

Ecological correlates of the distribution of species of the family Cholevidae (Coleoptera) in the Cantabrian Mountains of northwest Spain

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Abstract

We investigated ecological correlates of the distribution of species of the Cholevidae in the Cantabrian Mountains in northwest Spain. Within the study region, the probability of occurrence of most species appears to be influenced mainly by environmental factors which vary on a local rather than regional scale, although some species showed certain affinity for particular altitude ranges. Soil water content, ground-level insolation and detritus availability appear to be important local-scale determinants of the distribution of many of the species studied.

Keywords: Cholevidae, Spain, biogeography, environmental correlates of distribution, habitat selection.

Résumé

Nous avons étudié les corrélations écologiques de la distribution d'espèces de Cholevidae dans les Monts Cantabriques, au nord-ouest de l'Espagne. Dans la région étudiée, la probabilité d'occurrence de la plupart des espèces semble être influencée principalement par des facteurs environnementaux qui varient à une échelle locale plutôt que régionale, bien que certaines espèces présentent des affinités pour des gradients d'altitude particuliers. Le contenu hydrique du sol, l'ensoleillement à la surface et la disponibilité en débris semblent être les déterminants les plus importants à l'échelle locale de la distribution de beaucoup d'espèces étudiées.

INTRODUCTION

Very little information has been published on the geographical distribution and autecological characteristics of the epigeal species of the Cholevidae (JEANNEL, 1936). We have observed some species to be necrophagous, though in general the cholevids appear to be somewhat non-specialist detritivores. This apparent lack of specialization, by comparison with other families such as the Silphidae (TIZADO *et al.*, 1992), may be attributable to the fact that cholevids typically occur in the

surface layers of the soil or "hole-in-the-ground" microhabitats (for example, at the entries to caves and animal burrows) with rather low detritus availability.

The aim of the work reported here was to investigate ecological correlates of the distribution of species of the Cholevidae in the Orocantabrian phytogeographical Province (RIVAS-MARTÍNEZ *et al.*, 1984) of the northwest Iberian Peninsula.

MATERIALS AND METHODS

Coleoptera were sampled at 74 sites distributed among 38 areas in the Orocantabrian phytogeographical Province (fig. 1). At each site, one trap baited with liver was laid from May to September 1988-1989 and changed fortnightly. A detailed description of the study area and sampling method is given in NUÑEZ *et al.* (1989).

A total of 7,829 cholevid specimens belonging to 20 species of seven genera were trapped in the course of this sampling programme. The species were *Catops coracinus* Kellner, 1846, *Catops grandicollis* Erichson, 1837, *Catops fuliginosus* Erichson, 1837, *Catops fuscus* (Panzer, 1794), *Catops nigricans* (Spence, 1815), *Catops nigriclavus* Gerhardt, 1900, *Catops quadraticollis* Aubé, 1850, *Catops ventricosus* Weise, 1877, *Catops tristis* (Panzer, 1794), *Choleva cisteloides* (Frölich, 1799), *Choleva jeanneli* Britten, 1922, *Choleva punctata* Brisout, 1866, *Notidocharis zariquieyi* (Jeannel, 1924), *Ptomaphagus medius* Rey, 1889, *Ptomaphagus tenuicornis* (Rosenhauer, 1856), *Sciodrepoides fumatus* (Spence, 1815), *Sciodrepoides watsoni* (Spence, 1815), *Speonemadus vandallitiae* (Heyden, 1870), *Nargus velox* (Spence, 1815) and an unidentified *Nargus* species.

Cholevids were trapped in 37 of the 38 sampling areas (no specimens in Collada de Aralla). To identify regional-scale correlates of cholevid distribution, both ecological profiles analysis and cluster analyses of the 37 areas using various distance measures were used. To investigate whether altitude affects species distribution, ecological profiles analysis (DAGET *et al.*, 1972) was used. To identify local-scale environmental factors affecting the distribution of cholevid species among sites mainly correspondence analysis (LEGENDRE & LEGENDRE, 1979) with a reduced data set (see below) was used.

RESULTS AND DISCUSSION

Regional-scale correlates of distribution

To investigate possible regional-scale distribution patterns, the 37 areas were clustered using various distance measures based on relative or absolute abundance of the different species at each site. The tree diagrams obtained were in most cases difficult to relate to ecological similarities among areas; *only point out* Ward's agglomerative method using chord distance (ORLÓCI, 1967) that revealed three well-defined groups of areas (fig. 2): group A, characterized by scarcely humidified dry soils; group B, mostly wet meadows; and group C, mostly diverse habitats. It thus seems that environmental factors which vary on a large geographical scale (latitude and longitude) have little influence on the distribution of cholevids within the study region.

