

Article (refereed)

Vanbergen, Adam J.; Woodcock, Ben A.; Koivula, M.; Niemela, Jari; Kotze, D. Johan; Bolger, Tom; Golden, Valerie; Dubs, Florence; Boulanger, Guillaume; Serrano, Jose; Lencina, Jose Luis; Serrano, Artur; Aguiar, Carlos; Grandchamp, Anne-Catherine; Stofer, Silvia; Szel, Gyozo; Ivits, Eva; Adler, Petra; Markus, Jochum; Watt, Allan D.. 2010 Trophic level modulates carabid beetle responses to habitat and landscape structure: a pan-European study. *Ecological Entomology*, 35 (2). 226-235. [10.1111/j.1365-2311.2010.01175.x](https://doi.org/10.1111/j.1365-2311.2010.01175.x)

© 2010 The Royal Entomological Society

This version available <http://nora.nerc.ac.uk/9348/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the authors and/or other rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. Some differences between this and the publisher's version remain. You are advised to consult the publisher's version if you wish to cite from this article.

<http://www3.interscience.wiley.com/>

Contact CEH NORA team at
noraceh@ceh.ac.uk

1 Trophic level modulates carabid beetle responses to 2 habitat and landscape structure: a pan-European study

3
4 Adam J. Vanbergen^{1*}, Ben A. Woodcock², Matti Koivula³, Jari Niemelä⁴, D. Johan Kotze⁴,
5 Tom Bolger⁵, Valerie Golden⁵, Florence Dubs⁶, Guillaume Boulanger⁶, Jose Serrano⁷, José
6 Luís Lencina⁷, Artur Serrano⁸, Carlos Aguiar⁸, Anne-Catherine Grandchamp⁹, Silvia Stofer⁹,
7 Győző Szél¹⁰, Eva Ivits¹¹, Petra Adler¹², Jochum Markus¹², and Allan D. Watt¹

8
9 ¹ NERC Centre for Ecology and Hydrology, Bush Estate, Penicuik, Edinburgh EH26 0QB, UK

10 ² NERC Centre for Ecology and Hydrology, Crowmarsh Gifford, Wallingford, OX10 8BB, UK

11 ³Department of Biological and Environmental Sciences, P. O. Box 35, FI-40014 University of Jyväskylä,
12 Finland

13 ⁴Department of Biological and Environmental Sciences, P. O. Box 65, FI-0014 University of Helsinki, Finland

14 ⁵Department of Zoology, University College Dublin, Belfield, Dublin 4, Ireland

15 ⁶ UMR 137 BioSol. Institut de Recherche pour le Développement - Centre Ile de France / Universités de Paris
16 VI, VII et XII, 32, Avenue Henri de Varagnat, F-93143 Bondy Cedex - France

17 ⁷ Department of Zoology, Faculty of Veterinary, University of Murcia. Aptdo 4021, 30071 Murcia, Spain

18 ⁸ Faculdade de Ciências da Universidade de Lisboa, Departamento de Biologia Animal/Centro de Biologia
19 Ambiental, R. Ernesto de Vasconcelos, Ed. C2, 3º Piso, Campo Grande, 1749-016 Lisboa, Portugal

20 ⁹ Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstr. 111, CH-8903 Birmensdorf,
21 Switzerland

22 ¹⁰ Hungarian Natural History Museum, Department of Zoology, H-1088 Budapest, Barossu. 13, Hungary

23 ¹¹ Joint Research Centre (JRC) - European Commission Institute for Environment and Sustainability, Rural,
24 Water and Ecosystems Resources Unit, AGRI-ENV Action, via E. Fermi, 1; TP 460, 21020 Ispra (VA), Italy

25 ¹² Abt. Fernerkundung und LIS, Tennenbacherstr. 4, D-79106 Freiburg, Germany

26
27 *Author for correspondence Adam J. Vanbergen Centre for Ecology and Hydrology, Bush Estate, Penicuik,
28 Edinburgh EH26 0QB, UK email: ajv@ceh.ac.uk

29
30
31 Running title: *Trophic diversity, habitat, & landscape structure*

32

1 **Abstract**

2

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

5 2. We tested how activity density and species richness of carabid trophic groups responded to
6 local habitat and landscape structure (forest percentage cover and habitat richness) in 48
7 landscape parcels (1 km²) across eight European countries.

8 3. Local habitat affected activity density, but not species richness, of both trophic groups.

9 Activity densities were greater in rotational cropping compared with other habitats;
10 phytophage densities were also greater in grassland than forest habitats.

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

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

20

21 **Keywords: ground beetle, predator, trophic rank, herbivore, granivore**

22 **Introduction**

23

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

31

32 Such variation in landscape structure will affect biodiversity as a function of taxon-specific
33 responses to different facets of this environmental heterogeneity (e.g. habitat area or diversity)
34 at different spatial scales (e.g. habitat to landscapes). For instance, many populations persist
35 in complex landscapes containing perennial habitat refuges and are prone to extinction in
36 structurally simple landscapes arising from habitat loss or degradation (Davies & Margules,
37 1998; Gonzalez *et al.*, 1998; Hanski, 1998; Lindenmayer *et al.*, 2002; Tews *et al.*, 2004;
38 Driscoll & Weir, 2005). Many examples show that a variety of insect taxa such as bees,
39 parasitoids, beetles, and soil invertebrates are affected by environmental heterogeneity from
40 microhabitat to landscape scales (Steffan-Dewenter *et al.*, 2002; de la Pena *et al.*, 2003; Thies
41 *et al.*, 2003; Eggleton *et al.*, 2005; Vanbergen *et al.*, 2007). Often the diversity of a given
42 taxon is influenced by heterogeneity at more than one spatial scale; hence it is desirable to
43 explicitly account for variation attributable to different habitats when assessing the impact of
44 landscape structure on invertebrate diversity (Chust *et al.*, 2003; Jeanneret *et al.*, 2003;
45 Kruess, 2003; Schweiger *et al.*, 2005; Hendrickx *et al.*, 2007).

46

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

64

65 What is needed are studies that use ecological or functional trait approaches to better
66 understand the response of insect diversity to spatial heterogeneity at both habitat and
67 landscape scales (Henle *et al.*, 2004). The advantage of a functional trait (e.g. trophic group)
68 approach is that it provides a direct link to mechanistic processes (e.g. herbivory or
69 predation), hence changes in functional group diversity in response to environmental
70 heterogeneity are of fundamental and applied interest. Furthermore, a functional approach
71 enables the comparison of insect diversity responses to landscape structure across large

72 geographic areas. Such trans-regional studies are rare (Sousa *et al.*, 2006; Hendrickx *et al.*,
73 2007; Billeter *et al.*, 2008) because interpretation is complicated where major differences
74 exist in climate, historical origins of landscapes, and local species pools. This use of
75 functional, instead of taxonomic, groups resolves the problem of regional variation in species
76 pools enabling generalisations to be made about invertebrate responses to landscape structure
77 across geographic regions (Davies *et al.*, 2003; Schweiger *et al.*, 2005).

78

79 This paper describes the pan-European diversity responses of carabid (Coleoptera, Carabidae)
80 beetle trophic groups to habitat type and landscape structure. Carabidae are widely-distributed
81 and abundant (Thiele, 1977) and are functionally diverse (Ribera *et al.*, 2001; Cole *et al.*,
82 2002) containing both predatory and phytophagous genera (Lang *et al.*, 1999; Symondson *et*
83 *al.*, 2002; Honek *et al.*, 2003). The phytophagous genera generally being dependent on seeds
84 from plants (grasses, umbellifers, and crucifers) associated with grassland and agricultural
85 habitats (Thiele, 1977; Stace, 1997). Carabid trophic groups are known to respond differently
86 to landscape structure and intensification in agricultural landscapes (Purtauf *et al.*, 2005;
87 Schweiger *et al.*, 2005). These earlier studies showed that both landscape structure and
88 intensification influenced the trophic structure of carabid assemblages (Schweiger *et al.*,
89 2005); and that decreasing cover of perennial habitat affected carabid functional group
90 richness negatively (Purtauf *et al.*, 2005). These studies were, however, restricted to a single
91 country (Purtauf *et al.*, 2005) or agricultural mosaics across a number of countries (Schweiger
92 *et al.*, 2005). The novelty of this paper is that it assesses the general responses of carabid
93 trophic group diversity to structure of forested and agricultural landscapes (n = 48) across
94 eight European countries.

95

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

103

104 **Methods**

105

106 Landscape study sites

107

108 Forty-eight landscape parcels (Appendix S1: Fig. S2) were selected comprising six 1 km²
109 landscape units (LU) sited in each of eight European countries (Finland, France, Hungary,
110 Ireland, Portugal, Scotland, Spain and Switzerland). These LUs were selected according to
111 pre-defined guidelines aimed at ensuring there was variation in landscape structure within and
112 between countries. These guidelines related to the predominating habitat within each
113 landscape unit: LU1 - old-growth forest (100%), LU2 - managed forest (100%), LU3 - forest-
114 dominated mosaic (> 50% forest, remainder being open, pastoral or agricultural habitats),
115 LU4 - mixed-use mosaic (approximately 50% forest and 50% open, pastoral or agricultural
116 habitats); LU5 - grassland dominated (>50%), LU6 - dominated by arable agriculture (>50%).
117 The actual proportions of forest and open habitats in the LUs (Appendix S1: Fig. S1) were
118 quantified from satellite images using GIS and were used in the calculation of landscape
119 structure (see below).

120

121 Carabid sampling

122

123 Carabid beetles at each LU were sampled using a systematic grid of 16 sampling plots spaced
124 200m apart (Appendix S1: Fig. S2), giving a total of 96 sampling plots per country. At each
125 of the 16 sampling plots in the 48 LUs, carabid beetles were collected using four pitfall traps
126 (8 cm in diameter, 10.5 cm in depth) placed 5 m apart in a regular 2×2 grid. To kill and
127 preserve beetles the traps were half filled with a 50% solution of either propylene or ethylene
128 glycol with water (the choice of which was consistent within a country). A plastic or stone
129 roof was placed a few centimetres above each trap to prevent flooding and disturbance from
130 mammals. The traps were emptied at 2 week intervals for a period of 10 weeks in 2001 from
131 the following dates: Finland May 15; France June 19; Hungary April 18; Ireland June 6;
132 Portugal April 30; Scotland May 4; Spain May 10; and Switzerland May 16. These sampling
133 periods reflected regional periods of peak activity. In 2001, it was not possible to sample LU4
134 and LU5 in Ireland and LU2 in Portugal; therefore, additional sampling in 2002 was used to
135 supplement the data set (sampling was conducted in Ireland from April 30, and in Portugal
136 from May 1). The catch in the four pitfall traps per sampling plot was pooled in the field to
137 give 16 data points per LU per country; data obtained for each species was then summed over
138 time to give a single value of activity-density for each species at each sampling plot within
139 each LU. Activity density is proportional to the interaction between carabid abundance and
140 activity and is used as a surrogate for true relative abundance (Thiele, 1977).

141

142 All carabid beetles were identified to species and lists produced following a standard
143 nomenclature (Löbl & Smetana, 2003). These species were then assigned to a trophic level,
144 either predominantly zoophagous (carnivore and carrion feeding) or predominantly
145 phytophagous (herbivore, granivore) (Thiele, 1977; Lindroth, 1992; Ribera et al., 2001;

146 Purtauf et al., 2005). This dichotomous classification reflects the fact that most carabid
147 species will eat either plant or animal material, but will actively prefer one or other food
148 source. Where no information on feeding ecology could be found for a particular species they
149 were assigned to the trophic group of con-generics.

150

151 Habitat classification and landscape structure

152

153 Habitat type at each sampling point was classified by fieldworkers following CORINE Level
154 3 nomenclature and subsequently grouped for analyses into broad habitat classes: broadleaf
155 forest (BF), coniferous forest (CF), mixed forest (MF), intensive (IG) and extensive (EG)
156 grassland, permanent (PC) and rotational (RC) cropping.

