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National-scale metacommunity dynamics of carabid beetles in UK farmland

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Summary

1. Understanding the wide-scale processes controlling communities across multiple sites is a foremost challenge of modern ecology. Here, data from a nation-wide network of field sites are used to describe the metacommunity dynamics of arable carabid beetles. This is done by modelling how communities are structured at a local level, by changes in the environment of the sampled fields and, at a regional level, by fitting spatial parameters describing latitudinal and longitudinal gradients.

2. Local and regional processes demonstrated independent and significant capacities for structuring communities. Within the local environment, crop type was found to be the primary determinant of carabid community composition. The regional component included a strong response to a longitudinal gradient, with significant increases in diversity in an east-to-west direction.

3. Carabid metacommunities seem to be structured by a combination of species sorting dynamics, operating at two different, but equally important, spatial scales. At a local scale, species are sorted along a resource gradient determined by crop type. At a wider spatial scale species appear to be sorted along a longitudinal gradient.

4. Nation-wide trends in communities coincided with known gradients of increased homogeneity of habitat mosaics and agricultural intensification. However, more work is required to understand fully how communities are controlled by the interaction of crops with changes in landscape structure at different spatial scales.

5. We conclude that crop type is a powerful determinant of carabid biodiversity, but that it cannot be considered in isolation from other components of the landscape for optimal conservation policy.

Key-words: arable crops, Farm Scale Evaluations, regional variation, species diversity, species sorting.

Introduction

Appreciation of how processes interact to determine species assemblages at multiple sites is one of the foremost challenges of contemporary ecology (Willis & Whittaker 2002). Progress is likely to become increasingly reliant on understanding how processes work at a level of complexity, transcending simply the effect of the local environment at each site (Kneitel & Chase 2004). For example, how the local environment interacts with the wider landscape and the spatial scale of processes operating at this level remains poorly understood (Bengtsson *et al*. 2002). Data sets which have the capacity to model wider spatial effects, together with local environmental parameters, may prove invaluable for studying how such processes control communities (Amarasekare 2003). The spatial component of species composition can be modelled effectively when sites have sufficient geographical replication (Legendre & Fortin 1989). The local environmental parameters are best modelled as variation which may affect the habitat quality at each site (Ricklefs 1987). Where such analyses are permissible there is the potential to link data with current metacommunity theory for increased understanding of how processes control species assemblages (Cottenie 2005). A metacommunity may be defined as a composite of local communities, linked dynamically by the dispersal and interaction of multiple species (Gilpin & Hanski 1991). A number of models describing

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metacommunity dynamics have been postulated (Leibold *et al*. 2004). Fitting one of these models to reflect the true behaviour of species in nature, however, requires partitioning of the effects of wider spatial and local environment processes and quantification of their independent capacities for structuring communities (Cottenie 2005). For example, significance of the spatial component in the absence of environmental effects at sites may indicate a mass effect (ME) dynamic, reflecting sufficient dispersal between local populations for communities to become spatially structured, independent of local resource gradients (Mouquet & Loreau 2002). However, the presence of significant local environmental effects provides evidence of a species sorting (SS) dynamic, with species assortment along local resource gradients (Chase & Leibold 2003). Understanding such metacommunity dynamics is not only important conceptually, but can also be of practical use for instructing conservation management. For example, if processes are operating at mainly local levels, management of individual habitats can be prioritized ahead of costly restructuring of landscapes.

The Farm Scale Evaluations (FSE) project, which tested whether the introduction of genetically modified herbicide-tolerant (GMHT) crops to the United Kingdom would contribute significantly to declines in farmland wildlife (Firbank *et al*. 2003), provided data well suited for assessing how factors varying at local and wider spatial scales affect communities. This study represents the largest field ecology experiment to date, with *c*. 260 sites covering most arable areas of the United Kingdom (Perry *et al*. 2003). Therefore, spatial analysis is possible, using the x and y coordinates of sites, to describe geographical trends in latitudinal and longitudinal terms. Each site consisted of an arable field for which comprehensive records of agronomic management and abiotic descriptors were collected, together with biotic data (Firbank *et al*. 2003). Therefore, assessment of local environmental effects is possible due to the numerous descriptors available, covering, for example, crop and soil type, arable plants in and around fields, management intensity and numerous invertebrate taxa. This included over 120 carabid beetle species, captured using a standard protocol (Brooks *et al*. 2003). Carabids provide a good subject for metacommunity studies due to their high species richness in farmland (Luff 2002). Their community composition is a good indicator of habitat type (Luff, Eyre & Rushton 1992) and abiotic factors (Eyre *et al*. 2005). Carabids are also good indicators of land management practices and the structure of landscapes (Luff & Woiwod 1995; Schweiger *et al*. 2005). The FSE data therefore provide an unrivalled opportunity to study how carabid metacommunity dynamics operate at a national-scale. Here, we achieve this by using multivariate techniques to: (a) build models from spatial and environmental variables and test their validity for describing communities; (b) use these models to decompose explained variance into spatial and environmental components; (c) identify the effect of specific parameters within these components on species and their diversity; and (d) relate these results to metacommunity dynamics and management of farmed landscapes in the United Kingdom.

