

Carabid beetle occurrence at the edges of oak and beech forests in NW Spain

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Abstract. We examined the occurrence of carabid beetles (Coleoptera, Carabidae) at the edges of oak (*Quercus pyrenaica*) and beech (*Fagus sylvatica*) forests in León, NW Spain. Pitfall traps were used to collect beetles from April to October 2002, and leaf litter cover and depth were measured. Traps were placed at three distances (0, 50 and 100 m) from the edges of eight forest patches. A total of 5436 carabids belonging to 43 species were collected. We found no statistically significant edge effect at the carabid assemblage level, i.e. the number of species and individuals was not higher at the edge compared to the forest interior. However, individual species were affected by distance from the edge. Five of the 14 species analysed responded predictably to the edge, three of them statistically significantly so. Four species did not respond in the predicted direction, two of them statistically significantly so. We found a considerable difference between forest types in terms of carabid assemblage composition and response to the edge. Oak forests were species richer and beech forests had a higher number of individuals. These differences were probably due to small-scale habitat heterogeneity in the oak forest patches, caused by man, and the homogeneous structure of beech forests. Leaf litter appeared to be one possible factor influencing the distribution of some species from the interior to the edge of forests.

INTRODUCTION

A consequence of fragmentation is an increase in edge habitat per unit area compared to continuous habitats (Haila, 1999; Matlack & Litvaitis, 1999). This edge habitat can have either positive or negative effects on organisms (Angelstam, 1992; Matlack & Litvaitis, 1999), and represents a zone characterised by extreme abiotic conditions that affect species and ecological processes (Debinski & Holt, 2000). The edge effect is complex and is defined as a group of phenomena, i.e. changes in environmental and biological conditions, which result from the interaction between two adjacent ecosystems separated by an abrupt transition zone (Murcia, 1995).

Abiotic changes that occur at the edge of forests include higher light intensity, temperature and wind, which may cause edges to be drier than forest interiors (Murcia, 1995; Didham, 1997a; Kapos et al., 1997; Laurance, 1997). Forest edges are also characterised by increased tree mortality, invasion of generalist plants and lower dicotyledonous seedling densities (Murcia, 1995; Kapos et al., 1997; Turton & Freiburger, 1997). These features vary with edge age and matrix type (Kolasa & Zalewski, 1995; Murcia, 1995; Donovan et al., 1997; Kapos et al., 1997).

The variability in the abiotic environment and vegetation characteristics at edges affect the distribution and composition of animals (Murcia, 1995; Didham, 1997b; Jokimäki et al., 1998) at different temporal and spatial scales (see Kolasa & Zalewski, 1995; Murcia, 1995; Risser, 1995). Examples of taxa sensitive to edge conditions include birds (Paton, 1994; McCollin, 1998), small mammals (Stevens & Husband, 1998) and amphibians (Demaynadier & Hunter, 1998).

Insects too are influenced by edge effects. Didham (1997b) argued that changes in abiotic factors that occur at edges are mainly responsible for the responses of invertebrates to fragmentation, especially in habitat specialist species. Carabid beetles have been used to study the effects of fragmentation (Niemelä et al., 1993; De Vries, 1996; Luff, 1996; Spence et al., 1996; Davies & Margules, 1998; Tischendorf, 1998; Abildsnes & Tømmerås, 2000) and are considered to be sensitive indicators of fragmentation (Niemelä, 2001; Rainio & Niemelä, 2003). However, the effects of habitat edges on carabids are ambiguous. Magura (2002) found a significantly higher species richness at the edge than in the interior of a forest in northern Hungary, while Kotze & Samways (2001) found no significant changes in carabid species richness across edges in Afrotropical forests in South Africa. Heliölä et al. (2001) showed that the carabid assemblage in the interior was similar to that at the edge of boreal forests in central Finland. This ambiguity may be because the response of individual species depends on their habitat requirements (Spence et al., 1996; Davies & Margules, 1998), and the different forest types studied.

The aim of this study is to test the effects of beech and oak forest edges on carabid beetle assemblages in NW Spain. We are unable to predict the pattern of overall carabid abundance at forest edges compared to interiors, as several authors record increases (Magura & Tóthmérész, 1998), decreases (Kotze & Samways, 2001; Magura et al., 2001a) or no change (Heliölä et al., 2001). We expect little change in the number of species, i.e. species richness, from the edge to the forest interior (Heliölä et al., 2001; Kotze & Samways, 2001), as open habitat species may be abundant at the edges and forest specialists in the interior. Should we find a higher carabid species richness at the forest edge we shall explore whether this is

due to the presence of edge-associated species (Spence et al., 1996; Matlack & Litvaitis, 1999; Heliölä et al., 2001; Magura et al., 2001b; Mólnar et al., 2001).

