

Local-scale distribution of cholevid beetles (Col., Leiodidae: Cholevinae) in the province of León (Spain)

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Received March 12, 1999; revised December 1, 1999; accepted December 8, 1999

Abstract — Ecological correlates of the distribution of nine common leiodid species were studied in three river valleys on the southern side of the Cantabrian Range in León, in northern Spain. Soil moisture content, substrate temperature variability and type of organic matter proved to be the key factors determining the distribution of species of this group. These factors may have important effects not only at the local level but also on the medium scale. © 2000 Éditions scientifiques et médicales Elsevier SAS

Coleoptera / Cholevinae / Spain / environmental factors / habitat selection

1. INTRODUCTION

Leiodids, especially the Cholevinae, are often non-specialist detritivores occupying a wide range of habitats including caves, vertebrate nests and burrows, animal corpses, leaf litter and humus, though always in epigeal or semiendogeal positions. Nevertheless, and despite the fact that many species have a wide distribution, there have been relatively few in-depth studies of habitat selection. Peck and Anderson [5], Zoia [11] and Ruzicka [7] have reported information on habitat selection by a number of species. We have previously described the complex structure of factors governing habitat selection by species occurring in the Orocantabrian phytogeographic area of north-west Spain, largely related to vegetation type [10]. Also, one of us [8] has reported information on the ecological characteristics of twenty species captured in northern Spain.

In the present study, we aim to advance understanding of the factors affecting the local-scale distribution of, and habitat selection by, various species of leiodid beetles. To this end, sampling was performed at stations in both the Eurosiberian and Mediterranean

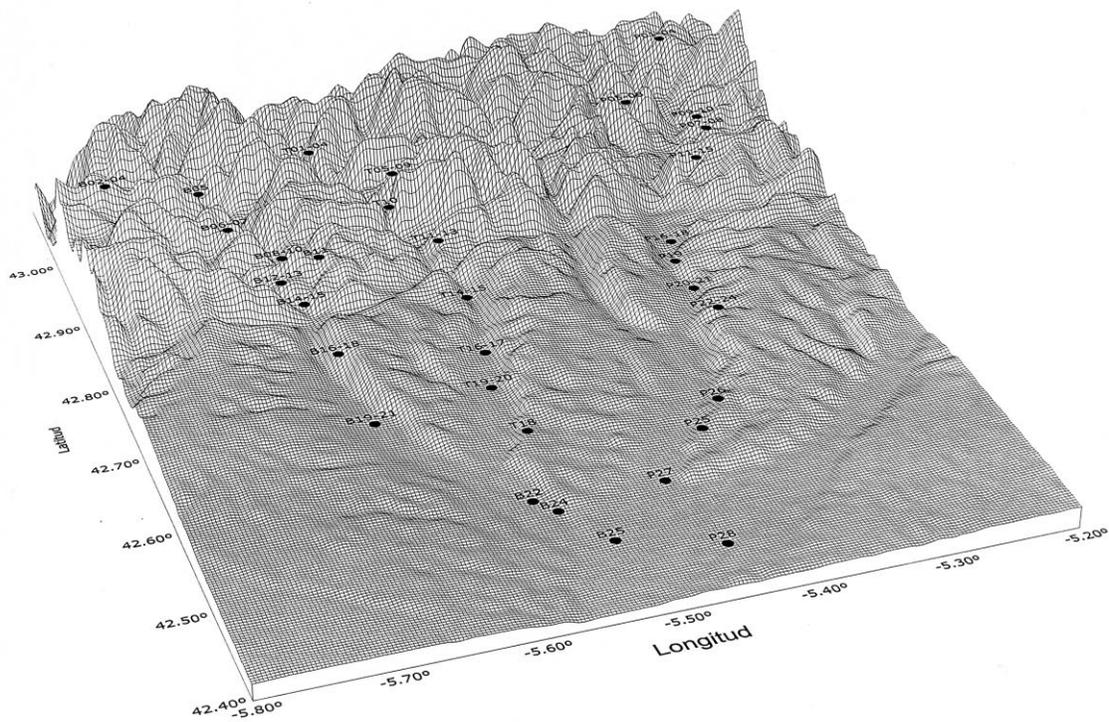
phytogeographic regions, in three watersheds on the southern side of the Cantabrian range in north-western Spain.