Methods

DATA

Analyses here reappraise data from the FSE covering spring crops of beet, maize and oilseed rape and winter oilseed rape. Sites were fields, each representing a single block in a randomized block design, within which conventional and GMHT treatments were applied randomly to half-fields (Perry *et al*. 2003). A total of 251 fields were used in analyses, ranging in size from 3 to 28 hectares. The network of these sites covered most lowland areas of the United Kingdom, with extremities of the Black Isle, Scotland (latitude 57·561), coastal Norfolk (longitude 1·510), coastal Dorset (latitude 50·656) and the Shropshire-Wales border (longitude – 2·894) in the north, east, south and west, respectively. Fields of different crops were, however, interdispersed geographically, except in Scotland where sites were limited to spring and winter oilseed rape (see Supplementary material, Fig. S1). Management of conventional half-fields reflected commercial practice accurately and sites mirrored the national distribution of each crop. All crops were surveyed for three growing seasons, each of which took place in discrete calendar years between 2000 and 2002, for spring crops. For winter oilseed rape each season spanned 2 calendar years, reflecting autumn drilling and summer harvests, leading to a period of sampling between 2000 and 2003. New, previously untested, fields provided the sites for each year. Response variables consisted of carabid species counts from 12 pitfall traps divided equally between positions at 2, 8 and 32 m from the margin of each half-field and run for 2-week periods. Traps were run three times per season within each field, during May, July and August for spring crops and late September to October, late April to May, and late June to July for winter oilseed rape (Brooks *et al*. 2003). There was no bias between sites of any crop or region for when trapping was conducted within these survey periods. Data were analysed in sets covering all crops and individual crops, within which sampling occasions and year totals were separated. However, data sets covering all crops used only the May and July samples for spring crops and late April to May and late June to July samples for winter oilseed rape, to ensure temporal consistency between crops. Replicates in analyses were captures summed across each conventional half-field. Species were ranked according to their abundance and lower ranks were removed from analyses until 95% of the total count was achieved. Carabid nomenclature and systematics follow Pope (1977). Extensive surveys of the biota, management and attributes of fields (Firbank *et al*. 2003) provided explanatory variables for carabid communities. These covered, for example, geographical location of sites, crop type, weeds and margin plants, pesticides, soil type and cultivation and carabid food resources such as seed rain, Collembola and slugs (see Supplementary material, Table S1 for full descriptions).

MODEL BUILDING

Effects of year were small and have been removed as part of the covariation fraction in all analyses. The importance of explanatory variables was investigated by building and refining models. This was required to reduce the number of spatial (68) and environmental (64) variables by approximately three-quarters, to subsets with the greatest explanatory power. Partial canonical correspondence analyses (pCCA) (Ter Braak 1988), using the CANOCO V 4·5 program (Ter Braak & Smilauer 2002), were used for developing multivariate models of the species–environment relationship. Models separated

spatial and environmental components. The spatial component was investigated with principal coordinates of neighbour matrices (PCNM) analysis (Borcard & Legendre 2002), combined with pCCA. This technique provides a powerful solution for describing the spatial structure of a heterogeneous network of sites, useful within the metacommunity context where dynamics reflect processes dependent upon site connectivity and ease of dispersal between them. This is achieved by generating a number of eigenvectors, in our case 68, which describe the distribution of sites and can be used as spatial parameters to build models describing the geographical variance of species. Spatial and environmental models were simplified by subjecting the explanatory variables to a forward selection procedure (Montgomery & Peck 1982) and retaining a subset with the highest eigenvalues (λ).

MODEL VALIDATION

Explained species variation was decomposed into unique spatial and environmental components, using the subsets of explanatory variables derived from model simplification, according to the methods of Borcard, Legendre & Drapeau (1992). This provided R^2 values for unique spatial or environmental effects, after partialling out their covariance. Significance tests of the first and all canonical axes (global) by Monte Carlo permutations (499) on residuals within a pCCA (Ter Braak & Smilauer 2002) established the explanatory power of these reduced models for describing the pure fractions of environmental and spatial variation. Additionally, the environmental variables were subjected to a forward selection procedure and significance tests to establish their hierarchical importance.

