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](10.1111/j.1365-2311.2010.01175.x)

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],

Győző Szél[10], Eva Ivits[11], Petra Adler[12], Jochum Markus[12], and Allan D. Watt[1]

[1] NERC Centre for Ecology and Hydrology, Bush Estate, Penicuik, Edinburgh EH26 0QB, UK
[2] NERC Centre for Ecology and Hydrology, Crowmarsh Gifford, Wallingford, OX10 8BB, UK
[3] Department of Biological and Environmental Sciences, P. O. Box 35, FI-40014 University of Jyväskylä, Finland
[4] Department of Biological and Environmental Sciences, P. O. Box 65, FI-0014 University of Helsinki, Finland
[5] Department of Zoology, University College Dublin, Belfield, Dublin 4, Ireland
[6] UMR 137 BioSol. Institut de Recherche pour le Développement - Centre Ile de France / Universités de Paris VI, VII et XII, 32, Avenue Henri de Varagnat, F-93143 Bondy Cedex - France
[7] Department of Zoology, Faculty of Veterinary, University of Murcia. Aptdo 4021, 30071 Murcia, Spain
[8] Faculdade de Ciências da Universidade de Lisboa, Departamento de Biologia Animal/Centro de Biologia Ambiental, R. Ernesto de Vasconcelos, Ed. C2, 3º Piso, Campo Grande, 1749-016 Lisboa, Portugal
[9] Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstr. 111, CH-8903 Birmensdorf, Switzerland
[10] Hungarian Natural History Museum, Department of Zoology, H-1088 Budapest, Barossu. 13, Hungary
[11] Joint Research Centre (JRC) - European Commission Institute for Environment and Sustainability, Rural, Water and Ecosystems Resources Unit, AGRI-ENV Action, via E. Fermi, 1; TP 460, 21020 Ispra (VA), Italy
[12] Abt. Fernerkundung und LIS, Tennenbacherstr. 4, D-79106 Freiburg, Germany

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

Running title: *Trophic diversity, habitat, & landscape structure*

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.

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

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).

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 & Tscharntke, 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 km^2

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 km^2) 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 1km^2

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 1km^2 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 $\times$ country combination

258   are shown in Tables S1 & S2 in Appendix S3.

259

260   Accounting for these significant habitat $\times$ 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 × 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

14

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 congenerics 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 papers 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 an useful approach to understanding biodiversity

393 change across regions (Kruess & Tscharntke, 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

References

Benton, T.G., Vickery, J.A., & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182-188.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekotter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., van Wingerden, W., Zobel, M., & Edwards, P.J. (2008) Indicators for biodiversity in agricultural landscapes: a pan-European study. *Journal of Applied Ecology*, **45**, 141-150.

Borrvall, C. & Ebenman, B. (2006) Early onset of secondary extinctions in ecological communties following the loss of top predators. *Ecology Letters*, **9**, 435-442.

Chust, G., Pretus, J.L., Ducrot, D., Bedos, A., & Deharveng, L. (2003) Response of soil fauna to landscape heterogeneity: Determining optimal scales for biodiversity modeling. *Conservation Biology*, **17**, 1712-1723.

Cole, L.J., McCracken, D.I., Dennis, P., Downie, I.S., Griffin, A.L., Foster, G.N., Murphy, K.J., & Waterhouse, T. (2002) Relationships between agricultural management and ecological groups of ground beetles (Coleoptera : Carabidae) on Scottish farmland. *Agriculture Ecosystems & Environment*, **93**, 323-336.

Colwell, R.K. (2005) EstimateS: statistical estimation of species richness and shared species from samples.

Dauber, J., Purtauf, T., Allspach, A., Frisch, J., Voigtlander, K., & Wolters, V. (2005) Local vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility. *Global Ecology and Biogeography*, **14**, 213-221.

