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Trophic level modulates carabid beetle responses to habitat and landscape structure: a pan-European study

ADAM J. VANBERGEN,[1] BEN A. WOODCOCK,[2] MATTI KOIVULA,[3] JARI NIEMELÄ,[4] D. JOHAN KOTZE,[4] TOM BOLGER,[5] VALERIE GOLDEN,[5] FLORENCE DUBS,[6] GUILLAUME BOULANGER,[6] JOSE SERRANO,[7] JOSÉ LUÍS LENCINA,[7] ARTUR SERRANO,[8] CARLOS AGUIAR,[8] ANNE-CATHERINE GRANDCHAMP,[9] SILVIA STOFER,[9] GYÖZÖ SZÉL,[10] EVA IVITS,[11] PETRA ADLER,[12] JOCHUM MARKUS[12] and ALLAN D. WATT[1] [1]NERC Centre for Ecology and Hydrology, Edinburgh, U.K., [2]NERC Centre for Ecology and Hydrology, Wallingford, U.K., [3]Department of Biological and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland, [4]Department of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland, [5]Department of Zoology, University College Dublin, Dublin, Ireland, [6]Institut de Recherche pour le Développement, UMR 137 BioSol., Centre Ile de France/Universités de Paris VI, Bondy Cedex, France, [7]Department of Zoology, University of Murcia, Murcia, Spain, [8]Departamento de Biologia Animal/Centro de Biologia Ambiental, Universidade de Lisboa, Lisbon, Portugal, [9]Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland, [10]Department of Zoology, Hungarian Natural History Museum, Budapest, Hungary, [11]Joint Research Centre (JRC), European Commission Institute for Environment and Sustainability, Rural, Water and Ecosystems Resources Unit, AGRI-ENV Action, Ispra (VA), Italy and [12]Abt. Fernerkundung und LIS, University of Freiburg, Freiburg, Germany

Abstract. 1. Anthropogenic pressures have produced heterogeneous landscapes expected to influence diversity differently across trophic levels and spatial scales.

2. We tested how activity density and species richness of carabid trophic groups responded to local habitat and landscape structure (forest percentage cover and habitat richness) in 48 landscape parcels (1 km^2) across eight European countries.

3. Local habitat affected activity density, but not species richness, of both trophic groups. Activity densities were greater in rotational cropping compared with other habitats; phytophage densities were also greater in grassland than forest habitats.

4. Controlling for country and habitat effects, we found general trophic group responses to landscape structure. Activity densities of phytophages were positively correlated, and zoophages uncorrelated, with increasing habitat richness. This differential functional group response to landscape structure was consistent across Europe, indicated by a lack of a country × habitat richness interaction. Species richness was unaffected by landscape structure.

5. Phytophage sensitivity to landscape structure may arise from relative dependency on seed from ruderal plants. This trophic adaptation, rare in Carabidae, leads to lower phytophage numbers, increasing vulnerability to demographic and stochastic processes that the greater abundance, species richness, and broader diet of the zoophage group may insure against.

Key words. Herbivore, granivore, ground beetle, predator, trophic rank.

Correspondence: Adam J. Vanbergen, Centre for Ecology and Hydrology, Bush Estate, Penicuik, Edinburgh EH26 0QB, U.K. E-mail: ajv@ceh.ac.uk

Introduction

Species extinction, replacement, and the modification of assemblage trophic structure can arise from fragmentation of primary forest (Didham *et al*., 1998; Davies *et al*., 2000), habitat conversion (Watt *et al*., 1997; Sala *et al*., 2000; Eggleton *et al*., 2002), and land-use intensification (Lawton *et al*., 1998; Benton *et al*., 2003; Jones *et al*., 2003). In Europe, as elsewhere, this suite of anthropogenic pressures has produced heterogeneous landscapes ranging from homogenous and intensively used monocultures to heterogeneous, low intensity land-use mosaics.

Such variation in landscape structure will affect biodiversity as a function of taxon-specific responses to different facets of this environmental heterogeneity (e.g. habitat area or diversity) at different spatial scales (e.g. habitat to landscapes). For instance, many populations persist in complex landscapes containing perennial habitat refuges and are prone to extinction in structurally simple landscapes arising from habitat loss or degradation (Davies & Margules, 1998; Gonzalez *et al*., 1998; Hanski, 1998; Lindenmayer *et al*., 2002; Tews *et al*., 2004; Driscoll & Weir, 2005). Many examples show that a variety of insect taxa such as bees, parasitoids, beetles, and soil invertebrates are affected by environmental heterogeneity from microhabitat to landscape scales (Steffan-Dewenter *et al*., 2002; de la Pena *et al*., 2003; Thies *et al*., 2003; Eggleton *et al*., 2005; Vanbergen *et al*., 2007). Often the diversity of a given taxon is influenced by heterogeneity at more than one spatial scale; hence it is desirable to explicitly account for variation attributable to different habitats when assessing the impact of landscape structure on invertebrate diversity (Chust *et al*., 2003; Jeanneret *et al*., 2003; Kruess, 2003; Schweiger *et al*., 2005; Hendrickx *et al*., 2007).