2. MATERIALS AND METHODS

Samples were obtained from a total of 73 sites at 34 locations, in the watersheds of the Bernesga, Torío and Porma rivers (León province, Spain; *figure 1*). At each sampling site, we placed a pitfall trap (diameter 7 cm, height 10 cm) containing beer as attractant and formol (3 ‰) as preservative. All traps were checked every 12 d between January 1991 and December 1992.

A total of 4 323 leiodid specimens, totalling nineteen species, were collected (see [9]). In the present study, we consider only the nine most abundant species or subspecies, namely *Ptomaphagus tenuicornis tenuicornis* (Rosenhauer 1856), *Speonemadus vandallitiae* (Heyden 1870), *Nargus velox velox* (Spence 1815), *N. brunneus* (Sturm 1839), *Choleva jeanneli* Britten 1992, *Catops grandicollis* Erichson 1837, *C. ventricosus ventricosus* Weise 1877, *C. fuliginosus* Erichson 1837 and *C. fuscus fuscus* (Panzer 1794).

The 73 sampling sites were classified on the basis of vegetation type into the following fifteen groups



Sites	Locations	Vegetation type	Sites	Locations	Vegetation type	Sites	Locations	Vegetation type
B02	Arbás del Puerto	Broom scrub	P01	Pto. de Señales	Pinewood	T01	Piornedo	Heath
B03	Arbás del Puerto	Heath	P02	Pto. de Señales	Broom scrub	T02	Piornedo	Broom scrub
B04	Arbás del Puerto	Rocky	P03	Pto. de Señales	Rocky	T03	Piornedo	Pasture
B05	Busdongo	Pinewood	P04	Pto. de Señales	Heath	T04	Piornedo	Rocky
B06	Villamanín	Willow stand	P05	Puebla de Lillo	Beechwood	T05	Getino	Beechwood
B07	Villamanín	Mowed meadow	P06	Puebla de Lillo	Pasture	T06	Getino	Pyrenean oak wood
B08	Ciñera	Beechwood	P08	Vegamián	Genista scrub	T07	Getino	Heath
B09	Ciñera	Broom scrub	P09	Camposolillo	Mowed meadow	T08	Getino	Willow stand
B10	Ciñera	Pyrenean oak wood	P10	Camposolillo	Willow stand	T09	Getino	Pasture
B11	Sta. Lucía de Gordón	Heath	P11	Embalse del Porma	Heath	T10	Hoces de Vegacervera	Genista scrub
B12	Huergas del Gordón	Heath	P12	Embalse del Porma	Pyrenean oak wood	T11	Matallana de Torio	Pyrenean oak wood
B13	Huergas del Gordón	Holm oak wood	P13	Embalse del Porma	Broom scrub	T12	Matallana de Torio	Broom scrub
B14	Peredilla	Pyrenean oak wood	P14	Embalse del Porma	Mowed meadow	T14	Pardavé	Holm oak wood
B16	La Seca	Broom scrub	P15	Embalse del Porma	Willow stand	T15	Pardavé	Pasture
B17	La Seca	Mowed meadow	P16	Palazuelo de Boñar	Mowed meadow	T16	Garrafe	Elm stand
B19	Lorenzana	Cropland	P17	Palazuelo de Boñar	Cropland	T17	Garrafe	Mowed meadow
B20	Lorenzana	Hedgerow	P18	Palazuelo de Boñar	Willow stand	T18	Villaobispo	Pinewood
B21	Lorenzana	Elm stand	P19	Candanedo	Pyrenean oak wood	T19	San Feliz de Torio	Willow stand
B22	Castrillo de la Ribera	Elm stand	P20	Lugán	Mowed meadow	T20	San Feliz de Torio	Cropland
B24	Alija de la Ribera	Poplar stand	P22	Cerezales del Condado	Holm oak wood			
B25	Villaroañe	Willow stand	P23	Cerezales del Condado	Hedgerow			
			P24	Cerezales del Condado	Mowed meadow			
			P25	Villimer	Elm stand			
			P26	Castrillo del Porma	Willow stand			
			P27	Puente Villarente	Poplar stand			
			P28	Villamoros de Mansilla	Cropland			

Figure 1. Three-dimensional map showing the 34 sampling locations. The listing below specifies the location and vegetation type of each of the 66 sampling sites with specimens.