Although the PCNM analysis provided the most powerful descriptors of a heterogeneous network of sites, it did not generate the explicit geographical eigenvectors necessary for describing national trends. Therefore, a third-order polynomial of x (longitude) and y (latitude) coordinates was tested within a pCCA, as this method fits a trend surface which describes accurately the spatial responses of most species (Legendre 1990). The degree of connection between neighbouring networks could not be compensated for in these analyses. Therefore, a more balanced design was achieved by removing 67 sites in northern and Scottish regions as their clustering became noticeably higher, leaving 130 sites. The nine spatial variables (monomials) were subjected to forward selection and Monte Carlo permutation tests and significant terms were retained in a simplified model.

Multiple linear regression was used to model responses of individual species and their diversity to geographical variation and the environmental descriptors highlighted as important in multivariate analyses, using the sites assessed for polynomial effects on communities. Diversity was calculated for each site using the log-series α index (Taylor, Kempton & Woiwod 1976). Species richness was computed for each site as S, total number of species present, corrected for the logged value of total number of individuals sampled at that site, N. Additionally, dominance (D) was calculated as $D = N_{max}/N$ at sites, where N_{max} represented number of individuals of the most abundant species (Berger & Parker 1970) and transformed to logits. Abundances of common species were analysed separately after $\log_{10}(\text{count} + 1)$ transformations.

Response variables were regressed against 23 x-variables formed from all main effects and interactions between two qualitative factors representing the four crops and 3 years, respectively, and a set of five quantitative variables representing a quadratic surface (LAT, LONG, LAT^2, LONG^2, LAT.LONG) in centred latitude (LAT) and centred longitude (LONG). In order to simplify the model and the variable selection process, terms were dropped from the full model according to a predetermined order giving preference to the early elimination of unimportant higher order interactions and spatial terms. Significant terms were retained in a simplified model, where they were refitted to obtain their parameter estimates. All regressions were performed using GenStat version 8 (Payne *et al.* 2005).

COMMUNITY CLASSIFICATION

Community composition was described further by a TWINSPAN classification (Hill, Bunce & Shaw 1975), using the program WinTWINS version 2·3 (Hill & Smilauer 2005). This hierarchical, divisive clustering method provides effective validation for canonical ordinations (Legendre & Legendre 1998). This is achieved by successive binary partition along first axes of correspondence analyses, refined by ordinations which reflect the indicator values of important species within these divisions. The results can be represented as a dendrogram showing clusters of similar sites and species which are good indicators of their ecological parity (Kent & Coker 1992).

Results

PARTITIONING REGIONAL AND LOCAL EFFECTS ON COMMUNITIES

A total of 123 carabid species were caught across all sites, 74 of which met the criteria for inclusion in ordinations covering all crop types (see Supplementary material, Table S2). The composition of carabid communities appears to be determined by a combination of regional and local factors, as decomposition of species variance showed roughly equal explanatory power for pure spatial and local environmental components. Overlap of these effects on communities is negligible due to the lack of covariance found between these fractions. The full model was able to explain 55·6% of total species inertia (Fig. 1). Repeats of this analysis for effects across the year, within individual crops, showed similar trends.

SPATIAL STRUCTURING OF COMMUNITIES

Carabid community composition has a strong spatial component, as it varies noticeably between regions. The significance of models describing the unique spatial component of variance using PCNM descriptors provide evidence for this, where P-values were universally $< 0{\cdot}01$ for global permutation tests and $< 0{\cdot}05$ for the first axes of most ordinations (Table 1 and Supplementary material, Table S3). This community variation has clear spatial trends, being orientated along primarily longitudinal, but also latitudinal gradients. This is demonstrated by forward selection within a pCCA of an up to third-order polynomial, which showed significance for x, y and x^2 variables. As monotonic effects of x and y vectors accounted for 77% of the explanatory power of these significant variables, a pCCA was constrained to only these parameters to provide a spatial ordination of approximate west–east (x) and south–north (y) gradients on the first two axes. The first axis represented the strongest gradient in a west–east direction

Table 1. Partial canonical correspondence analyses investigating the unique effect of: (i) spatial and (ii) environmental components in structuring carabid communities across all crops. The sum of all eigenvalues is the residual fraction of total species inertia remaining unexplained after partialling out year and either spatial or environmental effects. The sum of all canonical eigenvalues is the fraction of residual variance explained purely by the component listed