Davies, K.F. & Margules, C.R. (1998) Effects of habitat fragmentation on carabid beetles: experimental evidence. *Journal of Animal Ecology*, **67**, 460-471.

Davies, K.F., Margules, C.R., & Lawrence, K.F. (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology*, **81**, 1450-1461.

Davies, R.G., Eggleton, P., Jones, D.T., Gathorne-Hardy, F.J., & Hernandez, L.M. (2003) Evolution of termite functional diversity: analysis and synthesis of local ecological and 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. & Tscharntke, 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., & Tscharntke, 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., & Tscharntke, 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 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 $\pm$ SEM. Fitted lines are included where the slopes are statistically significant from zero (p < 0.05).

Figure 1.
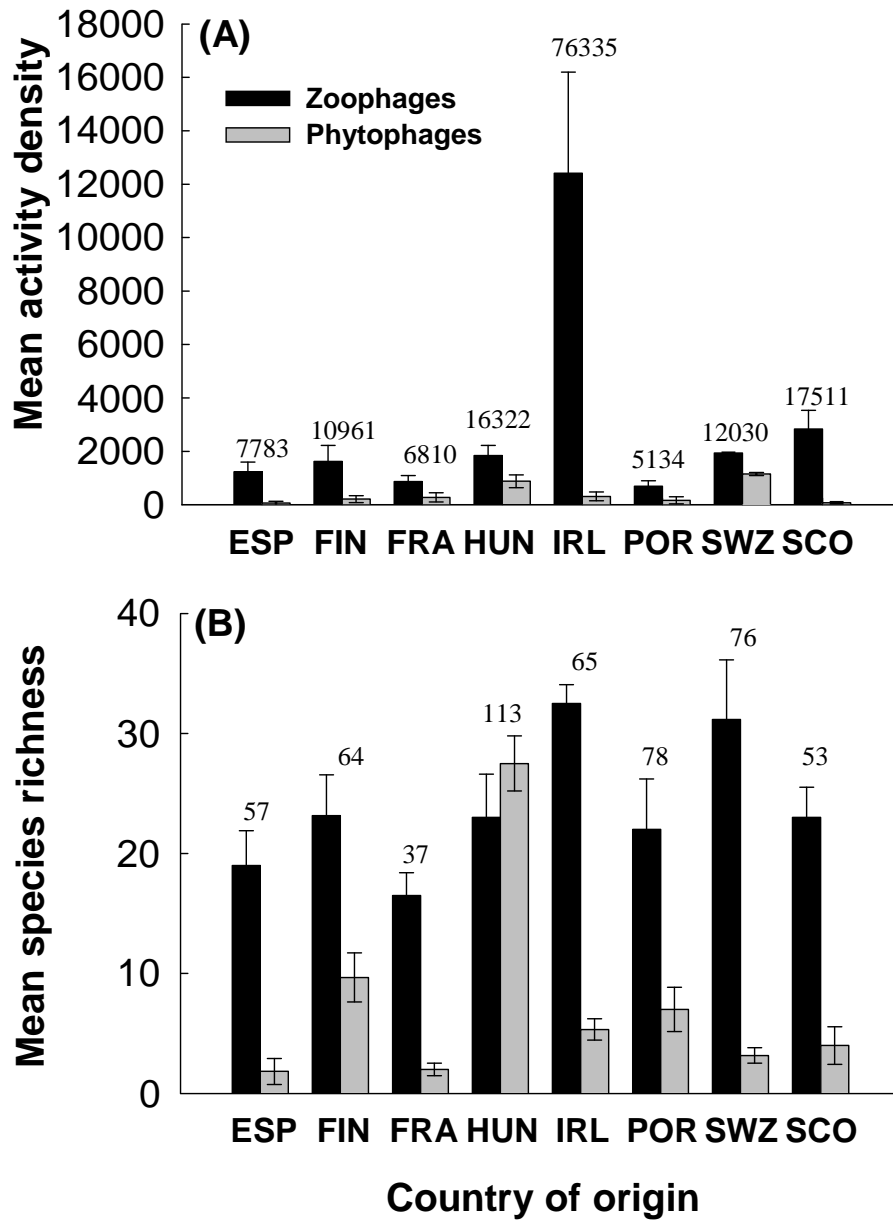
Figure 2
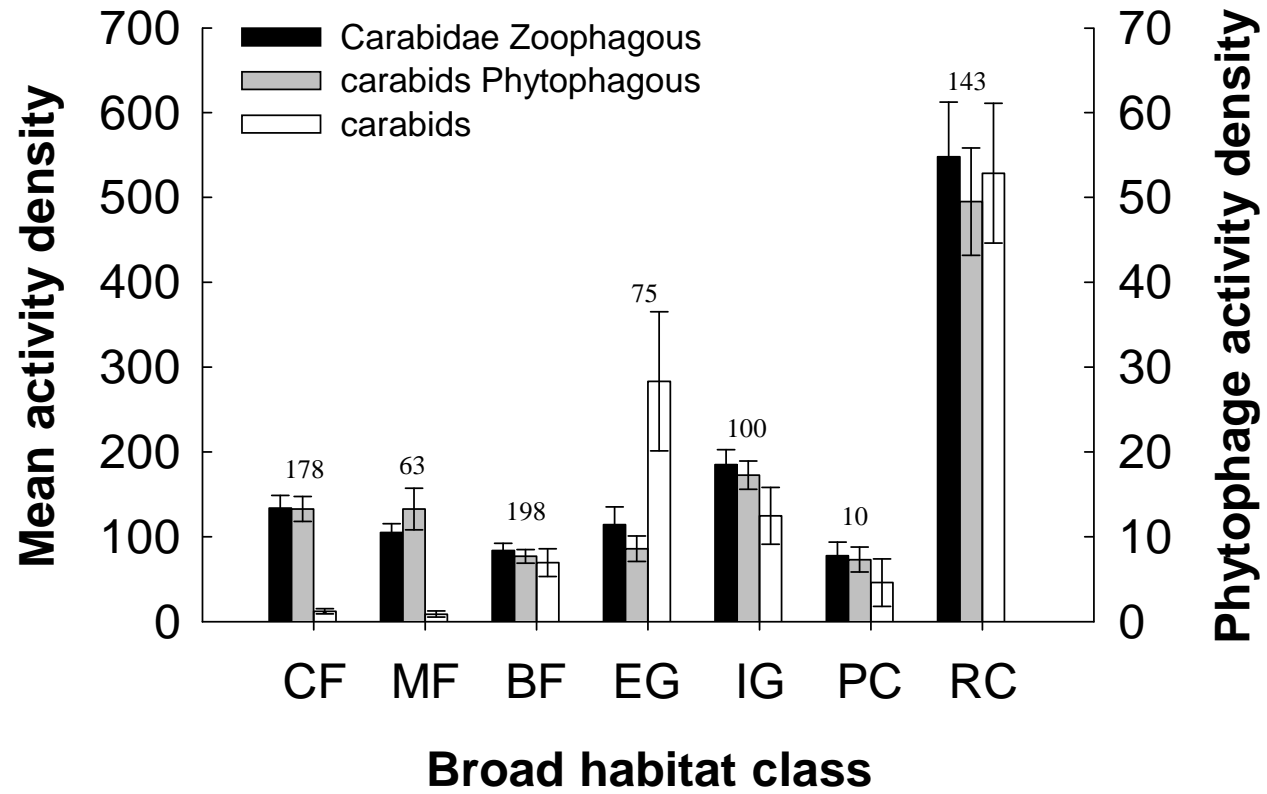