Moreover, different species within a taxon often respond differently to landscape structure (Steffan-Dewenter *et al*., 2002; Purtauf *et al*., 2005). An explanation is that ecological or functional traits predict the species sensitivity to landscape structure because, like most environmental pressures, it affects ecological assemblages in a non-random manner. One important trend is that the likelihood of extinction or demographic change tends to scale with trophic level, which itself co-varies with other species traits such as increased body size, home range area, and vulnerability to disturbance (Holt *et al*., 1999; Raffaelli, 2004). Predators, therefore, tend to be larger bodied, and more sensitive to habitat fragmentation because they require greater home ranges to meet their energetic needs (Holt *et al*., 1999; Duffy, 2003; Raffaelli, 2004; Borrvall & Ebenman, 2006; McCann, 2007). This means that environmental change is likely to lead to the extinction or reduced abundance of predators before species within lower trophic levels, such as phytophages. It is therefore likely that human alteration of landscape structure will differentially influence insect diversity according to trophic position (Kruess & Tscharntke, 2000; Thies *et al*., 2003). It should be noted, however, that there are examples where trophic level does not affect extinction probability, the responses were idiosyncratic across trophic groups, or lower trophic levels precede losses at higher trophic levels (Henle *et al*., 2004).

What is needed are studies that use ecological or functional trait approaches to better understand the response of insect diversity to spatial heterogeneity at both habitat and landscape scales (Henle *et al*., 2004). The advantage of a functional trait (e.g. trophic group) approach is that it provides a direct link to mechanistic processes (e.g. herbivory or predation), hence changes in functional group diversity in response to environmental heterogeneity are of fundamental and applied interest. Furthermore, a functional approach enables the comparison of insect diversity responses to landscape structure across large geographic areas. Such trans-regional studies are rare (Sousa *et al*., 2006; Hendrickx *et al*., 2007; Billeter *et al*., 2008) because interpretation is complicated where major differences exist in climate, historical origins of landscapes, and local species pools. This use of functional, instead of taxonomic, groups resolves the problem of regional variation in species pools enabling generalisations to be made about invertebrate responses to landscape structure across geographic regions (Davies *et al*., 2003; Schweiger *et al*., 2005).

This paper describes the pan-European diversity responses of carabid (Coleoptera, Carabidae) beetle trophic groups to habitat type and landscape structure. Carabidae are widely distributed and abundant (Thiele, 1977) and are functionally diverse (Ribera *et al*., 2001; Cole *et al*., 2002) containing both predatory and phytophagous genera (Lang *et al*., 1999; Symondson *et al*., 2002; Honek *et al*., 2003). The phytophagous genera generally being dependent on seeds from plants (grasses, umbellifers, and crucifers) associated with grassland and agricultural habitats (Thiele, 1977; Stace, 1997). Carabid trophic groups are known to respond differently to landscape structure and intensification in agricultural landscapes (Purtauf *et al*., 2005; Schweiger *et al*., 2005). These earlier studies showed that both landscape structure and intensification influenced the trophic structure of carabid assemblages (Schweiger *et al*., 2005); and that decreasing cover of perennial habitat affected carabid functional group richness negatively (Purtauf *et al*., 2005). These studies were, however, restricted to a single country (Purtauf *et al*., 2005) or agricultural mosaics across a number of countries (Schweiger *et al*., 2005). The novelty of this paper is that it assesses the general responses of carabid trophic group diversity to the structure of forested and agricultural landscapes ($n = 48$) across eight European countries.

We hypothesised that the response of carabid beetle activity densities, an abundance measure, and species richness to habitat type and landscape structure—percentage cover of forest and habitat richness—differed between trophic groups (zoophagous and phytophagous species). We predicted, firstly, that zoophages would be more sensitive to landscape structure than phytophages as a consequence of trophic position. Secondly, we predicted that phytophage activity densities and species richness would be greater in open habitats where dietary resources (grassland seeds) are readily available.

Methods

Landscape study sites

Forty-eight landscape parcels (Figure S2) were selected comprising six 1 km^2 landscape units (LU) sited in each of eight European countries (Finland, France, Hungary, Ireland, Portugal, Scotland, Spain and Switzerland). These LUs were selected according to predefined guidelines aimed at ensuring there was variation in landscape structure within and between countries. These guidelines related to the predominating habitat within each landscape unit: LU1, old-growth forest (100%); LU2, managed forest (100%); LU3, forest-dominated mosaic (>50% forest, remainder being open, pastoral or agricultural habitats); LU4, mixed-use mosaic (approximately 50% forest and 50% open, pastoral or agricultural habitats); LU5, grassland dominated (>50%); LU6, dominated by arable agriculture (>50%). The actual proportions of forest and open habitats in the LUs (Figure S1) were quantified from satellite images using GIS and were used in the calculation of landscape structure (see below).