In terms of individual species, habitat generalists are expected to be little influenced by the edge, while forest specialist species are expected to be negatively influenced. Open habitat species are expected to be more abundantly collected at forest edges than interiors. We also expect a greater effect at the edges of beech than oak forests, since oak forests are more heterogeneous with open and dry areas in the forest interior. Beech forest interiors are more homogeneous in terms of environmental conditions such as temperature and darkness. Consequently, the transition between forest interior and edge is expected to be more abrupt in beech than oak forests.

MATERIAL AND METHODS

Study area

Beech (*Fagus sylvatica*) and oak (*Quercus pyrenaica*) forests are widely distributed in the mountainous region of León, NW Spain. Historically, this area was strongly influenced by man (Luis-Calabuig et al., 2000) and is characterised by forest habitat surrounded by a mosaic of agricultural and pastoral land. Consequently, the landscape consists of sharp boundaries between forest and the surrounding habitat. Little is known, however, about the distribution patterns and responses of carabid beetles across these sharp boundaries in NW Spain. In fact, very few studies exist on the relationships between carabid beetles and their habitat requirements (vegetation and soil characteristics) in Spain (e.g. Salgado et al., 1998; Gutiérrez et al., 2004).

The study was carried out in eight forest patches in the province of León, NW Spain (42°37'–43°6'N, 4°55'–5°12'W). We selected four oak (*Quercus pyrenaica*) and four beech (*Fagus sylvatica*) patches, each separated by more than 2 km. Oak forests are included in the *Festuco heterophyllae-Querceto pyrenaicae* sigmetum in the Mediterranean Region (Penas et al., 1995), and are located at altitudes between 884 and 922 m. Forest interiors are sunny, dry, with nutrient poor and stony soil, and with open areas that create high habitat heterogeneity. Forest edges are dominated by shrubs of the association *Genistello tridentatae-Ericetum aragonensis cistetosum laurifolii* in wet areas and the *Cytiso scoparii-Genistetum polygaliphyllae lavanduletosum pedunculatae* association in dry areas. There are also small oak saplings and dense herbaceous vegetation with *Festuca* and *Trifolium* species at the edges.

Beech forests belong to the *Blechno spicanti-Fageto sylvaticae* sigmetum in the Eurosiberian Region (Penas et al., 1995), at altitudes between 1250 and 1433 m. Forest interiors are wet, shaded and with a deep leaf litter layer. Forest edges are characterised by meadow vegetation (*Merendero pyrenaicae-Cynosuretum cristati*) with few shrubs (*Cytisus* and *Genista* species).

Sampling method

We used glass pitfall traps (depth 80 mm, diameter 70 mm) to sample the beetles. Traps were partly filled with 30% alcohol and detergent. We placed two 30 cm long plastic guides (—o—) per trap to increase carabid catches (Winder et al., 2001), and covered the traps with flat stones to prevent the traps from filling up with rain water and leaves. Beetles were collected over their whole activity period from April to October 2002, by keeping the traps open for 12–15 days each month. Five traps (1–2 m apart) were placed in a line at three distances in each

forest patch (at the edge, at 50 m and at 100 m into the forest patches). This resulted in a total number of 120 pitfall traps. Beetles were identified using standard keys (Jeannel, 1941–1942; Lindroth, 1974; Trautner & Geigenmüller, 1987) and the nomenclature follows Serrano (2003).

We estimated the coverage and depth of leaf litter at each distance from the edge (0, 50 and 100 m) within a 2 m radius of each of the groups of five traps.

Statistical analysis

We pooled the carabid catches at each sampling point, i.e. the catches in the five traps in a line at each distance from the edge (0, 50 and 100 m), and for the whole trapping period. This resulted in four replicate samples per distance from the edge per forest type. Carabid species were classified as forest specialists, generalists or open habitat species, according to the literature (see Table 1).

Generalised Linear Models were used for the statistical analyses. Species collected from at least 6 of the 12 samples in each forest type were analysed individually, while the rest of the species were pooled according to their classification as forest, open habitat or generalist species (Table 1). The response variables in the models were the number of individuals (overall and for individual species) and number of species, and the predictor variables leaf litter cover, leaf litter depth and distance from the edge (see Quinn & Keough, 2002). Leaf litter variables were included in the models but we did not make specific predictions regarding the responses of the beetles to litter. The effects of litter were explored if found statistically significant in the models, repeating the analyses for those species without leaf litter cover and depth to evaluate the effects of these characteristics on the pattern relative to the distance from the forest edge.

