The influence of habitat type on the distribution of carabid beetles in traditionally managed "dehesa" ecosystems in NW Spain

Angela Taboada, D. Johan Kotze, José M. Salgado & Reyes Tárrega

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We investigated the responses of carabid beetles to habitat type at the local scale in traditionally managed "dehesa" ecosystems in NW Spain. The beetles were sampled from two habitat types (central grassland and surrounding forested zone) of five "dehesa" ecosystems, from May to October 2004. A total of 4,374 carabid individuals and 55 species were captured using pitfall trapping. Most of the species were collected from both habitat types, probably due to open spaces created between old-growth trees in the forested zone. Differences in carabid assemblage composition were found mainly due to *Harpalus* species characteristic from the central grassland and a few forest specialist species exclusively found in the forested zone. The maintenance of the "dehesa" structure may be of importance for carabid species adapted to the variety of habitats created, and requires the continuation of traditional management practices.

A. Taboada and J. M. Salgado, Department of Animal Biology, University of León, Campus de Vegazana s/n, E-24071 León, Spain; E-mail: dbaatp @unileon.es
D. J. Kotze, Department of Biological and Environmental Sciences, P. O. Box 65 (Biocenter 3, Viikinkaari 1), FI-00014 University of Helsinki, Finland
R. Tárrega, Department of Ecology, Genetics and Microbiology, University of León, Campus de Vegazana s/n, E-24071 León, Spain

1. Introduction

Historical land use and management practices, including forest burning and cutting to create agricultural land and pastures for livestock grazing, have altered and diversified the landscape in the Iberian Peninsula (Blanco *et al.* 1997, Luis-Calabuig *et al.* 2000). In some cases, these traditional practices have transformed the forested land to create "dehesa" ecosystems, where the use of resources coexists with areas of high biological diversity (Gómez-Limón & De Lucío Fernández 1999). A "dehesa" is an agro-forestry system with extensive grazing (sheep, goats, pigs and cattle); these multiple land-uses produce a landscape of high habitat heterogeneity (Blanco *et al.* 1997). The resulting anthropogenic mosaic (pasture, arable, woodland) produces a range of environmental conditions and niches that can enhance diversity (e.g., Pulido & Díaz 1997, Martín & López 2002).

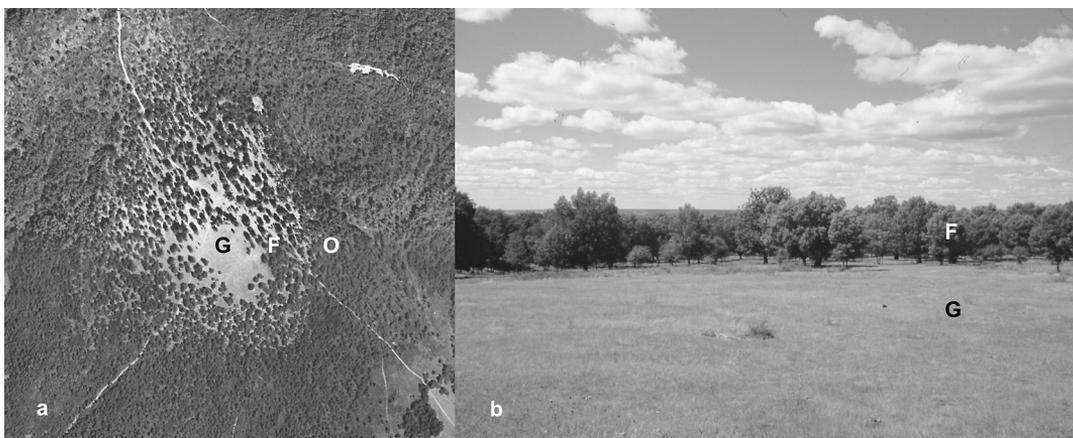The origin and evolution of the "dehesa"

Figure 1. Composition of the dehesa ecosystem and its relation to the surrounding oak forest. a) Aerial view and b) detailed view. Habitat types: G = Central grassland, F = Forested zone, O = Surrounding oak forest.

landscape have been intrinsically related to transhumance pastoral systems for centuries (Blanco *et al.* 1997). Well-developed "dehesa" systems were established as a permanent feature of the Spanish landscape from the early Middle Ages, when clearing, thinning and ploughing of continuous oak forests were frequently performed. These management practices were developed in order to obtain regularly-spaced retained trees (between 30 and 60 trees per ha) and to enhance grassland growth among the trees (Blanco *et al.* 1997, Joffre *et al.* 1999, Pulido *et al.* 2001). Most contemporary "dehesa" ecosystems were created during the second half of the 19th and the beginning of the 20th centuries as a result of increased human densities (Pulido *et al.* 2001).

The degree of habitat diversity (i.e., differences in vegetation structure and composition) in a "dehesa" ecosystem is mainly dependent on management practices and different products obtained (e.g., forage, firewood, charcoal, acorn, cork, tannin). Basically, the vegetation structure of a "dehesa" is composed of two layers (Joffre *et al.* 1999): a savannah-like open tree layer with scattered mature oaks (mainly *Quercus ilex* and *Q. suber*) and a grass dominated layer (usually native annual herbs for grazing). The maintenance of this two-layered vegetation structure requires continuous management such as: a) control of shrub invasion by uprooting, clearing and ploughing, b) preservation of the old-growth tree layer by regular pruning to favour horizontal branches (to provide shade, browsing and acorn production), and c) the enhancement of tree regeneration by the planting of new seedlings (Blanco *et al.* 1997).