Carabid sampling

Carabid beetles at each LU were sampled using a systematic grid of 16 sampling plots spaced 200 m apart (Figure S2), giving a total of 96 sampling plots per country. At each of the 16 sampling plots in the 48 LUs, carabid beetles were collected using four pitfall traps (8 cm in diameter, 10.5 cm in depth) placed 5 m apart in a regular 2 × 2 grid. To kill and preserve beetles the traps were half filled with a 50% solution of either propylene or ethylene glycol with water (the choice of which was consistent within a country). A plastic or stone roof was placed a few centimetres above each trap to prevent flooding and disturbance from mammals. The traps were emptied at 2-week intervals for a period of 10 weeks in 2001 from the following dates: Finland, 15 May; France, 19 June; Hungary, 18 April; Ireland, 6 June; Portugal, 30 April; Scotland, 4 May; Spain, 10 May; and Switzerland, 16 May. These sampling periods reflected regional periods of peak activity. In 2001, it was not possible to sample LU4 and LU5 in Ireland and LU2 in Portugal; therefore, additional sampling in 2002 was used to supplement the data set (sampling was conducted in Ireland from 30 April, and in Portugal from 1 May). The catch in the four pitfall traps per sampling plot was pooled in the field to give 16 data points per LU per country; data obtained for each species was then summed over time to give a single value of activity density for each species at each sampling plot within each LU. Activity density is proportional to the interaction between carabid abundance and activity and is used as a surrogate for true relative abundance (Thiele, 1977).

All carabid beetles were identified to species and lists produced following a standard nomenclature (Löbl & Smetana, 2003). These species were then assigned to a trophic level, either predominantly zoophagous (carnivore and carrion feeding) or predominantly phytophagous (herbivore, granivore) (Thiele, 1977; Lindroth, 1992; Ribera *et al*., 2001; Purtauf *et al*., 2005). This dichotomous classification reflects the fact that most carabid species will eat either plant or animal material, but will actively prefer one or other food source. Where no information on feeding ecology could be found for a particular species, they were assigned to the trophic group of congenerics.

Habitat classification and landscape structure

Habitat type at each sampling point was classified by fieldworkers following CORINE Level 3 nomenclature and subsequently grouped for analyses into broad habitat classes: broadleaf forest (BF), coniferous forest (CF), mixed forest (MF), intensive (IG) and extensive (EG) grassland, permanent (PC), and rotational (RC) cropping.

Landscape structure in each LU was quantified using a combination of remotely sensed land cover data and at the LU scale (1 km^2) subsequently checked by fieldworkers. Two satellite images, a Landsat 7 ETM+ multispectral image and an IRS-1C panchromatic image were used to create a single fused image with a 5-m spatial resolution for each LU. A hierarchic classification system based on the CORINE (Level 3 nomenclature) biotopes database (European Environment Agency) was defined and—together with ground knowledge of the LUs—used to visually interpret, and using GIS (ArcView 3.1) to classify the satellite images. These classified images were used to quantify, with the software FRAGSTATS, at the 1 km^2 spatial scale two metrics of landscape structure for each LU: (i) percentage cover of forest (includes coniferous, broadleaf, mixed, woodland scrub, and Mediterranean sclerophyllous types), and (ii) habitat richness (count of all CORINE Level 3 habitat types excluding aquatic and artificial surfaces). Percentage forest cover was selected because it was the dominant perennial habitat in the surveyed landscapes (Figure S1); perennial woody habitats represent stable refuges for carabids in contemporary landscapes dominated by agriculture (Petit & Usher, 1998). Habitat richness was selected as it represented the accumulation of ecological niches in the landscapes.

Statistical analyses

General linear mixed models (GLMMs) (proc mixed, SAS Institute 1999) were used to account for the nested hierarchical structure (three levels) of the data while testing the effect of habitat type and landscape structure on carabid communities across Europe. The three levels are sampling plot (768 plots = 8 countries × 6 LUs × 16 sampling plots) where carabid beetles were trapped and habitat type determined; landscape unit (48 1-km^2 LUs = 8 countries × 6 LUs); and country of origin ($n = 8$).

Response variables were activity density (count of individuals) and rarefied species richness within the Carabidae and trophic groups (zoophages, phytophages). Species richness was rarefied to account for differences in abundance between experimental plots using the Vegan version 1.15-0 package (Dixon, 2003) implemented in the R-statistical environment version 2.7.1 (R-Development, 2008). While species richness is an intuitive measure of biodiversity, it is problematic because the probability that additional species will be recorded increases with the more individuals sampled, thus comparison of species richness without standardisation can yield misleading patterns (Gotelli & Colwell, 2001). Rarefaction curves allow the comparison of species richness independently of the number of individuals captured by standardising sampling effort (Gotelli & Colwell, 2001). Note that while rarefaction curves are sample based, and sampling effort in the field (16 sampling points per LU) was standardised here, the fundamental unit with which species richness is compared remains the number of individuals sampled (Gotelli & Colwell, 2001). All species richness values were rarefied to 10 individuals. Samples with less than this number of individuals were excluded from these analyses, thus reducing the number of samples considered from an original 768 to 683 for zoophages and 704 for total Carabidae. The very high proportion (0.50) of zero values in the phytophage species richness dataset (cf. zoophages $= 0.02$) meant rarefaction of phytophage species richness at a sampling effort of 10 individuals would eliminate a large proportion (0.74) of the data. Consequently, rarefied species richness were analysed only for total Carabidae, and the zoophagous trophic group.