We assumed a clumped spatial distribution for carabid beetles (Niemelä et al., 1996) and consequently defined the response variables (i.e. abundance) in the analyses as following a negative binomial error distribution (White & Bennetts, 1996). Theta (θ), the dispersion parameter was, however, high for certain species, which were subsequently re-analysed by defining abundance as following a Poisson error distribution. Overall species richness was modelled following a Poisson error distribution.

In addition, we estimated distinctness in species composition at the three distances from the forest edge (0, 50 and 100 m) in each forest type, using the complementarity index in Colwell & Coddington (1995):

$$C_{jk} = U_{jk} / S_{jk},$$

where U_{jk} is the number of species unique to each distance within the forest type, defined as $U_{jk} = S_j + S_k - 2V_{jk}$, and S_{jk} is the total richness for two distances combined, defined as $S_{jk} = S_j + S_k - V_{jk}$. S_j and S_k represent the local richness at each distance, and V_{jk} is the number of species that occur at both distances. Complementarity values vary from 0 to 1, indicating high to low number of species in common, respectively.

RESULTS

A total of 5436 carabids belonging to 43 species were collected (Table 1). The most abundant species were the 2803 individuals of *Nebria asturiensis* (51.6% of the total catch), and 1321 individuals of *Pterostichus cantaber* (24.3%). Both species were collected from all 12 beech forests sites, but not from oak forests. *Cryobius cantabricus* (241 individuals) and *Carabus lineatus* (221 individuals) were also abundantly captured in beech forests. In oak forests, *Steropus globosus* was the most abundant

TABLE 1. Carabid beetles collected at three distances from the edges (0, 50 and 100 m) of beech and oak forest patches. Size = carabid beetle body size range in mm. Wings = wing morphology (b = brachypterous, micropterous or flightless, i.e. unable to fly; m = macropterous; D = dimorphic). Habitat = habitat association of the species (F = forest, G = generalist and O = open habitat species). Literature used: De la Fuente (1927), Jeannel (1941–1942), Lindroth (1974), Vázquez (1990), Andújar & Serrano (2001) and Ortuño & Marcos (2003).

