

Habitat-based conservation priorities for carabid beetles within the Picos de Europa National Park, northern Spain

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Abstract

Quick biodiversity studies on poorly studied taxa and areas are increasingly popular for setting conservation priorities over a wide range of spatial scales. However, the implementation of such studies is complicated by the variable extent to which the different criteria used in prioritisation are correlated to each other. Using methods of constrained ordination, we examined the species-habitat relationships of carabid beetles based on ground beetle assemblages from 22 sites in the Picos de Europa National Park, northern Spain. We found characteristic species assemblages for subalpine meadows, *Genista* shrublands, and pastures, whereas mown meadows, heathlands, beech and riparian woodlands were occupied by more habitat generalist species. Species associated with subalpine meadows and *Genista* shrublands tended to be mostly brachypterous and to have geographic ranges restricted to northern Spain. In contrast, we found no relationship between the degree of species' association with pastures and geographic range-wing size type. Although the species richness was higher in riparian woodlands and mown meadows, we suggest a higher conservation value for subalpine meadows and *Genista* shrublands across the landscape because they sustain characteristic assemblages dominated by species with restricted ranges and reduced powers of dispersal. Our study suggests that preserving areas in the landscape supporting higher biodiversity will not necessarily preserve those species potentially more susceptible to habitat loss and fragmentation. It also supports the feasibility of biodiversity studies based on multivariate techniques for setting conservation priorities over complex landscapes.

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1. Introduction

There is general consensus on the importance of reserve systems to preserve the rapidly declining biodiversity due to human impact (Wright, 1996; Primack and Ros, 2002). Central to this idea is the criteria for prioritisation of sites within (or among) reserves in order, for instance, to suggest particular protection plans, maintain extant or apply new management regimes (Primack and Ros, 2002). In areas in which

there is still a limited knowledge of biodiversity due to time and budget limitations, comprehensive ecological investigations on which to base conservation decisions are rarely available. This makes crucial the use of alternative rapid multi-species approaches to compare the capacity of different habitats to support biodiversity (e.g. Debinski and Brussard, 1994; Sparrow et al., 1994; Daily and Ehrlich, 1995). Such an approach is necessary for facing the difficult and urgent task of avoiding the extinction of as many species and populations as possible before they are even described (Ehrlich, 1992). Although there is a wide range of criteria for site selection, species diversity and (geographic) range size are probably the more important in most conservation studies at a wide range of spatial scales (e.g. Margules and Usher, 1981; Goldsmith, 1991; Debinski and Brussard, 1994; Kerr, 1997; Virolainen et al., 1998). Nevertheless, there is still a heated debate on the generality of

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the coincidence of centres of richness and endemism and on which one should receive priority (e.g. Prendergast et al., 1993; Kerr, 1997; Reid, 1998; Bonn et al., 2002; Vetaas and Grytnes, 2002).

Carabid beetles are widely recognised as potentially valuable indicators of environmental variation, because they are a highly diverse taxon, can be easily sampled, and are highly sensitive to changes in the physical and biological environment (Lövei and Sunderland, 1996). However, in Europe, most studies have been based on species diversity and composition, and seldom on patterns of geographic range size. This is likely the result of studies being mostly carried out in central and northern Europe, where the incidence of species with small range sizes is much lower than in southern Europe. Some recent studies on other beetle families in southern Europe have shown strong associations between species with small geographic ranges and particular habitat types (Ribera and Vogler, 2000; Verdú et al., 2000).

The Iberian peninsula is one of the richest areas both in total number of species and endemics for carabid beetles in Europe (Zaballos and Jeanne, 1994), although there is still an extremely poor knowledge of their distribution and habitat requirements. In Spain, the extent of the area under protection has markedly increased during 1980–2000 (Morillo and Gómez-Campo, 2000), providing increased potential for effective preservation of carabids and other fauna and flora. However, it is still a matter of urgency to formulate some guidelines concerning whether some particular habitats contain a larger proportion of species with small geographic ranges and whether they in turn have the more diverse faunas. This will be an important step in planning conservation efforts within the nature reserves and parks, and will give the basis for monitoring the changes in biodiversity derived from potential habitat modifications in the future.

The main aim of the present study focuses on the determination of conservation priorities for ground beetles in a series of habitats in the Picos de Europa National Park in northern Spain. Previously, we have shown that this area is particularly rich in northern-Iberian endemic carabid beetles, which in turn were more widely distributed at a regional scale than others with larger geographic ranges (Gutiérrez and Menéndez, 1997). Here, we test to what extent four conservation criteria were associated with each other among different habitats in order to set priorities for conservation management. Two criteria were relative to the community (species richness and composition), and two to the individual species (range size and dispersal ability). The assumption is that high species richness, a more characteristic species composition, and high incidence of species with small range sizes and low dispersal ability increases the conservation value of the habitat.

2. Methods

2.1. Study area

The field work was carried out in the Picos de Europa National Park, ca 20 km from the northern coast of Spain (centred on 43°15'N, 5°00'W; Fig. 1). This is the oldest and second largest national park in Spain, and along with Ordesa y Monte Perdido, and Aigüestortes National Parks (both in the Pyrennes), they are intended to be representative of Eurosiberian mountain ecosystems. The Picos de Europa National Park (formerly named Montaña de Covadonga national park) had 16925 ha until 1995, and it only included the western range of the Picos de Europa. In 1995, it was enlarged to its current extent of 64660 ha by the addition of the central and eastern ranges.

The Picos de Europa is a predominantly limestone mountain range with a marked elevational gradient from ca 200 to 2600 m a.s.l. The climate is extremely wet, particularly in the northern slopes, with precipitation values exceeding 1500 mm/year in most sites. The main vegetation types are limestone rocky outcrops with *Genista* spp. shrubland (*G. hispanica* ssp. *occidentalis* and *G. legionensis*), heathlands (*Erica vagans*, *Daboecia cantabrica*, *Ulex gallii*), beech woodlands (*Fagus sylvatica*) and pastures (*Cynosurus cristatus*). At high elevation, subalpine meadows (a mixture of communities dominated by *Nardus stricta* and *Festuca burnatii*) occurs in those sites with relatively gentle slopes. Mown meadows (*Arrhenatherum bulbosum*) and riparian woodlands (*Alnus glutinosa*) are restricted to a few lowlands localities, while holm oak woodlands (*Quercus rotundifolia*) are confined to basal rocky slopes of the limestone gorges. A detailed description of the vegetation and climate in the area is given by Rivas-Martínez et al. (1984).

2.2. Sampling

In 1992, we sampled carabid beetles at 22 sites classified into the seven major vegetation types and covering most of the elevational range of the study area (250–2050 m; Fig. 1): beech woodlands (five sites), riparian woodlands (two sites), rocky outcrops with *Genista* shrubland (four sites), heathlands (three sites), mown meadows (two sites), pastures (three sites), and subalpine meadows (three sites). For each site, we also obtained elevation (in m), northing and easting (in km within the corresponding 100 km UTM square, 30TUN) from the 1:25000 map of the area (Adrados, 1990).

We sampled each of the 22 sites with 10 pitfall traps placed 3 m apart in a straight line, totalling 220 traps. Traps were plastic cups with an opening diameter of 68 mm and a volume of 200 ml, partially filled with 100 ml

of a 4% solution of formalin as preservative. We made two small holes in each trap above the level of the preservative liquid to avoid rain flooding (van den Bergher, 1992). Because of the difficult approach to most sampling sites (only by walking), the traps were opened for two periods of 12–19 days during the season of most carabid activity in the study area: 16 May–7 June 1992, and 12 July–5 September 1992. Four study sites were sampled during the whole season in 1993 (see later), and for those cases, sampling over the two limited periods accounted for 60–89% of the total species pool for the whole season.