The categorical variable, LU nested within country, was fitted as a random effect to account for spatial variability among the landscapes across countries. Fixed explanatory variables tested were: year, country of origin, habitat (categorical variables), percentage forest cover per LU, and habitat richness per LU (continuous variables). Two-way interactions between country and each landscape parameter, and between country and habitat tested if the response of the Carabidae and the trophic groups was consistent across countries (non-significant interaction). The effect of the different broad habitat classes on the carabid groups were tested within GLMMs using pairwise differences of least-square means with multiple adjustments (Bonferroni) for the P-values and confidence limits. Denominator degrees of freedom were estimated using the Satterthwaite approximation (Littell *et al.*, 1996). Explanatory fixed effects and two-way interactions were individually fitted by forward stepwise selection. Non-significant terms ($P > 0.05$) were dropped—interactions prior to main effects—before the next stepwise addition. This stepwise procedure halted when the simplest model containing only significant terms was found; F-ratios for each explanatory variable adjusted for other variables (SAS Type 3 tests) are reported. The explanatory variables obtained did not differ from those obtained by backward elimination from the full model. Residual plots were inspected to ensure assumptions of normality and homogeneity of variance were met following $\log_{10}$(activity density) and $\sqrt{}$(standardised species richness) transformation.

Results

Trophic group diversity across countries

A total of 152 863 carabids belonging to 292 species were collected from the eight countries. Mean activity density and distribution across the 48 LUs for all species collected are given in Appendix S1.

In general, trophic structure of the assemblages was consistently skewed with more zoophagous than phytophagous individuals and species in all the countries surveyed (Fig. 1). Of the 292 species collected, 200 (68%) were classified as belonging to the predominantly zoophagous trophic group, and 92 (32%) belonging to the predominantly phytophagous group (Appendix S1). Overall, the zoophagous group was more abundant ($\text{mean} = 2055.2 \pm 333.2$ SEM) than the phytophagous group ($\text{mean} = 928.2 \pm 472.1$ SEM). The country of origin explained a significant amount of the variability in both total carabid and trophic guild species richness and activity density (Fig. 1, Tables 1 and 2). Only in the case of the Hungarian dataset was there no significant difference in the species richness of the two trophic groups (Fig. 1B). Much of this between-country variability in carabid diversity is likely to be due to multiple, unmeasured environmental influences (e.g. climate, soil) in the different landscapes across Europe. The inclusion

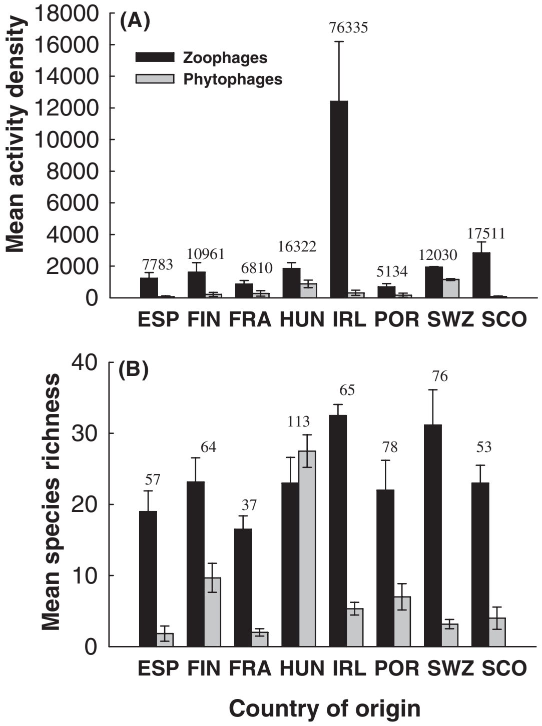

Fig. 1. The influence of country: ESP (Spain), FIN (Finland), FRA (France), HUN (Hungary), IRL (Ireland), POR (Portugal), SWZ (Switzerland), and SCO (Scotland), and trophic guild on mean (± SEM) carabid (A) activity density and (B) species richness. Total carabid activity density (A) and species recorded (B) are given by the numbers above each grouped bar.

Table 1. GLMM results summary for activity density of Carabidae and trophic groups (zoophages, phytophages) in relation to source country, habitat, and composition (percentage forest cover) and heterogeneity (habitat richness) of 1 km^2 landscape units (LUs).