Table I. Numbers of each of the nine leiodid species in each vegetation type. C ful, *Catops fuliginosus*; C fus, *C. fuscus fuscus*; C gra, *C. grandicollis*; C ven, *C. ventricosus ventricosus*; C jea, *Choleva jeanneli*; N bru, *Nargus brunneus*; N vel, *N. velox velox*; P ten, *Ptomaphagus tenuicornis tenuicornis*; S van, *Speonemadus vandalitiae*; sites, total number of sites with that vegetation type.

	C ful	C fus	C gra	C ven	C jea	N bru	N vel	P ten	S van	Sites
Genista scrub	1	0	2	0	0	0	0	0	2	2
Heath	3	6	1	4	0	3	1	5	6	7
Rocky	1	1	0	0	0	0	0	0	3	3
Poplar stand	2	2	1	0	0	0	2	0	2	2
Cropland	3	4	2	0	3	0	1	0	1	7
Holm oak wood	3	0	0	0	0	1	0	3	2	4
Beechwood	2	1	0	2	0	0	0	1	3	3
Pyrenean oak wood	3	5	3	2	2	3	0	5	6	6
Elm stand	2	4	1	0	1	0	3	0	1	4
Pasture	0	1	0	0	0	0	1	0	2	5
Pinewood	2	0	0	1	0	0	1	1	3	3
Broom scrub	3	4	3	3	2	3	0	5	7	7
Mowed meadow	2	7	2	0	4	0	0	0	6	8
Willow stand	2	5	0	0	2	0	2	0	3	10
Hedgerow	2	0	1	0	0	0	2	0	0	2
Total	31	40	16	12	14	10	13	20	47	73

(table I): beechwoods (*hayedos*), Pyrenean oak (*Quercus pyrenaica*) woodland (*melojares*), holm oak woodland (*encinares*), pinewoods (*pinares*), elm stands (*olmedas*), poplar stands (*choperas*), hedgerows (i.e. seminatural and generally thorny linear thickets separating areas of cultivated ground) (*sebes*), broom scrub (*piornales*), heath (*brezales*), *Genista* scrub (*aulagares*), willow stands (in some cases scrub, in some cases riverine communities with larger trees) (*saucedas*), pastures (*pastizales*), mowed meadows (*prados de siega*), cropland (*cultivos*) or rocky sites (*gujarrales*).

As well as the 9×66 species-by-sites abundance matrix obtained in the present study, we also considered the matrix obtained by merging this matrix with the equivalent 20×69 matrix obtained in a previous study [10], both excluding sites without specimens. The two species-by-site abundance matrices were analysed with the aid of correspondence analyses, with subsequent consideration of all factors whose eigenvalue exceeded $100/(F - 1)$, where F is the maximum number of factors possible for that analysis [4]. Species diversity was quantified by the method of Hutchinson [3]. Habitat preference was investigated by log-linear analysis, using the power divergence (PD) statistic of Cressie and Read [1], with the λ value of 2/3 recommended for tables with disperse values.

3. RESULTS AND DISCUSSION

Correspondence analysis is an exploratory technique related to principal components analysis which finds multidimensional representation of the association between the row and column categories of a two-way contingency table. Then, this approach is an interesting technique because it permits the generation of hypotheses on the relationship between rows (i.e. species) and underlying factors.

3.1. Local-scale environmental factors

Correspondence analysis of the 9×66 species-by-sites abundance matrix extracted three principal factors that together explained 65.4 % of total variance (29.0, 19.7 and 16.7 %; table II, figure 2).