Here we investigate the responses of carabid beetles to habitat type (defined by the variability in the composition of the vegetation layer) at the local scale in traditionally managed "dehesa" ecosystems in NW Spain. We selected a *Quercus pyrenaica* "dehesa" system that typically consists of two main habitat types: 1) a central grassland area and 2) a surrounding forested zone characterised by scattered old-growth trees, which are maintained for livestock shelter and feeding purposes (Fig. 1).

We aim to determine if the carabid assemblages inhabiting the "dehesa" ecosystem differ between the central grassland and the surrounding forested zone despite their spatial proximity. We ask whether differences in environmental conditions due to tree development in the forested area influence the presence of carabid species according to their habitat preferences [see Reyes-López *et al.* (2003) for ants]. Shade provided by the scattered trees in the forested zone increases microhabitat humidity, decreases temperature and contributes to leaf litter development and organic matter content (Joffre *et al.* 1999), leading also to modifications in the vegetation composition. These changes in environmental conditions may make the forested zone suitable for forest specialist species, even though these zones are not considered true forest ecosystems. Open hab-

itat species are expected to thrive in the central grassland and generalist species are expected to be less influenced by the differences between the two habitat types.

2. Material and methods

2.1. Study area and sampling method

The study was conducted in NW Spain (42º36'–42º39' N, 4º58'–5º05' W), in the Mediterranean Region 980–1,030 m a.s.l. We selected five *Quercus pyrenaica* "dehesa" ecosystems [*Festuco heterophyllae–Querceto pyrenaicae* sigmetum; Penas *et al.* (1995)] at least 1 km apart, surrounded by continuous oak forests and with a similar grazing intensity (sheep and goats). Each "dehesa" ecosystem included the two habitat types described above, and we sampled carabid beetles in five central grassland sites (size range 2.09–8.23 ha) and five surrounding forested sites (size range 11.50–24.64 ha).

Grazed and open central grasslands are dominated by a variety of herb species such as *Aira caryophyllea*, *Cynosurus cristatus*, *Medicago lupulina*, *Ornithopus compressus*, *Trifolium arvense*, *T. campestre*, *T. glomeratum*, *T. pratense*, *T. strictum*, and *Vulpia bromoides* (Díez *et al.* 1994, 1995). The surrounding forested zone is characterised by a more complex vegetation structure consisting of several layers: oak trees, oak saplings, shrubs and annual and perennial herbs (Table 1).

Vegetation sampling in these forested zones were carried out in June–July 2004: (a) understory vegetation cover (shrubs, herbs and saplings) was visually estimated in 20 systematically placed 1 m × 1 m quadrats per site; (b) oak tree characteristics (perimeter, height, canopy diameter and distance between trees) were measured from 40 trees per site.

We used plastic pitfall traps (depth 86 mm, diameter 60 mm) covered by 10 cm × 10 cm roofs and partly filled with 25% propylene glycol to collect the beetles. Pitfall catches reflect carabid activity-density (e.g., Thomas 1998) that will be referred to here as abundance or number of individuals. Five sampling points were placed in each of the ten sites. Each sampling point consisted of

Table 1. Structural characteristics of the vegetation at the five forested zones. Dominant herb (annual and perennial herbs) and scarce (<5% cover) shrub species at each zone are given. Oak saplings (<1m height) are indicated when cover was greater than 2%. Mean ± Standard Deviation distance between oak trees, tree height, perimeter and canopy diameter are also given.

	Annual herbs	Perennial herbs	Shrubs	Mean ±SD tree dist. (m)	Mean ±SD tree ht. (m)	Mean ±SD tree perim. (cm)	Mean ±SD canopy diam. (m)
1	*Aira caryophyllea* *Cynorosus echinatus* *Tuberaria guttata*	*Agrostis capillaris* *Festuca rubra* *Plantago lanceolata*	*Crataegus monogyna*	7.70 ± 3.76	8.46 ± 4.42	73.33 ± 71.47	6.49 ± 4.66
2	*Tuberaria guttata*	*Agrostis capillaris* *Carex muricata* *Festuca rubra*	*Erica cinerea* *Halimium umbellatum* Oak saplings	7.65 ± 5.32	11.03 ± 4.14	123.40 ± 112.32	7.45 ± 4.97
3	*Aira caryophyllea* *Cynosurus echinatus* *Tuberaria guttata* *Vulpia bromoides*	*Agrostis capillaris*	*Halimium umbellatum* Oak saplings	9.66 ± 5.17	10.20 ± 4.70	98.68 ± 102.69	6.83 ± 4.50
4	*Aira caryophyllea* *Tuberaria guttata* *Vulpia bromoides*	*Agrostis capillaris* *Hieracium castellanum* *Hieracium gr. pilosella* *Plantago lanceolata*	*Thymus serpyllum*	7.18 ± 4.34	10.18 ± 4.96	87.80 ± 91.43	6.08 ± 4.27
5	*Aira caryophyllea* *Trifolium campestre*	*Agrostis capillaries* *Carex muricata* *Festuca rubra* *Hieracium gr. pilosella*	*Calluna vulgaris* *Erica umbellate* *Lithodora diffusa* *Thymus serpyllum* Oak saplings	5.53 ± 3.13	13.88 ± 2.10	86.20 ± 48.26	6.64 ± 3.03