Fraction of explanatory data/date	No. sites	Eigenvalues				Total species inertia	Sum of all eigenvalues	Sum of all canonical eigenvalues	Monte Carlo permutation tests			
									Axis 1		Global	
		Axis 1	Axis 2	Axis 3	Axis 4				*F*-ratio	*P*-value	*F*-ratio	*P*-value
Spatial component												
Year	197	0·058	0·044	0·040	0·038	2·428	1·563	0·531	4·297	0·005	1·427	0·005
Mid April–May	208	0·065	0·058	0·047	0·046	3·171	2·088	0·707	3·621	0·075	1·247	0·005
Mid June–July	221	0·069	0·065	0·053	0·046	3·300	2·153	0·798	3·987	0·005	1·415	0·005
Environmental component												
Year	197	0·114	0·046	0·038	0·034	2·428	1·629	0·597	8·335	0·005	1·493	0·005
Mid April–May	208	0·120	0·073	0·053	0·044	3·171	2·186	0·806	6·514	0·005	1·452	0·005
Mid June–July	221	0·163	0·083	0·052	0·043	3·300	2·176	0·821	9·727	0·005	1·582	0·005

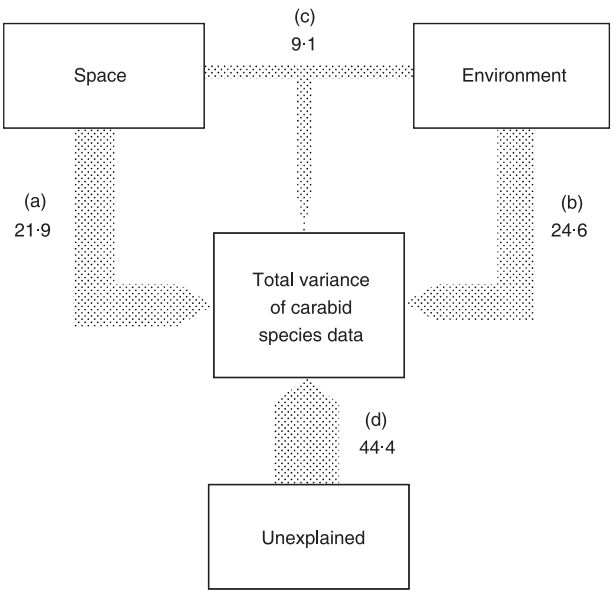

Fig. 1. Partitioning of the explanatory power of spatial and environmental variables describing arable carabid community composition within the United Kingdom. This diagram shows effects after removal of the variance explained by experimental year (1·9%) from a total species inertia of 2·428. The width of each arrow is proportional to the variance accounted for by that component; (a) space only; (b) environment only; (c) covariance between space and environment; and (d) unexplained. The numbers indicate the percentage of species variation accounted for by each of these components. Model schematic follows that of Borcard *et al*. (1992).

(eigenvalue = 0·056, *F*-value = 3·78, *P*-value < 0·01) and the second axis represented a less strong, but still significant, south–north gradient (eigenvalue = 0·047, *F*-value = 3·18, *P*-value < 0·01). There is regional variation in the importance of different taxa within assemblages. For example, *Bembidion* Latreille spp. and seed feeders, such as *Amara* Bonelli spp., showed a west or south-westerly ordination, whereas species more associated with intensive agriculture, such as *Pterostichus madidus* (Fabricius), *Pterostichus melanarius* (Illiger) and *Calathus fuscipes* (Goeze), showed an easterly ordination (see Supplementary material, Fig. S2).

ENVIRONMENTAL STRUCTURING OF COMMUNITIES

Communities are also structured by the local environment, where the type of crop appears most influential. This is demonstrated by the significance of models corrected for spatial effects and reduced to the most important subset of explanatory environmental variables (Table 1 and Supplementary material, Table S3). Crop type was hierarchically most important in forward selection of significant variables (see Supplementary material, Table S4). Winter oilseed rape was differentiated significantly from beet and maize on the first axis of ordinations, with spring oilseed rape uncorrelated with these crops on the second axis (Fig. 2). Significant marginal effects were found for seed rain which was collinear to winter rape, and for cover of bare ground which was collinear to beet and maize (see Supplementary material, Table S4). The importance of taxa within assemblages varies between the communities associated with different crops. For example, *Amara* spp. were ordinated mainly towards winter oilseed rape and *Bembidion* spp. were ordinated towards beet and maize (Fig. 2). Communities within individual crops are most influenced by previous crops in the rotation and soil type (see Supplementary material, Table S4).