157

158 Landscape structure in each LU was quantified using a combination of remotely sensed land
159 cover data and at the LU scale (1 km²) subsequently checked by fieldworkers. Two satellite
160 images, a Landsat 7 ETM+ multispectral image and an IRS-1C panchromatic image were
161 used to create a single fused image with a 5-m spatial resolution for each LU. A hierarchic
162 classification system based on the CORINE (Level 3 nomenclature) biotopes database
163 (European Environment Agency) was defined and - together with ground knowledge of the
164 LUs - used to visually interpret and using GIS (ArcView 3.1) classify the satellite images.

165 These classified images were used to quantify, with the software FRAGSTATS, at the 1km²
166 spatial scale two metrics of landscape structure for each LU: 1) percentage cover of forest
167 (includes coniferous, broadleaf, mixed, woodland scrub, and Mediterranean sclerophyllous
168 types) 2) habitat richness (count of all CORINE Level 3 habitat types excluding aquatic and
169 artificial surfaces). Percentage forest cover was selected because it was the dominant
170 perennial habitat in the surveyed landscapes (Appendix S1: Fig. S1); perennial woody

171 habitats represent stable refuges for carabids in contemporary landscapes dominated by
172 agriculture (Petit & Usher, 1998). Habitat richness was selected as it represented the
173 accumulation of ecological niches in the landscapes.

174

175 Statistical Analyses

176

177 General linear mixed models (GLMMs) (proc mixed, SAS Institute 1999) were used to
178 account for the nested hierarchical structure (3 levels) of the data while testing the effect of
179 habitat type and landscape structure on carabid communities across Europe. The three levels
180 are sampling plot (768 plots = 8 countries × 6 LUs × 16 sampling plots) where carabid beetles
181 were trapped and habitat type determined; landscape unit (48 1km² LUs = 8 countries × 6
182 LUs); and country of origin (n = 8).

183

184 Response variables were activity density (count of individuals) and rarefied species richness
185 within the Carabidae and trophic groups (zoophages, phytophages). Species richness was
186 rarefied to account for differences in abundance between experimental plots using the Vegan
187 version 1.15-0 package (Dixon, 2003) implemented in the R-statistical environment version
188 2.7.1 (R-Development, 2008). While species richness is an intuitive measure of biodiversity it
189 is problematic because the probability that additional species will be recorded increases with
190 the more individuals sampled, thus comparison of species richness without standardisation
191 can yield misleading patterns (Gotelli & Colwell, 2001). Rarefaction curves allow the
192 comparison of species richness independently of number of individuals captured by
193 standardising sampling effort (Gotelli & Colwell, 2001). Note that while rarefaction curves
194 are sample based, and sampling effort in the field (16 sampling points per LU) was
195 standardised here, the fundamental unit with which species richness is compared remains the

196 number of individuals sampled (Colwell, 2005). All species richness values were rarefied to
197 10 individuals. Samples with less than this number of individuals were excluded from these
198 analyses, thus reducing the number of samples considered from an original 768 to 683 for
199 zoophages and 704 for total Carabidae. The very high proportion (0.50) of zero values in the
200 phytophage species richness dataset (c.f. zoophages = 0.02) meant rarefaction of phytophage
201 species richness at a sampling effort of 10 individuals would eliminate a large proportion
202 (0.74) of the data. Consequently, rarefied species richness were analysed only for total
203 Carabidae, and the zoophagous trophic group.

204

205 The categorical variable: LU nested within country, was fitted as a random effect to account
206 for spatial variability among the landscapes across countries. Fixed explanatory variables
207 tested were: year, country of origin, habitat (categorical variables), percentage forest cover per
208 LU, and habitat richness per LU (continuous variables). Two-way interactions between
209 country and each landscape parameter and between country and habitat tested if the response
210 of the Carabidae and the trophic groups was consistent across countries (non-significant
211 interaction). The effect of the different broad habitat classes on the carabid groups were tested
212 within GLMMs using pair-wise differences of least-square means with multiple adjustments
213 (Bonferroni) for the p -values and confidence limits. Denominator degrees of freedom were
214 estimated using the Satterthwaite approximation (Littell *et al.*, 1996). Explanatory fixed
215 effects and two-way interactions were individually fitted by forward step-wise selection. Non-
216 significant terms ($P > 0.05$) were dropped - interactions prior to main effects - before the next
217 step-wise addition. This step-wise procedure halted when the simplest model containing only
218 significant terms was found; F -ratios for each explanatory variable adjusted for other
219 variables (SAS Type 3 tests) are reported. The explanatory variables obtained did not differ
220 from those obtained by backward elimination from the full model. Residual plots were

221 inspected to ensure assumptions of normality and homogeneity of variance were met
222 following \log_{10} (activity density) and square-root (standardised species richness)
223 transformation.

224

225 **Results**

226

227 *Trophic group diversity across countries*

228

229 A total of 152, 863 carabids belonging to 292 species were collected from the eight countries.
230 Mean activity density and distribution across the 48 LUs for all species collected are given in
231 Appendix S2.

232

233 In general, trophic structure of the assemblages was consistently skewed with more
234 zoophagous than phytophagous individuals and species in all the countries surveyed (Fig. 1).
235 Of the 292 species collected 200 (68%) were classified as belonging to the predominantly
236 zoophagous trophic group, and 92 (32%) belonging to the predominantly phytophagous group
237 (Appendix S2). Overall, the zoophagous group was more abundant (mean = 2055.2 ± 333.2
238 SEM) than the phytophagous group (mean = 928.2 ± 472.1 SEM). The country of origin
239 explained a significant amount of the variability in both total carabid and trophic guild species
240 richness and activity density (Fig.1, Table 1 & 2). Only in the case of the Hungarian dataset
241 was there no significant difference in the species richness of the two trophic groups (Fig. 1B).
242 Much of this between-country variability in carabid diversity is likely to be due to multiple,
243 unmeasured environmental influences (e.g. climate, soil) in the different landscapes across
244 Europe. The inclusion of the fixed effect ‘country’ and the random term ‘LU nested within
245 country’ in the GLMMs controlled for this country and landscape-specific variation when

246 testing for an overall effect of habitat and landscape structure on diversity of Carabidae and
247 carabid trophic groups. There was no evidence of an effect of sampling year (45 LUs sampled
248 in 2001, three more in 2002) on either activity density or rarefied species richness (Tables 1 &
249 2).

250

251 *Trophic group diversity and habitat type*

252

253 Activity densities (Table 1) and rarefied species richness (Table 2) of both trophic groups
254 were affected by the interaction between country and habitat. This indicated that there were
255 country-specific associations between habitat type and trophic group diversity. One
256 interpretation is that this interaction reflected differences in species pools across the European
257 sites. The mean activity density and species richness for each habitat × country combination
258 are shown in Tables S1 & S2 in Appendix S3.

259

260 Accounting for these significant habitat × country interactions, the habitat type at the
261 sampling plot had a strong influence on the activity density of Carabidae and both trophic
262 groups (Table 1, Fig. 2); but did not affect rarefied species richness of Carabidae or the
263 zoophage trophic group (Table 2). The influence of habitat on activity density, however,
264 differed between the phytophagous and zoophagous groups with, as predicted, a tendency for
265 phytophage abundance to be greater in open habitat (Fig. 2). Pair-wise comparisons of least-
266 square means (with Bonferroni adjustment) showed zoophage densities were significantly
267 greater under rotational cropping (RC) compared with all the other broad habitat classes:
268 broadleaf forest (BF): $t = -6.80$, adj. $P < 0.001$; coniferous forest (CF): $t = -5.83$, adj. P
269 < 0.001 ; mixed forest (MF) $t = -3.53$, adj. $P = 0.009$; extensive grassland (EG) $t = -7.54$, adj. P
270 < 0.001 ; intensive grassland (IG) $t = -5.41$, adj. $P < 0.001$). The association of total Carabidae

271 activity densities with habitat type (data not shown) followed the same pattern as for
272 zoophages (above). Phytophages were similarly more abundant in rotational cropping systems
273 (Fig. 2) compared with all other habitat (BF $t = -10.82$, adj. $P < 0.001$; CF $t = -13.10$, adj. P
274 < 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
275 $= -5.16$, adj. $P < 0.001$). In addition, however, there were greater numbers of phytophage
276 individuals in intensive (IG) and extensive (EG) grassland plots compared with the broadleaf
277 (IG $t = -5.15$, adj. $P < 0.001$; EG $t = -5.31$, adj. $P < 0.0001$), coniferous (IG $t = -7.96$, adj. P
278 < 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.
279 $P < 0.001$) forest plots (Fig.2). Altogether, both phytophage and zoophage activity densities
280 were greater in rotational cropping compared with the other habitats; phytophages were also
281 more abundant in grassland habitats compared with forest habitats.

282

283 *Trophic group diversity and landscape structure*

284

285 Carabid beetle trophic level modulated the response of activity density – but not species
286 richness - to landscape structure (Fig. 3, Table 1 & 2), contrary to our prediction, however,
287 this activity density response did not scale with increasing trophic level. These data show that
288 activity density of the lower trophic level (phytophages) was the most sensitive to landscape
289 heterogeneity (Fig. 3A; Table 1). Zoophage activity density was independent of variation in
290 landscape structure (Fig. 3B, Table 1). In contrast phytophage activity density was positively
291 correlated (Fig.3A, Table 1) with increasing habitat richness, but uncorrelated with increasing
292 forest cover (Table 1). The rarefied species richness of total Carabidae or zoophages was not
293 affected by either landscape parameter (Table 2); as already mentioned above the large
294 number of zeros in phytophage species richness precluded a comparable analysis of this
295 trophic group.

296

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

302

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

306

307 **Discussion**

308

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

317

318 This greater sensitivity of phytophage diversity departs from the majority of evidence that
319 sensitivity to landscape structure scales with increasing trophic level (Didham et al., 1998;
320 Gilbert *et al.*, 1998; Holt et al., 1999; Davies et al., 2000), but agrees with other documented

321 departures from this general trend (Henle et al., 2004 and references therein). At lower trophic
322 levels in a community the abundance of species or populations is – due to thermodynamic
323 constraints – generally greater than that at higher trophic levels, somewhat buffering lower
324 trophic levels against environmental heterogeneity, demographic and stochastic processes
325 (Spencer, 2000; Raffaelli, 2004). This applies particularly when considering a whole
326 community comprising many plant and animal taxa. This paper, however, focussed on trophic
327 levels within a single insect taxon, the Carabidae, here the zoophagous trophic group were
328 more numerous compared with the phytophagous group, and the phytophages were the most
329 sensitive to landscape structure. This may be explained by a degree of dependence of the
330 phytophages on ruderal plant species (see below), and their relatively low abundance
331 increasing sensitivity to any stochastic processes. In contrast, there may be an amount of
332 redundancy in the response of the speciose and abundant zoophage group to landscape
333 structure - whereby in response to an environmental gradient a reduction in the abundance of
334 one species is balanced by increasing abundance of others (Spencer, 2000; Raffaelli, 2004)
335
336 The relatively lower abundance and species richness of the phytophagous trophic group, and
337 greater sensitivity to increasing habitat richness, may be explained by the relatively
338 uncommon – within Carabidae – trophic adaptation of granivory (Thiele, 1977). While the
339 majority of Carabidae are able to consume both animal and plant material (Thiele, 1977), we
340 classified genera according to preference for either animal or plant diet. This classification led
341 to the predominance within the phytophagous group of genera (e.g. *Amara*, *Harpalus*, and
342 *Zabrus*, Appendix S2) to a large extent specialising on plant seed diet from grasses,
343 umbellifers, and crucifers (Thiele, 1977; Stace, 1997; Tutin *et al.*, 2001; Purtauf et al., 2005).
344 This relative dependency of the phytophages on seeds from ruderal plants (Thiele, 1977), and
345 the frequent association of these plants with disturbed sites (Ribera et al., 2001), means the

346 phytophages can be regarded as habitat specialists typical of grassland and agricultural
347 habitats. Indeed, at a habitat level, as predicted, the abundance of phytophages was generally
348 greater in open agricultural and grassland habitat compared with forest habitats. In contrast,
349 zoophagous carabid species are on the whole consumers of a wide variety of animal protein
350 both alive and dead (Thiele, 1977; Symondson & Liddell, 1993; McKemey *et al.*, 2003).
351 Consequently, these zoophages may be buffered from variation in environmental
352 heterogeneity at both habitat and landscape scales because of their relatively greater ability to
353 switch to alternative prey in different habitat types.