Table 2. Generalised linear model results. df = degrees of freedom. Residual Deviance is the amount of variation not explained by the models; p values in parentheses (boldface if *p* <0.05; χ^2 distribution). The Central grassland (Grassl.) coefficients are the basic intercepts of the models; Forest = forested zone. Theta (with SE) is the aggregation value (for negative binomial models only) with lower values indicating a higher degree of aggregation.

| | Null Dev. | Resid. Dev. (*p*) | | | Coeff. | | | | |
		Size	Ants	Habitat type	Size	Ants	Grassl.	Forest	Theta (SE)
Residual df	9	8	7	6					
Abundance	272.79	264.40 (**0.004**)	263.56 (0.361)	16.91 (**<0.001**)	−0.051	9.49×10^{-5}	−1.248	0.870	
Rarefied Richness	4.26	4.25 (0.902)	3.79 (0.497)	3.79 (0.976)	0.009	1.85×10^{-4}	2.675	−0.009	
Calathus fuscipes	14.56	14.17 (0.536)	14.17 (0.946)	10.80 (0.067)	−0.039	3.94×10^{-4}	−3.419	1.409	2.00 (0.86)
Carabus amplipennis	44.85	11.52 (**<0.001**)	9.35 (0.140)	7.44 (0.167)	0.093	-1.75×10^{-3}	−7.708	1.896	3.00 (2.29)
Harpalus distinguendus	58.67	16.61 (**<0.001**)	14.25 (0.124)	12.08 (0.141)	−0.207	-9.00×10^{-4}	−0.791	−1.283	2.29 (1.34)
Harpalus ebeninus	25.40	24.85 (0.459)	18.54 (**0.012**)	7.56 (**<0.001**)	−0.119	5.91×10^{-3}	−13.350	5.977	0.99 (0.66)
Harpalus rufipalpis	29.81	15.01 (**<0.001**)	11.39 (0.057)	8.56 (0.093)	−0.317	1.92×10^{-3}	−5.068	2.165	1.30 (0.70)
Harpalus serripes	17.70	11.15 (**0.011**)	8.64 (0.113)	8.44 (0.652)	0.070	5.17×10^{-3}	−10.640	−1.408	0.44 (0.26)
Nebria salina	18.54	16.61 (0.164)	12.86 (0.053)	10.09 (0.096)	−0.114	-9.17×10^{-4}	−4.407	2.107	1.69 (0.88)
Poecilus kugelanni	35.23	28.33 (**0.009**)	20.21 (**0.004**)	12.76 (**0.006**)	0.057	1.87×10^{-3}	−7.920	2.063	2.60 (1.69)
Steropus gallega	25.26	20.22 (**0.025**)	14.99 (**0.022**)	12.68 (0.128)	−0.095	-2.53×10^{-3}	−3.567	1.505	1.54 (1.24)
Steropus globosus	22.44	22.17 (0.603)	12.53 (**0.002**)	10.57 (0.161)	0.060	1.95×10^{-3}	−5.782	0.771	3.71 (1.76)
Syntomus foveatus	25.31	13.30 (**<0.001**)	13.14 (0.690)	11.21 (0.165)	0.005	4.69×10^{-4}	−4.412	−2.550	1.11 (0.58)
Trechus obtusus	16.13	12.91 (0.073)	12.91 (0.939)	11.96 (0.329)	−0.018	-2.22×10^{-4}	−5.489	1.621	0.92 (0.50)
Trechus quadristriatus	23.49	15.60 (**0.005**)	15.10 (0.476)	12.04 (0.081)	−0.034	-2.46×10^{-4}	−6.256	2.911	0.97 (0.61)
Zabrus silphoides	26.11	12.64 (**<0.001**)	11.04 (0.206)	10.54 (0.478)	−0.173	1.10×10^{-3}	−4.973	0.786	1.66 (0.99)
Generalist group	27.65	22.31 (**0.021**)	16.89 (**0.020**)	10.63 (**0.012**)	0.193	2.00×10^{-3}	−7.412	−3.274	2.43 (1.46)
Open habitat group	13.18	11.23 (0.162)	10.37 (0.354)	10.37 (0.972)	−0.006	7.55×10^{-4}	−4.635	−0.033	2.91 (1.39)

three traps 50–200 cm apart (i.e., 15 traps per site, 150 traps in total). Sampling points were at least 30 m apart and as far as possible from site edges. Beetles were collected continuously from 28 May to 4 October in 2004, and traps were emptied every 20–25 days. Beetles were identified using standard keys (Jeannel 1941–1942, Lindroth 1974, Trautner & Geigenmüller 1987), and follow the nomenclature in Serrano (2003). We counted the number of ants (Formicidae) collected in the traps due to high abundances obtained.