EFFECTS ON INDIVIDUAL SPECIES AND DIVERSITY

A mean of 22 carabid species per field (n = 198, SE = 0·3) were caught (see Supplementary material, Table S2). Variation in community composition between regions and crops includes changes in species diversity. This is shown by the significance of longitude and crop within a reduced multiple regression model of log-series α, with independent and strong trends for increased diversity in an east–west direction and in winter oilseed rape compared to beet and maize crops (Fig. 3 and Supplementary material, Table S5). Species richness showed

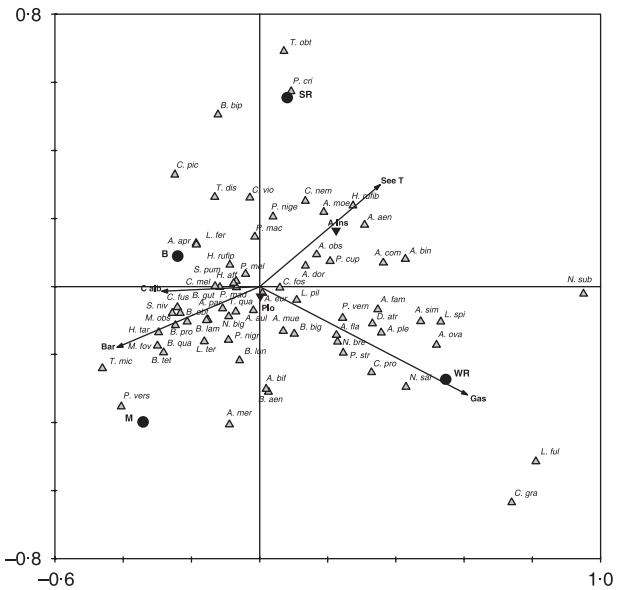

Fig. 2. Partial canonical correspondence ordination of summer carabid assemblage response to the unique effects of the local environment, after correcting for spatial and year effects. Significant environmental variables structuring the community are: solid circles for the centroids of crops; beet (B), maize (M), spring oilseed rape (SR) and winter oilseed rape (WR); inverted triangles for presence/absence of insecticide application (A Ins) or ploughing (Plo); and solid line vectors for the quantitative variables; seed rain counts (See T), gastropod counts (Gas), percentage of bare ground (Bar) and abundance of the weed *Chenopodium album* (C. alb). Upright triangles represent species centroids (see Fig. S2 in Supplementary material for descriptions of species abbreviations).

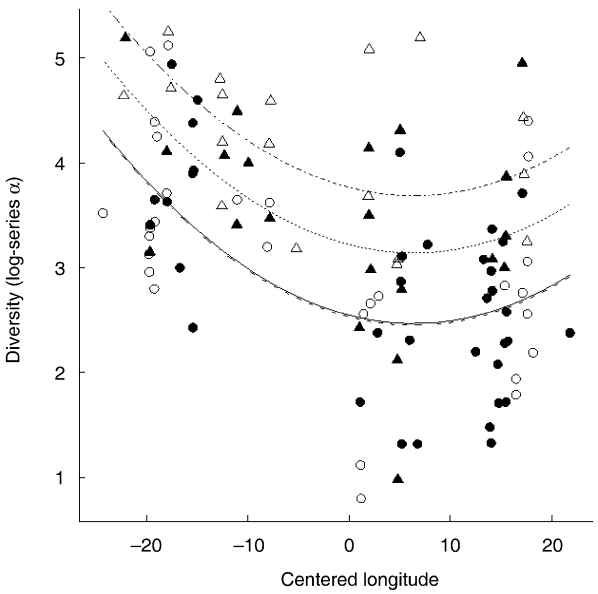

Fig. 3. Plot of site species diversity (log-series α) against United Kingdom longitude. Crop type at sites: beet (solid circles), maize (open circles), spring oilseed rape (solid triangles), winter oilseed rape (open triangles). Fitted model (α = CROP + LONG + LONG^2 + LAT), where LONG = longitude and LAT = latitude and all spatial variables were centred on their means. Fitted values are obtained at LAT = 0, shown by lines as follows; beet (solid), maize (long dash), spring oilseed rape (short dash) and winter oilseed rape (intermittent dots and dashes). LONG and LONG^2 are significant terms (see Table S5 in Supplementary material).

similar trends to log-series α and dominance increased significantly in a west–east direction and was highest in beet and maize crops (see Supplementary material, Table S5). Independent spatial and crop effects were often observed in regression models of common species. For example, *Nebria brevicollis* (Fabricius) and *Bembidion lampros* (Herbst) had significantly greater abundance in a westerly direction, while *Nebria salina* Fairmaire & Laboulbene and *P. madidus* increased in an easterly direction. *Pterostichus cupreus* (Linnaeus) and *Amara* spp. increased in a south-westerly direction and had greater abundance in winter oilseed rape, whereas *Bembidion* spp. were more numerous in beet and maize (see Supplementary material, Table S6a and S6b).