Nomenclature follows the monograph by Zaballo and Jeanne (1994). We were not able to obtain confident identifications of specimens of genus *Trechus* and some of genus *Amara*. They were included in the multivariate analyses, but were excluded from the subsequent analysis involving geographic ranges (see later).

Because the sampling efforts differed among the sites, and on some sampling occasions a few pitfall traps were lost due to cattle trampling, for each species and locality we standardised the catches to number of individuals per 10 traps and 30 days. These were the modal classes

of the number of traps and trapping session duration, respectively.

The information on the geographic range of carabid beetles is still fairly limited due to lack of comprehensive faunal studies. We classified the species' geographic ranges into two rough categories: (1) restricted: species usually restricted to the northern half of the Iberian peninsula; and (2) widespread: species with Mediterranean, European and Palearctic distributions. In addition, we classified the species according to the degree of hindwing development into: (1) macropterous: hindwings fully developed; (2) brachypterous: hindwings shorter than elytra when spread or reduced to stumps; (3) polymorphic: individuals with different degrees of hindwing development. Excluding the six polymorphic species, the cross-classification of geographic range size and hindwing development produced four categories: brachypterous-restricted ($N=20$), macropterous-restricted ($N=2$), brachypterous-widespread ($N=18$), and macropterous-widespread ($N=44$) species. The literature sources for geographic ranges are given by Gutiérrez and Menéndez (1997).

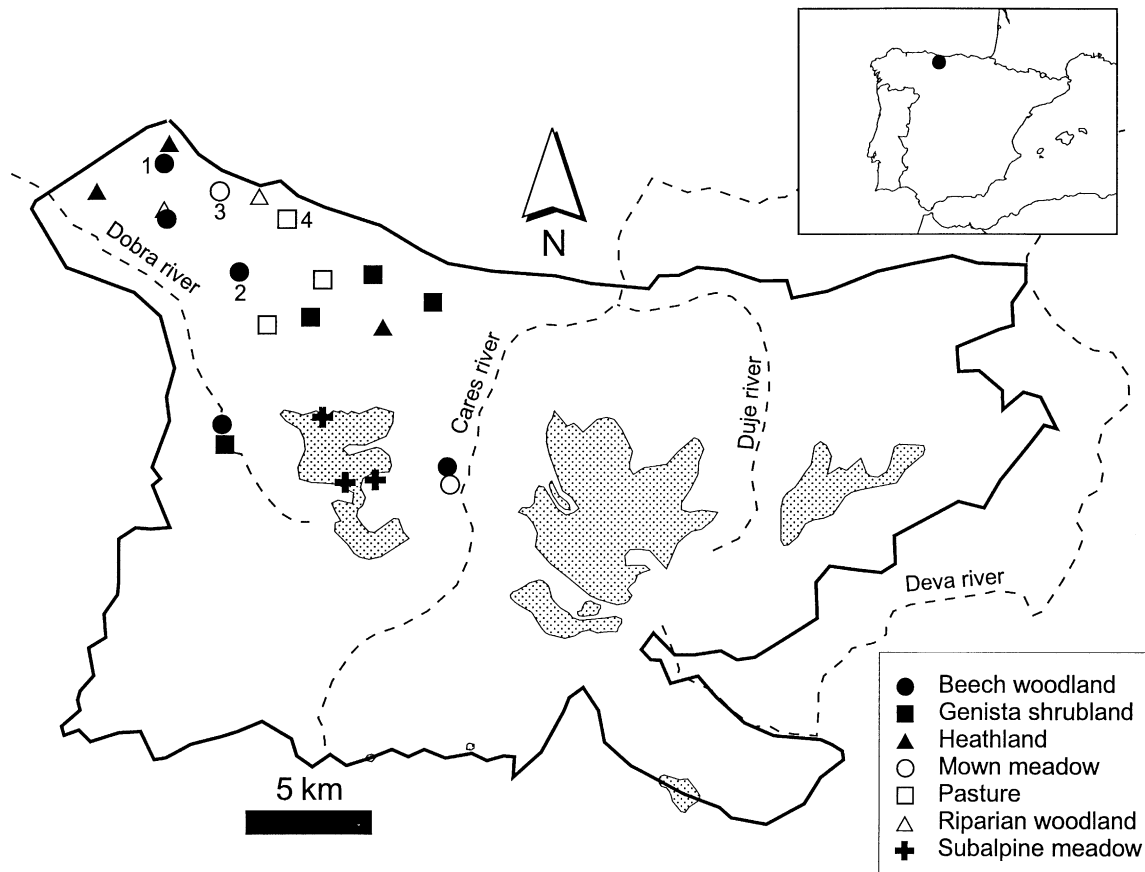


Fig. 1. Map of the Picos de Europa National Park. The park limit is denoted by the bold line, and rivers by dashed lines. The dotted areas show elevations above 2000 m. The three main ranges of the Picos de Europa are delimited by the four major rivers shown in the figure. Numbers next to symbols denote repeated sites in 1993: 1=Auseva; 2=Pome; 3=La Casilla; 4=Las Tremonas. The location of the national park in the Iberian peninsula is also shown.

To test the consistency of carabid assemblages from one year to another, we re-sampled in 1993 four of the sites sampled in 1992. We used exactly the same sampling protocol during the same time periods in spring and summer 1993, and standardised the catches to number of individuals per 10 traps and 30 days.

2.3. Statistical analyses

Differences in species composition and abundance among sites were evaluated using methods of constrained ordination, canonical correspondence analysis (CCA) and partial CCA, performed by CANOCO software (ter Braak, 1986; ter Braak and Smilauer, 1998). To avoid undue influence of a few abundance values, we log-transformed ($\ln[x + 1]$) the species' abundance values prior to analysis (e.g. *Calathus uniseriatus* accounted for ca. 18% of total catches). CCA is a multivariate method which relates the community species composition to environmental variables, assuming a unimodal response of species' abundance. We checked the appropriateness of CCA by performing a preliminary detrended correspondence analysis (DCA) with detrending by segments, which provides an estimate of the length of the extracted axes in units of standard deviation (SD). DCA is an unconstrained (i.e. not including environmental variables) ordination technique which assumes unimodal responses of species' abundance. As the first axis was 6.379 SDs in length, considerably greater than the range 1.5–3 SDs (the minimum threshold recommended for performing unimodal methods; ter Braak and Prentice, 1988), we confirmed the appropriateness of CCA for our data set.

First, we performed a CCA on the species \times samples matrix including the full set of environmental variables. When performing CCAs, elevation, easting and northing were continuous variables, and vegetation type was a categorical or nominal variable. Easting and northing were both spatial variables to account for any potential spatial pattern in species composition (Legendre, 1993). Vegetation type had seven categories and was transformed into the same number of dummy variables (instead of $[n - 1]$ to avoid multicollinearity problems) to allow for selection of any of the vegetation type categories during the stepwise procedure (see later; ter Braak, 1990). Because not all variables could have a significant influence on the species data matrix, we proceeded to generate a reduced model using a forward stepwise selection of the environmental variables. The statistical significance of the models (full and reduced) and after the inclusion of each new environmental variable during forward selection, was evaluated by the *F*-ratio based on the trace and 4999 unrestricted Monte Carlo permutations, the realistic minimum for estimating a significance level of ca. 0.01 (Manly, 1994). After the forward selection procedure, we calculated corrected

P-critical values using the sequential Bonferroni correction to control for the overall size of the test (ter Braak 1990; see Rice, 1989 for details).

