May and mid-August which coincides with the greatest level of carabid activity (Aviron et al., 2005; Luff, 2007). The sampling fortnight for each tetrad was randomly assigned during the May-August period to avoid clusters of sites in close spatial proximity trapping species during the same time period. All pitfall traps were one third filled with ethylene glycol (50%) and water (50%) and individual pitfalls within each pair were separated by a 15 m gap. This is considered to be above the distance of interaction between pitfall traps when sampling carabid beetles (Digweed et al., 1995; Ward et al., 2001). All individuals collected were pooled for each tetrad and identified to species level using Luff (2007) and a binocular microscope.

Life-history and ecological traits

Five carabid life-history and ecological traits (body size, wing system, breeding season, dominant habitat preference and soil moisture requirements) that related to dispersal, phenology and habitat specialism functions were selected (Schweiger et al., 2005; Barbaro and van Halder, 2009; Duflot et al., 2014) (refer to Table S1 in Appendix 1). Values recorded for each trait were obtained from British carabid field guides (Forsythe, 2000; Luff, 2007) and with reference to other published literature (Ribera et al., 2001; Taboada et al., 2004; Schweiger et al., 2005; Barbaro and van Halder, 2009). Average body-size (mm) was recorded as a continuous value (range 3.1 mm to 25 mm) for each species measuring from the tip of the mandibles to the apex of the elytra. In the Results and Discussion sections, the term 'small-bodied' refers to carabid species measuring less than 4.5 mm in length and 'large-bodied' applies to those that are greater than 10 mm. Carabid wing system was classified into 3 categories (macropterous, dimorphic and apterous); breeding season into 3 categories (spring, summer and autumn); habitat preference into 6 categories (woodland, grassland, agricultural, heath, open and all habitats) and soil moisture requirements into 4 categories (near running or standing water, damp soil, damp-dry soil and dry soil). Habitat preference and soil moisture requirement categories were chosen to reflect the natural variability of traits possessed by carabids, while ensuring that each category was large enough (at least 100 individuals from 6 species) to avoid statistical bias (Duflot et al., 2014).

Landscape heterogeneity spatial analysis

ArcGIS v.10.0 (ESRI, 2011) was used to digitize and quantify the whole landscape matrix in each 2 x 2 km tetrad. Three groups of explanatory variables were recorded: (i) 12 landscape composition variables (number and proportional cover of different landcover types), (ii) 12 landscape configuration variables (metrics representing shape and spatial patterning of landcover variables) and (iii) 2 additional constraining variables (Table 1).

Landscape composition variables

The dominant landcover types within the study region were included plus other habitats considered potentially significant for woodland carabids, either in terms of their anthropogenic effects (urban areas, main roads and railways), or direct relevance as semi-natural or linear habitat in farmed landscapes (Table 1). Where feasible, some habitat types were combined to ensure the heterogeneity of the whole landscape mosaic was represented using the most parsimonious number of variables: broadleaved and mixed woodland possess similar ecological characteristics and are often spatially contiguous within woodland patches, while scrub and rough grassland were interchangeably classified by OS MasterMap data (Ordnance Survey, 2010) (Table 1). Scattered trees included all forms of open canopy tree cover (broadleaved and coniferous species, orchards and parkland trees). Inland water encompassed all forms of running and standing freshwater including small rivers, streams, lakes, ponds, marshes and reed beds. Main transport routes that intersected the landscape matrix included motorways, A roads, B roads and railways. Minor residential roads were not included as these were spatially correlated with the urban land-use polygons. Unpaved tracks and lanes including woodland rides were also excluded as they were unlikely to pose the same effects as tarmacked main roads. All hedgerows were classified into three categories (H1 – H3) based on their structural characteristics and digitised as polylines from the latest Google Maps aerial imagery and field observations:

• H1: Hedgerows which are low and intensively managed; without trees. Up to approximately 1.5 metres high; average width 2.5 metres

• H2: Hedgerows which contain small / juvenile trees or taller shrubs. Greater than 1.5 metres high; average width 7 metres

• H3: Hedgerows which contain mature trees. Structurally similar to a linear strip of broadleaved woodland; average width 15 metres

The contribution of each hedge type as a habitat area was calculated using the average width values obtained from field measurements. Finally a GIS geoprocessing clip was used to ensure seamless landcover with no overlap between the different variable layers for each study tetrad.

Landscape configuration variables

Landscape configuration metrics were created using information on the number, amount and spatial pattern of the landcover variables (Table 1). Discrete woodland patches were at least 15 metres apart or where woodland was dissected by a main transport route as this poses a barrier to movement for many flightless carabids (Koivula, 2005). Functionally, 15 metres is considered to be above the 'interaction distance' and mean rate of daily movement for common woodland carabids (Digweed *et al.*, 1995; Brouwers and Newton, 2009a). Woodland habitat extending beyond a tetrad border was taken into account when calculating the sample woodland patch metrics. Isolated woodlands were defined as having no other woodland or any category of hedgerow within 25 m of their edge, while the length of hedgerows was used as a proxy for structural connectivity within tetrads. All proximity calculations were taken from the centre of the sample woodland using Euclidean distance to the nearest neighbour feature.

Table 1: Summary of the landscape composition, landscape configuration and additional constraining variables calculated for each 2 x 2 km study tetrad.