Figure 3
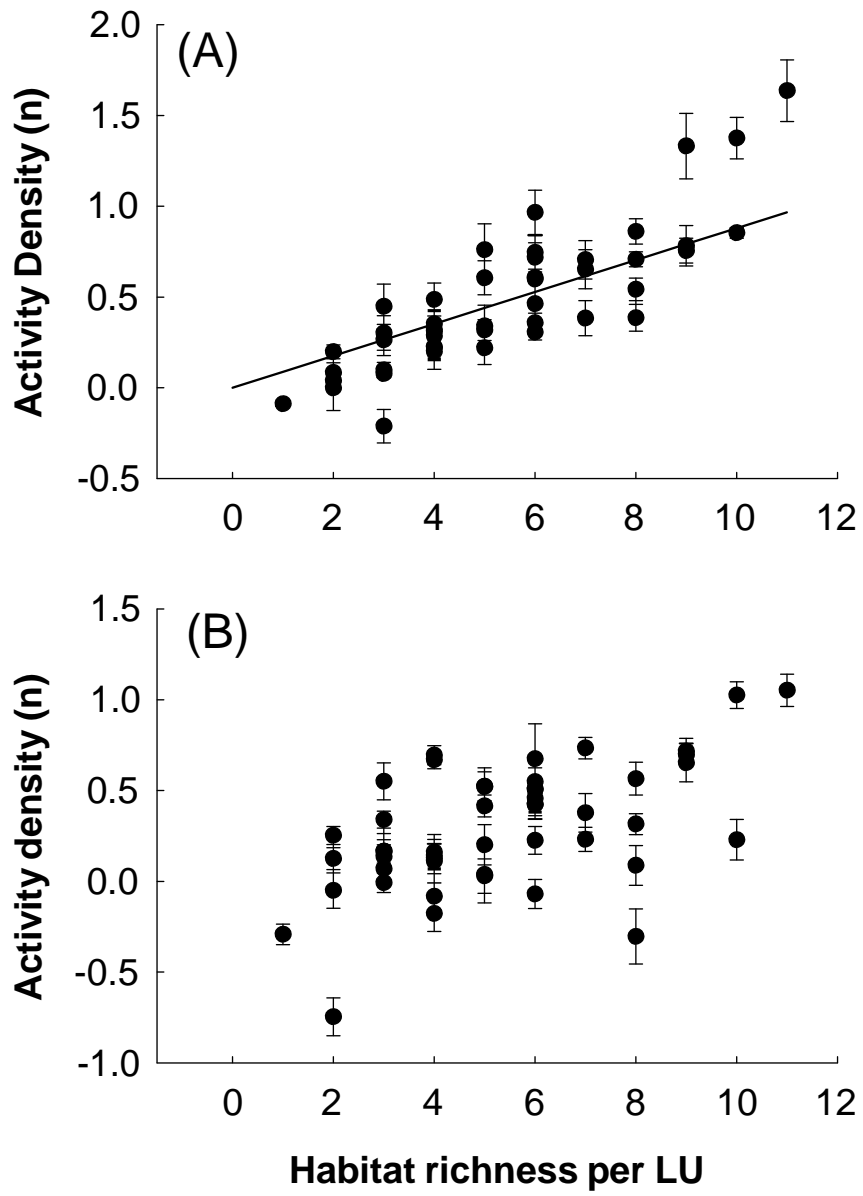
Table 1. GLMM results summary for activity density of Carabidae and trophic groups (zoophages, phytophages) in relation to source country, habitat, and composition (percentage forest cover) and heterogeneity (habitat richness) of $1km^2$ landscape units (LUs). Numerator (ndf) and Denominator (ddf) degrees 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	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