Sites with high positive loadings on factor I included elm stands (B21, B22 and T16), poplar stands (B24), hedgerows (B20, P23), cropland (P28), willow stands (B25, T19) and the pasture at Pardavé (T15), all characterized by high soil moisture content, and in some cases with frequent waterlogging. Sites with high negative loadings on this factor were all drier sites, including several Pyrenean oak woodland sites (B14, P19 and T06) and the *Genista* scrub at Vegamián (P08). Most sites are scattered fairly evenly along this axis, although the ten sites with highest positive loadings (group A in figure 2a) form a reasonably well-defined cluster.

Table II. Results of correspondence analysis of the 9 × 66 species-by-sites matrix, showing co-ordinates (COORD) and partial contributions to inertia (PCON) of each species on the first three axes extracted.

Factor	I		II		III	
Singular value	0.827		0.681		0.632	
Percents	29.04		19.71		16.66	
Species	COORD	PCON	COORD	PCON	COORD	PCON
<i>C. fuliginosus</i>	-0.243	0.010	0.125	0.004	0.239	0.016
<i>C. f. fuscus</i>	0.276	0.024	-0.813	0.312	0.729	0.291
<i>C. grandicollis</i>	0.239	0.004	0.324	0.010	-0.243	0.007
<i>C. v. ventricosus</i>	-0.507	0.017	-0.054	0.000	-0.554	0.035
<i>Ch. jeanneli</i>	0.107	0.000	-1.080	0.034	1.417	0.068
<i>N. brunneus</i>	-0.611	0.021	0.925	0.070	-0.047	0.000
<i>N. v. velox</i>	2.294	0.751	0.584	0.072	-0.432	0.046
<i>P. t. tenuicornis</i>	-0.623	0.078	1.207	0.434	0.638	0.141
<i>S. vandalitiae</i>	-0.472	0.094	-0.321	0.064	-0.739	0.396

Factor II is clearly related to factor I, as can be seen from the linear relationship shown in *figure 2a*. Eight sites with high positive loadings on this axis form a well-defined group (group B in *figure 2a*): these sites include holm oak woodland sites (B13, P22 and T14), the Pyrenean oak woodland site at Matallana de Torío (T11), two broom scrub sites (P13, T12) and two heath sites (B11, B12). Sites with high negative loadings on this factor included upland heaths (B03, T01 and T07) and notably pastures (B07, P14, P16 and T17). This factor appears to separate sites with bare soil, without a significant herb layer, from sites in which the herb layer is well developed. However, it should be stressed that the general trend is for Orocantabrian holm oak woodland sites (*Cephalanthero longifoliae-Querceto rotundifoliae* S.) to have relatively high positive loadings on this axis. Such sites have deep, well-drained soils and generally face south [6], suggesting that this factor may in fact be more closely related to substrate temperature variability than to herbaceous cover (though clearly the two are related, since herbaceous cover reduces temperature variability at soil surface).

Factor III is again related to factor I (soil moisture content), as indicated by the linear relationship shown in *figure 2b*. However, the group A sites do not conform to this relationship, which is attributable to the fact that these sites undergo frequent periods of high soil moisture content. The relationship with substrate temperature variability (*figure 2c*) is likewise linear for many sites with a high negative loading on factor II, but this tendency is inverted for sites with high positive loading on factor II, so that the plot shows a curved trend. Clustered around the point of inflexion of this curve are upland sites with very low leiodid abundances and species diversity, such as pinewoods (P01, P05), rocky sites (P03, P04), willow

stands (P06, T08) and the Piornedo pasture site (T03), at which we found only *S. vandalitiae* (a humus-dwelling species abundant throughout the study area [8]). The sites plotted along the negative factor II tail of the curve are characterized by low substrate temperature variation, and include pastures (B07, B17, P09, P14, P16, P20 and T17), two elm stands (P25, T16) and the Porma willow scrub sites (P10, P18 and P26). The sites plotted along the positive factor II tail of the curve are characterized by increasing substrate temperature variation (and substrate dryness), and include Pyrenean oak woodland sites (B10, B14, P12, P19, T06 and T11), with all the holm oak woodland sites plotted at the end of the tail (B13, P22 and T14). In both directions, species diversity initially increases, but at high-negative and high-positive loadings on factor II, diversity declines with species such as *C. fuscus fuscus* (negative loadings) and *P. tenuicornis tenuicornis* (positive loadings) becoming dominant. The curved trend observed in this factor space may be related to dietary differences among leiodids, particularly in relation to the characteristics of the organic matter available: in this view, sites plotted close to the point of inflexion have low organic matter content, while sites plotted along the tails of the curve are occupied by species that are specialized in particular types of organic matter.