Taxon/trophic group	Fixed effects	Estimate	$F_{(\text{ndf, ddf})}$	P
Carabidae	Sampling year	MPE	$0.78_{(1,46)}$	0.380
	Country of origin	**MPE**	**$6.45_{(7,49)}$**	**<0.001**
Random effect estimate:	**Habitat**	**MPE**	**$8.02_{(6,440)}$**	**<0.001**
LU(country) = 0.085	**Country × habitat**	**MPE**	**$3.40_{(26,319)}$**	**<0.001**
Residual variance = 0.140	Forest	0.000	$0.00_{(1,44)}$	0.984
	Country × forest	MPE	$1.44_{(7,35)}$	0.222
	Habitat richness	0.052	$3.90_{(1,38)}$	0.056
	Country × habitat richness	MPE	$0.55_{(7,31)}$	0.793
Zoophages	Sampling year	MPE	$1.02_{(1,46)}$	0.317
	Country of origin	**MPE**	**$7.52_{(7,48)}$**	**<0.001**
Random effect estimate:	**Habitat**	**MPE**	**$5.06_{(6,431)}$**	**<0.001**
LU(country) = 0.101	**Country × habitat**	**MPE**	**$4.96_{(26,528)}$**	**<0.001**
Residual variance = 0.147	Forest	0.000	$0.03_{(1,43)}$	0.854
	Country × forest	MPE	$1.31_{(7,34)}$	0.276
	Habitat richness	0.055	$3.83_{(1,38)}$	0.058
	Country × habitat richness	MPE	$0.83_{(7,31)}$	0.567
Phytophages	Sampling year	MPE	$0.11_{(1,46)}$	0.738
	Country of origin	**MPE**	**$15.93_{(7,56)}$**	**<0.001**
Random effect estimate:	**Habitat**	**MPE**	**$36.96_{(6,534)}$**	**<0.001**
LU(country) = 0.031	**Country × habitat**	**MPE**	**$3.98_{(26,460)}$**	**<0.001**
Residual variance = 0.145	Forest	−0.002	$2.15_{(1,54)}$	0.148
	Country × forest	MPE	$1.11_{(7,43)}$	0.377
	Habitat richness	**0.088**	**$23.52_{(1,40)}$**	**<0.001**
	Country × habitat richness	MPE	$0.44_{(7,30)}$	0.869

Numerator (ndf) and denominator (ddf) degrees of freedom were estimated using Satterthwaite's approximation. Estimate = parameter slope, MPE = multiple parameter estimates. Bold type indicates parameters retained in final models.

of the fixed effect 'country' and the random term 'LU nested within country' in the GLMMs controlled for this country and landscape-specific variation when testing for an overall effect of habitat and landscape structure on diversity of Carabidae and carabid trophic groups. There was no evidence of an effect of sampling year (45 LUs sampled in 2001, three more in 2002) on either activity density or rarefied species richness (Tables 1 and 2).

Trophic group diversity and habitat type

Activity densities (Table 1) and rarefied species richness (Table 2) of both trophic groups were affected by the interaction between country and habitat. This indicated that there were country-specific associations between habitat type and trophic group diversity. One interpretation is that this interaction reflected differences in species pools across the European sites. The mean activity density and species richness for each habitat × country combination are shown in Tables S1 and S2.

Accounting for these significant habitat × country interactions, the habitat type at the sampling plot had a strong influence on the activity density of Carabidae and both trophic groups (Table 1, Fig. 2), but did not affect rarefied species richness of Carabidae or the zoophage trophic group (Table 2). The influence of habitat on activity density, however, differed between the phytophagous and zoophagous groups with, as predicted, a tendency for phytophage abundance to be greater in open habitat (Fig. 2). Pairwise comparisons of least-square means (with Bonferroni adjustment) showed zoophage densities were significantly greater under rotational cropping (RC) compared with all the other broad habitat classes: broadleaf forest (BF): $t = -6.80$, adj. $P < 0.001$; coniferous forest (CF): $t = -5.83$, adj. $P < 0.001$; mixed forest (MF) $t = -3.53$, adj. $P = 0.009$; extensive grassland (EG) $t = -7.54$, adj. $P < 0.001$; intensive grassland (IG) $t = -5.41$, adj. $P < 0.001$). The association of total Carabidae activity densities with habitat type (data not shown) followed the same pattern as for zoophages (above). Phytophages were similarly more abundant in rotational cropping systems (Fig. 2) compared with all other habitat (BF $t = -10.82$, adj. $P < 0.001$; CF $t = -13.10$, adj. $P < 0.001$; MF $t = -8.25$, adj. $P < 0.001$; IG $t = -5.17$, $P < 0.001$; EG $t = -3.67$, adj. $P = 0.006$; PC $t = -5.16$, adj. $P < 0.001$). In addition, however, there were greater numbers of phytophage individuals in intensive (IG) and extensive (EG) grassland plots compared with the broadleaf (IG $t = -5.15$, adj. $P < 0.001$; EG $t = -5.31$, adj. $P < 0.0001$), coniferous (IG $t = -7.96$, adj. $P < 0.001$; EG $t = -7.79$, adj. $P < 0.001$), and mixed (IG $t = 4.84$, adj. $P < 0.001$; EG $t = 5.18$, adj. $P < 0.001$) forest plots (Fig. 2). Altogether, both phytophage and zoophage activity densities were greater in rotational cropping compared with the other habitats; phytophages were also more abundant in grassland habitats compared with forest habitats.