2.2. Data analysis

We pooled the carabid catches of each site and for the whole trapping period, and classified the species as forest specialists, generalists or open habitat species, according to the literature (Jeannel 1941–1942, Lindroth 1974, Vázquez 1990, Campos 2003, Ortuño & Marcos 2003 & Peláez 2004; see Appendix).

Generalised linear models (GLM) were used to test for differences in carabid abundance and species richness between the two habitat types. Species representing at least 50 individuals and collected from at least five of the ten sites were analysed individually. The remaining species were pooled into groups according to the above mentioned habitat classification in order to include them into the analysis. *Calathus granatensis* and the forest specialist group were not tested, as they were clearly associated with the forested zone. The response variables in the models were number of individuals (overall and for individual species) and overall number of species (i.e., species richness). Abundance data were modelled following a negative binomial error distribution (White & Bennetts 1996) unless specified otherwise (see Table 2), and species richness data were modelled following a Poisson error distribution. The predictor variable was habitat type (central grassland and forested zone). Site size and mean ant abundance per site were included into the models as exploratory variables. Ants

were included into the models because in previous studies potential competitor groups explained a large amount of the variability found in the carabid assemblages and individual species (Taboada *et al.* unpubl.). As a result of management practices and the "dehesa" habitat configuration, central grasslands are unavoidably smaller than surrounding forested zones and, consequently, size and habitat type were statistically confounded in the models (Pearson's correlation: $r = 0.75$, df = 8, $p = 0.001$). Therefore, the predicted values obtained (see Figs. 2 and 3) were based on: a) the mean size of each habitat type (i.e., 4.22 ha for central grasslands and 17.65 ha for forested zones) in order to get a more realistic prediction for each habitat type independently of size, and on b) the overall mean size (i.e., the mean size of the ten sites, 10.94 ha, which is located outside the true size ranges of both habitat types) in order to obtain a valid (although less realistic) comparison between habitat types by taking size into account.

We performed a Detrended Correspondence Analysis (DCA) to correlate carabid species and sites (Jongman *et al.* 1995), assuming a unimodal (Gaussian) response of carabid beetle abundances to the environment. Species with at least 15 individuals (26 species) were included in this analysis, avoiding the inclusion of scarce species according to our dataset.

Unequal trapping effort (19% trap loss) was corrected by including the number of days the traps per site were active as an offset term in the abundance models, and by rarefying species richness data to 200 individuals. Abundance data for the DCA analysis were standardised to 100 trapping days. Data analyses were carried out with the R statistical package (R Development Core Team 2005).

3. Results

We collected 4,374 carabid individuals and 55 species (Appendix). Overall carabid abundance was statistically significantly higher in the forested zone (Table 2, Fig. 2a). Rarefied species richness did not differ significantly between the two habitat types (Table 2, Fig. 2b).

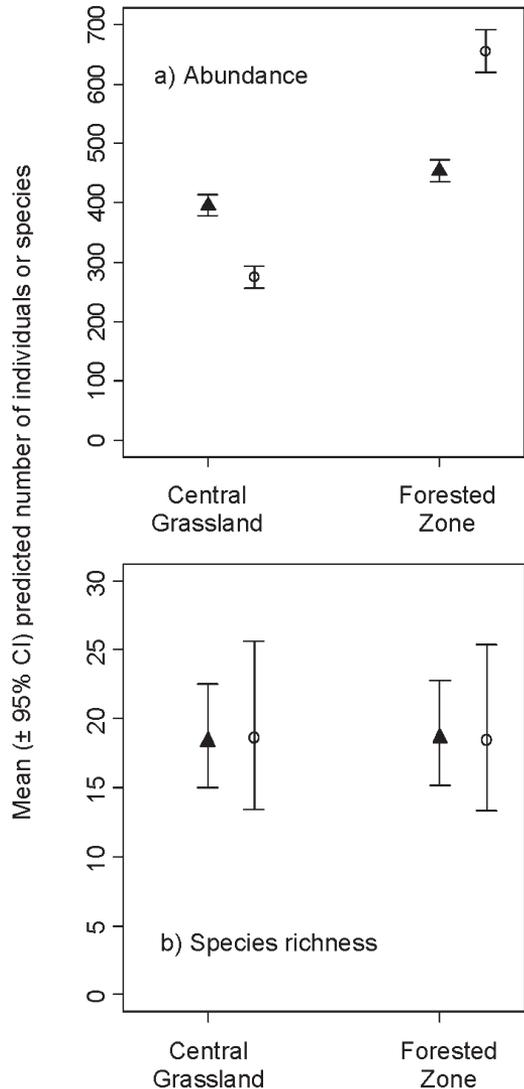Both habitat types supported mainly open

Figure 2. Mean (±95% Confidence Interval) predicted number of carabid individuals and species at the two habitat types. Predictions were obtained with: the mean size of each habitat type (▲) and the overall mean size (○); see text. Predicted values for abundance were standardised to the mean number of active trapping days per site (i.e., 1,543 days). Predicted values for species richness were obtained after rarefaction to 200 individuals.

habitat (57.8% and 48.6% in central grasslands and forested zones, respectively) and generalist species (42.2% and 37.9%, respectively). No forest specialist species were captured from the central grasslands, but 13.5% of the species captured exclusively from the forested zones were forest