354

355 Our findings support previous research that showed generalised diversity responses of
356 invertebrate trophic groups to landscape structure across geographic regions (Purtauf *et al.*,
357 2005; Schweiger *et al.*, 2005). Schweiger *et al.* (2005) showed with a pan-European analysis
358 that arthropod assemblages across an array of trophic levels was – in order of importance –
359 structured by landscape structure, management intensity, and local habitat effects (Schweiger
360 *et al.*, 2005). This earlier study also demonstrated that both phytophagous and zoophagous
361 assemblages were associated with high diversity landscapes (Schweiger *et al.*, 2005). Land-
362 use intensity is another driver of assemblage structure (e.g. Schweiger *et al.* 2005; Sousa *et al.*
363 2006) that, lacking intensification data, we did not test.

364

365 Another landscape-scale study found that carabid species richness was negatively related to
366 the reduction in percentage cover of perennial habitats (Purtauf *et al.*, 2005) that were
367 hypothesised to provide refuges from agricultural disturbance (Ribera *et al.*, 2001). This paper
368 found no evidence that increasing cover of perennial habitat (forest and woodland) enhanced
369 trophic group diversity. Moreover, Purtauf *et al.*, (2005) showed only a weak differentiation
370 between zoophagous and phytophagous responses to perennial habitat cover, while trophic

371 group activity densities were unaffected by perennial habitat cover. These discrepancies
372 between our findings and Purtauf *et al.* (2005) may be partly explained by methodological
373 differences. Firstly, the earlier study did not assume that congeners shared the same diet;
374 some species were thus excluded from analysis which might influence the results obtained.
375 Secondly, Purtauf *et al.* (2005) included a small and discrete omnivorous group; in this paper,
376 carabid omnivory is assumed, but with a strong preference for plant or animal material.
377 Thirdly, Purtauf *et al.*, examined the effect of perennial habitat on carabids within agricultural
378 landscapes; whereas our study included forested landscapes supporting only forest specialists
379 (e.g. certain *Calathus* and *Cychrus* species) and relatively low carabid species richness – the
380 majority of European carabid beetles are open habitat associates (Thiele, 1977). Finally, this
381 paper's geographic scope was much greater (c.f. Purtauf *et al.* 2005: 1 country, 2 regions, 36
382 landscapes, 14108 individuals, and 84 species) providing greater turnover in assemblage
383 composition among our landscapes.

384

385 Ecological processes governing carabid diversity operate at both habitat and landscape scales
386 for phytophages, but only at habitat scales for zoophages. Phytophage sensitivity to landscape
387 structure is a consequence of the relative rarity of this trophic group among Carabidae. While
388 a functional group approach is advocated in this paper it should be noted that taxonomy
389 remained essential, in assigning species to trophic groups and in interpreting patterns in
390 trophic group diversity. This paper demonstrates that diversity is affected by heterogeneity at
391 multiple spatial scales, and that functional traits, such as trophic group, that can predict the
392 magnitude or direction of responses are a useful approach to understanding biodiversity
393 change across regions (Kruess & Tschardt, 2000; Thies *et al.*, 2003; Raffaelli, 2004;
394 Dauber *et al.*, 2005; Purtauf *et al.*, 2005; Schweiger *et al.*, 2005; Hendrickx *et al.*, 2007).
395 Moreover in revealing carabid trophic group responses that are consistent across European

396 landscapes it adds to growing evidence of generic responses of invertebrate diversity to land-
397 use and landscape structure in European landscapes (Sousa et al., 2006; Hendrickx et al.,
398 2007; Schweiger *et al.*, 2007; Billeter et al., 2008).

399

400 **Acknowledgements**

401 This paper is an output from the European Union-funded project ‘Biodiversity assessment tools (BIOASSESS)’
402 (EVK4-1999-00280). We thank David Elston and Adam Butler of Biomathematics and Statistics Scotland for
403 help with the statistics. Thanks go to the following persons: France: C. Gerard (Laboratory of Zoology in the
404 National Museum of Natural History, France), E. Federoff (National Botanic Garden, France) and local farmers
405 for permission to access their land; Portugal: Direction of Companhia das Lezírias (Eng. Sérvulo Correia) and
406 the Portuguese Air Force (Cnte Norte Jacinto) for permission and facilities for field work, M. Santos-Reis and F.
407 Petrucci Fonseca for logistical support in the field. Finland: Finnish Forest and Park Service for field work
408 permission, J. Blomqvist, L. Hiisivuori and P.-K. Leppänen for field assistance, M. Koivula was partly financed
409 by the Izaak Walton Killam Postdoctoral Fellowship, University of Alberta, Canada; Ireland: C. Teo and several
410 landowners for help and access to their land, S. Dolan for field and lab work; Spain: J. Jiménez (National Park of
411 Cabañeros) and V. del Castillo for permission to access to land, D. Salgado, C. Ruiz, C. Andújar and J. A.
412 Carvajal for field work; Scotland: Glen Tanar Estate, Finzean Estate partnership, Forestry Commission, Birse
413 Community Trust, Mr. B. Ross, and the Macroboberts Trust for permission to access their land, C. Beaudoin, M.
414 Hardy, C. Dawson for field work, and D. Mann, J. Hogan, G. McGavin (Oxford University Museum);
415 Switzerland: E. Ruoss and P. Hofstetter (Biosphere Reserve) for local support and contacts with the landowners.
416 Thanks to Oliver Schweiger, Chris Binckley and anonymous referees for comments on an earlier version of this
417 manuscript.

1 **References**

- 2 Benton, T.G., Vickery, J.A., & Wilson, J.D. (2003) Farmland biodiversity: is habitat
3 heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182-188.
- 4 Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J.,
5 Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekotter, T., Dietz, H.,
6 Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F.,
7 Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M.,
8 Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans,
9 M., Simova, P., Verboom, J., van Wingerden, W., Zobel, M., & Edwards, P.J. (2008)
10 Indicators for biodiversity in agricultural landscapes: a pan-European study. *Journal of*
11 *Applied Ecology*, **45**, 141-150.
- 12 Borrvall, C. & Ebenman, B. (2006) Early onset of secondary extinctions in ecological
13 communities following the loss of top predators. *Ecology Letters*, **9**, 435-442.
- 14 Chust, G., Pretus, J.L., Ducrot, D., Bedos, A., & Deharveng, L. (2003) Response of soil fauna
15 to landscape heterogeneity: Determining optimal scales for biodiversity modeling.
16 *Conservation Biology*, **17**, 1712-1723.
- 17 Cole, L.J., McCracken, D.I., Dennis, P., Downie, I.S., Griffin, A.L., Foster, G.N., Murphy,
18 K.J., & Waterhouse, T. (2002) Relationships between agricultural management and ecological
19 groups of ground beetles (Coleoptera : Carabidae) on Scottish farmland. *Agriculture*
20 *Ecosystems & Environment*, **93**, 323-336.
- 21 Colwell, R.K. (2005) EstimateS: statistical estimation of species richness and shared species
22 from samples.
- 23 Dauber, J., Purtauf, T., Allspach, A., Frisch, J., Voigtlander, K., & Wolters, V. (2005) Local
24 vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of
25 differing mobility. *Global Ecology and Biogeography*, **14**, 213-221.
- 26 Davies, K.F. & Margules, C.R. (1998) Effects of habitat fragmentation on carabid beetles:
27 experimental evidence. *Journal of Animal Ecology*, **67**, 460-471.
- 28 Davies, K.F., Margules, C.R., & Lawrence, K.F. (2000) Which traits of species predict
29 population declines in experimental forest fragments? *Ecology*, **81**, 1450-1461.
- 30 Davies, R.G., Eggleton, P., Jones, D.T., Gathorne-Hardy, F.J., & Hernandez, L.M. (2003)
31 Evolution of termite functional diversity: analysis and synthesis of local ecological and
32 regional influences on local species richness. *Journal of Biogeography*, **30**, 847-877.

1 de la Pena, N.M., Butet, A., Delettre, Y., Morant, P., & Burel, F. (2003) Landscape context
2 and carabid beetles (Coleoptera : Carabidae) communities of hedgerows in western France.
3 *Agriculture Ecosystems & Environment*, **94**, 59-72.

4 Didham, R.K., Lawton, J.H., Hammond, P.M., & Eggleton, P. (1998) Trophic structure
5 stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments.
6 *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **353**,
7 437-451.

8 Dixon, P. (2003) VEGAN, a package of R functions for community ecology. *Journal of*
9 *Vegetation Science*, **14**, 927-930.

10 Driscoll, D.A. & Weir, T. (2005) Beetle responses to habitat fragmentation depend on
11 ecological traits, habitat condition, and remnant size. *Conservation Biology*, **19**, 182-194.

12 Duffy, J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecology*
13 *Letters*, **6**, 680-687.

14 Eggleton, P., Bignell, D.E., Hauser, S., Dibog, L., Norgrove, L., & Madong, B. (2002)
15 Termite diversity across an anthropogenic disturbance gradient in the humid forest zone of
16 West Africa. *Agriculture Ecosystems & Environment*, **90**, 189-202.

17 Eggleton, P., Vanbergen, A.J., Jones, D.T., Lambert, M.C., Rockett, C., Hammond, P.M.,
18 Beccaloni, J., Marriott, D., Ross, E., & Giusti, A. (2005) Assemblages of soil macrofauna
19 across a Scottish land-use intensification gradient: influences of habitat quality, heterogeneity
20 and area. *Journal of Applied Ecology*, **42**, 1153-1164.

21 Gilbert, F., Gonzalez, A., & Evans-Freke, I. (1998) Corridors maintain species richness in the
22 fragmented landscapes of a microecosystem. *Proceedings of the Royal Society of London*
23 *Series B-Biological Sciences*, **265**, 577-582.

24 Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M., & Evans-Freke, I. (1998)
25 Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science*, **281**,
26 2045-2047.

27 Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the
28 measurement and comparison of species richness. *Ecology Letters*, **4**, 379-351.

29 Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41-49.

30 Hendrickx, F., Maelfait, J.P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S.,
31 Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekotter, T., Dirksen, J.,
32 Herzog, F., Liira, J., Roubalova, M., Vandomme, V., & Bugter, R. (2007) How landscape
33 structure, land-use intensity and habitat diversity affect components of total arthropod
34 diversity in agricultural landscapes. *Journal of Applied Ecology*, **44**, 340-351.