Table 2. GLMM results summary for rarefied species richness of Carabidae and a trophic group (zoophages) to source country, habitat, and composition (percentage forest cover) and heterogeneity (habitat richness) of 1 km^2 landscape units (LUs).

Taxon/trophic group	Fixed effects	Estimate	$F_{(\text{ndf, ddf})}$	*P*
Carabidae	Sampling year	MPE	$0.26_{(1,46)}$	0.612
	Country of origin	**MPE**	$\mathbf{3.45_{(7,49)}}$	**0.005**
Random effect estimate:	**Habitat**	**MPE**	$\mathbf{0.54_{(6,411)}}$	**0.775**
LU(country) = 0.032	**Country × habitat**	**MPE**	$\mathbf{2.34_{(26,488)}}$	**>0.001**
Residual variance = 0.061	Forest	−0.001	$0.84_{(1,41)}$	0.366
	Country × forest	MPE	$1.75_{(7,34)}$	0.130
	Habitat richness	0.028	$2.86_{(1,35)}$	0.100
	Country × habitat richness	MPE	$0.78_{(7,28)}$	0.612
Zoophages	Sampling year	MPE	$0.28_{(1,46)}$	0.602
	Country of origin	**MPE**	$\mathbf{2.44_{(7,46)}}$	**0.033**
Random effect estimate:	**Habitat**	**MPE**	$\mathbf{0.73_{(6,387)}}$	**0.627**
LU(country) = 0.031	**Country × habitat**	**MPE**	$\mathbf{1.73_{(26,480)}}$	**0.015**
Residual variance = 0.059	Forest	−0.001	$1.03_{(1,42)}$	0.317
	Country × forest	MPE	$1.40_{(7,33)}$	0.237
	Habitat richness	0.014	$0.64_{(1,34)}$	0.428
	Country × habitat richness	MPE	$0.83_{(7,29)}$	0.570

Numerator (ndf) and denominator (ddf) degrees of freedom were estimated using Satterthwaite's approximation. Phytophage models were not run because the large numbers of zeros at the habitat (plot) scale for this trophic group precluded rarefaction. Bold type indicates parameters retained in final models.

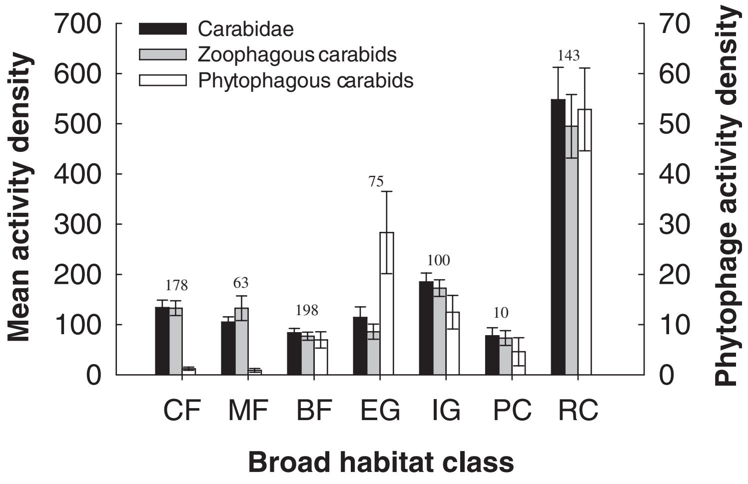

Fig. 2. The effect of source habitat on the mean activity density (± SEM) of Carabidae and carabid trophic groups (zoophages and phytophages); numbers above grouped bars indicate the number of sampling plots in each habitat class where carabids were collected. Habitat classes: coniferous forest (CF); mixed forest (MF); broadleaf forest (BF); extensive grassland (EG); intensive grassland (IG); permanent cropping (PC); and rotational cropping (RC).

Trophic group diversity and landscape structure

Carabid beetle trophic level modulated the response of activity density—but not species richness—to landscape structure (Fig. 3, Tables 1 and 2), contrary to our prediction. However, this activity density response did not scale with increasing trophic level. These data show that activity density of the lower trophic level (phytophages) was the most sensitive to landscape heterogeneity (Fig. 3A; Table 1). Zoophage activity density was independent of variation in landscape structure (Fig. 3B, Table 1). In contrast, phytophage activity density was positively correlated (Fig. 3A, Table 1) with increasing habitat richness, but uncorrelated with increasing forest cover (Table 1). The rarefied species richness of total Carabidae or zoophages was not affected by either landscape parameter (Table 2). As already mentioned above, the large number of zeros in phytophage species richness precluded a comparable analysis of this trophic group.