Figure 3. Mean (±95% CI) predicted number of individuals of the most representative species at the two habitat types. Predictions were obtained with: the mean size of each habitat type (▲) and the overall mean size (○). Predicted values were standardised to the mean number of active trapping days per site (i.e., 1,543 days).
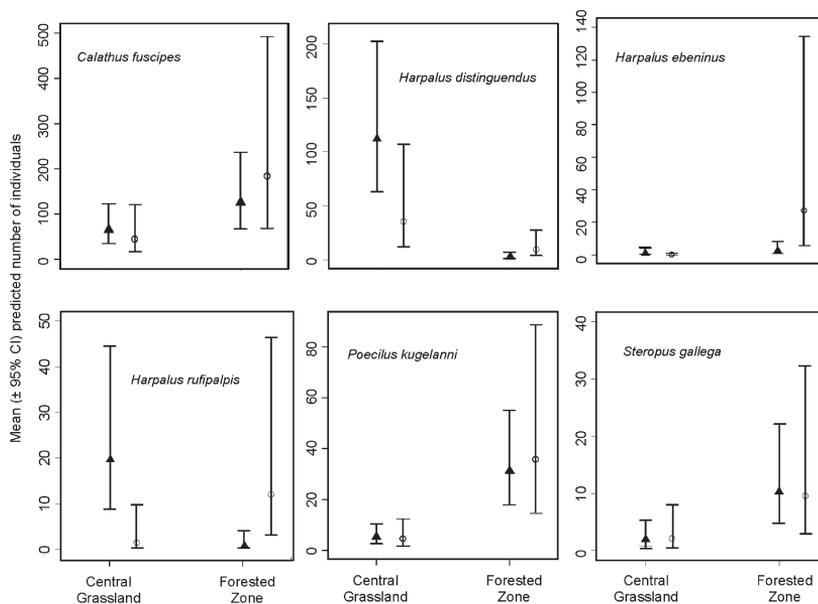
specialists, including *Calathus rotundicollis*, *Calosoma inquisitor*, *Carabus lusitanicus* and *Notiophilus biguttatus* (Appendix). *Calathus granatensis*, a generalist species according to the literature, was also exclusively collected from the forested zones.

The most abundant species were collected from both central grasslands and forested zones: *Calathus fuscipes* (1,071 individuals, 24.5% of the total catch), *Steropus globosus* (769 individuals, 17.6%) and *Harpalus distinguendus* (612 individuals, 14%), all generalist species. Only two (*Harpalus ebeninus* and *Poecilus kugelanni*) of the 14 species tested, responded statistically significantly to habitat type (i.e., responded positively to the forested zone, Table 2). Nine of the 14 species tested responded statistically significantly to the size of the studied sites, and the number of ants was a significant predictor of the abundance of four beetles tested (Table 2).

In general, habitat size had a negligible effect on the species responses to habitat type as most of the species tested responded in the same direction when we compared the predicted values obtained from the overall mean size to the predicted values obtained from the mean size of each habitat type (Fig. 3).

We identified three types of responses of the species to habitat type: (a) most of the species responded either as generalists or are mainly asso-

ciated to the forested zone, independently of size (for example, *Calathus fuscipes*, *Harpalus ebeninus*, *Poecilus kugelanni* and *Steropus gallega*; Table 2, Fig. 3); (b) two species responded as generalists in the statistical sense (i.e., no statistically significant difference between the two habitat types) and as open habitat species in the ecological sense (*Harpalus distinguendus* and *Harpalus serripes*; Table 2, Fig. 3); and (c) two species responded highly negatively to habitat size (*Harpalus rufipalpis* and *Zabrus silphoides*; Table 2, Fig. 3).

In addition, species in the open habitat group (24 species) were not statistically significantly associated with either of the habitat types, while the generalist group (11 species) was statistically significantly associated with the central grasslands (Table 2). The forest specialist group (five species) responded to habitat type as expected (not tested as it was clearly associated with the forested zone).