- 1 Henle, K., Davies, K.F., Kleyer, M., Margules, C., & Settele, J. (2004) Predictors of species
2 sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207-251.
- 3 Holt, R.D., Lawton, J.H., Polis, G.A., & Martinez, N.D. (1999) Trophic rank and the species-
4 area relationship. *Ecology*, **80**, 1495-1504.
- 5 Honek, A., Martinkova, Z., & Jarosik, V. (2003) Ground beetles (Carabidae) as seed
6 predators. *European Journal of Entomology*, **100**, 531-544.
- 7 Jeanneret, P., Schupbach, B., & Luka, H. (2003) Quantifying the impact of landscape and
8 habitat features on biodiversity in cultivated landscapes. *Agriculture Ecosystems &*
9 *Environment*, **98**, 311-320.
- 10 Jones, D.T., Susilo, F.X., Bignell, D.E., Hardiwinoto, S., Gillison, A.N., & Eggleton, P.
11 (2003) Termite assemblage collapse along a land-use intensification gradient in lowland
12 central Sumatra, Indonesia. *Journal of Applied Ecology*, **40**, 380-391.
- 13 Kruess, A. (2003) Effects of landscape structure and habitat type on a plant-herbivore-
14 parasitoid community. *Ecography*, **26**, 283-290.
- 15 Kruess, A. & Tschamntke, T. (2000) Species richness and parasitism in a fragmented
16 landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia*, **122**, 129-
17 137.
- 18 Lang, A., Filser, J., & Henschel, J.R. (1999) Predation by ground beetles and wolf spiders on
19 herbivorous insects in a maize crop. *Agriculture Ecosystems & Environment*, **72**, 189-199.
- 20 Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M.,
21 Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., & Watt,
22 A.D. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in
23 tropical forest. *Nature*, **391**, 72-76.
- 24 Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Nix, H., & Lindenmayer, B.D.
25 (2002) Effects of forest fragmentation on bird assemblages in a novel landscape context.
26 *Ecological Monographs*, **72**, 1-18.
- 27 Lindroth, C.H. (1992) Ground beetles of Fennoscandia: a zoogeographic study Amerind
28 Publishing, New Delhi, India.
- 29 Littell, R.C., Milliken, G.A., Stroup, W.W., & Wolfinger, R.D. (1996). SAS system for mixed
30 models. SAS Institute Inc., Cary, North Carolina, USA.
- 31 Löbl, I. & Smetana, A. (2003) Catalogue of Palearctic Coleoptera Apollo Books.
- 32 McCann, K. (2007) Protecting biostructure. *Nature*, **446**, 29-29.

1 McKemey, A.R., Symondson, W.O.C., & Glen, D.M. (2003) Predation and prey size choice
2 by the carabid beetle *Pterostichus melanarius* (Coleoptera : Carabidae): the dangers of
3 extrapolating from laboratory to field. *Bulletin of Entomological Research*, **93**, 227-234.

4 Petit, S. & Usher, M.B. (1998) Biodiversity in agricultural landscapes: the ground beetle
5 communities of woody uncultivated habitats. *Biodiversity and Conservation*, **7**, 1549-1561.

6 Purtauf, T., Dauber, J., & Wolters, V. (2005) The response of carabids to landscape
7 simplification differs between trophic groups. *Oecologia*, **142**, 458-464.

8 R-Development (2008) R: A language and environment for statistical computing. In R
9 Foundation for Statistical Computing, Vienna, Austria.

10 Raffaelli, D. (2004) How extinction patterns affect ecosystems. *Science*, **306**, 1141-1142.

11 Ribera, I., Doledec, S., Downie, I.S., & Foster, G.N. (2001) Effect of land disturbance and
12 stress on species traits of ground beetle assemblages. *Ecology*, **82**, 1112-1129.

13 Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald,
14 E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A.,
15 Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. (2000)
16 Biodiversity - Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770-1774.

17 Schweiger, O., Maelfait, J.P., Van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M.,
18 Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekotter, T.,
19 Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M., & Bugter, R. (2005)
20 Quantifying the impact of environmental factors on arthropod communities in agricultural
21 landscapes across organizational levels and spatial scales. *Journal of Applied Ecology*, **42**,
22 1129-1139.

23 Schweiger, O., Musche, M., Bailey, D., Billeter, R., Diekotter, T., Hendrickx, F., Herzog, F.,
24 Liira, J., Maelfait, J.P., Speelmans, M., & Dziock, F. (2007) Functional richness of local
25 hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe.
26 *Oikos*, **116**, 461-472.

27 Sousa, J.P., Bolger, T., da Gama, M.M., Lukkari, T., Ponge, J.F., Simon, C., Traser, G.,
28 Vanbergen, A.J., Brennan, A., Dubs, F., Ivitis, E., Keating, A., Stofer, S., & Watt, A.D.
29 (2006) Changes in Collembola richness and diversity along a gradient of land-use intensity: A
30 pan European study. *Pedobiologia*, **50**, 147-156.

31 Spencer, M. (2000) Are predators rare? *Oikos*, **89**, 115-122.

32 Stace, C. (1997) *New Flora of the British Isles* Cambridge University Press, Cambridge.

33 Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., & Tschardt, T. (2002) Scale-
34 dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421-1432.

1 Symondson, W.O.C., Glen, D.M., Ives, A.R., Langdon, C.J., & Wiltshire, C.W. (2002)
2 Dynamics of the relationship between a generalist predator and slugs over five years.
3 *Ecology*, **83**, 137-147.

4 Symondson, W.O.C. & Liddell, J.E. (1993) The detection of predation by *Abax*
5 *parallelepipedus* and *Pterostichus madidus* (Coleoptera, Carabidae) on Mollusca using a
6 quantitative ELISA. *Bulletin of Entomological Research*, **83**, 641-647.

7 Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., & Jeltsch, F.
8 (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of
9 keystone structures. *Journal of Biogeography*, **31**, 79-92.

10 Thiele, H.U. (1977) *Carabid Beetles In Their Environments* Springer Verlag, Berlin.

11 Thies, C., Steffan-Dewenter, I., & Tschardt, T. (2003) Effects of landscape context on
12 herbivory and parasitism at different spatial scales. *Oikos*, **101**, 18-25.

13 Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M., & Webb, D.A.,
14 eds. (2001) *Flora Europaea*. Vol. Vols I to V. Cambridge University Press.

15 Vanbergen, A.J., Watt, A.D., Mitchell, R.J., Truscott, A.M., Palmer, S.C.F., Ivits, E.,
16 Eggleton, P., Jones, T.H., & Sousa, J.P. (2007) Scale-specific correlations between habitat
17 heterogeneity and soil fauna diversity along a landscape structure gradient. *Oecologia*, **153**,
18 713-725.

19 Watt, A.D., Stork, N.E., McBeath, C., & Lawson, G.L. (1997) Impact of forest management
20 on insect abundance and damage in a lowland tropical forest in southern Cameroon. *Journal*
21 *of Applied Ecology*, **34**, 985-998.

22
23

Figure legends

Figure 1. The influence of country: FIN (Finland), FRA (France), HUN (Hungary), IRE (Ireland), POR (Portugal), SCO (Scotland), ESP (Spain) and SWZ (Switzerland), and trophic guild on mean (\pm 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.

Figure 2. The effect of source habitat on the mean activity density (\pm 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: broadleaf forest (BF); coniferous forest (CF); mixed forest (MF); extensive grassland (EG); intensive grassland (IG); permanent cropping (PC); and rotational cropping (RC).

Figure 3. Partial residual relationships on the linear predictor scale of (A) phytophagous and (B) zoophagous activity densities with the habitat richness per 1 km² 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 \pm SEM. Fitted lines are included where the slopes are statistically significant from zero ($p < 0.05$).

Figure 1.