Composition model	Variables	Mean	Min	Max
Woodland habitat	Area (ha) of broadleaved/mixed woodland	95 ha	29 ha	200 ha
	Area (ha) of coniferous plantation	14 ha	0 ha	135 ha
Semi-natural habitat	Area (ha) of scrub/rough grassland	1 ha	0 ha	4 ha
	Area (ha) of scattered trees	4 ha	0 ha	19 ha
	Area (ha) of inland water	1 ha	0 ha	7 ha
Linear habitat [a]	Area (ha) of low, managed hedge (H1)	2 ha	0.2 ha	5 ha
	Area (ha) of shrubby hedge (H2)	3 ha	0.6 ha	8 ha
	Area (ha) of mature hedge with trees (H3)	8 ha	1 ha	25 ha
Agricultural habitat	Area (ha) of arable land	131 ha	21 ha	220 ha
	Area (ha) of improved grassland	76 ha	5 ha	156 ha
Man-made habitat	Area (ha) of urban land-use	18 ha	0.4 ha	71 ha
	Length (m) of main transport routes	2.2 km	0 km	4.7 km
Configuration model	**Variables**	**Mean**	**Min**	**Max**
Woodland	Number of woodland patches	19	6	45
configuration	Length (m) of woodland edge	8.7 km	19.9 km	35.6 km
	Number of isolated woodland patches	4	0	14

in the matrix [b]	Perimeter: Area ratio of sample wood patch	1.6	0.5	3.3
	Distance (m) to nearest woodland patch	279 m	37 m	624 m
Hedgerow connectivity [a]	Length (km) of all hedgerow types	16 km	5 km	46 km
	Length (km) of low, managed hedge (H1)	7 km	0.8 km	21 km
	Length (km) of shrubby hedge (H2)	4 km	0.7 km	11 km
	Length (km) of mature hedge with trees (H3)	6 km	0.8 km	17 km
Proximity from centre of sample wood patch to matrix features	Distance (m) to nearest transport route	652 m	121 m	> 2 km
	Distance (m) to nearest patch of scrub	431 m	56 m	> 2 km
	Distance (m) to nearest water feature	513 m	48 m	> 2 km

Constraining variables	
Sampling Date	Date of first carabid collection after 7 days (fortnight mid-point)
Spatial Location	British National Grid coordinate (XY) at tetrad mid-point

[a] Full hedgerow category descriptions outlined in 'landscape composition variables' section.

[b] Woodland configuration includes both broadleaved and mixed habitats due to their contiguous nature. Variables representing woodland habitats, semi-natural habitats and urban areas were derived from OS MasterMap (Ordnance Survey, 2010); agricultural habitats were obtained from UK Land Cover Map 2000 (Fuller *et al.*, 2002); linear habitats were digitised from aerial imagery (Terra Metrics, 2009); transport routes were from OS Strategi data (Ordnance Survey, 2012).

Additional constraining variables

Constraining variables can hamper the detection of true landscape effects on carabid communities (Table 1). During analyses, the effects of Sampling Date (given that carabids were sampled in tetrads over different time periods), and spatial autocorrelation were accounted for (Heikkinen *et al.*, 2004; Oliver *et al.*, 2010).

Statistical analyses

Direct gradient analyses, variation partitioning and response trait analyses were performed in Canoco v.5 (ter Braak and Šmilauer, 2012) to ascertain the importance of landscape heterogeneity on woodland carabid communities with respect to the four questions posed. For all analyses, the full matrix of carabids recorded were log (x+1) transformed to reduce the impact of abundant species on the results (Vanbergen *et al.*, 2005; ter Braak and Šmilauer, 2012). Prior to analyses a log (x+1) transformation was also applied to a selection of the landscape composition variables (those measured in ha) to maximise the linearity of their relation and ensure that the ecological importance of all the landcover types was considered (Cleveland, 1993; ter Braak and Šmilauer, 2012).

The effect of i) landscape composition and ii) landscape configuration variables (Table 1) on woodland carabid communities were analysed separately in different models using partial canonical correspondence analyses (pCCA) followed by partial interactive forward selection (pIFS). Partial methods were used to take account of, and remove any explanatory effect of Sampling Date on the carabid community variation. For each model, a constrained ordination (pCCA) containing all the landscape composition, or all the landscape configuration variables (Table 1) was run first to check for significance of the joint effects (ter Braak and Šmilauer, 2012). A global permutation test is considered significant where p-value < 0.05 using 9999 Monte-Carlo permutations. Due to the relatively high number of explanatory variables, a conservative p-value < 0.01 was used in order to firmly reject the null hypothesis that 'species communities are randomly attributed to each study tetrad irrespective of the landscape heterogeneity'. Multicollinearity between explanatory variables can occur in spatially defined landscapes where landcover composition sums to 1 (Heikkinen *et al.*, 2004). In both pCCA models the correlation matrix and variance inflation factors (VIF) were consulted during the global permutation test to check for collinearity (ter Braak and Šmilauer, 2012). Correlation coefficients among the final explanatory variables were all less than 0.6 (*cf*. Aviron *et al.*, 2005; Radford and Bennett, 2007).

Following significant global permutation (pCCA) results for each model, partial interactive forward selection (pIFS) was used to identify a subset of landscape composition and landscape configuration variables which best summarized the carabid community variation. In both models, significant explanatory variables were determined by p-value < 0.05 and confirmed using p-values set by the false discovery rate method adjusted for Type 1 error (ter Braak and Šmilauer, 2012). Bi-plots were used to provide a graphical representation of the results. Landscape arrows point in the direction of the steepest increase in a variables value; a small angle between arrows indicates a positive correlation in landscape values while opposing arrows represent a landscape gradient e.g., from grassland to woodland landcover. Within the Canoco v.5 software, the approximate optima of individual carabid species in respect to values for each of the landscape variables was inferred by projecting the species symbols onto the landscape arrows shown on each bi-plot. This inference of niche optima is underpinned by some assumptions, including that species have unimodal distributions along the landscape variable of interest (see Legendre and Legendre, 1998, p.600), but provides a useful indication of species response in respect to different landscape values (ter Braak and Šmilauer, 2012).