COMMUNITY CLASSIFICATION

The TWINSPAN classification confirmed the results of other analyses, with clustering determined by clear trends in the geographical locations of fields and their crop types. For example, the first division produced clusters representing either spring oilseed rape sites in the west and winter oilseed rape, for which *Amara similata* (Gyllenhal), *Amara ovata* (Fabricius) and *P. cupreus* were good indicator species, or spring oilseed rape in eastern, northern or Scottish regions and beet and maize sites, for which *C. fuscipes*, *Bembidion tetracolum* Say and *P. madidus* acted as indicators (Fig. 4).

Discussion

Our results show that two distinct processes control carabid communities. The significant independent effects found for both the local environment mediated mainly by crop type, and wider spatial processes mediated mainly by an east–west gradient, helps to elucidate the underlying metacommunity dynamics of carabids within this data set. It has been suggested that when these environmental and spatial components are significant, metacommunities are structured by a combination of SS and ME dynamics at local and regional scales, respectively (Cottenie 2005). The local SS dynamic reflects the assortment of species to complementary niches along a resource gradient (Chase & Leibold 2003), provided in this case by the different crops. The ME dynamic describes a sink–source process of immigration, sufficient for carabid communities to have spatial structure by becoming homogenized within discrete geographical areas (Mouquet & Loreau 2002). However, we found a continuum of community variation along geographical axes, implying the presence of an SS dynamic along a resource gradient, but in this case operating at a wide-spatial scale. Regardless of the precise definition of this dynamic, these findings highlight the need to consider processes hierarchically to gain insight into the mechanisms underlying community formation (Schluter & Ricklefs 1993; Whittaker, Willis & Field 2001). Previous studies assessing hierarchical effects on carabid communities have considered wider environmental