Results from the DCA analysis (Fig. 4) showed that the carabid assemblage composition of the two habitat types clearly differed, mainly due to the presence of *Harpalus* species (open and generalist species) in the central grasslands, and forest specialist species (e.g., *Calathus rotundicollis* and *Calosoma inquisitor*) and other abundantly collected species at the forested zones (e.g., *Poecilus kugelanni*).
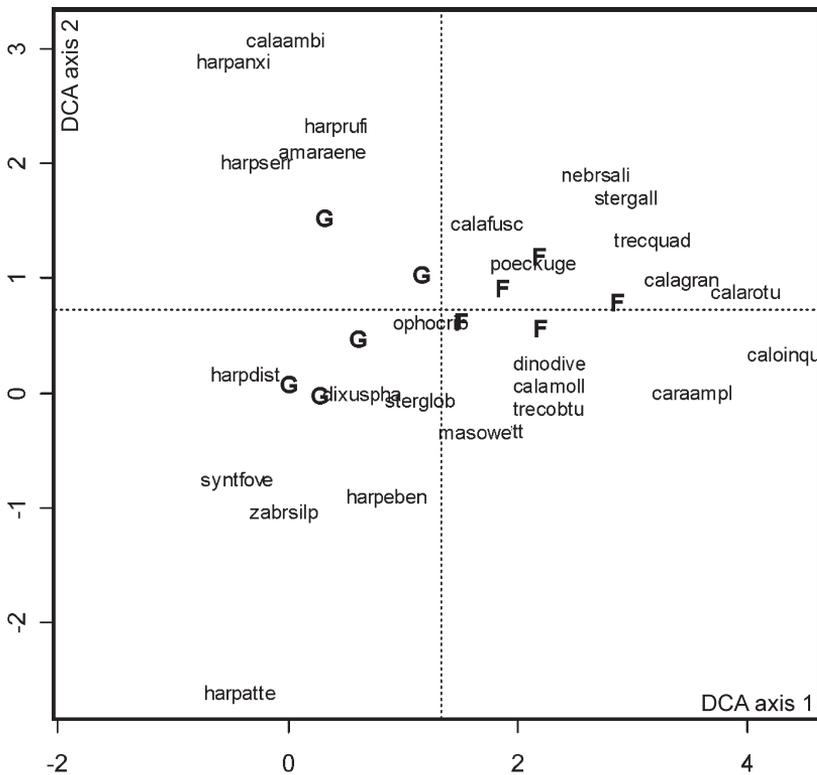
Figure 4. Detrended Correspondence Analysis (eigenvalues and axis lengths: 0.52 and 2.86 SD for axis 1, and 0.21 and 1.54 SD for axis 2, respectively) for carabid species and sites. Habitat types: G = Central grassland, F = Forested zone. Carabid names are a combination of 4 (genus name) by 4 (species name) letters. For example, calaambi = *Calathus ambiguus*.

4. Discussion

Even though the two habitat types sampled here were quite different in terms of vegetation structure, we showed that they were quite similar regarding to the carabid beetles – most species did not respond to habitat type (i.e., were collected from both central grasslands and forested zones). Some of these species were collected from the forested zones but were mainly characteristic of the open central grasslands, such as species of the genus *Harpalus*, as shown in the DCA analysis. These species may prefer the environmental conditions that characterise the central grassland, like higher temperature and lower moisture, but may also occasionally move into the surrounding forested zone. Human-created spaces between old-growth trees in the forested zone may allow these species to move from and to the central grassland (Koivula & Niemelä 2003). Besides, as temperature has a significant effect on carabid beetle movement (Raworth & Choi 2001), it may also have influenced pitfall catches in the central grasslands (i.e., higher temperatures imply higher

movement rates and consequently a higher activity-density measure from pitfall traps).

On the other hand, some species were more abundantly found in the forested zone, but cannot be considered as true forest specialist species. These species may be associated to specific environmental conditions created under the oak trees (see Reyes-López *et al.* 2003). For example, *Poecilus kugelanni* was abundantly found in meadow areas characterised by non grazed tall grasses (Taboada *et al.* unpubl.) that are also characteristic of the immediate oak tree surroundings in the forested zone.

Differences between the two habitat types were also found in terms of higher overall abundance and carabid assemblage composition, mainly due to high numbers of *Harpalus* species collected from the central grasslands and due to species collected exclusively from the forested zones, as reflected in the DCA analysis. The maintenance of the forested zone characterised by mature oak trees, with great canopy cover, perimeter and height, positively influenced the presence of a few forest specialist species. These spe-

cies may move from the well-developed surrounding oak forest (see Taboada *et al.* 2004) to the forested zone due to shade and humidity provided by tree development, and probably the more diverse microhabitats created by leaf litter accumulation (Koivula *et al.* 1999). Some species, such as *Carabus lusitanicus* and *Notiophilus biguttatus*, were found in low numbers in the surrounding forested zone, but in case of the rare *Calosoma inquisitor* the forested zone of the "dehesa" probably provides a suitable habitat.

Our results further suggest that ants are a significant predictor of the distribution of four carabid species tested. We found either positive or negative responses of carabids to ants. Although ants appear to affect carabid abundance and species richness negatively (Lövei & Sunderland 1996, Hawes *et al.* 2002), individual species responded differently to the presence of wood ants, depending on their daily activity patterns [e.g., in spruce boreal forests; Koivula *et al.* (1999, 2002)] and their abilities to avoid direct encounters and predation by ants [in mixed pine-birch forests; Reznikova & Dorosheva (2004)] or in their ability to produce defensive chemicals [e.g., formic acid; Will *et al.* (2000)].

In terms of carabid beetle assemblages, the forested zones of the "dehesas" are not that different from the central grasslands and cannot be considered as true forest ecosystems. Furthermore, main differences in carabid beetles are expected between the open "dehesa" ecosystem (i.e., central grassland and surrounding forested zone together) and the closed oak forest, a hypothesis that will be addressed in the future. It may well be that the "dehesa" carabid beetles constitute a unique assemblage that depends on habitat diversity of the "dehesa" ecosystem, making it worthy of conservation efforts.