	Size	Wings	Habitat	Beech Forest			Oak Forest			
				0 m	50 m	100 m	0 m	50 m	100 m	Total
<i>Agonum (Agonum) viridicupreum viridicupreum</i> (Goeze, 1777)	8.0–10.0	m	O				1			1
<i>Amara (Amara) aenea</i> (De Geer, 1774)	6.0–8.0	m	O	1						1
<i>Amara (Percosia) equestris equestris</i> (Duftschmid, 1812)	8.0–13.0	m	G		1		2			3
<i>Amara (Leironotus) glabrata</i> Dejean, 1828	6.0–7.0	b	O				1			1
<i>Amara (Amara) ovata</i> (F., 1792)	8.0–10.0	m	O					1		1
<i>Anchomenidius astur</i> (Sharp, 1873)	5.0–5.5	b	F		1					1
<i>Bembidion (Nepha) callosum subconnexum</i> De Monte, 1953	3.5–4.0	m	G				1			1
<i>Calathus (Calathus) fuscipes graecus</i> Dejean, 1831	10.0–15.0	b	G	81	5	2	12	3	4	107
<i>Calathus (Neocalathus) granatensis</i> Vuillefroy, 1866	9.5–12.0	D	G					9	30	39
<i>Calathus (Neocalathus) melanocephalus melanocephalus</i> (L., 1758)	6.0–8.0	D	O					1		1
<i>Calathus (Neocalathus) rotundicollis</i> Dejean, 1828	9.0–12.0	D	F	14	19	19	1	44	30	127
<i>Carabus (Oreocarabus) amplipennis getschmanni</i> Lapouge, 1924	18.0–22.0	b	F	53	12	3	1	4	3	76
<i>Carabus (Chrysocarabus) lineatus lineatus</i> Dejean, 1826	24.0–32.0	b	F	59	61	101				221
<i>Carabus (Mesocarabus) lusitanicus complanatus</i> Dejean, 1826	20.0–26.0	b	F				1		8	9
<i>Carabus (Mesocarabus) macrocephalus macrocephalus</i> Dejean, 1826	25.0–30.0	b	F	19	15	17				51
<i>Carabus (Archicarabus) nemoralis prasinotinctus</i> Heyden, 1880	20.0–26.0	b	G	2	1		2	13	11	29
<i>Carabus (Megodontus) violaceus aurichalceus</i> Kraatz, 1879	20.0–34.0	b	G	1						1
<i>Cryobius cantabricus cantabricus</i> (Schaufuss, 1862)	7.5–8.0	b	F	55	71	115				241
<i>Cychrus spinicollis spinicollis</i> Dufour, 1857	13.0–18.0	b	F	3	4	11				18
<i>Cymindis (Cymindis) alternans alternans</i> Rambur, 1837	7.5–9.0	b	O				1	1		2
<i>Dinodes (Dinodes) dives kricheldorffi</i> (Wagner, 1932)	11.0–12.0	b	O						1	1
<i>Harpalus (Harpalus) ebeninus</i> Heyden, 1870	10.0–12.0	b	O						1	1
<i>Harpalus (Harpalus) rufipalpis rufipalpis</i> Sturm, 1818	7.0–9.0	m	O						1	1
<i>Harpalus (Harpalus) serripes serripes</i> (Quensel, 1806)	10.0–12.0	m	O				1			1
<i>Laemostenus (Pristonychus) terricola terricola</i> (Herbst, 1783)	10.0–18.0	b	G	2	7	13				22
<i>Lebia (Lebia) marginata</i> (Geoffroy, 1785)	4.0–4.5	m	O					2		2
<i>Leistus (Leistus) barnevillei</i> Chaudoir, 1867	7.0–9.0	b	F	3	10					13
<i>Leistus (Leistus) nitidus</i> (Duftschmid, 1812)	7.5–9.0	b	F	5	29	19				53
<i>Licinus (Licinus) aequatus angustus</i> Chevrolat, 1840	11.0–14.0	b	G		1	1				2
<i>Microlestes negrita negrita</i> Wollaston, 1854	2.2–2.8	D	G				1			1
<i>Nebria (Nebria) asturiensis</i> Bruneau de Miré, 1964	10.5–13.5	b	F	558	960	1285				2803
<i>Notiophilus biguttatus</i> (F., 1779)	5.0–5.5	D	G	25	15	28		3		71
<i>Ophonus (Metophonus) puncticeps</i> Stephens, 1828	6.0–9.0	m	O				1			1
<i>Orthomus (Orthomus) hispanicus</i> (Dejean, 1828)	9.0–11.0	b	O				2			2
<i>Panagaeus cruxmajor</i> (L., 1758)	7.5–8.0	m	G					1		1
<i>Poecilus (Macropoecilus) kugelanni</i> (Panzer, 1797)	12.0–14.0	m	O	1				3	7	11
<i>Poecilus (Poecilus) versicolor</i> (Sturm, 1824)	9.0–11.0	m	O				11			11
<i>Pterostichus (Oreophilus) cantaber</i> (Chaudoir, 1868)	13.0–16.0	b	F	217	454	650				1321
<i>Steropus (Steropidius) gallega</i> (Fairmare, 1859)	13.0–16.0	b	G	21	2	2				25
<i>Steropus (Sterocorax) globosus ebenus</i> (Quensel, 1806)	13.5–20.0	b	G				61	3	44	108
<i>Trechus (Trechus) obtusus asturicus</i> Jeannel, 1921	3.2–4.0	D	O				3	29	6	38
<i>Trechus (Trechus) quadristriatus</i> (Schrank, 1781)	3.2–4.0	m	O			1	1	11	2	15
<i>Zabrus (Iberoabrus) silphoides asturiensis</i> Heyden, 1880	11.0–16.5	b	O				1			1
Number of individuals				1120	1668	2267	105	128	148	5436
Number of species				18	18	15	19	15	13	43