3.2. Medium-scale environmental factors

With the aim of studying these factors on a larger scale and of investigating possible effects of the attractant used, we performed a second correspondence analysis, this time considering the 21 × 142 species-by-sites abundance matrix obtained by including equivalent data obtained in a previous study of 20 species at 69 sites in the Cantabrian

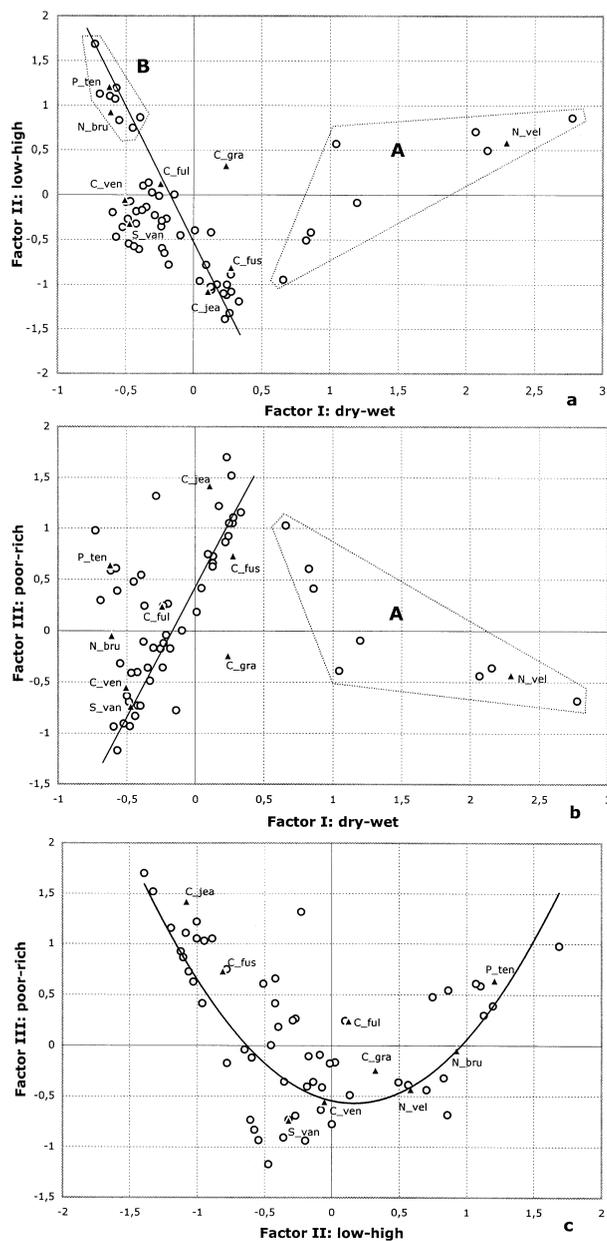


Figure 2. Plots of sites (circles) and species (triangles; see *table I* for co-ordinates) in the spaces defined by the first three factors extracted by correspondence analysis of the 9×66 species-by-sites abundance matrix. The linear (a and b) and parabolic (c) curves fitted to each plot (see text) are also shown.

mountains [10]. This analysis extracted seven factors which together explained 78.0% of total variance (16.2, 13.9, 11.2, 9.6, 8.6, 8.1, 5.7 and 4.7%).