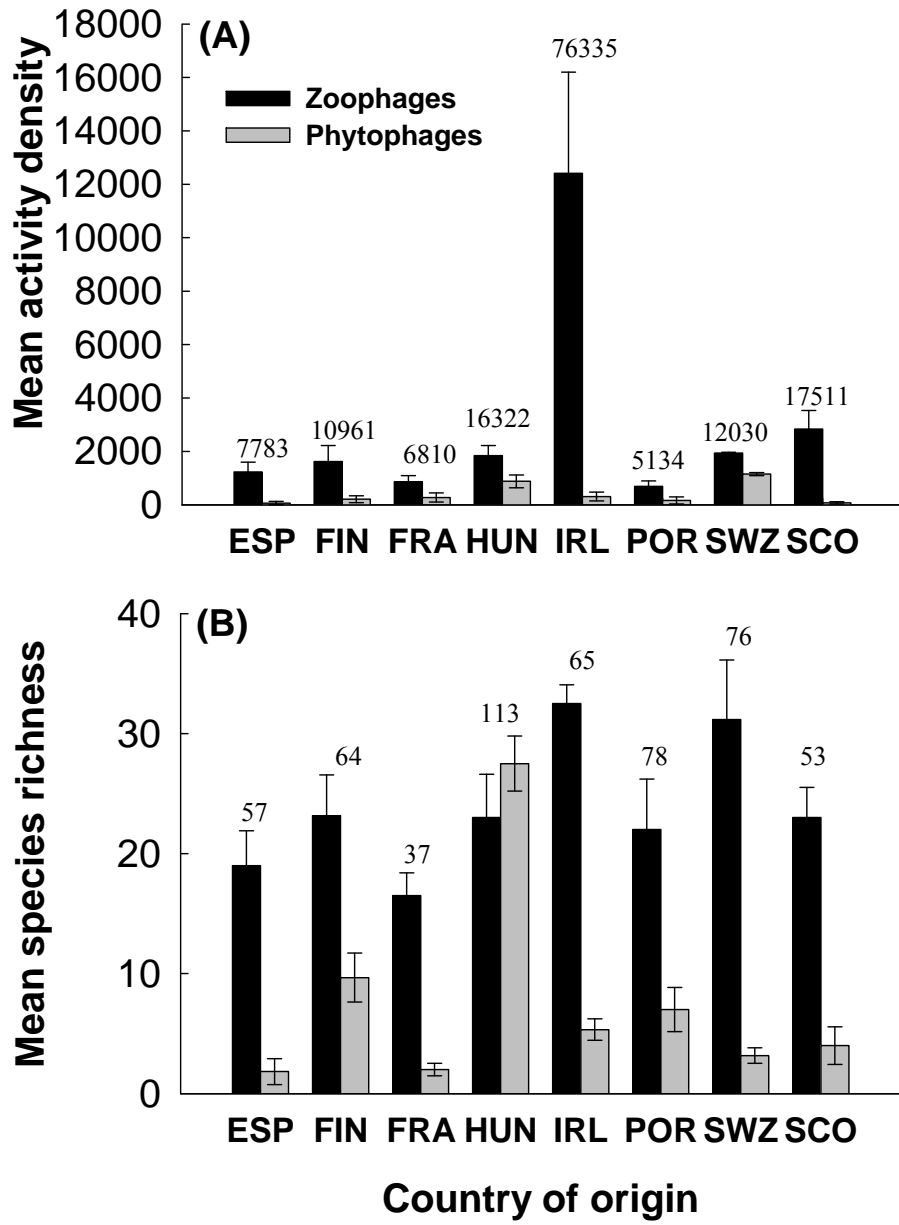


Figure 2

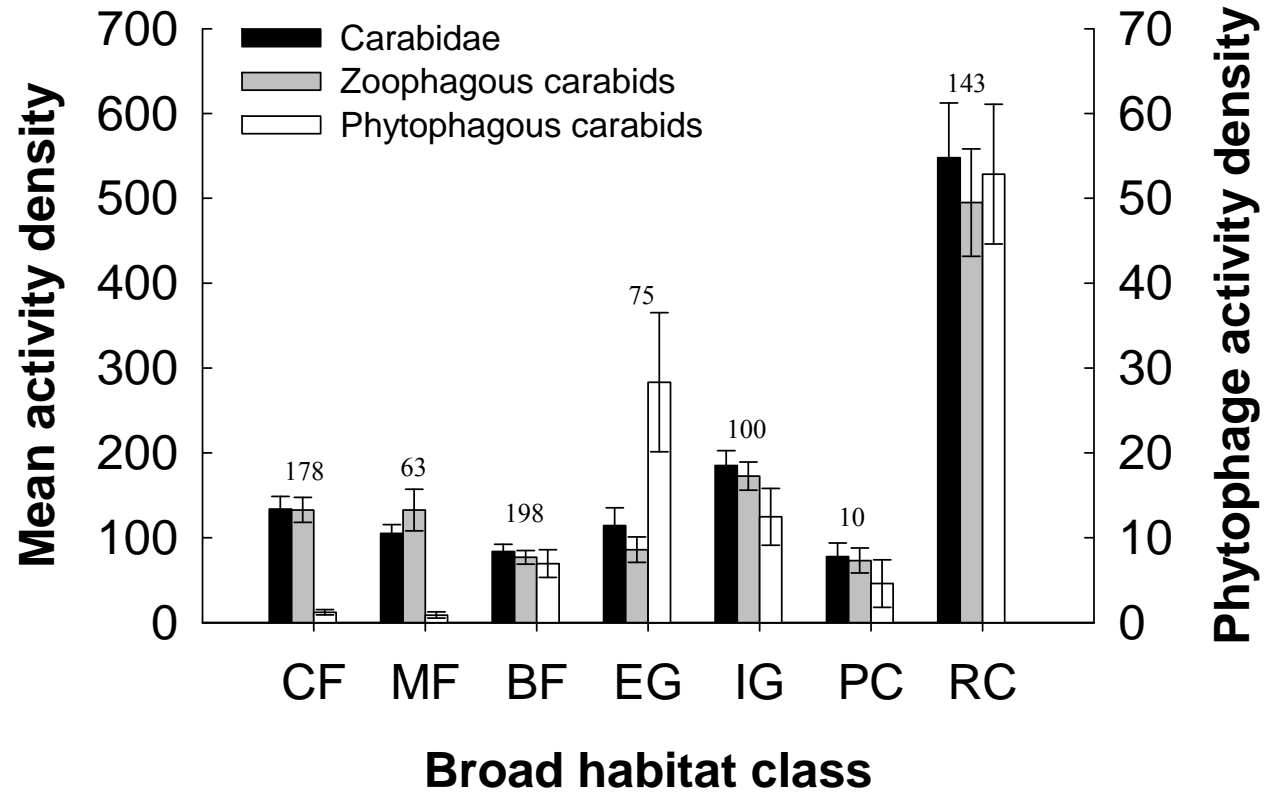


Figure 3

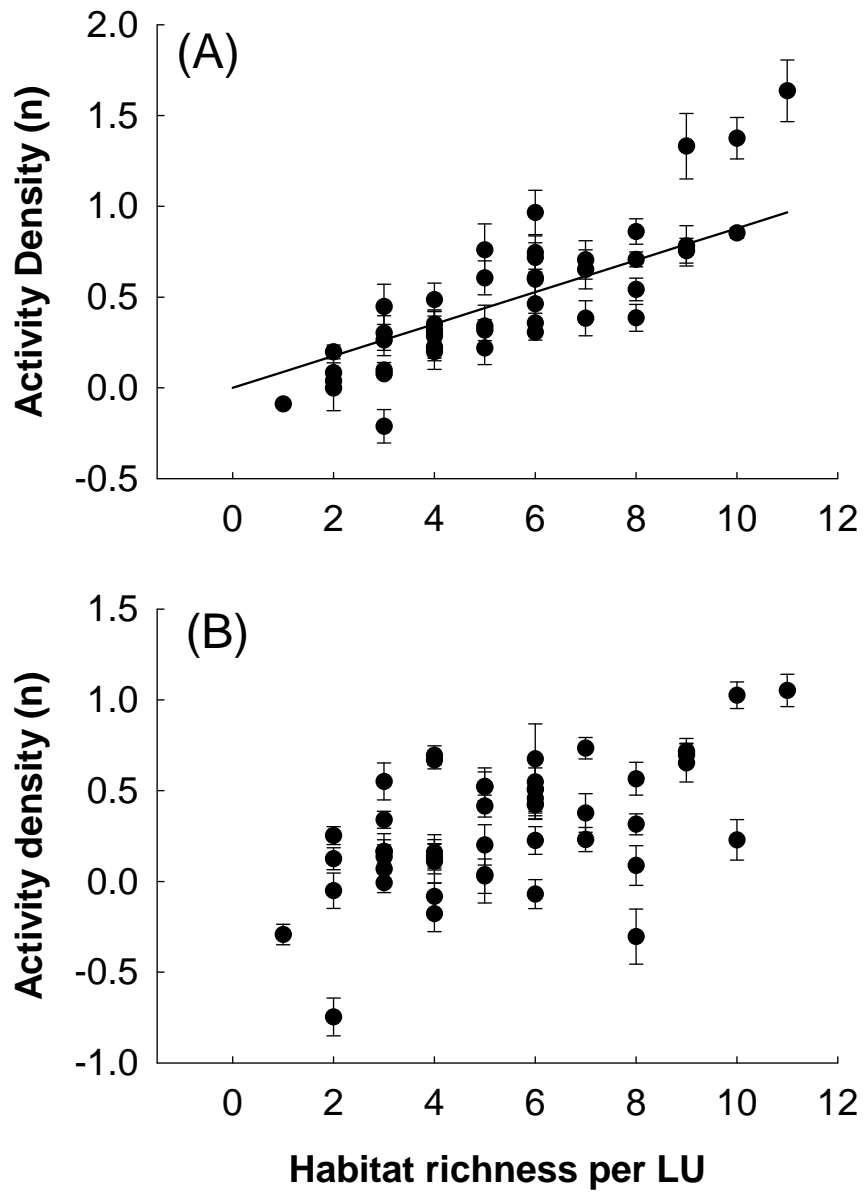


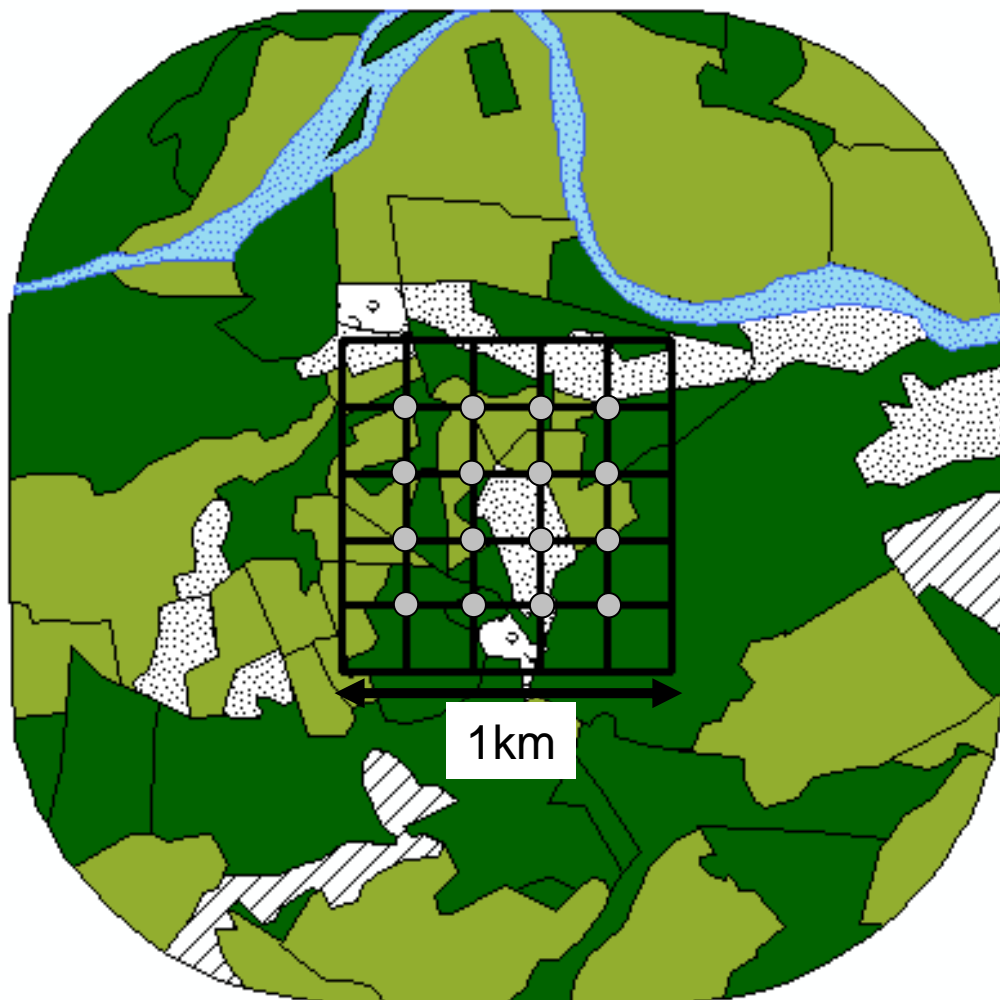
Table 1. GLMM results summary for activity density of Carabidae and trophic groups (zoophages, phytophages) in relation to source country, habitat, and composition (percentage forest cover) and heterogeneity (habitat richness) of 1km² landscape units (LUs). Numerator (ndf) and Denominator (ddf) degrees of freedom were estimated using Satterthwaite's approximation. Estimate = parameter slope, MPE = multiple parameter estimates. Bold type indicates parameters retained in final models.

Taxon/Trophic group	Fixed effects	Estimate	F (ndf, ddf)	p
Carabidae Random effect estimate: LU(Country) = 0.085 Residual variance = 0.140	Sampling year	MPE	0.78 (1,46)	0.380
	Country of origin	MPE	6.45 (7,49)	<0.001
	Habitat	MPE	8.02 (6,440)	<0.001
	Country × Habitat	MPE	3.40 (26,319)	<0.001
	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 Random effect estimate: LU(Country) = 0.101 Residual variance = 0.147	Sampling year	MPE	1.02 (1,46)	0.317
	Country of origin	MPE	7.52 (7,48)	<0.001
	Habitat	MPE	5.06 (6,431)	<0.001
	Country × Habitat	MPE	4.96 (26,528)	<0.001
	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 Random effect estimate: LU(Country) = 0.031 Residual variance = 0.145	Sampling year	MPE	0.11 (1,46)	0.738
	Country of origin	MPE	15.93 (7,56)	<0.001
	Habitat	MPE	36.96 (6,534)	<0.001
	Country × Habitat	MPE	3.98 (26,460)	<0.001
	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

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 1km² landscape units (LUs). 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.

Taxon/Trophic group	Fixed effects	Estimate	F (ndf, ddf)	p
Carabidae Random effect estimate: LU(Country) = 0.032 Residual variance = 0.061	Sampling year	MPE	0.26 _(1,46)	0.612
	Country of origin	MPE	3.45 _(7,49)	0.005
	Habitat	MPE	0.54 _(6,411)	0.775
	Country × habitat	MPE	2.34 _(26,488)	<0.001
	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 Random effect estimate: LU(Country) = 0.031 Residual variance = 0.059	Sampling year	MPE	0.28 _(1,46)	0.602
	Country of origin	MPE	2.44 _(7,46)	0.033
	Habitat	MPE	0.73 _(6,387)	0.627
	Country × habitat	MPE	1.73 _(26,480)	0.015
	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

Fig. S2. An example of a GIS map (ArcView 3.1) of a 1km² landscape unit (LU) containing a grid of 16 sampling plots, 200m 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.



Scotland LU4
Mixed-use mosaic

Vanbergen et al
Appendix S2.