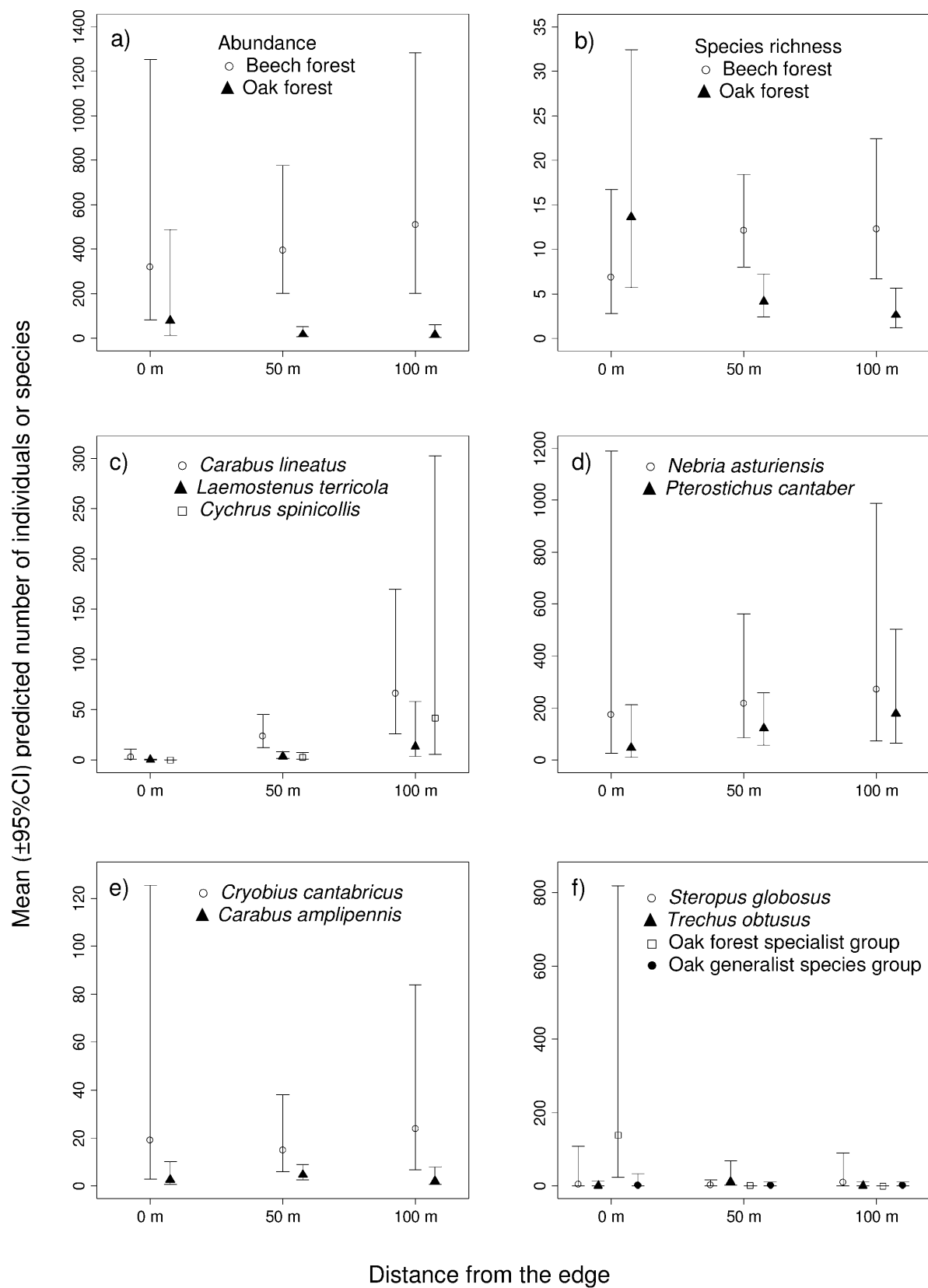


Fig. 1. Carabid beetle responses to distance from the edge. Mean ($\pm 95\%$ confidence intervals) predicted number of individuals or species at three distances (0, 50 and 100 m) from the forest edge.

TABLE 2. Generalised Linear Model results. Degrees of freedom (df) = 1 for Leaf litter cover and Leaf litter depth, and 2 for Distance. Residual Deviance is the amount of variation not explained by the models. P-values smaller than 0.05 (χ^2 distribution) are in bold face. Theta is the aggregation value (for negative binomial error models only) with lower values indicating a higher degree of aggregation. Theta SE is the standard error of Theta. Prediction Holds indicates the species response to distance from the edge coincided with the predicted response according to their classification as forest (F), generalist (G) or open habitat species (O). Y = yes the species responded as predicted, N = no it did not respond as predicted, ? = uncertain response.