Factor I clearly separated the samples of the two studies (*figure 3c*), despite the fact that some of the

sites were included in both studies. This can only be attributed to differences in the sampling procedure itself, and is most probably due to the fact that we used beer as attractant in the present study, but liver in our previous study [10]. Plots of sites in the spaces defined by the other factors show patterns similar to those observed when only the 66 sites of the present study are considered (cf. *figures 2a, 3b*, for example), and similar to those obtained considering only the 69 sites of our previous study [10]. They can thus be interpreted in the same way: factors II, V and VI reflect soil moisture content, substrate temperature variability and type of organic matter content in the samples of the present study, while factors III, IV and VII reflect the same variables in the samples of our previous study.

These factors thus appear to be stable on the medium scale, although the evident independence of the principal factors of the two sampling programmes should be stressed: this independence is apparent even in the case of related factors such as temperature and humidity (*figure 3a*), and may be attributable to the different attractants which were used and to differences in the way that environmental factors act on these attractants (for example, high temperatures have different effects on the decomposition of a meat food source such as liver than on the decomposition of a plant food source such as beer).

3.3. Environmental preferences of the different species

Only two species showed significant variation in probability of occurrence (presence/absence) among vegetation types (*table I*): *Nargus velox velox*, attributable to its high probability of occurrence in hedgerows, elm stands and poplar stands; and *Ptomaphagus tenuicornis tenuicornis*, attributable to its high probability of occurrence in heath, broom scrub, holm oak woodland and Pyrenean oak woodland (for both species $PD > 23.68$, $df = 14$, $P < 0.05$).

However, log-linear modelling of the presence/absence data, considering both vegetation type and river basin, indicated that there was no significant interaction either between 'species' and 'river-basin' or between 'species' and 'vegetation-type'. Likewise, association analysis of the 'species/vegetation-type' table (*table I*) did not reveal any significant association (Cochran-Mantel-Haenszel general association = 132.5, $df = 112$, $P = 0.09$). These findings suggest that leiodid habitats cannot be usefully classified in terms of vegetation type, presumably because of variability in other factors (such as those detected in our correspondence analyses) within individual vegetation types. The cases in which presence/absence does appear to show any association with vegetation type (i.e. *Nargus velox velox* and *Ptomaphagus*