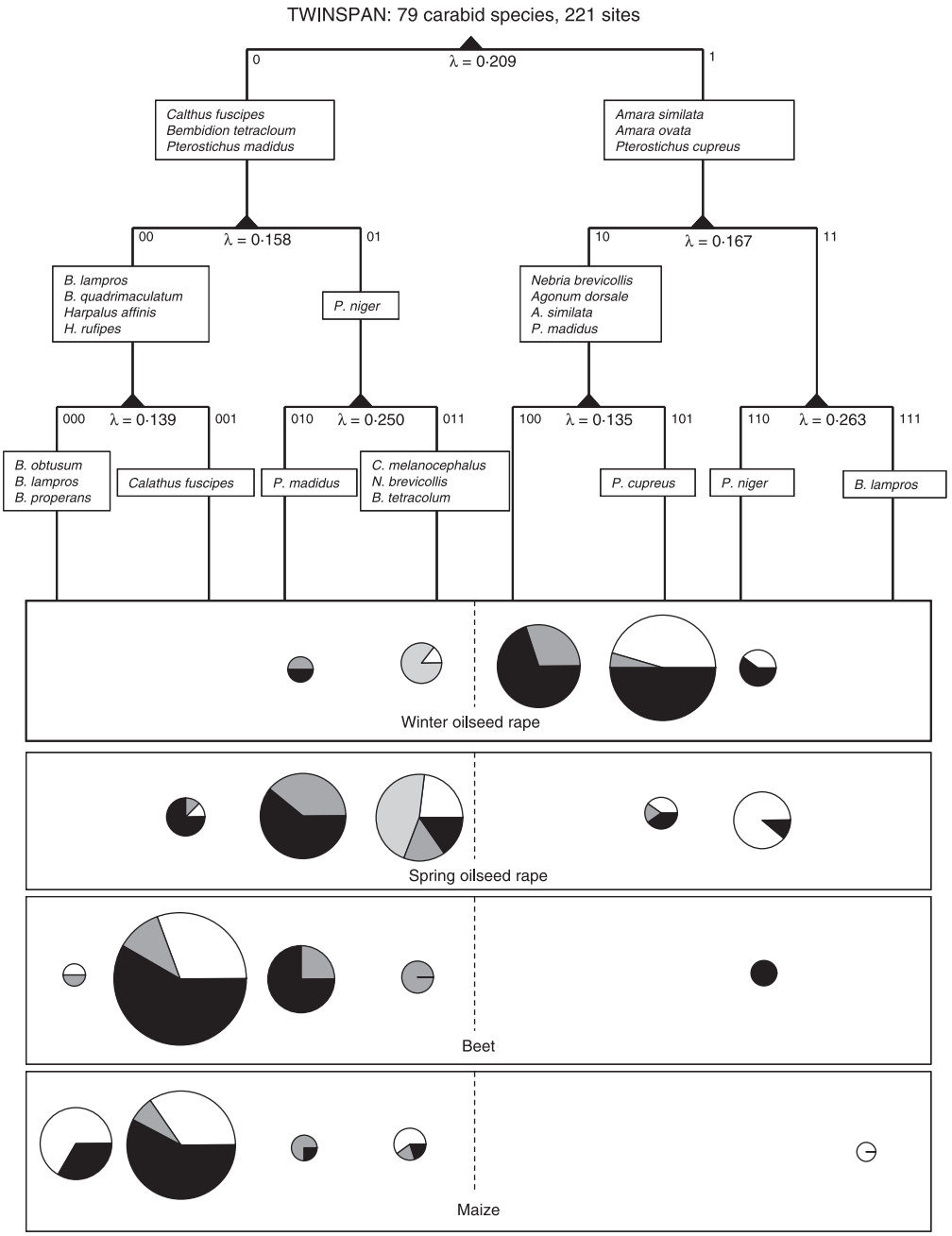

Fig. 4. The first three levels and seven divisions of a TWINSPAN classification of carabid communities. λ = the eigenvalue of each division. Species shown are those acting as indicators for divisions. Vertical lines before pie charts point to each final group. Pie charts provide a schematic of the numbers of sites representing different crops and regions within each final group. Each pie represents how important a crop is within each group; their size is proportional to the number of sites of the indicated crop type within the group. Slices within the pies represent the proportions of these sites belonging to different regions of the United Kingdom: west (white); east (black); north (dark grey) and Scotland (light grey) (see Fig. S1 for map of regions). The community variation between groups increases with horizontal distance across the pies.

factors only within discrete areas of landscape at fairly low replication. These showed mixed results, with over-riding importance attributed to either field use (Jeanneret, Schüpbach & Luka 2003; Weibull, Östman & Granqvist 2003) or landscape factors (Petit & Usher 1998; Aviron *et al*. 2005; Schweiger *et al*. 2005; Vanbergen *et al*. 2005). Our analyses provide high geographical replication of sites, sufficient to model the spatial component of such wider-scale effects and partition it from that of the local environment.

Our results show conclusively that crop type is a powerful local determinant of carabid biodiversity. The partitioning of different resources between crops is likely to be responsible for this effect, as this will produce an environmental gradient promoting local SS dynamics. For example, beet and maize are row crops providing an open architecture for much of the season, favourable to the thermo-physiological requirements of *Bembidion* spp. (Baker & Dunning 1975). Weed seeds, however, are more abundant in winter oilseed rape and may

explain the contrasting ordination of species known to forage on them (Tooley & Brust 2002). These crop effects on carabid communities accord with previous observations, especially for higher diversity in winter-sown compared to spring root crops (Hance & Grégoire-Wibo 1987; Holland & Luff 2000). The descriptive power of crop type is not surprising, as it represents a composite of specific habitat architecture, weeds and agronomic practice.

Crop also appears to have a more important role than GMHT management, as exploratory analyses showed this treatment had a negligible effect on community variation across all half-fields. This is also not surprising, as species responses to conventional and GMHT management were idiosyncratic, leading to similar overall captures and diversity between these treatments (Brooks *et al*. 2003). This contrasts markedly with the crop effects found here and points to a less fundamental role for GMHT management in structuring communities. Rotational effects, soil type and cultivation intensity also seemed to influence local SS dynamics less than crop types. This is because their importance became apparent only in analyses of individual crops, where their effects were not masked by differences in the current crop type. Field size, seedbank diversity and hedge cover, however, had little effect on community variation.

We can be confident in concluding from our study that a strong longitudinal species coenocline exists across lowland United Kingdom, with increased diversity in the west. More work is clearly needed to identify the causes of this community variation. However, we can highlight a number of possible explanations that may prove productive areas for future research. For example, trends for more diverse communities coincide with a progressive decrease in proportion and intensification of arable land but increase in landscape heterogeneity in an east–west direction (Haines-Young *et al*. 2003). There is therefore a likelihood of an interaction between crops and non-cropped habitats in the wider landscape. This is probable, as arable carabid assemblages can be considered as an early successional stage (Tonhasca 1993), consisting of eurytopic species which are drawn from a much wider species pool during annual invasions of disturbed field habitats (Turin 2000). As crop type appears to control the assemblages invading fields, this provides a good demonstration of the importance attached to regional species pools, from which taxa can be filtered to form communities in distinct habitats (Zobel 1997; Noda 2004). The composition and diversity of such species pools is likely to be influenced by landscape structure for a number of reasons. Most carabid species rely on non-cropped habitats, such as hedgerows, to complete their life cycles (Lee & Landis 2002). For example permanent grassland, which is more prevalent in the west, can provide a good over-wintering habitat for larvae (Anderson 1997). Also, carabid diversity in such non-cropped habitats is often greater than in cultivated land (Fournier & Loreau 1999), thereby contributing to the species pool. Diversity of uncultivated vegetation often diminishes with landscape simplification (Gabriel, Thies & Tscharntke 2005), which may explain why phytophagous *Amara* spp. have a westerly ordination, as they have been correlated with species-rich plant assemblages in farmland (Holland, Perry & Winder 1999). Many other carabids are generalist predators (Luff 2002), a functional group which can be influenced disproportionately by landscape variation due to effects being tiered through lower trophic levels (Purtauf, Dauber & Wolters 2005). For example, some carabid prey, such as Collembola and earthworms, can be affected by landscape structure (Dombos 2001; Lagerlöf, Goffre & Vincent 2002). Also, prey provision may be improved by increased frequency of non-cropped habitats, as this change in landscape structure has been associated with better carabid nutritional status and fecundity (Bommarco 1999). Spatial structuring of non-cropped areas may also be important, as corridors (Schweiger *et al*. 2005) and fragmentation (Niemelä 2001) of preferential habitat can have positive and negative effects, respectively, on carabids. Soil moisture and climate are also important for carabid communities (Eyre *et al*. 2005) and may affect regional species pools. This may alter species phenology in different areas, contributing to the importance of the spatial component in our data set.