	Null deviance	Residual deviance (p values)			Coefficients							Theta SE	Prediction holds
		Leaf litter cover	Leaf litter depth	Distance	Intercept	Leaf litter cover	Leaf litter depth	Distance 50 m	Distance 100 m	Theta			
Residual df	11	10	9	7									
BEECH FOREST													
Abundance	18.18	13.96 (0.040)	13.03 (0.334)	12.59 (0.802)	5.116	0.018	−0.109	0.214	0.468	4.49	1.82		
Richness	5.55	5.06 (0.484)	3.82 (0.266)	2.93 (0.638)	2.624	−0.001	−0.094	0.577	0.586				
<i>Calathus rotundicollis</i>	17.88	17.24 (0.423)	15.72 (0.218)	12.93 (0.248)	−0.086	0.008	0.505	−4.126	−3.633	1.05	0.60	? (G/O)	
<i>Carabus amplipennis</i>	80.59	11.83 (<0.001)	11.17 (0.417)	8.70 (0.291)	4.258	−0.049	0.063	0.575	−0.264			N (O)	
<i>Carabus lineatus</i>	30.68	30.07 (0.436)	23.96 (0.013)	14.52 (0.009)	3.575	−0.006	−0.336	2.216	3.259	6.04	4.10	Y	
<i>Cryobius cantabricus</i>	16.19	14.20 (0.158)	13.79 (0.523)	12.77 (0.599)	2.048	0.020	−0.100	−0.246	0.216	2.78	1.30	N (G)	
<i>Cychrus spinicollis</i>	31.37	30.08 (0.255)	21.82 (0.004)	6.37 (<0.001)	3.209	−0.047	−0.998	7.746	10.503			Y	
<i>Laemostenus terricola</i>	27.42	22.97 (0.035)	20.55 (0.120)	11.45 (0.010)	1.164	−0.034	−0.301	4.540	5.907			N (F)	
<i>Leistus nitidus</i>	15.12	12.70 (0.119)	12.50 (0.659)	12.09 (0.814)	−2.673	0.074	−0.030	−1.862	−2.748	0.49	0.27	? (G/O)	
<i>Nebria asturiensis</i>	17.09	13.88 (0.073)	13.27 (0.435)	13.11 (0.921)	4.229	0.023	−0.125	0.222	0.438	2.28	0.91	Y	
<i>Notiophilus biguttatus</i>	17.10	17.10 (0.982)	15.40 (0.193)	14.49 (0.634)	0.436	0.048	−0.243	−1.418	−1.102	1.59	0.99	? (G/O)	
<i>Pterostichus cantaber</i>	21.79	14.86 (0.008)	14.82 (0.826)	13.46 (0.508)	4.035	0.001	−0.045	0.975	1.366	3.69	1.65	Y	
Forest specialist group	102.88	102.74 (0.700)	89.93 (<0.001)	88.81 (0.573)	2.395	−0.040	0.356	0.033	−0.311				
OAK FOREST													
Abundance	17.78	16.54 (0.265)	15.90 (0.425)	14.38 (0.468)	2.956	0.059	−0.395	−1.532	−1.597	1.18	0.52		
Richness	31.20	31.14 (0.805)	25.90 (0.022)	20.68 (0.074)	1.676	0.046	−0.370	−1.186	−1.656				
<i>Calathus fuscipes</i>	19.04	16.97 (0.150)	14.57 (0.121)	12.16 (0.300)	0.849	0.068	−0.672	−2.543	−2.925	2.32	2.68	N (O)	
<i>Carabus nemoralis</i>	21.47	14.31 (0.007)	13.96 (0.557)	9.15 (0.090)	−1.660	0.168	−0.594	−4.692	−7.505	0.98	0.68	? (G/O)	
<i>Steropus globosus</i>	18.57	17.23 (0.249)	13.05 (0.041)	11.96 (0.581)	3.061	0.035	−1.186	−0.711	0.754	0.43	0.27	Y	
<i>Trechus obtusus</i>	16.73	14.27 (0.117)	14.24 (0.851)	10.36 (0.144)	−0.584	0.069	−1.180	3.206	0.560	0.50	0.30	? (G/O)	
Forest specialist group	204.64	57.72 (<0.001)	48.87 (0.003)	5.68 (<0.001)	−1.544	0.133	0.379	−6.151	−7.701				
Generalist group	22.85	16.17 (0.010)	12.85 (0.069)	12.64 (0.899)	−0.387	0.104	−1.182	0.004	−0.434	0.79	0.64		
Open habitat group	13.94	13.92 (0.891)	13.70 (0.637)	12.36 (0.512)	1.474	0.036	−0.359	−0.603	−1.355	1.37	0.73		

species collected (108 individuals) followed by *Calathus rotundicollis* (75 individuals).

We found a considerable difference in overall abundance and species richness between forest types. In beech forests we collected 5055 individuals of 22 species and 381 individuals of 29 species in oak forests, i.e. beech forests had a higher total number of individuals and oak forests were species richer. Only eight of the 43 species collected were common to both forest types (Table 1). 58.6% (17 species) of the species captured in oak forests were open habitat species and 10.3% (3 species) forest specialists. 13.6% (3 species) of the species collected in beech forests were open habitat species, and 50% (11 species) forest specialists.

The results of the hypotheses tested and the estimated coefficients from the Generalised Linear Models are given in Table 2. Theta values indicated aggregated distributions for all species, except *Carabus amplipennis*,

Cychrus spinicollis and *Laemostenus terricola*, which were collected from beech forests.