Those environmental variables which proved to be significant after the stepwise forward selection procedure were used as external variables in further partial CCAs to explain specific habitat gradients (Spitzer et al., 1993, 1997). Partial constrained ordinations correspond to partial regression, in which the effect of covariables is first partialled out before testing the explanatory power of the environmental variables of interest. One partial CCA was performed for each environmental variable, using the remaining ones as covariables in the analyses. For instance, to examine the position of species along the axis of subalpine meadow, we carried out a partial CCA using subalpine meadow as (dummy) environmental variable, and pasture and *Genista* shrubland as covariables (see later results). The optimum of species on the environmental axis is expressed by its score on the first (constrained) axis, large values being typical for those species occurring mostly in the particular habitat (in the earlier example, in subalpine meadows).

We used Kruskal–Wallis non-parametric tests with a posteriori Student Newman Keuls (SNK) comparisons of mean ranks for unequal sample sizes to examine whether species of different geographic range and wing size types had their optimum on different habitats (Zar, 1999).

We examined the temporal consistency of carabid assemblages using DCA with detrending by segments on 26 samples (22 sites + four repeated sites) \times species matrix. If assemblages are persistent over the study period, we should expect similar sample scores along the axes of major variation for a specific site in 1992 and 1993 relative to scores of other sites sampled in 1992.

Given that sampling effort varied among sites, we used non-parametric methods to estimate species richness. Some of those methods are relatively simple to apply, and are based on occurrences of rare species in samples. In particular, the Chao 2 and second-order jackknife have proven to provide relatively unbiased estimates of species richness for small numbers of samples, including pitfall traps (Colwell and Coddington, 1994; Brose, 2002). Both are based on the number of species that occur in only one sample as well as the number that occur in two samples. Using the occurrence of species in the operating traps (9 or 10) over the whole study period, we estimated species richness at each site by computing the second-order jackknife estimate (S_4 ; Colwell and Coddington, 1994):

$$S_4 = S_{\text{obs}} + \left(\frac{L(2n - 3)}{n} - \frac{M(n - 2)^2}{n(n - 1)} \right),$$

where S_{obs} is the observed number of species at a site, L is the number of species that occur in only one sample,

M is the number of species that occur in exactly two samples, and n is the number of samples (Colwell and Coddington, 1994). We used Kruskal–Wallis non-parametric test with a posteriori SNK comparisons of mean ranks for unequal sample sizes to compare the estimated species richness among vegetation types.

3. Results

3.1. Species composition

We caught a total of 5006 individuals from 93 species in the 22 localities, including 30 specimens of *Trechus* spp. and two indeterminate specimens of genus *Amara* (Appendix). The results obtained from the CCA using the full set of environmental variables revealed that the first three axes explained 39% of the variance of the species data (Table 1). Using forward stepwise selection of environmental variables, we found that a reduced set of three categorical variables explained significantly 30.3% of the variance in species data (Table 1). The first axis was positively related to subalpine meadow, the second negatively to *Genista* shrubland and positively to pasture, and the third positively to *Genista* shrubland (absolute values of correlation coefficients >0.4 ; Table 2). Both the percentage of explained variance in species data, and the species–environment correlation coefficients for the first three axes were only slightly smaller than those of the CCA including the full set of variables (drop of 8.7%), suggesting that they were relevant explanatory variables for species composition (Table 1).

Table 1
Eigenvalues, cumulative explained variance (%) of species data and species–environment correlation coefficients for the first three axes obtained by CCA using the full set and the reduced set of environmental variables selected by stepwise procedure

Analysis	Axis			F	P
	1	2	3		
<i>Eigenvalues</i>					
CCA, full set	0.736	0.679	0.532	2.411	0.0002
CCA, reduced set	0.703	0.548	0.476	2.614	0.0002
<i>Cumulative explained variance</i>					
CCA, full set	14.7	28.3	39.0		
CCA, reduced set	14.1	23.6	30.3		
<i>Correlation coefficients</i>					
CCA, full set	0.989	0.942	0.981		
CCA, reduced set	0.972	0.933	0.948		

The F -test value and significance (after 4999 Monte-Carlo permutations) for each model are also shown.

The observed patterns in species composition are visualised in CCA plots, showing the first three axes (Fig. 2). For simplicity, we refer only to those species with 10 or more individuals in the total catch (abundant species henceforth) and axis scores >1 in at least one CCA axis. The first axis separated the sites with subalpine meadows from the remaining sites. *Calathus uniseriatus*, *Cymindis alternans*, *Haptoderus ehlersi*, *Iniopachis auriculatus*, *Nebria sobrina* and *Zabrus consaguineus*, which are restricted to the Cantabrian range, were the abundant carabid species associated with that habitat type. The second axis separated the sites containing pastures from the others. Because these assemblages were both rich in species and individuals, a relatively large number of abundant species were associated with that habitat, *Agonum muelleri*, *A. viduum*, *Chlaeniellus nigricornis*, *Clivina fossor*, *Lagarus vernalis*, *Metallina lampros*, *M. properans*, *Poecilus coerulescens* and *P. cupreus*, which all have large geographic ranges. *Elaphrus pyrenaicus* was the only abundant species associated with pastures that had a restricted geographic range. The third axis separated the sites with *Genista* shrubland from other vegetation types. *Harpalus ebeninus* (restricted to the Cantabrian range), *Calathus fuscipes*, *Cicindela campestris* and *Licinus aequatus* (widespread) were abundant species with high scores in that type of habitat. Other species with restricted geographic ranges were strongly associated with *Genista* shrublands, but occurred in low numbers.

3.2. Geographic ranges and wing size

The summarised results of the partial CCA analyses using one of the significant environmental variables at each time are shown in Table 3. The correlation between the first species axis and the first environmental axis was relatively high in the three models, and they all were significant. The mean scores obtained from each model and for each type of carabid species (geographic ranging size category) are visualised in Fig. 3. We excluded macropterous-restricted species from analyses due to low sample size ($N=2$). For subalpine meadow and

Table 2
Intra-set correlations of environmental variables with the first three ordination axes of the CCA performed for the carabid data set

Variable	F	P	Correlation coefficients		
			Axis 1	Axis 2	Axis 3
Subalpine meadow	3.09	0.0004	0.932	0.316	−0.177
Pasture	2.63	0.0006	−0.385	0.856	0.346
<i>Genista</i> shrubland	2.12	0.0012	0.185	−0.506	0.843

Variables were selected using a stepwise procedure. Only significant variables after sequential Bonferroni correction of the critical P -value are included. P -value is the uncorrected significance of the F -tests for each variable after 4999 Monte-Carlo permutations.