The long-term maintenance of the "dehesa" landscape strongly depends upon varied local uses (Gómez-Limón & De Lucío Fernández 1999). Over the last 60 years, great changes in the Mediterranean rural landscape, together with changes in the agriculture policies of the European Union, resulted in either the intensification of agricultural and livestock farming or the abandonment of traditional and non-competitive land uses, leading to the disappearance of "dehesa" ecosystems. Transformation of "dehesas" into simplified agricultural lands in case of intensification, or into closed oak forested lands (i.e., due to invasion by young trees and shrubs from the surroundings) in case of abandonment, have lead to the alteration of the vegetation composition and structure in these ecosystems (Díez *et al.* 1991, Gómez-Limón & De Lucío Fernández 1999, Plieninger *et al.* 2003, Peco *et al.* 2005). This loss in habitat diversity in the "dehesa" ecosystem may affect the fauna, and especially those specialist species adapted to habitat heterogeneity (Niemelä *et al.* 1996, Stoate *et al.* 2001). Indeed, in case of carabid beetles, the assemblage composition is expected to vary along landscape transformations due to land use intensification (Fournier & Loreau 1999, Vanbergen *et al.* 2005) and abandonment (Burel & Baudry 1995, Purtauf *et al.* 2004).

Preserving the characteristic habitat diversity of "dehesas" in NW Spain means that specific and traditional practices are needed, such as shrub control (by cutting or grazing by goats), tree care (cutting branches, removing old trees, sanitary care, planting of new trees) and livestock management (i.e., balanced feeding in the whole area) (Blanco *et al.* 1997, Plieninger *et al.* 2003). Ultimately, the preservation of "dehesas" requires that conservation policies integrate participatory planning approaches that consider the motivations of local people (landowners and land-users) and the appreciation of "dehesa" incomes (Plieninger *et al.* 2004) as most "dehesas" are privately owned or local renting systems.

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Appendix. Carabid beetles collected in the five central grasslands and the five forested zones. Wings (W) = wings morphology (b = brachypterous, micropterous or flightless, i.e. unable to fly; m = macropterous; D = dimorphic). Habitat (H) = habitat association of the species (F = forest, G = generalist and O = open habitat species). Literature used: Jeannel (1941–1942), Lindroth (1974), Vázquez (1990), Campos (2003), Ortuño and Marcos (2003) and Peláez (2004).

	W	H	Central grassland					Forested zone					Total
			1	2	3	4	5	1	2	3	4	5	
Amara (*Amara*) *aenea* (De Geer, 1774)	m	O	1	4	–	9	7	4	–	1	1	3	30
Amara (*Bradytus*) *apricaria* (Paykull, 1790)	m	O	1	–	–	–	–	–	–	–	–	–	1
Amara (*Amara*) *eurynota* (Panzer, 1796)	m	O	1	–	–	–	–	2	–	–	–	–	3
Amara (*Amara*) *familiaris* (Duftschmid, 1812)	m	O	1	–	–	1	–	2	–	–	1	–	5
Bembidion (*Metallina*) *lampros* (Herbst, 1784)	D	G	1	–	–	–	–	–	–	–	–	–	1
Bembidion (*Emphanes*) *normannum* Dejean, 1831	m	O	–	–	–	–	–	–	1	–	–	–	1
Bembidion (*Phyla*) *tethys* Netolitzky, 1926	m	G	–	8	1	–	–	2	–	–	–	–	11
Brachinus (*Brachinoaptinus*) *bellicosus* Dufour, 1820	b	O	–	–	–	–	–	–	1	–	–	1	2
Brachinus (*Brachynidius*) *variventris* Schaufuss, 1862	m	O	1	1	–	–	–	–	–	–	–	–	2
Calathus (*Neocalathus*) *ambiguus* (Paykull, 1790)	m	G	–	–	12	18	–	–	–	–	–	–	30
Calathus (*Calathus*) *fuscipes graecus* Dejean, 1831	b	G	42	9	194	26	78	59	27	200	286	150	1,071
Calathus (*Neocalathus*) *granatensis* Vuillefroy, 1866	D	G	–	–	–	–	–	29	37	22	61	20	169
Calathus (*Neocalathus*) *mollis mollis* (Marsham, 1802)	D	O	2	2	5	–	1	16	5	6	5	1	43
Calathus (*Neocalathus*) *rotundicollis* Dejean, 1828	D	F	–	–	–	–	–	18	43	–	34	3	98
Calosoma (*Calosoma*) *inquisitor inquisitor* (Linnaeus, 1758)	m	F	–	–	–	–	–	4	20	–	–	4	28
Carabus (*Oreocarabus*) *amplipennis getschmanni* Lapouge, 1924	b	G	1	–	–	–	–	22	17	1	6	12	59
Carabus (*Mesocarabus*) *lusitanicus complanatus* Dejean, 1826	b	F	–	–	–	–	–	2	5	3	1	3	14
Carabus (*Archicarabus*) *nemoralis prasinotinctus* Heyden, 1880	b	G	–	–	–	–	–	–	–	–	1	6	7
Cicindela (*Cicindela*) *campestris campestris* Linnaeus, 1758	m	O	1	–	–	–	–	–	–	–	1	–	2
Cryptophonus tenebrosus (Dejean, 1829)	m	G	1	–	–	–	–	–	–	–	–	–	1
Dinodes (*Dinodes*) *dives kricheldorffi* (Wagner, 1932)	b	O	–	2	9	–	–	8	6	8	1	–	34
Dixus sphaerocephalus (Olivier, 1795)	m	G	3	1	2	1	2	5	–	1	–	–	15
Graniger femoralis (Coquerel, 1858)	m	O	1	–	–	–	–	–	–	–	–	–	1
Harpalus (*Harpalus*) *anxius* (Duftschmid, 1812)	m	O	–	16	–	46	–	–	–	–	–	–	62
Harpalus (*Harpalus*) *attenuatus* Stephens, 1828	m	G	–	23	–	1	1	–	–	–	–	–	25
Harpalus (*Harpalus*) *decipiens decipiens* Dejean, 1829	m	O	–	–	1	–	–	–	–	–	–	–	1
Harpalus (*Harpalus*) *distinguendus distinguendus* (Duftschmid, 1812)	m	G	266	62	50	49	159	3	–	19	4	–	612
Harpalus (*Harpalus*) *ebeninus* Heyden, 1870	m	O	–	16	1	–	–	5	–	28	5	–	55
Harpalus (*Harpalus*) *honestus* (Duftschmid, 1812)	m	G	–	–	2	–	–	–	–	–	–	–	2
Harpalus (*Harpalus*) *neglectus neglectus* Audinet–Serville, 1821	D	O	–	2	–	–	–	–	–	–	–	–	2
Harpalus (*Harpalus*) *oblitus patruelis* Dejean, 1829	m	G	2	1	–	3	–	–	–	–	–	–	6
Harpalus (*Harpalus*) *rufipalpis rufipalpis* Sturm, 1818	m	O	3	6	51	40	5	–	–	29	3	–	137
Harpalus (*Harpalus*) *serripes serripes* (Quensel, 1806)	m	G	–	30	3	31	–	2	–	3	–	–	69
Masoreus wetterhallii wetterhallii (Gyllenhal, 1813)	m	O	–	1	5	–	–	5	–	4	–	–	15
Microlestes abeillei abeillei (Brisout de Barneville, 1885)	m	G	–	–	1	–	1	–	–	–	–	–	2
Microlestes corticalis (Dufour, 1820)	m	O	1	1	–	–	3	1	–	–	–	–	6
Microlestes negrita negrita Wollaston, 1854	D	O	2	2	–	–	–	1	–	–	–	–	5
Nebria (*Nebria*) *salina* Fairmaire & Laboulbène, 1856	m	O	2	2	8	5	3	7	19	1	48	4	99
Notiophilus biguttatus (Fabricius, 1779)	D	F	–	–	–	–	–	2	5	–	5	–	12
Olisthopus elongatus Wollaston, 1854	m	O	1	1	1	1	1	–	–	–	–	–	5
Ophonus (*Metophonus*) *brevicollis* (Audinet–Serville, 1821)	m	O	1	–	–	–	–	–	–	–	–	–	1
Ophonus (*Hesperophonus*) *cribricollis* (Dejean, 1829)	m	O	3	–	1	–	3	3	–	1	7	–	18