Neither overall abundance nor species richness responded statistically significantly, at the 5% risk level, to distance from the forest edge in either forest type (Table 2). Generally, however, in beech forest mean carabid abundance and richness decreased from the forest interior to the edge (Fig. 1a, b). We found the opposite in oak forests where both mean carabid abundance and richness (at the 7% risk level) were higher at the edge (Fig. 1a, b). There was a high mean number of species at the edges of oak forests (Fig. 1b), which seemed to be responsible for the higher overall richness of oak compared to beech forests – 10 species were collected only at oak forest edges, but their abundances were low (Table 1).

The results of the complementarity calculation indicate that samples along the beech forest gradient were more similar, as they had a higher number of species in

common than in oak forests (beech forest complementarity values ranged between 0.26–0.35 and oak forest values between 0.53–0.69).

Three species responded statistically significantly to distance from the edge in beech forests (*Carabus lineatus*, *Cychrus spinicollis* and *Laemostenus terricola*) and none in oak forests (Table 2). The first two species are forest specialists and they responded predictably to the edge as they increased in abundance towards the forest interior (Fig. 1c). According to the literature, *Laemostenus terricola* is a generalist species, but our results indicated that it is associated with forest interiors (Fig. 1c).

Leaf litter cover and depth in oak and beech forests were higher in the interior (mean value for cover = 62.3% and 98.2%, and depth = 3.97 cm and 8.93 cm, respectively) and lower at the edge (mean value for cover = 6.2% and 37.9%, and depth = 0.25 cm and 2.14 cm, respectively). In both forest types, we found that half of the species analysed were significantly correlated with one of the leaf litter characteristics (either leaf litter cover or depth). We repeated the analysis for these species without leaf litter cover and depth. *Pterostichus cantaber* and *Carabus amplipennis* then responded significantly to distance from the edge (null deviance = 21.53 and 51.83, residual deviance = 13.46 and 11.12, $p = 0.018$ and <0.001 , respectively). Both species are considered to be forest specialists but only *Pterostichus cantaber* increased in abundance with distance from the edge (Fig. 1d). *Nebria asturiensis*, a forest specialist, showed a similar distribution pattern to *Pterostichus cantaber*, but not statistically significantly so (Fig. 1d). The rest of the species did not respond either predictably or statistically significantly to distance from the edge (Table 2, Fig. 1e, f). For example, *Cryobius cantabricus*, a forest species according to the literature, appeared to be a generalist species, and both *Leistus nitidus* and *Calathus rotundicollis*, considered to be forest species, appeared to be either generalist or open habitat species (Table 2).

The beech forest specialists group showed no significant correlation with distance from the edge, but responded positively to leaf litter depth (Table 2). In oak forests we found a significant correlation between the forest specialists group and distance from the edge (Table 2), but this group did not respond as predicted – mean number of individuals was higher at the edge (Fig. 1f). The generalist species group responded positively to distance once leaf litter characteristics were removed (null deviance = 102.99, residual deviance = 79.78, $p = <0.001$), but did not show a clear pattern of distribution because of low numbers of individuals (Fig. 1f). The oak forest open habitat species group did not respond statistically significantly to distance from the edge (Table 2).

DISCUSSION

The main results were: 1) no statistically significant edge effects at the carabid beetle assemblage level in either forest type, 2) three forest species correlated significantly and predictably to distance from the beech forest edge, 3) different carabid beetle responses to the

edge were recorded in beech and oak forests (i.e. mean carabid abundance and species richness were higher in beech forest interiors and at oak forest edges), and 4) leaf litter, the only environmental variable measured, appeared to be an important factor affecting the distribution of some species from forest interior to edge.

No edge effects on carabid beetle assemblages

Our results showed that there was no significant correlation between either abundance or species richness and distance from the edge, i.e. no edge effect at the carabid assemblage level. This result is similar to that found by Kotze & Samways (2001) at Afromontane forest edges in South Africa. However, several studies in Hungary have shown a significant edge effect on carabid beetles along oak-hornbeam forest-grassland transects (Magura et al., 2001a, b; Molnár et al., 2001; Magura, 2002).

In general, environmental conditions at the edge influence abundance, diversity, species interactions and functional roles of insects (Didham, 1997a), and quite often result in an increase in species richness (Murcia, 1995; Risser, 1995). This increased species richness at the edge was, however, not observed for carabid beetles at oak and beech forest edges in NW Spain. To evaluate the validity of this result, a sampling strategy with more replication is needed, as the small number of sites used in this study may have been partly responsible for not showing an effect, if it exists.