Consistency in the response of carabid trophic groups to variation in landscape structure among the different countries was explicitly tested by fitting statistical interactions (country of origin × forest or habitat richness) in the GLMMs. The lack of statistical significance for these interactions (Tables 1 and 2) indicates that the response was very consistent and can be considered a generic response of trophic group diversity.

Habitat richness and percentage forest cover, estimated by remote sensing for each LU, were not correlated (Pearson's correlation coefficient $r = -0.074$, $P = 0.618$), and thus the presented GLMMs (Tables 1 and 2) of trophic group diversity were not confounded by such an effect.

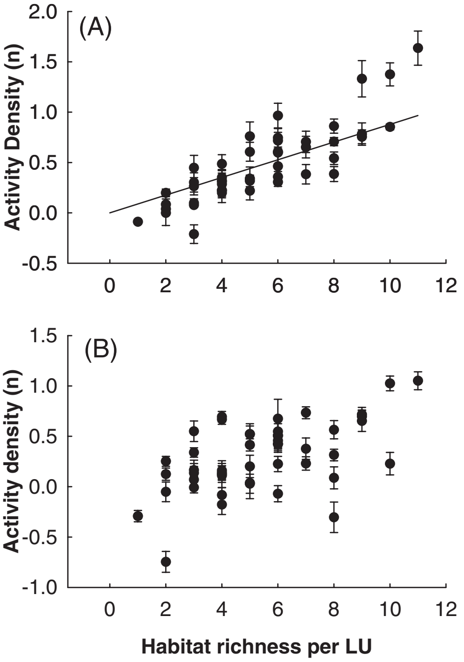

Fig. 3. Partial residual relationships on the linear predictor scale of (A) phytophagous and (B) zoophagous activity densities with the habitat richness per 1 km^2 landscape unit (LU), controlling for the influence of other fixed and random effects in final models. Data points ($n = 47$) are mean partial residuals per LU ± SEM. Fitted lines are included where the slopes are statistically different from zero ($P < 0.05$).

Discussion

The response of carabid beetle activity density and species richness to variation in landscape structure was, as hypothesised, modulated according to trophic group. The prediction that higher trophic levels (i.e. zoophages) would be most sensitive to landscape structure was not supported by these data. Instead phytophage—and not zoophage—activity densities were positively correlated with increasing landscape habitat richness. This relationship between phytophage densities and habitat richness was consistent (indicated by non-significant interaction with country) across an array of different biomes demonstrating the generality of this functional group response to landscape structure across Europe.

This greater sensitivity of phytophage diversity departs from the majority of evidence that sensitivity to landscape structure scales with increasing trophic level (Didham *et al.*, 1998; Gilbert *et al.*, 1998; Holt *et al.*, 1999; Davies *et al.*, 2000), but is consistent with some other studies (Henle *et al.*, 2004 and references therein). At lower trophic levels in a community the abundance of species or populations is—due to thermodynamic constraints—generally greater than that at higher trophic levels, somewhat buffering lower trophic levels against environmental heterogeneity, demographic and stochastic processes (Spencer, 2000; Raffaelli, 2004). This applies particularly when considering a whole community comprising many plant and animal taxa. This paper, however, focused on trophic levels within a single insect taxon, the Carabidae. Here the zoophagous trophic group were more numerous compared with the phytophagous group, and the phytophages were the most sensitive to landscape structure. This may be explained by a degree of dependence of the phytophages on ruderal plant species (see below), and their relatively low abundance increasing sensitivity to any stochastic processes. In contrast, there may be an amount of redundancy in the response of the speciose and abundant zoophage group to landscape structure—whereby in response to an environmental gradient a reduction in the abundance of one species is balanced by increasing the abundance of others (Spencer, 2000; Raffaelli, 2004).

The relatively lower abundance and species richness of the phytophagous trophic group, and greater sensitivity to increasing habitat richness, may be explained by the relatively uncommon—within Carabidae—trophic adaptation of granivory (Thiele, 1977). While the majority of Carabidae are able to consume both animal and plant material (Thiele, 1977), we classified genera according to preference for either animal or plant diet. This classification led to the predominance within the phytophagous group of genera (e.g. *Amara*, *Harpalus*, and *Zabrus*, see Appendix S1) to a large extent specialising on plant seed diet from grasses, umbellifers, and crucifers (Thiele, 1977; Stace, 1997; Tutin *et al.*, 2001; Purtauf *et al.*, 2005). This relative dependency of the phytophages on seeds from ruderal plants (Thiele, 1977), and the frequent association of these plants with disturbed sites (Ribera *et al.*, 2001), means the phytophages can be regarded as habitat specialists typical of grassland and agricultural habitats. Indeed, at a habitat level, as predicted, the abundance of phytophages was generally greater in open agricultural and grassland habitat compared with forest habitats. In contrast, zoophagous carabid species are on the whole, consumers of a wide variety of animal protein both alive and dead (Thiele, 1977; Symondson & Liddell, 1993; McKemey *et al.*, 2003). Consequently, these zoophages may be buffered from variation in environmental heterogeneity at both habitat and landscape scales because of their relatively greater ability to switch to alternative prey in different habitat types.