28

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 1km^2 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	Sampling year	MPE	0.26 $_{(1,46)}$	0.612
	Country of origin	**MPE**	**3.45 $_{(7,49)}$**	**0.005**
Random effect estimate:	**Habitat**	**MPE**	**0.54 $_{(6,411)}$**	**0.775**
LU(Country) = 0.032	**Country × habitat**	**MPE**	**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**	**2.44 $_{(7,46)}$**	**0.033**
Random effect estimate:	**Habitat**	**MPE**	**0.73 $_{(6,387)}$**	**0.627**
LU(Country) = 0.031	**Country × habitat**	**MPE**	**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

Vanbergen et al Appendix S1.

Fig. 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
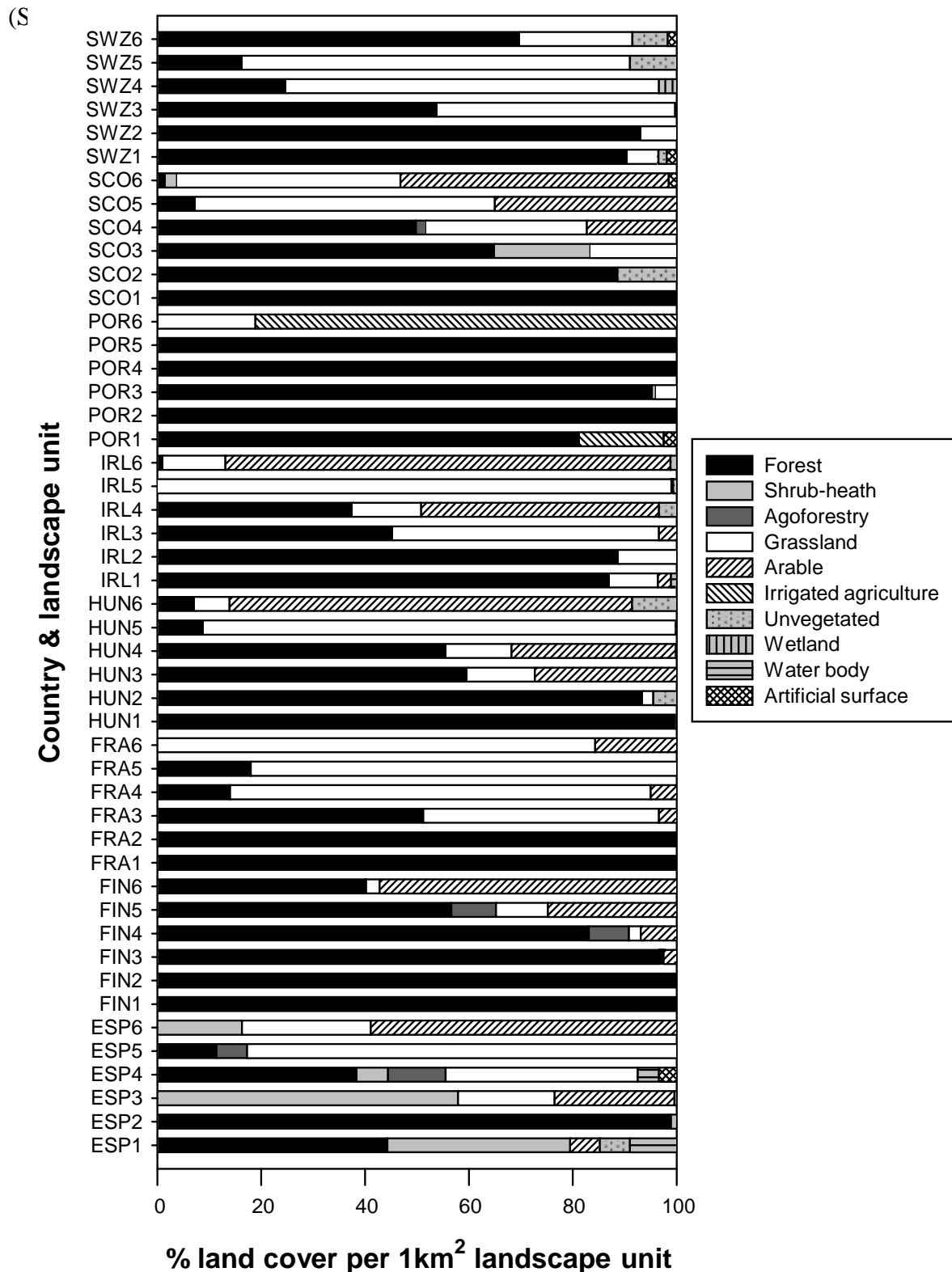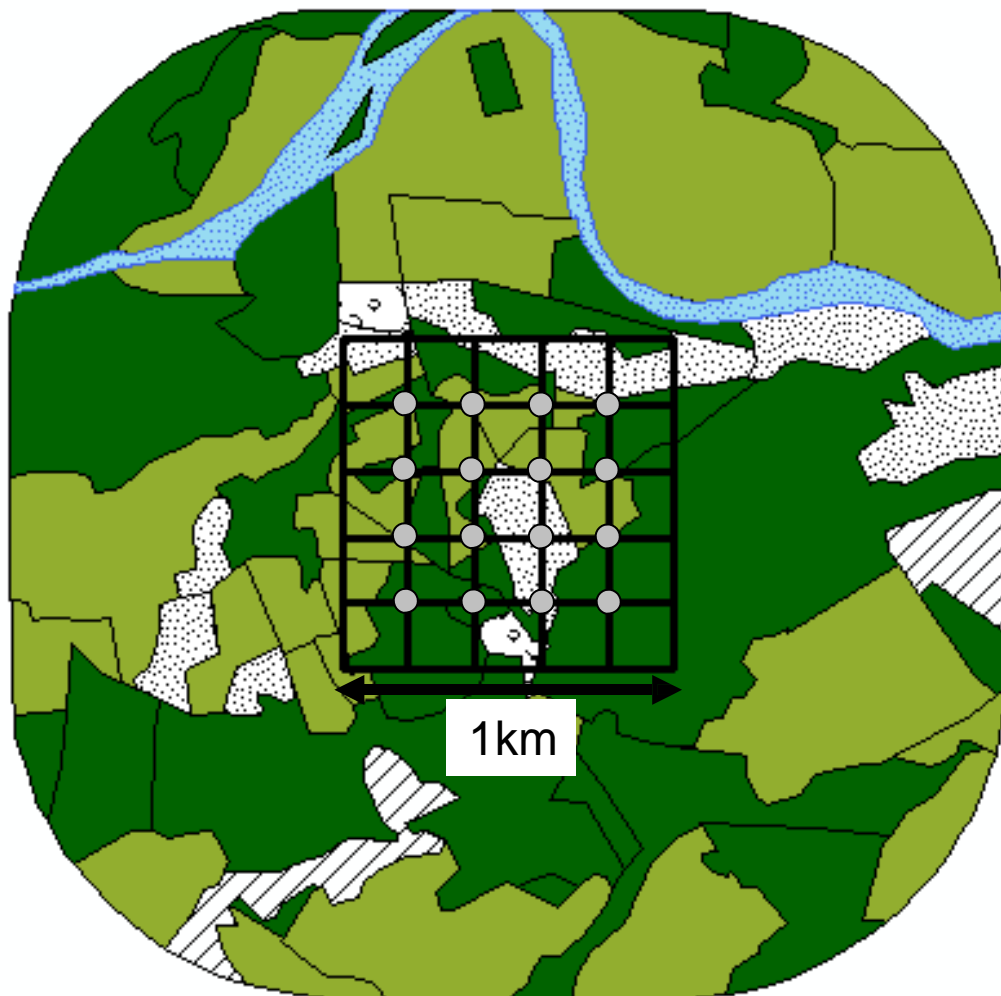
(S