Variation partitioning was performed to ascertain the unique contributions of the landscape composition variables and the landscape configuration variables (identified by pIFS), plus their

shared effect in explaining carabid community variation. Specialized variation partitioning with principal coordinates of neighbour matrices (PCNM) was used to test for spatial autocorrelation. Tetrads in close proximity to each other can possess more similar landscape or biotic conditions than those from a random set of observations (Heikkinen *et al.*, 2004). The PCNM method separates the variation explained by spatial location from that explained by landscape variables by representing space as geographic (X Y) Euclidean distances among cases (Borcard and Legendre, 2002).

Finally, response trait analyses were used test the null hypothesis that 'carabid communities within study tetrads that are significantly associated with landscape variables, cannot be explained by species life-history or ecological traits'. The sequential two stage test confirmed the results of partial interactive forward selection and then summarized any relationships which existed between the range of species traits possessed by the whole carabid community and the landscape variables.

Results

Carabid dynamics

A total of 4677 individuals from 76 species were identified during the sampling period. Woodland and widespread generalist species were the most frequently recorded carabids. The five most commonly occurring species were *Pterostichus madidus* (1809, 39% of the total), *Abax parallelepipedus* (1354, 29% of the total), *Pterostichus melanarius* (303, 6% of the total), *Nebria brevicollis* (162, 3% of the total) and *Calathus rotundicollis* (155, 3% of the total) representing 78% of the total carabid composition. Other species recorded frequently but in lower abundances included those inhabiting grasslands, open habitats, agricultural land and heathland.

Effect of spatial location

Principal coordinates of neighbour matrices (PCNM) found no spatially conditioned variation in the landscape composition (p = 0.260) or landscape configuration variables (p = 0.530) which could explain the community composition of carabid species.

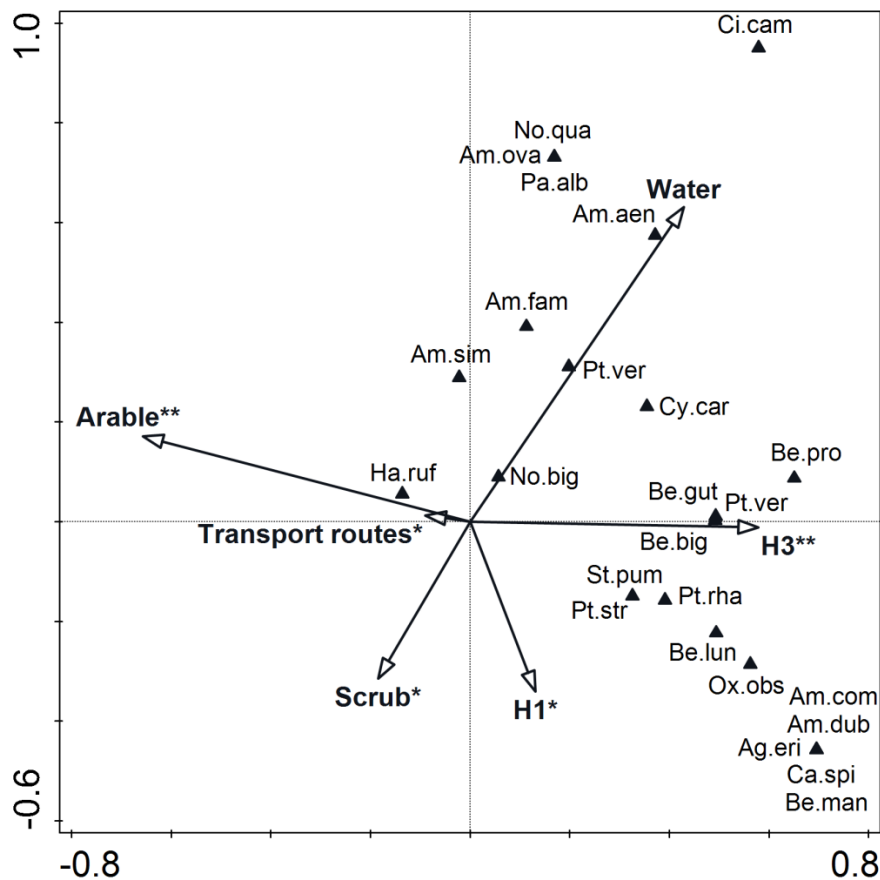**Landscape composition and carabid communities**

Figure 2: Partial canonical correspondence analysis (pCCA) bi-plot illustrating key landscape composition variables explaining differences in carabid assemblages as identified by partial interactive forward selection (pIFS). Significance of variables determined by Monte-Carlo global permutation tests; no symbol $p < 0.1$, *$p < 0.05$, **$p < 0.01$. Bi-plot displays 25 species with the largest fit in the ordination space. Refer to Table S1 in Appendix 1 for full species names and Methods section for hedgerow descriptions.