Possible correlations with altitude were investigated by ecological profiles analysis. The ratio of sampled factor entropy to maximal factor entropy was high ($Q_L > 0.99$), indicating that the altitudinal range had been well sampled. Sampled factor entropy was 2.79 bits, and the mean species-factor mutual information value was 0.17 bits, indicating that altitude is an important determinant of some species distribution (BLONDEL, 1985). Examination of the ecological profiles of those

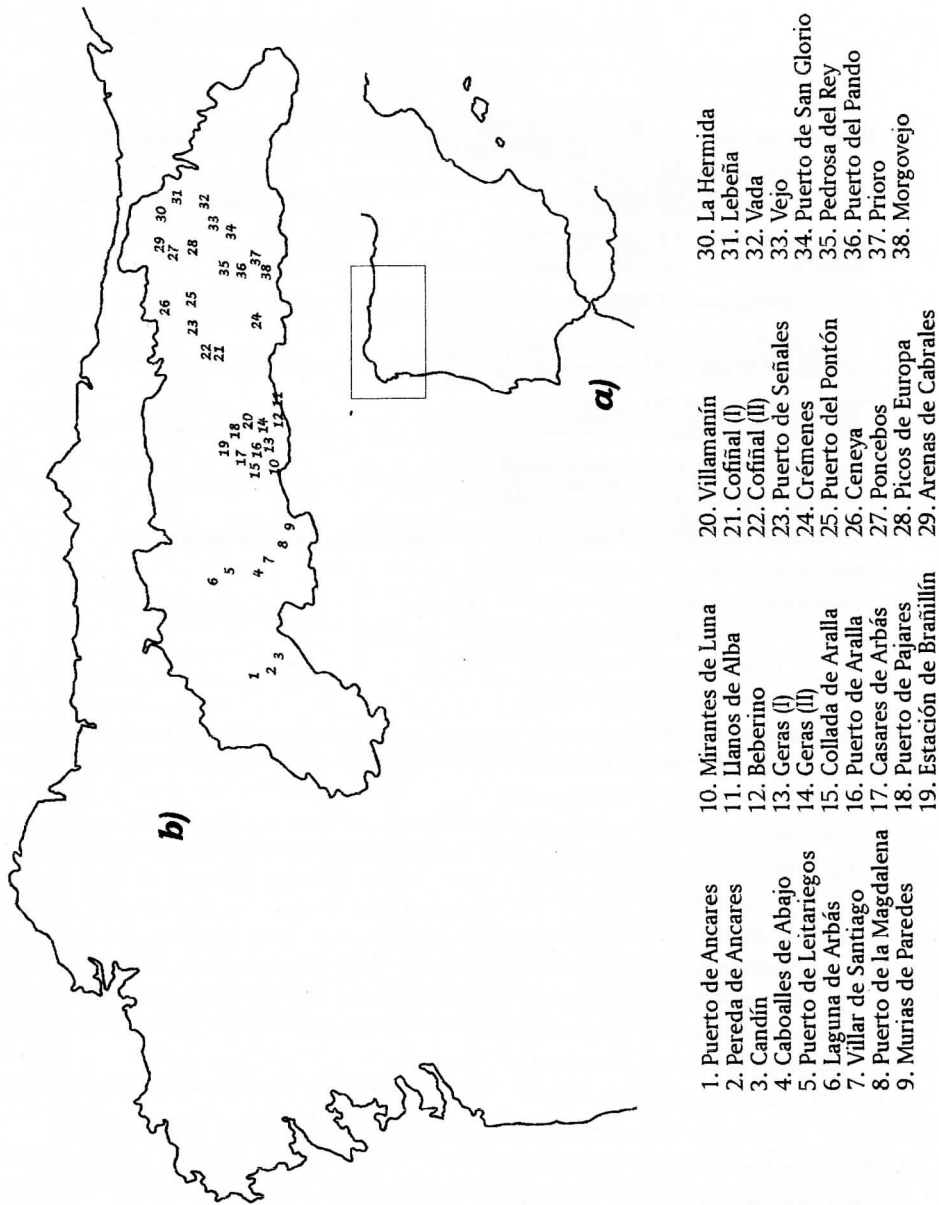


FIG. 1. – a) Map of the Iberian Peninsula, showing the location of the study region.
 b) Map of the study region, showing the location of the 38 sampling areas.