Fig. S2. An example of a GIS map (ArcView 3.1) of a 1km^2 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
Amara aenea	(Degeer, 1774)	PHY	23	11.73	48.02
Amara anthobia	Villa & Villa, 1833	PHY	2	0.48	2.68
Amara apricaria	(Paykull, 1790)	PHY	3	0.29	1.41
Amara aulica	(Panzer, 1797)	PHY	5	0.33	1.74
Amara bifrons	(Gyllenhal, 1810)	PHY	7	2.00	9.12
Amara brunnea	(Gyllenhal, 1810)	PHY	5	0.56	1.81
Amara chaudoiri incognita	Fassati, 1946	PHY	1	0.02	0.14
Amara communis	(Panzer, 1797)	PHY	9	1.25	5.61
Amara consularis	(Duftschmid, 1812)	PHY	4	0.42	2.07
Amara convexior	Stephens, 1828	PHY	7	2.63	8.19
Amara cursitans	(Zimmermann, 1832)	PHY	1	0.02	0.14
Amara equestris	(Duftschmid, 1812)	PHY	2	0.25	1.36
Amara eurynota	(Panzer, 1797)	PHY	6	2.33	12.81
Amara familiaris	(Duftschmid, 1812)	PHY	10	0.88	2.23
Amara fervida	Coquerel, 1858	PHY	1	0.02	0.14
Amara fulva	(Müller, 1776)	PHY	8	0.67	1.87
Amara infima	(Duftschmid, 1812)	PHY	1	0.04	0.29
Amara ingenua	(Duftschmid, 1812)	PHY	1	0.83	5.77
Amara lucida	(Duftschmid, 1812)	PHY	4	0.23	0.83
Amara lunicollis	Schiødte, 1837	PHY	10	1.85	7.23
Amara majuscula	(Chaudoir, 1850)	PHY	1	0.02	0.14
Amara montivaga	Sturm, 1825	PHY	3	0.19	0.91
Amara municipalis	(Duftschmid, 1812)	PHY	1	0.02	0.14
Amara nitida	Sturm, 1825	PHY	4	0.42	1.88
Amara ovata	(F., 1792)	PHY	7	1.04	4.72
Amara plebeja	(Gyllenhal, 1810)	PHY	9	8.33	32.38
Amara quenseli	(Schönherr, 1806)	PHY	1	0.02	0.14
Amara saphyrea	Dejean, 1828	PHY	5	1.33	5.62
Amara similata	(Gyllenhal, 1810)	PHY	8	0.40	1.16
Amara tibialis	(Paykull, 1798)	PHY	1	0.02	0.14
Amara tricuspidata	Dejean, 1831	PHY	3	0.06	0.24
Bradycellus csikii	Laczó, 1912	PHY	1	0.02	0.14
Bradycellus harpalinus	(Audinet-Serville, 1821)	PHY	2	0.06	0.32
Bradycellus verbasci	(Duftschmid, 1812)	PHY	2	0.04	0.20
Diachromus germanus	(L., 1758)	PHY	1	0.02	0.14
Dixus clypeatus	(Rossi, 1790)	PHY	1	0.06	0.43
Dixus sphaerocephalus	(Olivier, 1795)	PHY	1	0.02	0.14
Graniger cordicollis	Serville, 1821	PHY	1	0.02	0.14
Harpalus affinis	(Schrank, 1781)	PHY	5	0.58	2.42
Harpalus albanicus	Reitter, 1900	PHY	2	0.04	0.20
Harpalus anxius	(Duftschmid, 1812)	PHY	2	0.10	0.52
Harpalus atratus	(Latreille, 1804)	PHY	2	0.23	1.45
Harpalus attenuatus	(Stephens, 1828)	PHY	3	0.33	1.60
Harpalus azureus	(F., 1775)	PHY	4	0.21	0.85
Harpalus autumnalis	(Duftschmid, 1812)	PHY	2	0.04	0.20
Harpalus calceatus	(Duftschmid, 1812)	PHY	3	0.94	5.66

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

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

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

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

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

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.

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

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.

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