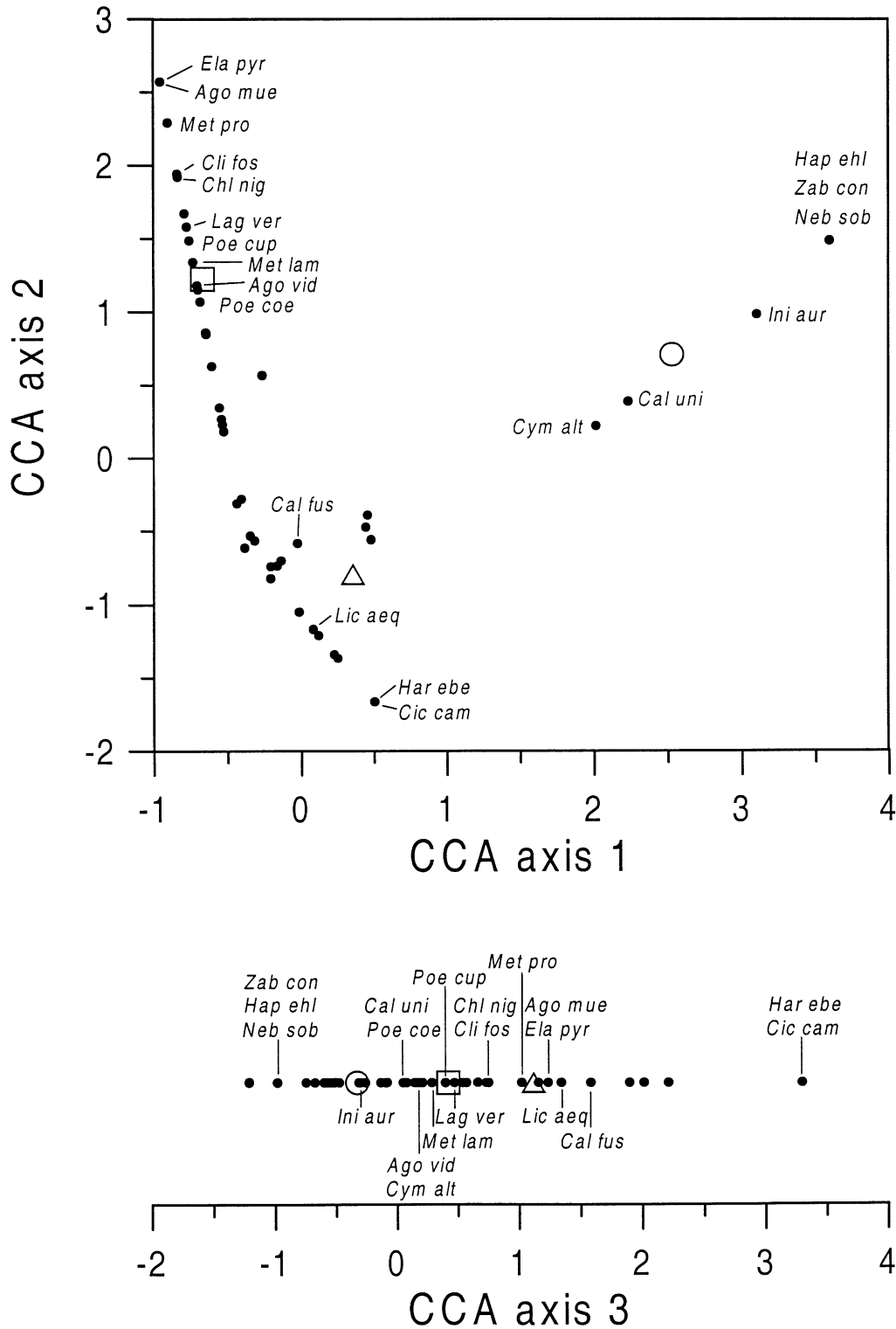


Fig. 2. CCA ordination plots (first three axes) for the carabid beetles in the Picos de Europa using the environmental variables selected by forward stepwise procedure (Tables 1 and 2). Centroids of categorical environmental variables are represented by open symbols, the species by solid symbols. Open circle: subalpine meadow; open square: pasture; open triangle: *Genista* shrubland. Only those species with 10 or more individuals in the total catch and axis scores greater than 1 in at least one of the CCA axis are shown. Species' abbreviations: *Ago mue* = *Agonum muelleri*; *Ago vid* = *Agonum viduum*; *Cal fus* = *Calathus fuscipes*; *Cal uni* = *Calathus uniseriatus*; *Chl nig* = *Chlaeniellus nigricornis*; *Cic cam* = *Cicindela campestris*; *Cli fos* = *Clivina fossor*; *Cym alt* = *Cymindis alternans*; *Ela pyr* = *Elaphrus pyrenaicus*; *Hap ehl* = *Haptoderus ehlersi*; *Har ebe* = *Harpalus ebeninus*; *Ini aur* = *Iniopachys auriculatus*; *Lag ver* = *Lagarus vernalis*; *Lic aeq* = *Licinus aequatus*; *Met lam* = *Metallina lampros*; *Met pro* = *Metallina properans*; *Neb sob* = *Nebria sobrina*; *Poe coe* = *Poecilus coerulescens*; *Poe cup* = *Poecilus cupreus*; *Zab con* = *Zabrus consanguineus*.

Genista shrubland axes, brachypterous-restricted species tended to have large CCA scores, whereas both brachypterous-widespread and macropterous-widespread species had small scores (Kruskal–Wallis tests, $H=11.223$, d.f. = 2, $P=0.004$; and $H=13.032$, d.f. = 2, $P=0.001$, for subalpine meadow and *Genista* shrubland, respectively). We found no significant effect of geographic range–wing size type on species scores along the pasture axis ($H=1.404$, d.f. = 2, $P=0.496$).

3.3. Between-year variation in species composition

We caught 864 individuals in the four repeated sites in 1993. We found three previously unrecorded species, *Dyschirius semistriatus*, *Amara nitida* and *Amara lucida* in the same site, La Casilla (Fig. 1). Because DCA (but not CCA) is sensitive to samples with a substantial proportion of species that occur only in a few sites (Jongman et al., 1995), we excluded a mown meadow

Table 3

Summary of the partial CCA analyses performed using at each time one of the three significant environmental variables selected by forward stepwise procedure

Analysis	Environmental variable	Co-variables	Species–environment correlation	<i>F</i>	<i>P</i>
1	Subalpine meadow (SM)	P, GS	0.977	3.445	0.0002
2	Pasture (P)	SM, GS	0.932	2.295	0.0112
3	<i>Genista</i> shrubland (GS)	SM, P	0.937	1.927	0.0136

The co-variables included in each analysis, the correlation of the first species with the first environmental axis, and the value and significance of the *F*-test (after 4999 permutations) for the first environmental axis are shown. Co-variable abbreviations are included in the environmental variable column.