Partial canonical correspondence analysis (pCCA) testing joint effects of all landscape composition variables explained 44.8% of the total variation in woodland carabid assemblages (F = 1.5, p < 0.001). Partial interactive forward selection identified six explanatory variables explaining 26.7% of the variation (Figure 2). Variation in woodland carabid communities could not be attributed to one dominant landscape composition variable. Rather, assemblages were most strongly influenced by increased amounts of mature hedgerows containing trees (H3) (p = 0.007), low-lying intensively managed hedgerows (H1) (p = 0.019), and decreased amounts of arable land (p = 0.009) in the landscape (Figure 2). Combined, these three variables contributed equally to approximately 16% of the total explained variation. Other explanatory variables included the amount of inland water (p = 0.079), scrub/rough grassland (p = 0.034) and length of transport routes (p = 0.025) (Figure 2). Variations in landscape composition impacted most

strongly on species less frequently encountered in the study such as *Amara similata* (11 individuals from 4 tetrads) and *Bembidion lunulatum* (19 individuals, 3 tetrads). Other more habitually occurring species such as *Harpalus rufipes* (67 individuals, 12 tetrads), *Pterostichus strenuus* (63 individuals, 16 tetrads) and *Notiophilus biguttatus* (48 individuals, 18 tetrads) also exhibited a response, indicating the result was not solely influenced by the presence of infrequently trapped species (Figure 2).

The cluster of *Bembidion*, *Amara*, and *Agonum* species ordinated at the apex of the H3 arrow on the bi-plot (Figure 2) indicates their prevalence in tetrads that contained more than 6 km of mature hedge. The opposing projection of the arable arrow suggests the same species were negatively impacted when arable land exceeded 110 ha or 27% of the matrix cover. The absence of any carabids at this end of the bi-plot implies extensive arable cover was unfavorable for many of the species studied. Species ordinated between the H3 and H1 arrows showed high scores in respect to these two variables indicating an association with tetrads that contained substantial hedgerow networks (Figure 2). *Notiophilus quadripunctatus*, *Amara ovata*, *Paranchus albipes* and *Cicindela campestris* were strongly associated with increased amounts of inland water, however with the exception of *P. albipes* none of these species are hydrophilic (Luff, 2007).

Landscape configuration and carabid communities

All landscape configuration variables explained 38.8% of the total variation in carabid assemblages and the global permutation test was significant (pCCA, F = 1.4, p = 0.002). Interactive forward selection identified six explanatory variables, accounting for 25.9% of the total carabid variation (Figure 3). Mature hedges (H3) (p = 0.008) and low-lying hedges (H1) (p = 0.053) when included as linear connecting elements explained 11% of the total variation and were associated with the same cluster of *Bembidion, Amara* and *Agonum* species observed in the landscape composition model (Figures 2 and 3). These species were also associated with woodland edge habitat (p = 0.029) and an increased number of wood patches (p = 0.010). Frequently trapped woodland species *A. parallelepipedus* and *P. madidus* optimally occurred where woodland was less fragmented. However, of the 25 species on the bi-plot they were the least negatively affected by the presence of isolated wood patches (p = 0.011) and close proximity of transport routes (p = 0.015), despite being brachypterous (Luff, 2007).
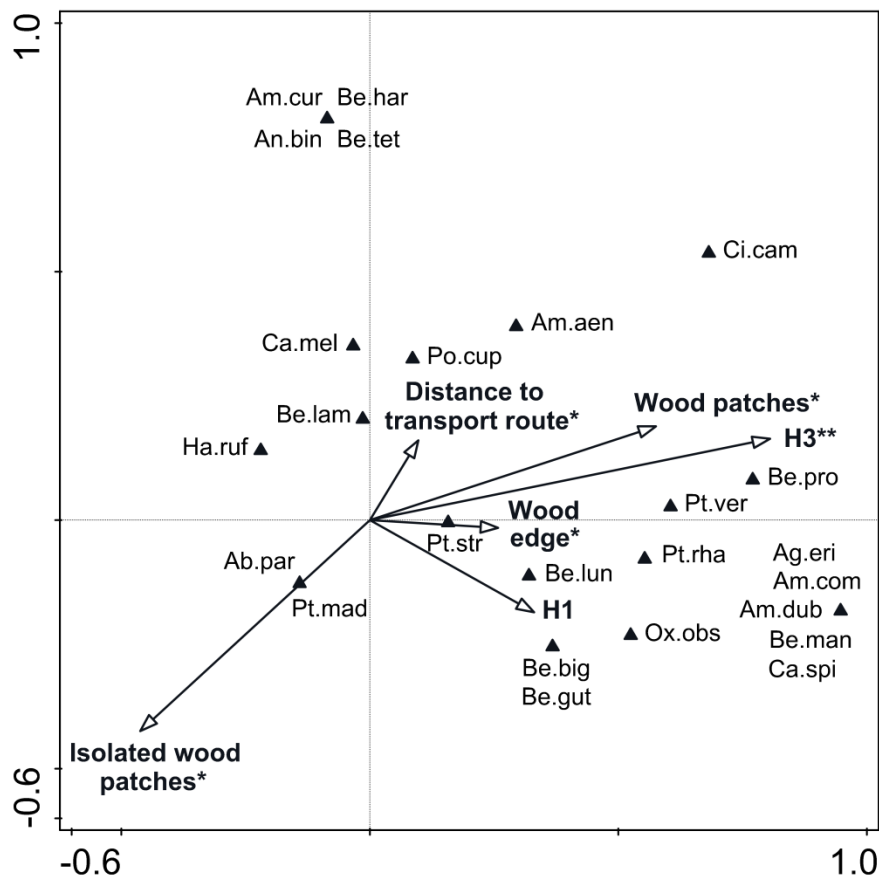
Figure 3: Partial canonical correspondence analysis (pCCA) bi-plot illustrating key landscape configuration variables explaining differences in carabid assemblages as identified by partial interactive forward selection (pIFS). Significance of variables determined by Monte-Carlo global permutation tests; no symbol $p < 0.1$, *$p < 0.05$, **$p < 0.01$. Bi-plot displays 25 species with the largest fit in the ordination space. Refer to Table S1 in Appendix 1 for full species names and Methods section for hedgerow descriptions.