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

Species	Authority	Trophic group	Distribution	Mean	SD
<i>Amara aenea</i>	(Degeer, 1774)	PHY	23	11.73	48.02
<i>Amara anthobia</i>	Villa & Villa, 1833	PHY	2	0.48	2.68
<i>Amara apricaria</i>	(Paykull, 1790)	PHY	3	0.29	1.41
<i>Amara aulica</i>	(Panzer, 1797)	PHY	5	0.33	1.74
<i>Amara bifrons</i>	(Gyllenhal, 1810)	PHY	7	2.00	9.12
<i>Amara brunnea</i>	(Gyllenhal, 1810)	PHY	5	0.56	1.81
<i>Amara chaldoiri incognita</i>	Fassati, 1946	PHY	1	0.02	0.14
<i>Amara communis</i>	(Panzer, 1797)	PHY	9	1.25	5.61
<i>Amara consularis</i>	(Duftschmid, 1812)	PHY	4	0.42	2.07
<i>Amara convexior</i>	Stephens, 1828	PHY	7	2.63	8.19
<i>Amara cursitans</i>	(Zimmermann, 1832)	PHY	1	0.02	0.14
<i>Amara equestris</i>	(Duftschmid, 1812)	PHY	2	0.25	1.36
<i>Amara eurynota</i>	(Panzer, 1797)	PHY	6	2.33	12.81
<i>Amara familiaris</i>	(Duftschmid, 1812)	PHY	10	0.88	2.23
<i>Amara fervida</i>	Coquerel, 1858	PHY	1	0.02	0.14
<i>Amara fulva</i>	(Müller, 1776)	PHY	8	0.67	1.87
<i>Amara infima</i>	(Duftschmid, 1812)	PHY	1	0.04	0.29
<i>Amara ingenua</i>	(Duftschmid, 1812)	PHY	1	0.83	5.77
<i>Amara lucida</i>	(Duftschmid, 1812)	PHY	4	0.23	0.83
<i>Amara lunicollis</i>	Schiødte, 1837	PHY	10	1.85	7.23
<i>Amara majuscula</i>	(Chaudoir, 1850)	PHY	1	0.02	0.14
<i>Amara montivaga</i>	Sturm, 1825	PHY	3	0.19	0.91
<i>Amara municipalis</i>	(Duftschmid, 1812)	PHY	1	0.02	0.14
<i>Amara nitida</i>	Sturm, 1825	PHY	4	0.42	1.88
<i>Amara ovata</i>	(F., 1792)	PHY	7	1.04	4.72
<i>Amara plebeja</i>	(Gyllenhal, 1810)	PHY	9	8.33	32.38
<i>Amara quenseli</i>	(Schönherr, 1806)	PHY	1	0.02	0.14
<i>Amara saphyrea</i>	Dejean, 1828	PHY	5	1.33	5.62
<i>Amara similata</i>	(Gyllenhal, 1810)	PHY	8	0.40	1.16
<i>Amara tibialis</i>	(Paykull, 1798)	PHY	1	0.02	0.14
<i>Amara tricuspidata</i>	Dejean, 1831	PHY	3	0.06	0.24
<i>Bradycellus csikii</i>	Laczó, 1912	PHY	1	0.02	0.14
<i>Bradycellus harpalinus</i>	(Audinet-Serville, 1821)	PHY	2	0.06	0.32
<i>Bradycellus verbasci</i>	(Duftschmid, 1812)	PHY	2	0.04	0.20
<i>Diachromus germanus</i>	(L., 1758)	PHY	1	0.02	0.14
<i>Dixus clypeatus</i>	(Rossi, 1790)	PHY	1	0.06	0.43
<i>Dixus sphaerocephalus</i>	(Olivier, 1795)	PHY	1	0.02	0.14
<i>Graniger cordicollis</i>	Serville, 1821	PHY	1	0.02	0.14
<i>Harpalus affinis</i>	(Schrank, 1781)	PHY	5	0.58	2.42
<i>Harpalus albanicus</i>	Reitter, 1900	PHY	2	0.04	0.20
<i>Harpalus anxius</i>	(Duftschmid, 1812)	PHY	2	0.10	0.52
<i>Harpalus atratus</i>	(Latreille, 1804)	PHY	2	0.23	1.45
<i>Harpalus attenuatus</i>	(Stephens, 1828)	PHY	3	0.33	1.60
<i>Harpalus azureus</i>	(F., 1775)	PHY	4	0.21	0.85
<i>Harpalus autumnalis</i>	(Duftschmid, 1812)	PHY	2	0.04	0.20
<i>Harpalus calceatus</i>	(Duftschmid, 1812)	PHY	3	0.94	5.66

<i>Harpalus caspius</i>	Schauberger, 1928	PHY	2	0.21	1.30
<i>Harpalus cupreus</i>	Dejean, 1829	PHY	1	0.02	0.14
<i>Harpalus distinguendus</i>	(Duftschmid, 1812)	PHY	7	10.52	41.42
<i>Harpalus dispar</i>	Dejean, 1929	PHY	2	0.17	0.91
<i>Harpalus flavicornis</i>	Dejean, 1829	PHY	1	0.02	0.14
<i>Harpalus froelichii</i>	Sturm, 1818	PHY	4	4.54	24.61
<i>Harpalus griseus</i>	(Panzer, 1797)	PHY	4	3.17	20.92
<i>Harpalus hirtipes</i>	(Panzer, 1797)	PHY	5	0.54	2.02
<i>Harpalus honestus</i>	(Duftschmid, 1812)	PHY	1	0.02	0.14
<i>Harpalus latus</i>	(L., 1758)	PHY	6	0.48	1.77
<i>Harpalus neglectus</i>	Audinet-Serville, 1821	PHY	3	0.13	0.61
<i>Harpalus oblitus</i>	Dejean, 1829	PHY	5	3.10	13.58
<i>Harpalus picipennis</i>	(Duftschmid, 1812)	PHY	5	0.42	1.37
<i>Harpalus progrediens</i>	Schauberger, 1922	PHY	1	0.02	0.14
<i>Harpalus pumilus</i>	(Sturm, 1818)	PHY	3	0.08	0.35
<i>Harpalus punctatostrigatus</i>	Dejean, 1829	PHY	2	0.25	1.28
<i>Harpalus pygmaeus</i>	Dejean	PHY	2	0.13	0.73
<i>Harpalus quadripunctatus</i>	Dejean, 1829	PHY	7	1.23	6.65
<i>Harpalus rubripes</i>	(Duftschmid, 1812)	PHY	7	1.15	4.36
<i>Harpalus rufibarbis</i>	(F., 1792)	PHY	10	54.54	192.72
<i>Harpalus rufipalpis</i>	Sturm, 1818	PHY	6	12.75	83.80
<i>Harpalus rufipes</i>	Degeer, 1794)	PHY	14	46.56	163.46
<i>Harpalus serripes</i>	(Quensel, 1806)	PHY	6	1.98	7.00
<i>Harpalus servus</i>	(Duftschmid, 1812)	PHY	2	0.13	0.64
<i>Harpalus signaticornis</i>	(Duftschmid, 1812)	PHY	2	0.04	0.20
<i>Harpalus smaragdinus</i>	(Duftschmid, 1812)	PHY	2	0.08	0.45
<i>Harpalus tardus</i>	(Panzer, 1797)	PHY	8	12.75	41.52
<i>Harpalus xanthopus</i>	Gemming & Harold, 1868	PHY	1	0.02	0.14
<i>Oedesis villosulus</i>	Reiche, 1859	PHY	1	0.06	0.43
<i>Ophonus nitidulus</i>	(Stephens, 1828)	PHY	2	0.08	0.40
<i>Ophonus opacus</i>	Dejean, 1829	PHY	1	0.17	1.15
<i>Ophonus rufibarbis</i>	F., 1792	PHY	1	0.08	0.58
<i>Ophonus puncticeps</i>	Stephens, 1828	PHY	1	0.04	0.29
<i>Ophonus puncticollis</i>	Paykull, 1798	PHY	2	0.10	0.59
<i>Ophonus stictus</i>	(Stephens, 1828)	PHY	1	0.02	0.14
<i>Ophonus subsinuatus</i>	Rey, 1886	PHY	5	1.04	5.55
<i>Parophonus maculicornis</i>	(Duftschmid, 1812)	PHY	1	0.02	0.14
<i>Poecilus cupreus</i>	(L., 1758)	PHY	16	50.65	173.91
<i>Scybalicus oblongiusculus</i>	(Dejean, 1829)	PHY	1	0.04	0.29
<i>Stenolophus mixtus</i>	(Herbst, 1784)	PHY	1	0.02	0.14
<i>Stenolophus teutonius</i>	(Schränk, 1781)	PHY	5	0.96	5.63
<i>Synuchus vivalis</i>	(Illiger, 1798)	PHY	9	2.23	10.29
<i>Trichotichnus laevicollis</i>	(Duftschmid, 1812)	PHY	3	0.06	0.24
<i>Zabrus ignavus</i>	Csiki 1907	PHY	1	0.02	0.14
<i>Zabrus spinipes</i>	F., 1798	PHY	3	2.33	15.44
<i>Zabrus tenebrioides</i>	(Goeze, 1777)	PHY	5	0.46	2.34
<i>Abax ovalis</i>	(Duftschmid, 1812)	ZOO	4	1.65	6.28
<i>Abax parallelepipedus</i>	(Piller & Mitterpacher, 1783)	ZOO	18	249.65	724.09
<i>Abax parallelus</i>	(Duftschmid, 1812)	ZOO	3	0.10	0.42
<i>Acupalpus brunnius</i>	(Sturm, 1825)	ZOO	5	0.60	2.32
<i>Acupalpus cantabricus</i>	Piochard de la Brulerie, 1867	ZOO	1	0.06	0.43
<i>Agonum afrum</i>	(Duftschmid, 1812)	ZOO	1	0.02	0.14
<i>Agonum albipes</i>	Fabricius, 1796	ZOO	8	1.40	4.12
<i>Agonum assimile</i>	(Paykull, 1790)	ZOO	11	11.71	34.38

<i>Agonum atratum</i>	(Duftschmid, 1812)	ZOO	1	0.02	0.14
<i>Agonum fuliginosum</i>	(Panzer, 1809)	ZOO	8	2.31	9.16
<i>Agonum gracilipes</i>	Duftschmid, 1812	ZOO	3	0.25	1.33
<i>Agonum marginatum</i>	(L., 1758)	ZOO	5	0.50	2.02
<i>Agonum moestum</i>	(Duftschmid, 1812)	ZOO	6	18.90	88.50
<i>Agonum muelleri</i>	Herbst, 1974	ZOO	23	41.60	103.87
<i>Agonum nigrum</i>	Dejean, 1828	ZOO	3	1.40	7.14
<i>Agonum obscurum</i>	(Herbst, 1784)	ZOO	4	1.90	12.13
<i>Agonum permolestum</i>	Puel, 1930	ZOO	1	0.58	4.04
<i>Agonum seipunctatum</i>	(L., 1758)	ZOO	4	0.10	0.37
<i>Agonum thoreyi</i>	Dejean, 1828	ZOO	2	0.19	1.16
<i>Agonum viduum</i>	(Panzer, 1797)	ZOO	4	3.19	11.00
<i>Agonum viridicupreum</i>	(Goeze, 1777)	ZOO	5	3.67	23.81
<i>Anchomenus dorsalis</i>	(Pontoppidan, 1763)	ZOO	17	212.92	851.03
<i>Anisodactylus binotatus</i>	(F., 1787)	ZOO	3	0.23	0.95
<i>Anisodactylus heros</i>	(F., 1801)	ZOO	1	0.02	0.14
<i>Apotomus rufus</i>	Rossi, 1790	ZOO	2	0.08	0.45
<i>Asaphidion flavipes</i>	(L., 1761)	ZOO	5	1.08	6.50
<i>Asaphidion stierlini</i>	Heyden, 1880	ZOO	1	0.02	0.14
<i>Badister bullatus</i>	(Schrank, 1798)	ZOO	6	0.15	0.41
<i>Badister lacertosus</i>	Sturm, 1815	ZOO	4	0.23	0.88
<i>Badister sodalis</i>	(Duftschmid, 1812)	ZOO	1	0.02	0.14
<i>Bembidion aeneum</i>	(Germar, 1824)	ZOO	4	2.33	13.90
<i>Bembidion ambiguum</i>	Dejean, 1831	ZOO	4	1.31	6.03
<i>Bembidion antoinei</i>	Puel, 1935	ZOO	1	0.02	0.14
<i>Bembidion biguttatum</i>	(F., 1779)	ZOO	1	0.02	0.14
<i>Bembidion bruxellense</i>	Wesmael, 1835	ZOO	3	0.35	2.04
<i>Bembidion deletum</i>	Audinet-Serville, 1821	ZOO	1	0.04	0.29
<i>Bembidion guttula</i>	(F., 1792)	ZOO	11	4.90	18.83
<i>Bembidion harpaloides</i>	Audinet-Serville, 1821	ZOO	7	0.44	1.34
<i>Bembidion laetum</i>	Brulle, 1838	ZOO	1	0.02	0.14
<i>Bembidion lampros</i>	(Herbst, 1784)	ZOO	16	13.33	38.23
<i>Bembidion lunulatum</i>	(Fourcroy, 1785)	ZOO	3	0.42	1.89
<i>Bembidion mannerheimii</i>	Sahlberg, 1827	ZOO	4	1.23	5.98
<i>Bembidion obtusum</i>	Audinet-Serville, 1821	ZOO	3	0.46	2.49
<i>Bembidion properans</i>	(Stephens, 1828)	ZOO	5	0.21	0.68
<i>Bembidion punctulatum</i>	Drapiez, 1820	ZOO	2	0.04	0.20
<i>Bembidion quinquestriatum</i>	Gyllenhal, 1810	ZOO	2	0.21	1.30
<i>Bembidion tethys</i>	Netolitzky, 1926	ZOO	8	0.79	2.56
<i>Bembidion tetracolum</i>	Say, 1823	ZOO	7	29.08	151.03
<i>Bembidion vicinum</i>	Lucas, 1846	ZOO	1	0.02	0.14
<i>Brachinus bellicosus</i>	Dufour, 1820	ZOO	1	0.02	0.14
<i>Brachinus crepitans</i>	(L., 1758)	ZOO	3	0.54	2.32
<i>Brachinus elegans</i>	Chaudoir, 1842	ZOO	3	0.08	0.35
<i>Brachinus explodens</i>	(Duftschmid, 1812)	ZOO	3	0.13	0.53
<i>Brachinus plagiatus</i>	Reiche, 1858	ZOO	1	0.02	0.14
<i>Brachinus sclopeta</i>	Fabricius, 1792	ZOO	2	33.00	227.45
<i>Brosicus cephalotes</i>	(L., 1758)	ZOO	2	0.04	0.20
<i>Calathus ambiguus</i>	(Paykull, 1790)	ZOO	6	45.27	237.21
<i>Calathus cinctus</i>	Motchulsky, 1850	ZOO	6	5.00	23.75
<i>Calathus circumseptus</i>	Germar, 1824	ZOO	1	0.06	0.43
<i>Calathus erratus</i>	(Sahlberg, 1827)	ZOO	8	46.85	146.52
<i>Calathus fuscipes</i>	(Goeze, 1777)	ZOO	19	100.60	226.98
<i>Calathus granatensis</i>	Vuillefroy, 1866	ZOO	11	23.08	75.50