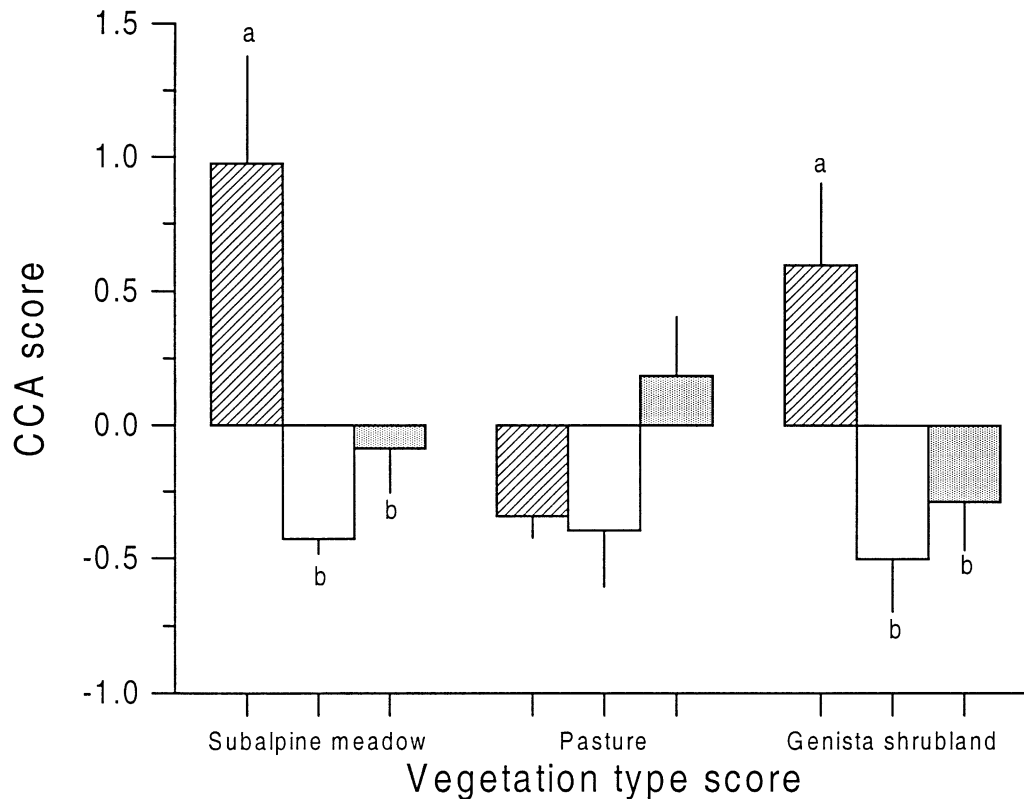


Fig. 3. Mean CCA species scores of each vegetation category for each geographic range and wing size type for 82 species of carabid beetles (macropterous-restricted species were excluded from analyses because of low sample size). Hatched bars: brachypterous-restricted species ($N=20$). Empty bars: brachypterous-widespread species ($N=18$). Dotted bars: macropterous-widespread species ($N=44$). CCA scores were obtained for each vegetation type category by constrained ordination using the other two remaining categories as covariables in the analyses (Table 3). Large CCA score values of a given vegetation category are for those species typical of that vegetation category. Letters indicate different groups for mean CCA scores at $P\leq 0.05$ using SNK tests.

sample with an extremely unusual species composition from the analysis. The first and second axes of DCA on 25 samples were, respectively, 0.767 and 0.489, and accounted for 17.3 and 11.0% of variance of species data. Fig. 4 shows that samples from a particular site collected in different years are closer (i.e. more similar) than samples from different sites in the same year.

3.4. Species richness

We found significant differences in estimated species richness (using second-order jackknife estimator) among the seven vegetation types ($H=13.283$; d.f. = 6; $P=0.039$; Fig. 5). Riparian woodlands and mown meadows had the largest mean estimated species richness, whereas subalpine meadows and beech woodlands were less diverse habitats. However, the SNK test was not able to detect significant differences between mean ranks, probably because the significance of the overall

test was close to the critical P -value (0.05) and the sample sizes were small (SNK test has lower power than Kruskal–Wallis test). The observed species richness showed a similar diversity site ranking to the jackknife estimates ($H=14.520$; d.f. = 6; $P=0.024$; Fig. 5).

Because the association between range size and wing development were examined with the constrained axes of the CCA (see earlier), our analyses do not exclude the possibility that habitats that do not show a characteristic species assemblage could show a high incidence of species with particular range sizes and wing development. We tested this possibility by comparing the proportions of species of each range size–wing development category among habitats using Kruskal–Wallis tests. We found significant differences in the proportion of brachypterous-restricted species among the seven vegetation types ($H=18.699$; d.f. = 6; $P=0.005$; Fig. 5). SNK test showed that subalpine meadows contained the

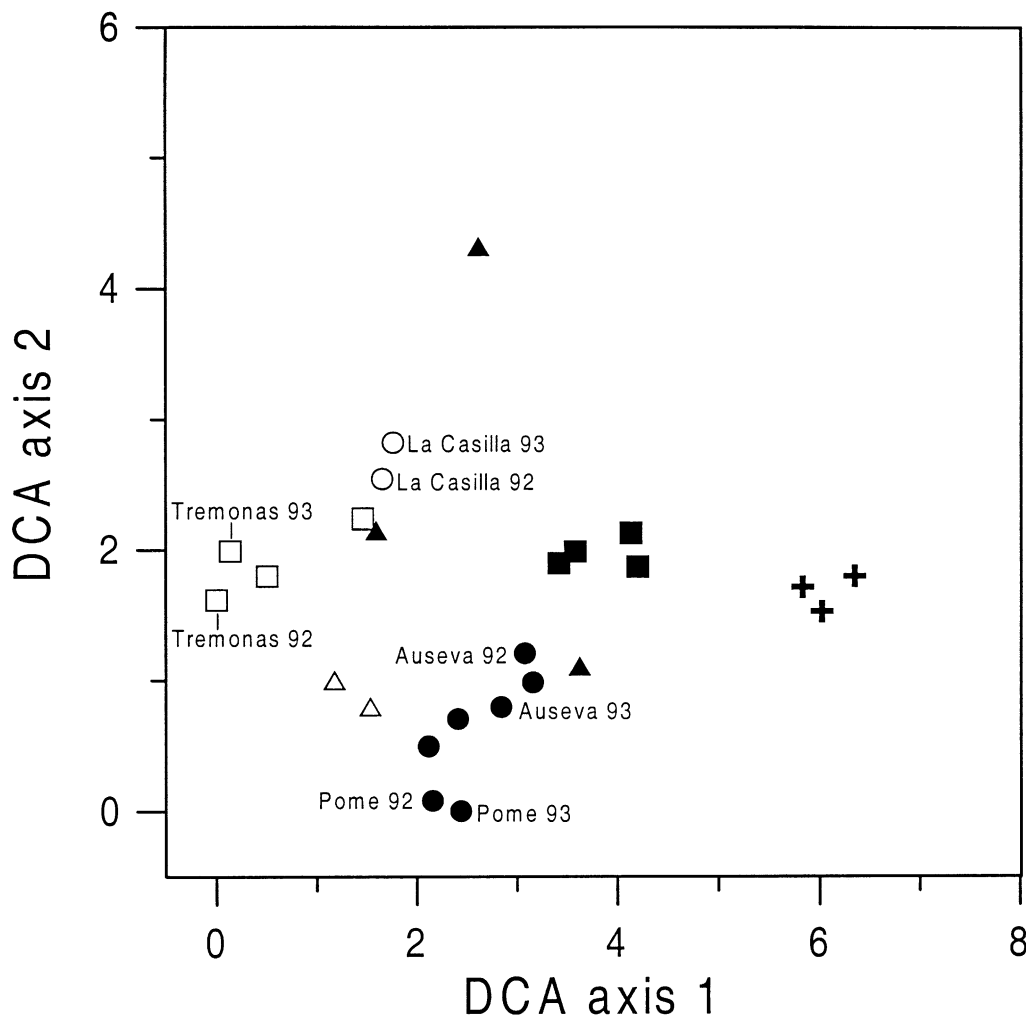


Fig. 4. DCA ordination plot based on carabid species composition in 25 samples (21 sites in 1992 + 4 repeated sites in 1993). Names are next to symbols for those sites sampled in 1992 and 1993. Axis units are number of SDs. Site symbols as in Fig. 1.

highest proportion of brachypterous-restricted species, whereas mown meadows and pastures had lowest proportions. The proportion of brachypterous-wide-spread species also showed significant differences among habitats ($H=14.520$; d.f. = 6; $P=0.024$; Fig. 5). Sub-alpine meadows had the largest proportion of species with those characteristics, whereas riparian woodlands had the smaller, but in this case the SNK tests failed to find any significant differences between mean ranks. The proportion of macropterous-widespread species also differed among habitats ($H=13.427$; d.f. = 6; $P=0.037$; Fig. 5), but no paired comparison became significant after SNK testing. Mown meadows contained the highest proportion of macropterous-wide-spread species, whereas *Genista* shrubland had the smallest.