Variation partitioning

Mature hedgerows containing trees (H3) and low, managed hedgerows (H1) were significant variables in both pIFS models. Partitioning their effects separately provided an indication of their relative importance as habitat cover and linear connections (Figure 4).

The total amount of variation captured by both landscape composition and configuration variables was 38.0% when representing hedgerows as habitat cover (Figure 4a). Landscape composition explained a substantially greater proportion of variation (22.9%, $p = 0.005$) than landscape configuration variables which, without hedgerows, only explained 11.3% and were non-significant ($p = 0.138$). Expressing hedgerows as linear elements increased the total variation explained to 39.2%: configuration variables now explained the largest proportion (21.7%) and

significance had increased (p = 0.002). Without hedgerows, landscape composition variables still contributed a significant 13.3% explanatory power (Figure 4b). The joint effect was small for both models indicating a low degree of explanatory overlap between landscape composition and landscape configuration variables (Figure 4).

a) Hedgerows expressed as habitat cover variables   b) Hedgerows expressed as linear structural elements
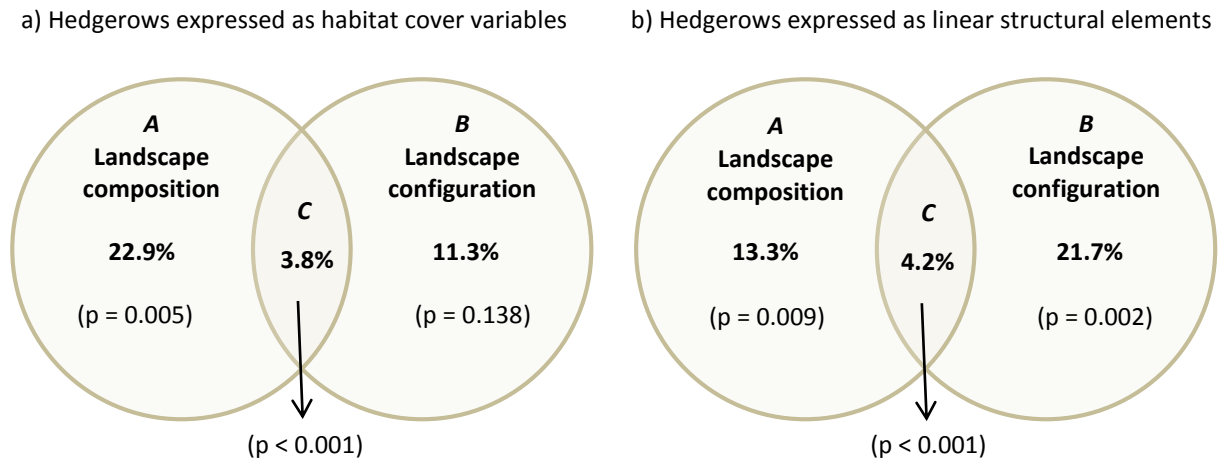

Figure 4: Results of variation partitioning for the total carabid community composition in terms of fractions of variation explained by landscape composition variables and landscape configuration variables. a) Hedgerow types H1 and H3 represented as habitat cover variables (included in group *A* and omitted from group *B*). b) Hedgerow types H1 and H3 represented as linear structural elements (omitted from group *A* and included in group *B*).

In both diagrams *A* and *B* are unique effects of landscape composition and landscape configuration variables respectively, and *C* indicates the joint effect.

Life-history traits and ecological groups

Body size was the only life-history trait to be significant in both models (6.7%, p = 0.009 and 7.4%, p = 0.003) (Table 2). The distribution of small-bodied carabids (< 4.5 mm) within woodlands was positively influenced by an increase in the total length of transport routes and woodland edge habitat while larger carabids (> 10 mm) reacted opposingly to both. Small-bodied species were also associated with large amounts of managed hedgerow cover (H1) in the tetrads. Variation in carabid response to the composition and configuration of the landscape could not be explained by flight capability (Table 2). In the landscape composition model, there was statistical evidence that breeding season was an explanatory trait shaping woodland carabid communities (8.8%, p = 0.026). Spring breeders were more frequently encountered in woodlands where the matrix contained increased hedgerow cover. A similar near-significant result was observed for the landscape configuration model (7.6%, p = 0.066) (Table 2).

Table 2: Results of response trait analyses showing the percentage of carabid community variation (as determined by landscape composition and configuration variables identified from partial interactive forward selection) which can be explained by carabid life-history and ecological traits possessed by the whole community.

Function	Life-history traits	Landscape composition			Landscape configuration		
		Explains %	F	p-value	Explains %	F	p-value
Dispersal	Body size (mm)	6.7%	3.2	0.009	7.4%	3.6	0.003
Dispersal	Wing system	5.8%	1.3	0.224	1.6%	0.7	0.635
Phenology	Breeding season	8.8%	2.1	0.026	7.6%	1.7	0.066
Specialism	Habitat preference	28.8%	2.3	0.019	9.9%	1.4	0.140
Specialism	Moisture requirements	30.8%	2.4	0.006	6.4%	1.5	0.068

Tetrads with greater amounts of mature hedges containing trees (H3) were associated with hydrophilic carabids found near standing or running water such as *Agonum ericeti* and *Bembidion biguttatum* (Figure 2). Species preferring open and agricultural habitats with drier soil conditions existed in woodlands surrounded by large amounts of arable land. Heathland species were identified from tetrads containing numerous woodland patches and increased amounts of inland water. Habitat generalists were suited to patchy woodland configurations where tetrads were most likely to represent a heterogeneous mix of landcover types. Woodland species dominated in damp, woodland habitats and were more positively associated with H3 as opposed to managed hedgerows H1. Overall, the effects of landscape composition on carabids were strongly related to species habitat and soil moisture preferences (28.8%, p = 0.019 and 30.8%, p = 0.006 respectively) (Table 2).