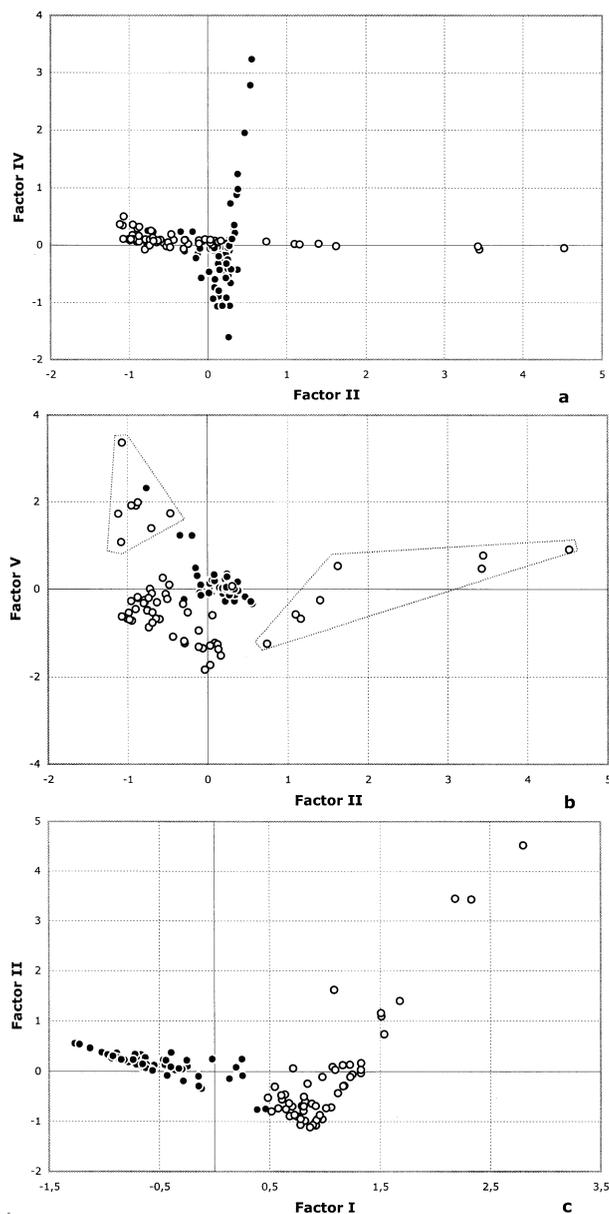


Figure 3. Plots of sites in the spaces defined by representative factors extracted by correspondence analysis of the 21×142 species-by-sites abundance matrix (the matrix obtained by pooling the data of the present study and that of our previous study of twenty species at 69 sites in the Cantabrian mountains). Samples from the present study are shown as white circles, and samples from our previous study as black circles.

tenuicornis tenuicornis) probably reflect a relationship between vegetation type and more proximal determinants of presence/absence.

Considering the data obtained in the present study (i.e. the 9×66 data matrix), four of the species studied

had very high loadings on particular factors in the correspondence analysis (i.e. high squared cosines values):

a) *Nargus velox velox* (90.3 % of variance in abundance explained by factor I): this species was found largely in soil-determined vegetation types like hedgerows, elm stands and poplar stands;

b) *Catops fuscus fuscus* (47.3 and 38.0 % of variance in abundance explained by factors II and III, respectively): this species was present at sites with low substrate temperature variation, notably sites with good herbaceous cover; 54 % of specimens of this species were collected in elm stands, pastures and willow stands, suggesting that this species may show some dietary specialization for decomposing plant matter;

c) *Ptomaphagus tenuicornis tenuicornis* (58.2 % of variance in abundance explained by factor II): this species shows a dietary specialization almost diametrically opposed to that of the preceding species, with preference for sites subject to marked substrate temperature variation; 98 % of specimens were collected from holm oak woodland, Pyrenean oak woodland, heath or broom scrub, perhaps indicating a preference for dry leaf litter;

d) *Speonemadus vandalitiae* (58.0 % of variance in abundance explained by factor III): this species appears to have been more strongly influenced by the presence of any organic matter than by other factors, since it was found mostly at sites with abundant litter; 59 % of specimens were from heath, Pyrenean oak woodland and broom scrub, though it was also present in a wide range of other habitats (13 % of meadow samples; the dominant species at rocky sites; present in all beechwoods and pinewoods sampled).

4. CONCLUSIONS

The results of the correspondence analysis of the data matrix obtained by pooling the data from the present study and from our previous one [10] indicate that the two sampling programmes cannot be usefully compared (probably because of the use of different attractants), which highlights the importance of using identical sampling procedures for large-scale studies.

Analysis of the data for the present sampling programme indicates that the local-scale distribution of the leiidids considered is governed by three principal factors, namely soil moisture content, substrate temperature variability and type of organic matter content. The same principal factors were detected in our previous study of the distribution of leiidids in the

Cantabrian Mountains [10]. Taken together, these findings suggest that these three factors are important on a regional scale, since they explain large proportions of variance in abundance at sites with widely differing vegetation types, in both the Mediterranean and Euro-siberian regions.

Four of the species considered show habitat preferences that are particularly well defined, namely *Nargus velox velox* (preference for moist Mediterranean habitats), *Catops fuscus fuscus* (preference for sites with decaying plant matter), *Ptomaphagus tenuicornis tenuicornis* (preference for sites with abundant leaf litter), and *Speonemadus vandalitiae* (preference for humus sites).

These three factors, and particularly substrate temperature variability and organic matter content, clearly interact, giving rise to a factor of key importance in determining the local-scale distribution of these species, namely availability of decomposing organic matter, since both soil moisture content and temperature variability affect the rate of decomposition of organic matter, and thus the rate at which organic matter becomes unavailable as a food source. A factor of this type – durational stability – was found to be the primary gradient in a study of ecological correlates of the distribution of a grasshopper species [2].

Finally, the present results make clear that leiodid habitats cannot be usefully classified in terms of vegetation type, since leiodid distribution appears to be governed by factors that may vary within vegetation types.

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