4. Discussion

4.1. Composition of carabid assemblages

Over the 2-year period 1992–1993, we found relatively similar DCA scores for a particular site in different years relative to other sites in the same year, suggesting that carabid assemblages were relatively predictable entities in terms of relative species composition. This means that the quick short term study shown here can give a relatively reliable picture of the species–habitat associations discussed later.

Our results suggest a strong dependence of species composition on some vegetation types, particularly those with a more open structure in the landscape. Surprisingly, no characteristic assemblages were found for

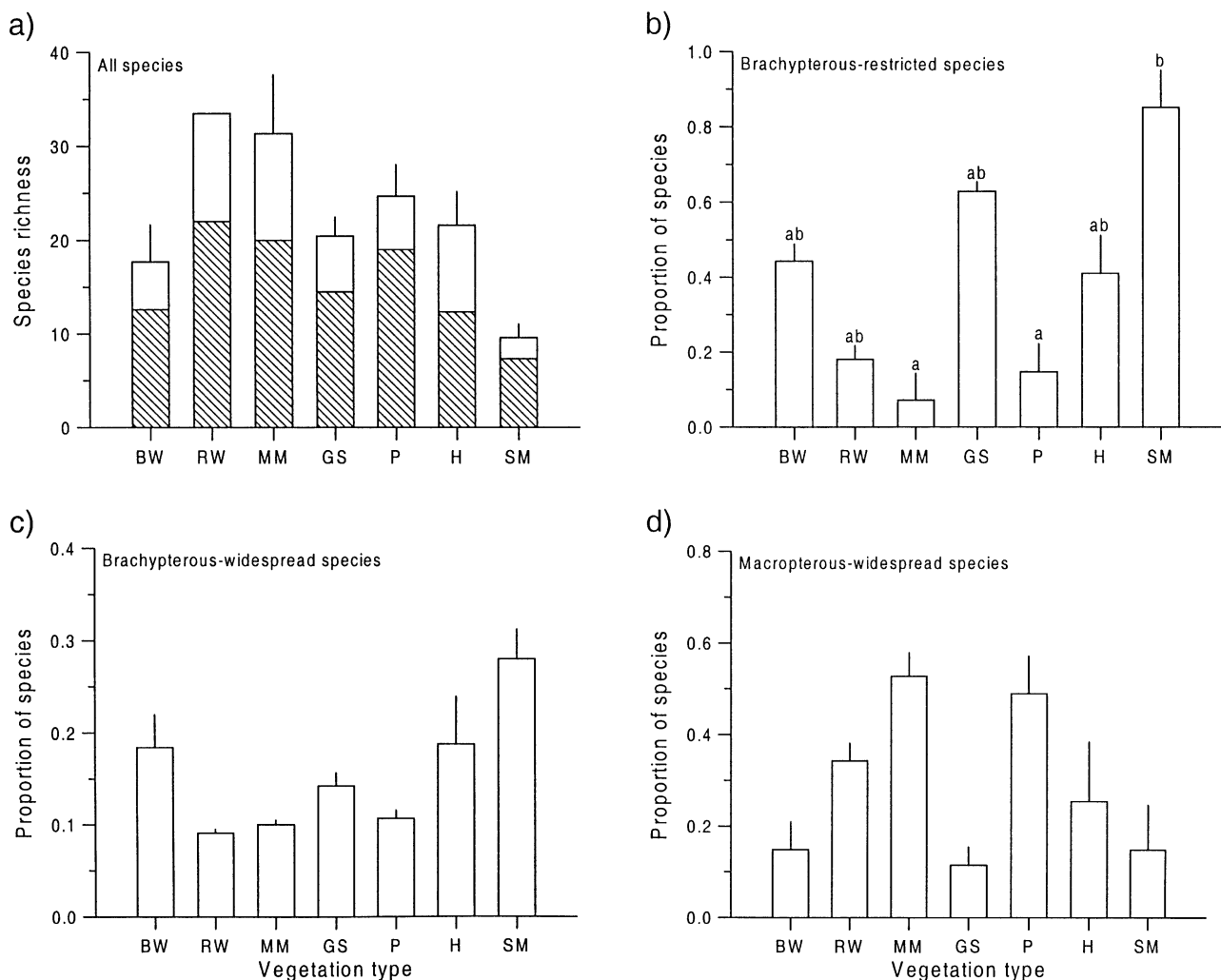


Fig. 5. (a) Mean estimated species richness using the second-order jackknife estimate for each vegetation type. The hatched area within the bars denote the mean observed species richness. (b) Mean proportion of brachypterous-restricted, (c) brachypterous-widespread, and (d) macropterous-widespread species for each vegetation type. Vertical lines indicate one standard error of the mean. Letters indicate different groups for means at $P \leq 0.05$. BW: beech woodland; RW: riparian woodland; MM: mown meadow; GS: *Genista* shrubland; P: pasture; H: heathland; SM: subalpine meadow. Note that the y-axes have different scales.

wooded areas, i.e. beech and riparian woodlands, in contrast with other previous studies (e.g. Niemelä and Halme, 1992; Baguette and Gérard, 1993; but see Eyre and Luff, 1994). In the case of beech woodlands, they were dominated by usually large-bodied and regionally widespread species of subfamilies Carabinae and Pterostichinae, as for instance *Chrysocarabus lineatus*, *Archicarabus nemoralis*, *Steropus gallega* and *Oreophilus cantaber* (Appendix). These are all habitat generalist species in this area and can occur in other non-wooded habitats. Nevertheless, it is worth noting that some characteristic woodland carabid species were not collected by our pitfall traps because they occur mainly on trees rather than on the ground (e.g. species of *Dromius* and other related genera). Riparian woodlands, on the other hand, showed a particular picture because they were more species rich, but yet had no characteristic assemblages. In our study area, riparian woodlands were narrow vegetation belts occupied by habitat generalist species that occurred in beech woodlands (see earlier), but also by more habitat specialist species in the area that occupy more open habitats as well, such as *Metallina lampros*, *Argutor strenuus* and *Chlaeniellus nigricornis*, among others. Thus, riparian woodlands would function as ecotones for which the identity of the adjacent vegetation is likely to have an important role in determining the carabid beetle composition. Eyre and Luff (1994) raised similar hypothesis to explain the carabid assemblages in North East England woodlands. Differences in carabid assemblages between different habitats have been found in a wide range of sites and areas, and they have been mostly attributed to differences in physical conditions, disturbance regimes, resources, presence of competitors and season (Lövei and Sunderland, 1996).

Although we found no relationship between species scores along pasture axis and geographic range-wing size type, most characteristic species of that habitat also occur elsewhere in Europe (Fig. 2), where they are associated with sites supporting high intensity of land disturbance (e.g. Ribera et al., 2001). This suggests that the carabid fauna of pastures is dominated by regionally habitat specialist but geographically widespread species. Pastures in the Picos de Europa are intensively grazed by cattle and sheep during spring and summer. On the other hand, brachypterous species with restricted geographical ranges tended to occupy subalpine meadows and *Genista* shrublands (Figs. 3 and 5), which are less disturbed habitats.