Discussion

Landscape studies conducted at an intermediate spatial scale, *c*. 500 x 500 m to 2 x 2 km (Heikkinen *et al*., 2004) are increasingly popular because they incorporate multiple landscape elements and are directly relevant to local scale management practices (Haslem and Bennett, 2008). In this study, 2 x 2 km provided the opportunity to site each tetrad within a comparable landscape type and avoid features uncharacteristic of lowland agricultural-woodland environments. This is inherently more difficult when working at larger-spatial scales or adopting a grid-based approach (Heikkinen *et al*., 2004; Hendrickx *et al*., 2007).

The forward selection results from the landscape composition and landscape configuration analyses are concordant, with carabid-landscape relationships matching well between the two models. In both cases, the joint effects of explanatory variables explained most of the variation in woodland carabid communities, with relatively low amounts attributable to individual landscape features. This supports the idea that landscapes function as entire ecological units rather than as separate components, and wildlife populations respond not only to the type and amount of habitats, but also the interactions and configuration of the different elements throughout the landscape (Rodewald, 2003; Devictor and Jiguet, 2007; Haslem and Bennett, 2008). The greater amount of total explained variation and small proportion of explanatory overlap between the landscape composition and landscape configuration models during variation partitioning further indicates that a more detailed understanding of how species respond can be achieved when considering both components simultaneously (Barbaro *et al.*, 2007).

The importance of semi-natural habitats and linear features within the matrix

Semi-natural habitats and linear features were both identified as key variables shaping woodland carabid communities. Despite contributing to a minute proportion of the total landcover in study tetrads, the importance of scrubland/rough grassland and water bodies confirms published evidence that heterogeneity provided by such habitats is vital for maintaining diverse populations in agriculturally modified environments (Schweiger *et al.*, 2005; Vanbergen *et al.*, 2005; Hendrickx *et al.*, 2007; Billeter *et al.*, 2008; Oliver *et al.*, 2010). Mature hedgerows containing trees and low, managed hedgerows were also key variables in both models. Hedgerows are an integral part of the landscape in Britain and other European countries (Hinsley and Bellamy, 2000; Billeter *et al.*, 2008; Duflot *et al.*, 2014) but they are rarely incorporated in matrix-wide studies at the level of detail provided here. The ordination and life-history trait results presented here, supplement other local scale studies. Notably, hedges can provide overwintering habitat for many field-based spring breeding carabids such as *Amara* spp. They may also replicate local site conditions similar to those found at woodland edges with similar carabid assemblages existing in both habitats (Thomas *et al.*, 2001; Taboada *et al.*, 2004). Mature hedges also frequently line river margins and can provide ditches or damp conditions which are suitable for the survival and dispersal of hydrophilic carabids in agricultural environments (Luff, 2007). Structurally, mature hedges are also known to facilitate the movement and dispersal of larger-bodied, woodland carabids such as *Pterostichus* spp. (Petit and Burel, 1998; Aviron *et al.*, 2005; Jopp and Reuter, 2005). The presence of *P. madidus* and *A. parallelepipedus* in tetrads containing isolated wood patches is unlikely to be because large species cope better with

isolation than smaller species (see Schweiger *et al.*, 2005), but because they have been physically unable to disperse (Petit and Burel, 1998; Jopp and Reuter, 2005). Essentially, they are remnant populations from a time when the woodland was part of a larger network (Lindborg and Eriksson, 2004). The most significant result in this study is the clear evidence that hedgerows are imperative structural landscape features for carabids. They explained a substantial proportion of the total variation of all the configuration variables and their elimination from the model during variation partitioning rendered the remaining variables of no significance. Therefore, carabid community response to woodland isolation, increased patchiness and edge habitat could only be identified when incorporating the interactions of hedgerows at the 2 x 2 km scale. By extrapolating the patterns presented in both models, the overall trend indicates that hedgerows provide useable habitat within the more inhospitable arable habitat unfavoured by many species and significant functional connectivity through the matrix, particularly where woodland exists in patchy configurations.

Life-history traits and ecological groups

Habitat preference and moisture requirements were the key ecological traits which determined how species responded to landscape composition. Judas *et al.*, (2002) suggested that for some carabid species, microclimatic habitat associations scale-up to distributions within a landscape. As the majority of carabids collected were typical of woodland habitats the negative influence of widespread arable land is not surprising as species will frequently respond most strongly to the extent of preferred or avoided elements in the landscape (Heikkinen *et al.*, 2004; Aviron *et al.*, 2005). Nonetheless, woodland communities did not notably respond to increased woodland cover, again indicating that diversity provided by other matrix habitats may be more important for species than the extent of focal habitat in a landscape (Kallimanis *et al.*, 2008; Oliver *et al.*, 2010; Fahrig *et al.*, 2011). At the species and trait level, some carabids with explicit habitat requirements, such as *P. albipes* which inhabits water margins (Luff, 2007), did display strong relationships with tetrads containing equivalent landcover types. However, this trend was also not clear-cut; *N. quadripunctatus* and *C. campestris* were associated with tetrads containing inland water and numerous woodland patches despite being typical of dry, heathland habitat not present within the tetrads at the time of study. Data obtained from the British Land-Utilisation Survey 1933-1949 (Clark, 2011) confirms that lowland heath was widespread throughout the majority of the tetrads prior to the onset of intensive agriculture. Wet mires, bodies of open water and woodland patches are commonly associated with lowland heath (Gimingham, 1972),

and indicate that species may persist at least for some decades, if elements of the original habitat which can be utilized by individuals are retained (Eyre and Luff, 2004).