Specific edge effects

The occurrence of three flightless forest specialist species in beech forests (*Carabus lineatus*, *Cychrus spinicollis* and *Pterostichus cantaber*) correlated significantly with distance from the edge, as predicted, i.e. they were more abundant in the forest interior. *Laemostenus terricola*, a generalist species collected in beech forests only, was also strongly influenced by the edge, showing a forest specialist distribution pattern. These findings support the results of Spence et al. (1996) and Davies & Margules (1998) who reported that individual carabid species were susceptible to edge effects and responded differently to the edge according to their habitat requirements.

Unexpectedly, the oak forest specialists group increased significantly in abundance at the forest edge. The reasons for this are unknown, but it is similar to the results of Spence et al. (1996) who showed that some old-growth forest specialists occurred in high numbers at forest-clearcut edges.

Although we found several species (open habitat and generalist species) only at the edges of oak forests, these can not be classified as edge associated species (Magura et al., 2001b; Molnár et al., 2001), because of their low abundance and they may be inhabitants of the adjacent, unsampled grassland (see Heliölä et al., 2001; Magura et al., 2001b).

Differences between beech and oak forests

We showed that carabid beetle assemblages in *Fagus sylvatica* and *Quercus pyrenaica* forests were different (see Thiele, 1977). We found mainly open habitat species in oak forests, and forest specialists in beech forests.

Beech forests had a higher number of individuals and oak forests were species richer.

Higher carabid species richness in oak forests is associated with a greater small-scale habitat heterogeneity in terms of vegetation structure. This habitat heterogeneity is a factor determining carabid beetle distribution in boreal forests in Finland (Halme & Niemelä, 1993; Niemelä et al., 1996). The carabid assemblage in beech forest interiors was very similar to that of the edge in terms of species composition and assemblage structure (i.e. abundance distribution), a pattern also found by Heliölä et al. (2001) for carabids at forest-clearcut edges in Finland.

Overall carabid abundance was higher in the interior of both forest types, as recorded by Kotze & Samways (2001) for Afromontane forests in South Africa, and by Magura et al. (2001a) from oak-hornbeam forests in Hungary. The high abundance in the interiors of beech forest was mainly because of the presence there of two abundant forest specialist species (*Nebria asturiensis* and *Pterostichus cantaber*). According to Thiele (1977), more uniform microclimatic conditions in beech forest interiors favours a few very abundant carabid species, which prefer moist and cool conditions. The abundance distribution of the beech forest species was similar to that found by Niemelä (1993) and Koivula (2002) in mature boreal forests in Finland and Niemelä et al. (1993) in Canada; and by Gutiérrez et al. (2004) in beech forests in Spain (but see also Koivula et al., 2002).

We found an unexpected difference between the two types of forests in the response of the carabid assemblages to the edge in beech and oak forests (mean carabid abundance and species richness were higher in the interiors of beech forest and edges of oak forest). This difference was probably associated with greater variability in oak forest structure compared to the more homogeneous beech forests. In the past, oak forests were heavily used by people in NW Spain (Luis-Calabuig et al., 2000) because they were more accessible than the beech forests, which are located in mountains near the Picos de Europa mountain range. Oak forest interiors are more similar to the edges as the canopy is not closed and there are open habitat sites. This allows generalist and open habitat species to disperse across the boundary between the oak interior and the edge.

Carabid beetle response to leaf litter

The effects of distance from the edge on the distribution patterns of carabids are probably due to the different environmental and biological conditions at different distances from the edge.

We found a great number of statistically significant correlations between leaf litter characteristics (cover and depth) and the species analysed. Leaf litter, therefore, appeared to be one of the factors that influence the distribution of carabid beetles from the interior to the edge of forests (see Koivula et al., 1999). It is worth pointing out that leaf litter was the only environmental variable measured, so its relationship with other variables is unknown. Magura et al. (2001a) and Magura (2002) reported that leaf litter cover significantly affects the distribution of

individual species in their habitats, e.g. open habitat species correlate negatively with leaf litter. Molnár et al. (2001) also found that leaf litter cover influenced carabid beetle diversity along forest-grassland transects in Hungary. For epigaeic invertebrates, such as carabid beetles, litter volume provides a "large area for life" (Giller, 1996) for many reasons. For example, more litter may provide more prey or space, or better protection against environmental conditions. Testing the effects of these variables on carabid beetle distribution patterns, will possibly reveal the processes determining their occurrence.

To conclude, the oak and beech forests harboured markedly different carabid beetle assemblages. Small-scale heterogeneity in the oak forests possibly determined the higher number of species there, while the homogeneous beech forest patches were characterised by a lower number of species of which a few were very abundant.

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