A recent work on aquatic beetles shows that species that occupy stable habitats (running water) have on average much smaller ranges than those occurring in unstable habitats (standing water; Ribera and Vogler, 2000). The authors suggest two possible, not incompatible, mechanisms operating at different temporal scales to explain that pattern: (1) larger range size because of

greater propensity to disperse which leads to the colonisation of a wide geographical area; and (2) larger range size because of reduced probability of allopatric speciation of species with high levels of gene flow (consequence of the need for frequent dispersal). Given the strong association between brachypterous-restricted species with more stable habitats, our results are more in line with an increased allopatric speciation rate in species occupying stable habitats, which could result in a smaller range size. Yet, in subalpine meadows, speciation rates could be reinforced by the fact that high-elevation habitats are more isolated and represent an energetically costly environment for flight (Thiele, 1977; Roff, 1990; Wagner and Lieberr, 1992; Gaston, 1994). In fact, Lieberr (1988) found that the levels of genetic heterogeneity in five carabid species were mostly positively associated with habitat persistence, which leads to a lower extinction rate for populations, and elevation, which limits gene flow in upland populations.

4.2. Conservation implications

Our study shows a lack of coincidence between habitats with high species richness and occurrence of species with small range sizes and reduced wing development. In addition, the more diverse habitats had no characteristic carabid fauna. In contrast, the habitats in which most species with restricted ranges and reduced wing development occurred, contained a low or medium number of species, but had a characteristic species composition. Therefore, our results suggest that, although species richness is the most used criterion in habitat prioritisation, it cannot be the preferred criterion in our study. Species richness has the advantage of being relatively easily assessed by site visit, but has the major problem of only dealing with species numbers and not with species identity. In contrast, rarity assessment requires an additional knowledge of the surrounding biogeographic region, but it deals explicitly with species identity, the current central issue in biology of conservation (Hanski and Simberloff, 1997). Thus, we suggest that conservation prioritisation should be given on the basis of species range sizes, rather than species richness.

Accordingly, subalpine meadows and *Genista* shrublands should be the priority habitats for carabid beetles within the Picos de Europa National Park, regardless of the fact that the number of species is relatively low in those habitats. Fortunately, setting conservation priorities for those areas of the landscape will not come into opposition with traditional land uses, because they are mostly limestone rocky areas traditionally regarded as unproductive and only marginally used for livestock grazing. Our results are in line with others that also have failed in finding a correspondence between more diverse habitats and those dominated by

rare species (e.g. Spitzer et al., 1997; Reid, 1998; Vetaas and Grytnes, 2002). Although it is difficult to formulate a general statement based only on correlative results, our recommendation is that, provided that a picture of species distributions is available, habitat prioritisation should be focused primarily on criteria, such as rarity, characteristic composition, and dispersal of species.

One striking result from our study is the fact that beech woodlands are particularly poor in terms of carabid beetle conservation. There was no characteristic fauna, the species richness was relatively low in that habitat type, and it contained only an intermediate proportion of species with small range sizes and reduced wing development. Beech woodlands have been traditionally regarded as emblematic habitats for faunal conservation in northern Spain. However, this assumption has probably arisen from a vertebrate-biased concept of species conservation. For instance, in the Cantabrian range, beech woodlands are thought to be crucial for the survival of the Cantabrian capercaillie (*Tetrao urogallus cantabricus*), which is probably the most charismatic species in the area after the brown bear (*Ursus arctos*) (Rodríguez and Obeso, 2000). Unfortunately, the bioindicator and flagship species concepts, i.e. charismatic species whose presence may indicate sites of high conservation value (Andelman and Fagan, 2000), do not seem to work in the present case. Separate conservation priorities should be given for preserving vertebrates such as capercaillie and insects such as carabid beetles in the Picos de Europa. This point and the one previously discussed support the importance of maintaining high habitat diversity for successful preservation of a wide range of species. In a similar study, Kati et al. (in press) found that the habitat which constituted the dominant vegetation type of a strictly protected area for black vulture (*Aegypius monachus*) in Greece was also less important for conserving Orthoptera in the Dardia reserve.

Finally, it is worth noting some of the potential limitations of quick biodiversity studies such as the one

presented here. Our approach is just based on a static picture of species–habitat associations, regardless of any population trends shown by the species. Hypothetically, macropterous-widespread species have large geographic ranges, but they could be suffering strong population declines of some concern. Nevertheless, evidence to date in other areas shows that poorly dispersing carabid species generally suffer decreasing trends in their distributions over time, whereas the occurrences of well dispersing species are more stable or increasing (Turin and den Boer, 1988). This supports the conservation value given to the habitats occupied by brachypterous-restricted species in our study.

The approach presented here has straightforward benefits to conservationists and land managers who wish to rank habitat patches in the landscape according to their ground beetle fauna. Our results suggest marked differences in the conservation value among habitats differing in structure and degree of human disturbance in a complex mountain landscape. They also suggest that conservation priorities based on species richness do not correspond at all with other criteria based on species identities, and the relatively limited potential value of using flagship indicator species for establishing conservation measures of less conspicuous taxa.

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Appendix. Regional distribution (number of sites occupied), total catches (number of individuals caught in 1992), body size (dry mass in mg), wing size and geographic range of species of carabid beetles found in the present study

Wing size categories: A: apterous; B: brachypterous; M: macropterous; P: polymorphic. Geographic range categories: W: widespread; R: restricted. See methods and results for a explanation of categories. Nomenclature follows Zaballos and Jeanne (1994). Body mass from Gutiérrez and Menéndez (1997)

Family, subfamily and species	Regional distribution	Total catches	Body mass	Wing size	Geographic range
Cicindelidae					
Cicindelinae					
<i>Cicindela campestris</i> Linnaeus, 1758	2	18	33.70	M	W

Appendix (continued)

Family, subfamily and species	Regional distribution	Total catches	Body mass	Wing size	Geographic range
Carabidae					
Carabinae					
<i>Megodontus purpurascens</i> Fabricius, 1787	5	14	189.50	A	W
<i>Chrysocarabus lineatus</i> Dejean, 1826	14	108	151.40	A	R
<i>Iniopachys auriculatus</i> Putzeys, 1872	3	15	64.80	A	R
<i>Hadrocarabus macrocephalus</i> Dejean, 1826	15	132	265.40	A	R
<i>Eucarabus deyrollei</i> Gory, 1839	9	59	38.12	A	R
<i>Archicarabus nemoralis</i> Müller, 1764	13	127	142.90	A	W
<i>Oreocarabus getschmanni</i> Lapouge, 1924	5	9	95.41	A	R
Cychrinae					
<i>Cychrus spinicollis</i> Dufour, 1857	3	4	35.17	A	R
Nebriidae					
Nebriinae					
<i>Leistus montanus</i> Stephens, 1828	1	1	5.70	M	W
<i>L. barnevillei</i> Chaudoir, 1867	1	2	5.80	A	R
<i>Nebria brevicollis</i> Fabricius, 1792	7	20	19.26	M	W
<i>N. sobrina</i> Schaufuss, 1862	2	21	21.28	A	R
<i>N. andarensis</i> Bolívar, 1923	1	1	19.40	A	R
Notiophilidae					
Notiophilinae					
<i>Notiophilus pusillus</i> Waterhouse, 1833	1	1	0.60	M	W
<i>N. rufipes</i> Curtis, 1829	1	1	2.40	M	W
<i>N. biguttatus</i> Fabricius, 1779	4	7	1.88	P	W
Elaphridae					
Elaphrinae					
<i>Elaphrus pyrenaicus</i> Fairmaire & Laboulbène, 1854	2	10	9.88	M	R
Loroceridae					
Lorocerinae					
<i>Lorocera pilicornis</i> Fabricius, 1775	5	38	4.33	M	W
Clivinidae					
Clivininae					
<i>Clivina fossor</i> Linnaeus, 1758	3	12	3.28	M	W
Trechidae					
Trechinae					
<i>Trechus</i> spp. Clairville, 1806	5	30	-	-	-
Bembidiinae					
<i>Philochtus biguttatus</i> Fabricius, 1779	1	4	1.40	M	W
<i>P. guttula</i> Fabricius, 1792	4	15	0.58	B	W
<i>Ocydromus deletus</i> Serville, 1821	1	3	1.85	M	W
<i>Metallina properans</i> Stephens, 1828	4	121	1.14	M	W
<i>M. lampros</i> Herbst, 1784	8	114	0.90	B	W
Pterostichidae					
Pterostichinae					
<i>Stomis pumicatus</i> Panzer, 1796	1	1	4.50	A	W