It was hypothesized that smaller species would respond differently in comparison to larger carabids and that this could be related to habitat specialization and flight capability. Smaller species (< 4.5 mm) were positively influenced, and many larger species negatively so by the presence of roads, railways and increased managed hedgerow cover within tetrads. Small carabids generally display higher rates of species turnover and are capable of readily dispersing between habitats making them suited to occupying disturbed or changeable environments such as road verges, woodland edges and managed hedgerows. Larger species, which are often flightless, slow-dispersers, are associated with more ecologically stable, long-lived habitats such as woodland or mature hedgerows (Kotze and O'Hara, 2003; Brouwers and Newton, 2009a; Korhonen *et al.*, 2010). Flight capability however provided no explanatory power suggesting that it is not consistently correlated with body size and dispersal power. Rather, carabid response can be better attributed to specific species habitat specialization which in some cases is correlated with wing-presence or absence (Kotze and O'Hara, 2003). For example, transport routes negatively affected large, flightless woodland specialists such as *Carabus* species (Luff, 2007). Conversely, woodland generalists' *A. parallelepipedus* and *P. madidus* were able to utilize the road and railway verge habitat and respond favourably despite being brachypterous and of comparable size (Brouwers and Newton, 2009a).

Conservation and policy implications

Carabid community response at a landscape scale is the result of complex interactions relevant to both the type and configuration of different habitats present but also individual species ecological requirements and life-history traits. Studying a diverse group such as carabids demonstrates that features considered unsuitable for one species may be readily utilized by others even when they are closely related. With demands for land-use intensifying plus additional factors such as climate change, there is a need to design and manage landscapes to increase heterogeneity and buffer populations by focusing on semi-natural and linear habitats (Schweiger *et al.*, 2005; Vanbergen *et al.*, 2005; Hendrickx *et al.*, 2007; Haslem and Bennett, 2008; Oliver *et al.*, 2010; Fahrig *et al.*, 2011). Although this is recognized in European policy, the biodiversity benefits of agri-environment schemes remain questionable (Davey *et al.*, 2010), arguably because the choice of options do not consider the type, configuration and interactions of the wider surroundings (Aviron *et al.*, 2005; Fahrig *et al.*, 2011). It has been demonstrated that defining different types of semi-natural and linear habitats improves understanding of specific

species-landscape interactions than can be achieved by grouping them together under one umbrella term (Haslem and Bennett, 2008). Information of this type can be applied at the individual landowner scale to inform conservation and land management decisions. Hedgerows or comparable linear habitat should be a priority option where woodlands exist as smaller, isolated patches in the surrounding landscape. Semi-natural habitats and linear features should also be actively preserved and matrix heterogeneity encouraged wherever possible (Aviron *et al.*, 2005; Hendrickx *et al.*, 2007; Haslem and Bennett, 2008). Mature hedgerows should be retained along water margins and where semi-natural habitat is threatened or lost to other land-use demands, effort should be focused on retaining or replacing features characteristic of the original environment as this may help encourage species to persist (Bakker and Berendse, 2001; Piessens and Hermy, 2006). In conclusion, agri-environment options should be targeted at the individual landowner level using ecological knowledge obtained about the current and, where appropriate, historic land-use to maximise biodiversity benefits.

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Appendix 1

Table S1: Record of carabid species life-history traits and individual bi-plot identification code

Species name	Bi-plot code	Average body size (mm)	Wing system	Breeding season	Dominant habitat	Soil moisture preference
Asaphidion curtum	Am.cur	4.1	Macropterous	Spring	Open	Near water
Bembidion aeneum	Be.aen	4	Dimorphic	Spring	Woodland	Near water
Bembidion biguttatum	Be.big	4.2	Macropterous	Spring	Grassland	Near water
Bembidion guttula	Be.gut	3.3	Macropterous	Spring	All	Near water
Bembidion lampros	Be.lam	3.5	Dimorphic	Spring	Open	Dry
Bembidion lunulatum	Be.lun	3.7	Macropterous	Spring	Open	Near water
Bembidion mannerheimii	Be.man	3.1	Apterous	Spring	Woodland	Damp
Bembidion obtusum	Be.obt	3.1	Dimorphic	Spring	Open	Dry
Bembidion properans	Be.pro	3.9	Dimorphic	Spring	Open	Dry
Bembidion quadrimaculatum	Be.qua	3.1	Macropterous	Spring	Open	Dry
Bembidion tetracolum	Be.tet	5.5	Apterous	Spring	Agricultural	Near water
Ocys harpaloides	Oc.har	5	Macropterous	Summer	Woodland	Damp
Carabus nemoralis	Ca.nem	23	Apterous	Spring	Open	Damp-Dry
Carabus problematicus	Ca.pro	24	Apterous	Summer	Woodland	Damp