Arable carabid assemblages are considered to be species rich (Luff 2002). Lack of interspecific competition is thought to promote such diversity (Niemelä 1993), but mechanisms for achieving this are poorly understood, especially as presence of dominance hierarchies precludes the equivalence of species required for neutral model dynamics (Hubbell 2001). The increased understanding of metacommunity dynamics achieved by our study can provide speculative explanations for how this diversity may be maintained and promoted. Our analyses could not describe explicitly the movement patterns of carabids. The metacommunity dynamics that they did describe, however, have noticeable consistency with their dispersal power and with mechanisms known to promote diversity in other taxa. Carabids have a range of dispersal power, with wing dimorphism providing opportunities for migration even when a species has predominantly ground locomotion, while other species are mainly macropterous and fly readily (den Boer 1977). This enables the assortment along wide-scale geographical gradients that we observed which, in turn, increases the spatial scale and level of their environmental stochasticity, a process known to reduce the strength of inter-specific interactions and promote coexistence (May 1973; Bonsall & Hastings 2004). Such traits, however, prevent universality of high dispersion, which leads to homogenization and decreased coexistence in communities (Kneitel & Miller 2003). Differences in dispersal power may also facilitate local SS dynamics and foster coexistence. A trade-off can exist between colonization and competition, where dispersive species move between patches to avoid those which are more competitive but sedentary (Nee & May 1992). This is feasible for carabids, as dominant species such as *P. melanarius* have low dispersal power and often stay within fields (Thomas, Parkinson & Marshall 1998), whereas lower-ranking species, such as *Amara* spp., are more dispersive (den Boer 1977). Also, theoretical modelling of species movement when colonizing patches has shown a strengthening of SS dynamics as patches

become temporally more heterogeneous (Law & Morton 1996). Thus, if the crops available for annual reinvasion by carabids have greater heterogeneity, the local environmental gradient and SS dynamics will be strengthened. This could promote species diversity because it will increase exchange of individuals between assemblages, a process known to stabilize species-rich communities (May 1973; Mouquet & Loreau 2002).

Our study highlights the need for increased understanding of how processes operate at different spatial scales in the wider landscape. This will not be easy, as there is increasing evidence that processes at this level have high dimensionality (Clark & Gelfand 2006). However, the rewards may be great, as although diversity of species within localities may reach an asymptote at high patch diversity (Mouquet & Loreau 2002), linear increases in diversity in response to more continuous environments are less limited (Pacala & Tilman 1994). Therefore, there is considerable potential for enhancing biodiversity through wide-scale manipulation of landscapes, as community diversity has been linked positively to ecosystem function (Loreau *et al*. 2001). This study has highlighted the potential geographical range and magnitude of processes operating at this scale in the United Kingdom landscape. It therefore provides a conceptual framework which may be useful to future studies aiming to advance understanding of ecosystem functioning at this level.

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Supplementary material

The following supplementary material is available for this article.

Fig. S1. Map showing the location of sites in the United Kingdom

Fig. S2. pCCA biplot of species responses to longitudinal and latitudinal gradients in the United Kingdom

Table S1. Full description of environmental variables used to build multivariate models

Table S2. List of all species captured from sites

Table S3. Partial canonical correspondence analyses of the pure spatial and environmental fractions of community variation for individual crops

Table S4. Forward selection of significant environmental variables within pCCAs

Table S5. Reduced multiple regression models relating species diversity parameters to spatial descriptors and crop type

Table S6a. Reduced multiple regression models of individual species responses to spatial descriptors and crop type

Table S6b. Parameters within reduced multiple regression models of individual species responses

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