<i>Calathus hispanicus</i>	Gautier, 1866	ZOO	1	2.60	18.04
<i>Calathus luctuosus</i>	Latreille, 1804	ZOO	1	0.02	0.14
<i>Calathus melanocephalus</i>	(L., 1758)	ZOO	16	58.85	206.51
<i>Calathus micropterus</i>	(Duftschmid, 1812)	ZOO	16	38.88	136.17
<i>Calathus minutus</i>	Gautier, 1866	ZOO	2	0.08	0.40
<i>Calathus mollis</i>	Marsham, 1802	ZOO	6	1.29	4.74
<i>Calathus rotundicollis</i>	Dejean, 1828	ZOO	11	9.81	29.96
<i>Callistus lunatus</i>	(F., 1775)	ZOO	1	0.02	0.14
<i>Calosoma inquisitor</i>	(L., 1758)	ZOO	1	0.02	0.14
<i>Calosoma maderae</i>	(F., 1775)	ZOO	3	17.21	118.49
<i>Calosoma sycophanta</i>	(L., 1758)	ZOO	2	0.04	0.20
<i>Carabus arvensis</i>	Herbst, 1784	ZOO	9	4.88	14.64
<i>Carabus auratus</i>	L., 1761	ZOO	2	0.60	3.90
<i>Carabus auronitens</i>	(F., 1792)	ZOO	11	18.06	58.67
<i>Carabus cancellatus</i>	Illiger, 1798	ZOO	3	0.42	2.13
<i>Carabus convexus</i>	F., 1775	ZOO	9	4.60	15.03
<i>Carabus coriaceus</i>	L., 1758	ZOO	5	0.73	3.78
<i>Carabus glabratus</i>	Paykull, 1790	ZOO	14	10.85	36.05
<i>Carabus granulatus</i>	L., 1758	ZOO	13	21.81	96.50
<i>Carabus hortensis</i>	L., 1758	ZOO	6	18.29	58.69
<i>Carabus intricatus</i>	L., 1761	ZOO	1	0.27	1.88
<i>Carabus irregularis</i>	F., 1792	ZOO	1	0.04	0.29
<i>Carabus lusitanicus</i>	Dejean, 1826	ZOO	13	15.94	37.21
<i>Carabus melancholicus</i>	F., 1798	ZOO	9	25.58	120.81
<i>Carabus monilis</i>	F., 1792	ZOO	5	3.27	20.64
<i>Carabus nemoralis</i>	Müller, 1764	ZOO	17	10.75	24.43
<i>Carabus problematicus</i>	Herbst, 1786	ZOO	13	56.75	157.31
<i>Carabus rugosus</i>	Deyrolle, 1858	ZOO	10	9.27	46.09
<i>Carabus sylvestris</i>	Dejean, 1826	ZOO	4	2.56	8.80
<i>Carabus violaceus</i>	L., 1758	ZOO	17	25.52	81.97
<i>Chlaenius chrysocephalus</i>	(Rossi 1790)	ZOO	2	2.13	14.43
<i>Chlaenius nigricornis</i>	(F., 1787)	ZOO	5	3.92	14.30
<i>Chlaenius nitidulus</i>	(Schrank, 1781)	ZOO	2	3.58	19.60
<i>Chlaenius olivieri</i>	(Crotch, 1870)	ZOO	4	3.65	22.81
<i>Chlaenius tristis</i>	(Schaller, 1783)	ZOO	2	0.04	0.20
<i>Chlaenius velutinus</i>	Duftschmid, 1812	ZOO	2	0.35	2.31
<i>Chlaenius vestitus</i>	(Paykull, 1790)	ZOO	1	0.06	0.43
<i>Cicindela campestris</i>	L., 1758	ZOO	6	0.33	1.36
<i>Cicindela maroccana</i>	Roeschke, 1891	ZOO	3	0.19	1.02
<i>Clivina fossor</i>	(L., 1758)	ZOO	12	7.83	30.98
<i>Cychrus attenuatus</i>	F., 1798	ZOO	8	14.00	45.03
<i>Cychrus caraboides</i>	(L., 1758)	ZOO	17	5.33	12.49
<i>Cymindis vaporariorum</i>	(L., 1758)	ZOO	1	0.02	0.14
<i>Demetrias atricapillus</i>	(L., 1758)	ZOO	1	0.02	0.14
<i>Dolichus halensis</i>	(Schaller, 1783)	ZOO	2	0.06	0.32
<i>Dromius agilis</i>	(F., 1787)	ZOO	1	0.02	0.14
<i>Dromius linearis</i>	(Olivier, 1795)	ZOO	2	0.13	0.73
<i>Drypta dentata</i>	(Rossi, 1790)	ZOO	1	0.02	0.14
<i>Drypta distincta</i>	Rossi, 1792	ZOO	1	0.08	0.58
<i>Dyschirius globosus</i>	(Herbst, 1784)	ZOO	1	0.08	0.58
<i>Elaphrus cupreus</i>	Duftschmid, 1812	ZOO	3	0.63	3.41
<i>Elaphrus uliginosus</i>	F., 1792	ZOO	3	0.13	0.53
<i>Elaphrus riparius</i>	(L., 1758)	ZOO	1	0.02	0.14
<i>Epomis circumscriptus</i>	(Duftschmid, 1812)	ZOO	1	0.02	0.14

<i>Laemostenus terricola</i>	(Herbst, 1784)	ZOO	6	0.54	1.65
<i>Leistus expansus</i>	Putzeys, 1874	ZOO	3	0.94	5.08
<i>Leistus ferrugineus</i>	(L., 1758)	ZOO	5	0.17	0.56
<i>Leistus fulvibarbis</i>	Dejean, 1826	ZOO	3	0.08	0.35
<i>Leistus nitidus</i>	Dufts Schmid, 1812	ZOO	5	0.29	1.22
<i>Leistus piceus</i>	Froelich, 1799	ZOO	4	0.19	0.73
<i>Leistus rufomarginatus</i>	(Dufts Schmid, 1812)	ZOO	2	0.04	0.20
<i>Leistus spinibarbis</i>	(F., 1775)	ZOO	7	11.13	38.88
<i>Leistus terminatus</i>	(Hellwig in Panzer, 1793)	ZOO	14	4.67	17.15
<i>Licinus depressus</i>	(Paykull, 1790)	ZOO	5	1.06	3.73
<i>Licinus punctatulus</i>	(F., 1792)	ZOO	3	0.06	0.24
<i>Loricera pilicornis</i>	(F., 1775)	ZOO	16	11.50	32.23
<i>Masoreus wetterhallii</i>	(Gyllenhal, 1813)	ZOO	2	0.13	0.73
<i>Microlestes luctuosus</i>	Holdhaus, 1904	ZOO	1	0.02	0.14
<i>Microlestes minutulus</i>	(Goeze, 1777)	ZOO	1	0.02	0.14
<i>Microlestes negrita</i>	Wollaston, 1854	ZOO	3	0.29	1.18
<i>Molops elatus</i>	(F., 1801)	ZOO	1	0.02	0.14
<i>Molops piceus</i>	(Panzer, 1793)	ZOO	5	0.65	2.29
<i>Nebria brevicollis</i>	(F., 1792)	ZOO	18	211.94	455.39
<i>Nebria rufescens</i>	Strom, 1768	ZOO	6	0.67	2.60
<i>Nebria salina</i>	Fairmaire & Laboulbène, 1854	ZOO	13	39.83	153.39
<i>Notiophilus aestuans</i>	Motschulsky, 1864	ZOO	1	0.02	0.14
<i>Notiophilus aquaticus</i>	(L., 1758)	ZOO	1	0.02	0.14
<i>Notiophilus biguttatus</i>	(F., 1779)	ZOO	20	3.15	6.19
<i>Notiophilus germinyi</i>	(Fauvel, 1863)	ZOO	2	0.06	0.32
<i>Notiophilus marginatus</i>	(Gene, 1839)	ZOO	3	0.13	0.53
<i>Notiophilus palustris</i>	(Dufts Schmid, 1812)	ZOO	2	0.04	0.20
<i>Notiophilus quadripunctatus</i>	Dejean, 1826	ZOO	5	0.19	0.61
<i>Notiophilus rufipes</i>	Curtis, 1829	ZOO	1	0.02	0.14
<i>Notiophilus substriatus</i>	Waterhouse, 1833	ZOO	1	0.02	0.14
<i>Olisthopus fuscatus</i>	Dejean, 1828	ZOO	3	0.15	0.74
<i>Olisthopus hispanicus</i>	Dejean, 1828	ZOO	4	0.15	0.55
<i>Olisthopus rotundatus</i>	(Paykull, 1790)	ZOO	3	0.60	3.38
<i>Olisthopus sturmii</i>	(Dufts Schmid, 1812)	ZOO	1	0.02	0.14
<i>Panagaeus bipustulatus</i>	(F., 1775)	ZOO	6	0.71	2.38
<i>Panagaeus cruxmajor</i>	(L., 1758)	ZOO	1	0.08	0.58
<i>Paranchus albipes</i>	F., 1796	ZOO	2	0.29	1.54
<i>Patrobus assimilis</i>	Chaudoir, 1844	ZOO	4	0.38	1.59
<i>Patrobus atrorufus</i>	(Ström, 1768)	ZOO	13	26.79	73.68
<i>Penetretus rufipennis</i>	(Dejean, 1828)	ZOO	4	0.40	1.43
<i>Poecilus kugelanni</i>	(Panzer, 1797)	ZOO	8	1.10	3.75
<i>Poecilus purpurascens</i>	(Dejean, 1828)	ZOO	5	0.40	1.28
<i>Poecilus sericeus</i>	Fischer von Waldheim, 1824	ZOO	1	0.02	0.14
<i>Poecilus versicolor</i>	(Sturm, 1824)	ZOO	13	20.81	87.31
<i>Pterostichus adstrictus</i>	Eschscholtz, 1823	ZOO	4	0.98	5.08
<i>Pterostichus aethiops</i>	(Panzer, 1797)	ZOO	2	0.23	1.32
<i>Pterostichus anthracinus</i>	(Illiger, 1798)	ZOO	2	1.81	11.84
<i>Pterostichus brevicornis</i>	Kirby, 1837	ZOO	1	0.02	0.14
<i>Pterostichus burmeisteri</i>	Heer, 1841	ZOO	5	7.56	31.01
<i>Pterostichus cristatus</i>	(Dufour, 1820)	ZOO	6	0.96	3.26
<i>Pterostichus cursor</i>	(Dejean, 1828)	ZOO	1	0.02	0.14
<i>Pterostichus diligens</i>	(Sturm, 1824)	ZOO	13	1.38	3.36
<i>Steropus globosus</i>	(Quensel, 1806)	ZOO	12	39.35	123.12
<i>Pterostichus macer</i>	(Marsham, 1802)	ZOO	1	0.02	0.14