Carabus violaceus	Ca.vio	25	Apterous	Autumn	Woodland	Damp
Acupalpus dubius	Ac.dub	2.7	Macropterous	Spring	Woodland	Near water
Anisodactylus binotatus	An.bin	11.5	Macropterous	Spring	Grassland	Damp
Bradycellus harpalinus	Br.har	4.3	Dimorphic	Autumn	All	Dry
Harpalus affinis	Ha.aff	10.5	Macropterous	Spring	Agricultural	Dry
Harpalus attenuates	Ha.att	8	Macropterous	Spring	Open	Dry
Harpalus latus	Ha.lat	9.5	Macropterous	Summer	Grassland	Dry
Harpalus rubripes	Ha.rub	10.2	Macropterous	Spring	Grassland	Dry
Harpalus rufipes	Ha.ruf	13.5	Macropterous	Summer	Agricultural	Dry
Ophonus rufibarbis	Op.ruf	8	Macropterous	Spring	Open	Damp-Dry
Ophonus schaubergerianus	Op.sch	9	Macropterous	Spring	Grassland	Dry
Leistus fulvibarbis	Le.ful	7.5	Macropterous	Summer	Woodland	Damp
Leistus rufomarginatus	Le.ruf	8.7	Macropterous	Summer	Woodland	Damp
Leistus spinnibarbis	Le.spi	9.3	Macropterous	Summer	Woodland	Damp
Nebria brevicollis	Ne.bre	12.5	Apterous	Autumn	All	Damp-Dry
Nebria salina	Ne.sal	12.5	Apterous	Autumn	Heath	Dry
Notiophilus biguttatus	No.big	5.5	Dimorphic	Summer	All	Damp-Dry
Notiophilus palustris	No.pal	5	Dimorphic	Summer	Woodland	Damp
Notiophilus quadripunctatus	No.qua	5.2	Dimorphic	Spring	Heath	Dry

Notiophilus rufipes	No.ruf	6	Macropterous	Spring	Woodland	Damp
Agonum ericeti	Ag.eri	7.2	Apterous	Summer	Heath	Near water
Agonum fuliginosum	Ag.ful	6.2	Apterous	Spring	Grassland	Damp
Oxypselaphus obscurus	Ox.obs	5.8	Apterous	Spring	Woodland	Damp
Paranchus albipes	Pa.alb	7.6	Macropterous	Spring	All	Near water
Platynus assimilis	Pl.ass	10.7	Macropterous	Spring	Woodland	Near water
Abax parallelepipedus	Ab.par	19.5	Apterous	Summer	Woodland	Damp
Poecilus cupreus	Po.cup	12	Macropterous	Spring	Grassland	Dry
Poecilus versicolor	Po.ver	11.5	Apterous	Summer	Grassland	Damp
Pterostichus madidus	Pt.mad	16	Apterous	Autumn	Woodland	Damp-Dry
Pterostichus melanarius	Pt.mel	15	Apterous	Autumn	Agricultural	Dry
Pterostichus niger	Pt.nig	18.5	Apterous	Autumn	Woodland	Damp
Pterostichus nigrita/ rhaeticus	Pt.rha	10.5	Macropterous	Spring	Grassland	Near water
Pterostichus oblongopunctatus	Pt.obl	10.8	Macropterous	Spring	Woodland	Dry
Pterostichus strenuus	Pt.str	6.6	Dimorphic	Spring	All	Damp-Dry
Pterostichus vernalis	Pt.ver	6.8	Dimorphic	Spring	Grassland	Damp
Stomis pumicatus	St.pum	7.5	Apterous	Spring	Woodland	Damp
Calathus fuscipes	Ca.fus	12	Dimorphic	Autumn	Grassland	Dry
Calathus melanocephalus	Ca.mel	7.2	Apterous	Autumn	Heath	Dry

Calathus rotundicollis	Ca.rot	9.5	Dimorphic	Autumn	Woodland	Damp-Dry
Synuchus vivalis	Sy.viv	7.3	Macropterous	Autumn	Grassland	Damp-Dry
Trechus obtusus	Tr.obt	3.8	Apterous	Autumn	Heath	Dry
Trechus quadristriatus	Tr.qua	3.9	Macropterous	Autumn	Agricultural	Dry
Amara aenea	Am.aen	7.6	Macropterous	Spring	Grassland	Dry
Amara communis	Am.com	7	Macropterous	Spring	Grassland	Damp-Dry
Amara convexior	Am.con	7.3	Macropterous	Spring	Grassland	Dry
Amara curta	Am.cur	6.3	Macropterous	Spring	Grassland	Dry
Amara eurynota	Am.eur	11	Macropterous	Autumn	Agricultural	Dry
Amara familiaris	Am.fam	6.4	Macropterous	Spring	Grassland	Dry
Amara lunicollis	Am.lun	8.2	Macropterous	Spring	Open	Damp-Dry
Amara nitida	Am.nit	7.8	Macropterous	Spring	Open	Dry
Amara plebeja	Am.ple	6.9	Macropterous	Spring	Agricultural	Near water
Amara ovata	Am.ova	8.7	Macropterous	Spring	Open	Dry
Amara similata	Am.sim	8.7	Macropterous	Spring	Open	Near water
Curtonotus aulicus	Cu.aul	12.5	Macropterous	Autumn	Open	Dry
Zabrus tenebrioides	Za.ten	15	Macropterous	Autumn	Agricultural	Dry
Badister bullatus	Ba.bul	6.5	Macropterous	Spring	Heath	Dry
Calodromius spilotus	Ca.spi	4.1	Macropterous	Summer	Woodland	Damp

Cicindela campestris	Ci.cam	14.5	Macropterous	Spring	Heath	Dry
Clivina fossor	Cl.fos	6.4	Dimorphic	Spring	Agricultural	Damp-Dry
Cychrus caraboides	Cy.car	16.5	Apterous	Autumn	Woodland	Damp
Loricera pilicornis	Lo.pil	7	Macropterous	Summer	Grassland	Near water
Panagaeus bipustulatus	Pa.bip	7	Macropterous	Spring	Grassland	Dry