Appendix (continued)

Family, subfamily and species	Regional distribution	Total catches	Body mass	Wing size	Geographic range
<i>Lagarus vernalis</i> Panzer, 1796	6	22	4.70	P	W
<i>Poecilus cupreus</i> Linnaeus, 1758	5	126	28.34	M	W
<i>P. coeruleus</i> Linnaeus, 1758	6	452	26.95	M	W
<i>P. kugelanni</i> Panzer, 1797	2	4	39.38	M	W
<i>Argutor diligens</i> Sturm, 1824	3	4	3.05	A	W
<i>A. strenuus</i> Panzer, 1797	5	38	3.69	P	W
<i>Bothriopterus angustatus</i> Duftschmid, 1812	1	1	20.60	M	W
<i>Melanius nigrita</i> Paykull, 1790	7	175	18.17	B	W
<i>Haptoderus ehlersi</i> Heyden, 1881	2	23	10.36	A	R
<i>H. aralarensis</i> Mateu, 1945	6	40	5.01	A	R
<i>Steropus gallega</i> Fairmaire, 1859	12	206	54.64	A	R
<i>Oreophilus cantaber</i> Chaudoir, 1868	11	237	35.26	A	R
<i>Pterostichus cristatus</i> Dufour, 1820	8	164	35.45	A	W
<i>P. dux</i> Schaufuss, 1862	10	262	94.26	A	R
<i>Abax ater</i> Villers, 1789	5	112	79.19	A	W
Platyninae					
<i>Europhilus fuliginosus</i> Panzer, 1809	2	5	2.88	M	W
<i>Agonum viduum</i> Panzer, 1797	4	172	6.65	M	W
<i>A. muelleri</i> Herbst, 1784	3	154	6.01	M	W
<i>Platynus assimilis</i> Paykull, 1790	4	73	15.93	M	W
<i>Anchomenus dorsalis</i> Pontoppidan, 1763	3	25	3.45	M	W
<i>Paranchus albipes</i> Fabricius, 1801	3	35	4.57	P	W
<i>Synuchus vivalis</i> Illiger, 1798	2	6	4.07	M	W
<i>Platyderus quadricollis</i> Chaudoir, 1866	2	2	3.27	A	R
<i>Anchomenidius astur</i> Sharp, 1872	1	2	8.98	A	R
<i>Calathus asturiensis</i> Vuillefroy, 1866	1	1	10.80	M	R
<i>C. melanocephalus</i> Linnaeus, 1758	1	1	6.80	A	W
<i>C. fuscipes</i> Goeze, 1777	8	140	25.88	A	W
<i>C. uniseriatus</i> Vuillefroy, 1866	6	879	21.05	A	R
<i>Actenipus oblongus</i> Dejean, 1828	3	4	61.86	A	W
Zabrinae					
<i>Amara (Zezea)</i> sp1 Csiki, 1929	1	1	22.60	M	-
<i>Amara (Amara)</i> sp2 Bonelli, 1810	2	2	11.45	M	-
<i>A. ovata</i> Fabricius, 1792	2	3	13.20	M	W
<i>A. montivaga</i> Sturm, 1825	1	3	10.80	M	W
<i>A. familiaris</i> Duftschmid, 1812	1	3	6.25	M	W
<i>A. communis</i> Panzer, 1797	2	14	9.73	M	W
<i>A. aenea</i> De Geer, 1774	3	39	8.79	M	W
<i>Percosia equestris</i> Duftschmid, 1812	2	8	14.33	M	W
<i>Bradytus apricarius</i> Paykull, 1790	1	1	12.20	M	W
<i>Cyrtonotus aulicus</i> Panzer, 1797	1	1	27.70	M	W
<i>Zabrus consanguineus</i> Chevrolat, 1865	3	100	51.00	A	R
Harpalidae					
Anisodactylinae					
<i>Anisodactylus binotatus</i> Fabricius, 1787	1	1	21.80	M	W
Harpalinae					
<i>Ophonus azureus</i> Fabricius, 1775	1	6	8.94	P	W
<i>Pseudophonus rufipes</i> De Geer, 1774	1	4	47.27	M	W
<i>Harpalus dimidiatus</i> Rossi, 1790	2	76	35.03	M	W

Appendix (continued)

Family, subfamily and species	Regional distribution	Total catches	Body mass	Wing size	Geographic range
<i>H. attenuatus</i> Stephens, 1828	1	5	15.40	M	W
<i>H. rubripes</i> Duftschmid, 1812	2	7	20.20	M	W
<i>H. latus</i> Linnaeus, 1758	1	5	12.68	M	W
<i>H. ebeninus</i> Heyden, 1870	4	40	21.27	A	R
<i>H. sulphuripes</i> Germar, 1824	1	31	10.16	A	W
<i>H. honestus</i> Duftschmid, 1812	1	12	12.56	M	W
<i>Paraphonus maculicornis</i> Duftschmid, 1812	1	15	4.85	M	W
Licinidae					
Licininae					
<i>Licinus aequatus</i> Serville, 1821	7	15	22.10	A	W
Badistrinae					
<i>Badister bullatus</i> Schrank, 1798	2	2	2.60	M	W
Callistidae					
Callistinae					
<i>Chlaeniellus nigricornis</i> Fabricius, 1787	4	82	14.92	M	W
<i>C. tristis</i> Schaller, 1783	1	1	29.10	M	W
Lebiidae					
Cymindinae					
<i>Cymindis alternans</i> Rambur, 1837	7	30	6.61	A	R
Lebiinae					
<i>Lamprias cyanocephalus</i> Linnaeus, 1758	1	2	2.35	M	W
Dromiinae					
<i>Dromius meridionalis</i> Dejean, 1825	1	1	2.10	M	W
<i>Philorhizus vectensis</i> Rye, 1873	1	1	0.65	A	W
<i>P. notatus</i> Stephens, 1828	1	1	0.43	A	W
<i>Syntomus foveatus</i> Fourcroy, 1785	4	173	0.59	A	W
<i>Microlestes maurus</i> Sturm, 1825	1	7	0.23	B	W
<i>M. minutulus</i> Goeze, 1777	1	21	0.39	M	W
<i>M. negrita</i> Wollaston, 1854	1	35	0.17	P	W
Brachinidae					
Brachininae					
<i>Brachinus explodens</i> Duftschmid, 1812	1	3	2.97	M	W
<i>B. sclopeta</i> Fabricius, 1792	1	2	3.70	M	W

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