Species			1	2	3	4	5	6	7	8	9	10	Total
Ophonus (*Metophonus*) *parallelus* (Dejean, 1829)	m	O	–	1	–	–	–	–	–	–	–	–	1
Poecilus (*Coelipus*) *crenulatus crenulatus* (Dejean, 1828)	m	O	–	–	–	3	–	–	–	–	–	–	3
Poecilus (*Macropoecilus*) *kugelanni* (Panzer, 1797)	m	O	1	–	14	6	7	23	19	116	9	35	230
Poecilus (*Poecilus*) *versicolor* (Sturm, 1824)	m	O	1	2	–	–	–	–	–	–	–	–	3
Pseudomasoreus canigoulensis (Fairmaire & Laboulbène, 1854)	m	F	–	–	–	–	–	–	1	–	–	–	1
Pseudoophonus (*Pseudoophonus*) *rufipes* (DeGeer, 1774)	m	O	–	–	–	–	–	–	–	–	1	–	1
Steropus (*Steropidius*) *gallega* (Fairmaire, 1859)	b	G	–	–	2	2	7	–	17	7	32	11	78
Steropus (*Sterocorax*) *globosus ebenus* (Quensel, 1806)	b	G	8	92	77	18	71	60	28	269	54	92	769
Syntomus foveatus (Geoffroy, 1785)	b	G	68	53	7	14	4	5	–	3	–	3	157
Synuchus vivalis vivalis (Illiger, 1798)	m	G	–	–	–	1	–	3	–	–	–	4	8
Trechus (*Trechus*) *obtusus asturicus* Jeannel, 1921	D	G	11	8	–	–	4	41	26	22	7	2	121
Trechus (*Trechus*) *quadristriatus* (Schrank, 1781)	m	G	–	–	2	7	–	41	36	14	31	4	135
Zabrus (*Iberozabrus*) *silphoides asturiensis* Heyden, 1880	b	O	29	33	10	2	9	3	–	18	1	–	105
Number of individuals			456	379	459	284	366	378	313	776	605	358	4,374
Number of species			28	26	23	21	18	29	18	22	24	18	55
Rarefied number of species			18	21	18	19	16	26	17	16	18	16	