<i>Pterostichus madidus</i>	(F., 1775)	ZOO	18	722.35	3136.63
<i>Pterostichus melanarius</i>	(Illiger, 1798)	ZOO	30	278.83	523.99
<i>Pterostichus multipunctatus</i>	(Dejean, 1828)	ZOO	4	40.73	255.22
<i>Pterostichus niger</i>	(Schaller, 1783)	ZOO	25	106.60	190.94
<i>Pterostichus nigrita</i>	(Paykull, 1790)	ZOO	23	10.48	25.75
<i>Pterostichus oblongopunctatus</i>	(F., 1787)	ZOO	21	17.48	36.30
<i>Pterostichus panzeri</i>	(Panzer, 1805)	ZOO	4	0.52	2.43
<i>Pterostichus pumilio</i>	(Dejean, 1828)	ZOO	3	0.15	0.65
<i>Pterostichus quadrifoveolatus</i>	Letzner, 1852	ZOO	1	0.02	0.14
<i>Pterostichus rhaeticus</i>	Heer, 1837	ZOO	2	0.15	0.71
<i>Pterostichus strenuus</i>	(Panzer, 1797)	ZOO	22	22.73	98.61
<i>Pterostichus unctulatus</i>	(Duftschmid, 1812)	ZOO	3	4.35	24.71
<i>Pterostichus vernalis</i>	(Panzer, 1796)	ZOO	20	4.23	14.22
<i>Scarites cyclops</i>	Bedel, 1895	ZOO	2	0.31	1.60
<i>Stomis pumicatus</i>	(Panzer, 1796)	ZOO	3	0.10	0.42
<i>Syntomus foveatus</i>	(Fourcroy, 1785)	ZOO	5	1.06	4.07
<i>Syntomus foveolatus</i>	Dejean, 1831	ZOO	2	0.13	0.73
<i>Syntomus fuscomaculatus</i>	(Motschulsky, 1844)	ZOO	1	0.02	0.14
<i>Syntomus pallipes</i>	(Dejean, 1825)	ZOO	2	0.04	0.20
<i>Trechus cunicolorum</i>	Méquignon, 1931	ZOO	2	0.04	0.20
<i>Trechus discus</i>	(F., 1792)	ZOO	1	0.04	0.29
<i>Trechus fulvus</i>	Dejean, 1831	ZOO	2	0.06	0.32
<i>Trechus micros</i>	(Herbst, 1784)	ZOO	5	1.27	7.38
<i>Trechus obtusus</i>	Erichson, 1837	ZOO	20	16.44	47.32
<i>Trechus quadristriatus</i>	(Schränk, 1781)	ZOO	19	33.40	118.24
<i>Trechus rivularis</i>	(Gyllenhal, 1810)	ZOO	3	0.10	0.47
<i>Trechus rubens</i>	(F., 1792)	ZOO	1	0.06	0.43
<i>Trechus secalis</i>	(Paykull, 1790)	ZOO	6	9.71	40.26
<i>Trichocellus placidus</i>	(Gyllenhal, 1827)	ZOO	3	0.08	0.35
<i>Trymosternus onychinus</i>	Dejean, 1825	ZOO	1	0.02	0.14

Table S1. Mean (\pm 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.

Habitat class	Spain	Finland	France	Hungary	Ireland	Portugal	Switzerland	Scotland
Phytophages								
Coniferous forest	0.00 (16)	2.08 \pm 0.99 (50)	0.88 \pm 0.46 (25)	7.11 \pm 1.44 (9)	0.380 \pm 0.15 (32)	–	0.00 (4)	0.33 \pm 0.23 (42)
Broadleaf forest	0.43 \pm 0.33 (37)	0.00 (1)	1.11 \pm 1.00 (27)	28.21 \pm 6.69 (42)	2.23 \pm 0.93 (13)	1.56 \pm 0.67 (70)	0.00 (1)	1.00 \pm 1.00 (7)
Mixed forest	–	1.19 \pm 0.36 (16)	–	–	–	–	0.68 \pm 0.50 (44)	2.33 \pm 2.33 (3)
Extensive grassland	–	0.00 (1)	14.52 \pm 3.39 (23)	54.50 \pm 21.58 (26)	–	9.50 \pm 9.50 (2)	15.39 \pm 8.51 (23)	–
Intensive grassland	13.85 \pm 13.19 (13)	27.33 \pm 20.88 (3)	40.67 \pm 14.17 (3)	–	7.20 \pm 1.98 (20)	4.13 \pm 2.05 (8)	17.22 \pm 10.46 (23)	9.63 \pm 4.51(30)
Permanent crop	–	9.20 \pm 4.96 (5)	0.00 (4)	–	–	–	0.00 (1)	–
Rotational agriculture	5.97 \pm 3.43 (30)	50.35 \pm 13.18 (20)	80.21 \pm 51.48 (14)	137.37 \pm 32.46 (19)	54.45 \pm 14.75 (31)	50.81 \pm 9.31 (16)	–	10.69 \pm 2.31 (13)
Zoophages								
Coniferous forest	40.13 \pm 9.79 (16)	49.76 \pm 9.22 (50)	75.64 \pm 13.80 (25)	52.56 \pm 10.52 (9)	431.31 \pm 52.12 (32)	–	81.50 \pm 23.39 (4)	95.10 \pm 10.18 (42)
Broadleaf forest	28.95 \pm 3.65 (37)	112.00 \pm 0.00 (1)	62.74 \pm 7.39 (27)	91.62 \pm 14.88 (42)	387.00 \pm 47.00 (13)	35.90 \pm 5.92 (70)	55.00 \pm 0.00 (1)	129.00 \pm 39.66 (7)
Mixed forest	–	79.38 \pm 22.74 (16)	–	–	–	–	115.95 \pm 12.06 (44)	65.00 \pm 5.51(3)
Extensive grassland	–	61.00 \pm 0.00 (1)	11.30 \pm 4.57 (23)	113.80 \pm 13.08 (26)	–	14.50 \pm 2.50 (2)	136.26 \pm 29.70 (23)	–
Intensive grassland	78.62 \pm 13.91 (13)	176.33 \pm 55.31 (3)	76.00 \pm 55.89 (3)	–	222.75 \pm 48.41 (20)	70.50 \pm 12.61(8)	127.32 \pm 24.13 (23)	251.17 \pm 32.45 (30)
Permanent crop	–	93.60 \pm 22.38 (5)	42.50 \pm 16.54 (4)	–	–	–	94.00 \pm 0.00 (1)	–
Rotational agriculture	155.57 \pm 40.62 (30)	238.75 \pm 33.36 (20)	66.21 \pm 35.25 (14)	197.11 \pm 33.21(19)	1651.23 \pm 161.70 (31)	65.69 \pm 7.75 (16)	–	340.00 \pm 63.07 (13)

Table S2. Mean (\pm 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.

Habitat class	Spain	Finland	France	Hungary	Ireland	Portugal	Switzerland	Scotland
Zoophages								
Coniferous forest	1.65 \pm 0.10 (14)	1.92 \pm 0.06 (34)	2.03 \pm 0.05 (24)	1.96 \pm 0.06 (8)	1.91 \pm 0.04 (32)	–	1.83 \pm 0.09 (4)	1.97 \pm 0.03 (42)
Broadleaf forest	1.78 \pm 0.06 (31)	2.02 \pm 0.00 (1)	1.94 \pm 0.04 (25)	1.79 \pm 0.05 (36)	2.08 \pm 0.05 (13)	1.79 \pm 0.05 (56)	2.05 0.00 \pm (1)	2.06 \pm 0.15 (7)
Mixed forest	–	2.06 \pm 0.09 (13)	–	–	–	–	1.83 \pm 0.04 (43)	2.03 \pm 0.06 (3)
Extensive grassland	–	2.07 \pm 0.00 (1)	1.86 \pm 0.12(8)	1.81 \pm 0.07 (23)	–	2.16 \pm 0.49 (2)	2.27 \pm 0.04 (20)	–
Intensive grassland	1.75 \pm 0.10 (13)	2.01 \pm 0.18 (3)	1.52 \pm 0.09 (2)	–	2.28 \pm 0.04 (20)	1.87 \pm 0.08 (8)	2.23 \pm 0.05 (22)	2.13 \pm 0.06 (30)
Permanent crop	–	1.98 \pm 0.11 (5)	1.88 \pm 0.06 (3)	–	–	–	1.96 \pm 0.00 (1)	–
Rotational agriculture	1.68 \pm 0.04 (30)	1.93 \pm 0.04 (20)	1.89 \pm 0.13 (6)	1.84 \pm 0.04 (19)	1.87 \pm 0.05 (31)	1.72 \pm 0.06 (16)	–	2.34 \pm 0.03 (13)
Carabidae (total)								
Coniferous forest	1.65 \pm 0.10 (14)	1.97 \pm 0.06 (34)	2.05 \pm 0.05 (24)	2.15 \pm 0.07 (8)	1.91 \pm 0.04 (32)	–	1.83 \pm 0.09 (4)	1.97 \pm 0.03 (42)
Broadleaf forest	1.79 \pm 0.06 (31)	2.02 \pm 0.00 (1)	1.95 \pm 0.04 (25)	2.06 \pm 0.05 (40)	2.09 \pm 0.05 (13)	1.84 \pm 0.05 (56)	2.05 0.00 \pm (1)	2.07 \pm 0.15 (7)
Mixed forest	–	2.04 \pm 0.09 (14)	–	–	–	–	1.81 \pm 0.04 (43)	2.09 \pm 0.01(3)
Extensive grassland	–	2.07 \pm 0.00 (1)	1.60 \pm 0.11(16)	2.07 \pm 0.05 (26)	–	2.06 \pm 0.39 (2)	2.30 \pm 0.04 (20)	–
Intensive grassland	1.77 \pm 0.10 (13)	2.17 \pm 0.18 (3)	1.49 \pm 0.25 (3)	–	2.33 \pm 0.04 (20)	1.95 \pm 0.07 (8)	2.24 \pm 0.05 (22)	2.17 \pm 0.06 (30)
Permanent crop	–	2.12 \pm 0.10 (5)	1.88 \pm 0.06 (3)	–	–	–	1.96 \pm 0.00 (1)	–
Rotational agriculture	1.71 \pm 0.05 (30)	2.11 \pm 0.04 (20)	1.68 \pm 0.14 (10)	2.18 \pm 0.03 (19)	1.93 \pm 0.05 (31)	1.95 \pm 0.04 (16)	–	2.37 \pm 0.03 (13)