Our findings support previous research that showed generalised diversity responses of invertebrate trophic groups to landscape structure across geographic regions (Purtauf *et al.*, 2005; Schweiger *et al.*, 2005). Schweiger *et al.* (2005) showed with a pan-European analysis that arthropod assemblages across an array of trophic levels was—in order of importance—structured by landscape structure, management intensity, and local habitat effects (Schweiger *et al.*, 2005). This earlier study also demonstrated that both phytophagous and zoophagous assemblages were associated with high diversity landscapes (Schweiger *et al.*, 2005). Land-use intensity is another driver of assemblage structure (e.g. Schweiger *et al.*, 2005; Sousa *et al.*, 2006) that, lacking intensification data, we did not test.

Another landscape-scale study found that carabid species richness was negatively related to the reduction in percentage cover of perennial habitats (Purtauf *et al.*, 2005) that were hypothesised to provide refuges from agricultural disturbance (Ribera *et al.*, 2001). This paper found no evidence that increasing cover of perennial habitat (forest and woodland) enhanced trophic group diversity. Moreover, Purtauf *et al*. (2005) showed only a weak differentiation between zoophagous and phytophagous responses to perennial habitat cover, while trophic group activity densities were unaffected by perennial habitat cover. These discrepancies between our findings and Purtauf *et al*. (2005) may be partly explained by methodological differences. Firstly, the earlier study did not assume that congenerics shared the same diet; some species were thus excluded from analysis which might influence the results obtained. Secondly, Purtauf *et al*. (2005) included a small and discrete omnivorous group; in this paper, carabid omnivory is assumed, but with a strong preference for plant or animal material. Thirdly, Purtauf *et al*., examined the effect of perennial habitat on carabids within agricultural landscapes. Whereas our study included forested landscapes supporting only forest specialists (e.g. certain *Calathus* and *Cychrus* species) and relatively low carabid species richness—the majority of European carabid beetles are open habitat associates (Thiele, 1977). Finally, this paper's geographic scope was much greater (cf. Purtauf *et al*., 2005: one country, two regions, 36 landscapes, 14 108 individuals, and 84 species) providing greater turnover in assemblage composition among our landscapes.

Ecological processes governing carabid diversity operate at both habitat and landscape scales for phytophages, but only at habitat scales for zoophages. Phytophage sensitivity to landscape structure is a consequence of the relative rarity of this trophic group among Carabidae. While a functional group approach is advocated in this paper, it should be noted that taxonomy remained essential in assigning species to trophic groups and in interpreting patterns in trophic group diversity. This paper demonstrates that diversity is affected by heterogeneity at multiple spatial scales, and that functional traits, such as trophic group, that can predict the magnitude or direction of responses are useful approaches to understanding biodiversity change across regions (Kruess & Tscharntke, 2000; Thies *et al*., 2003; Raffaelli, 2004; Dauber *et al*., 2005; Purtauf *et al*., 2005; Schweiger *et al*., 2005; Hendrickx *et al*., 2007). Moreover in revealing carabid trophic group responses that are consistent across European landscapes, it adds to growing evidence of generic responses of invertebrate diversity to land-use and landscape structure in European landscapes (Sousa *et al*., 2006; Hendrickx *et al*., 2007; Schweiger *et al*., 2007; Billeter *et al*., 2008).

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Supporting Information

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Figure S1. Realised percentage land-cover (CORINE level 3) derived from GIS maps (ArcView 3.1) of a fused satellite image (Landsat 7 ETM+ and IRS-1C for 48 landscape units, six landscape units (1–6) situated per European country: FIN (Finland), FRA (France), HUN (Hungary), IRE (Ireland), POR (Portugal), SCO (Scotland), ESP (Spain) and SWZ (Switzerland).

Figure S2. An example of a GIS map (ArcView 3.1) of a 1 km^2 landscape unit (LU) containing a grid of 16 sampling plots, 200 m apart, at which carabid assemblages were sampled. Dark shaded areas, forest; pale shaded areas, intensive grassland; white dotted areas, rotational crop land; hatched areas, shrub/heathland.

Appendix S1. The 292 ground beetle (Coleoptera; Carabidae) species assigned to a trophic group (PHY, phytophages; ZOO, zoophages), their distribution (number of landscape units where each species was recorded, maximum of 48 landscape units) and mean and standard deviation of activity density (number of individuals per landscape unit).

Table S1. Mean (± SEM) carabid trophic group activity densities between different countries and broad habitat classes. Numbers in parentheses indicate the number of sampling plots per country within a given habitat class; dash means that a particular habitat class was not present in a particular country.

Table S2. Mean (± SEM) species richness (Mao Tao rarefaction) of total Carabidae–including phytophages–and the zoophagous group among different countries and broad habitat classes. Numbers in parentheses indicate the number of sampling plots per country within a given habitat class;

dash means that a particular habitat class was not present in a particular country.

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