species with species-factor mutual information values greater than 0.10 bits (fig. 3) reveals the existence of four main groups: a) that comprising *Sciodrepoides fumatus* and *Catops coracinus*, from lower-altitude sites generally below 500 m, b) that

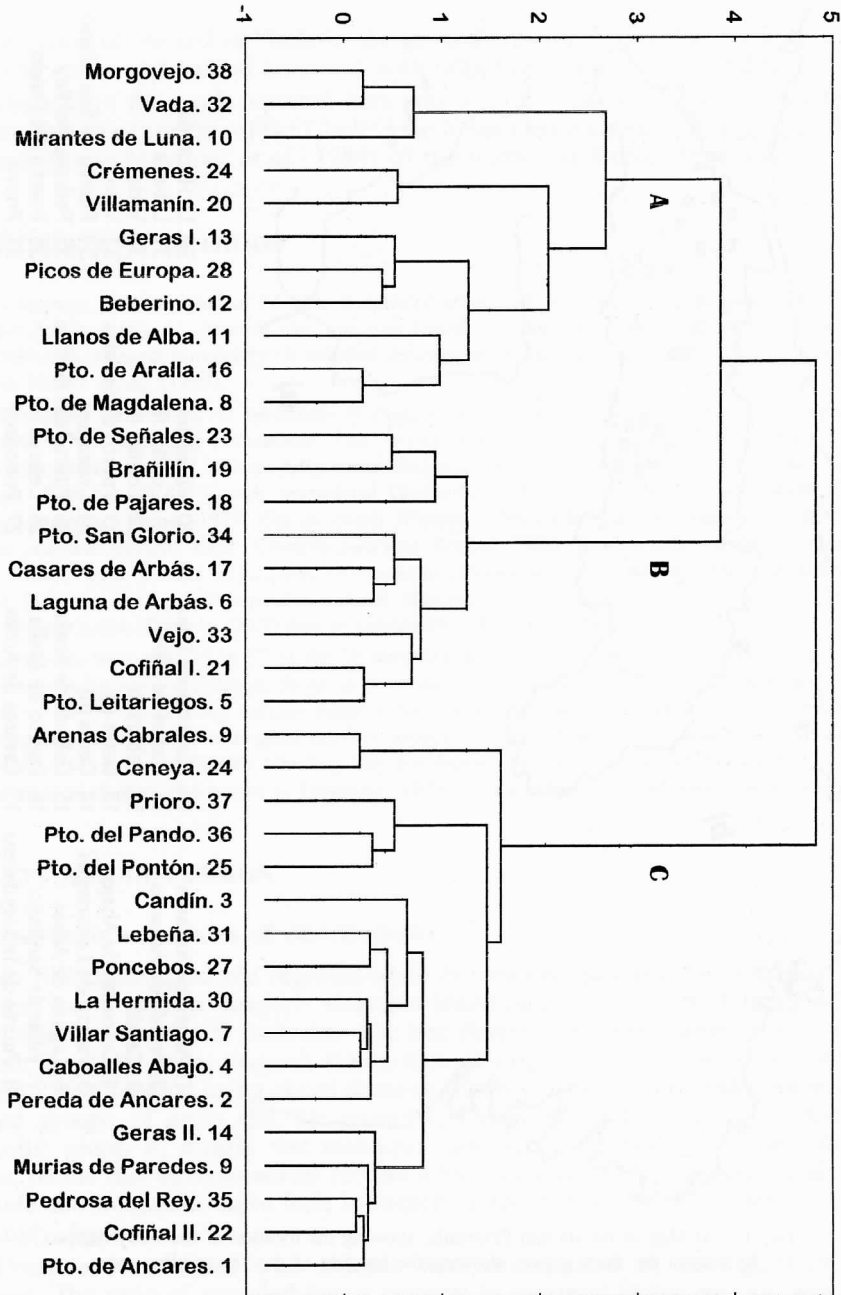


FIG. 2. - Tree diagram showing the results of clustering the 37 sampling areas. Chord distance was used as distance measure. Clustering was by Ward's agglomerative method. The locations of the sampling areas are shown in figure 1. Groups A, B and C are described in the text.

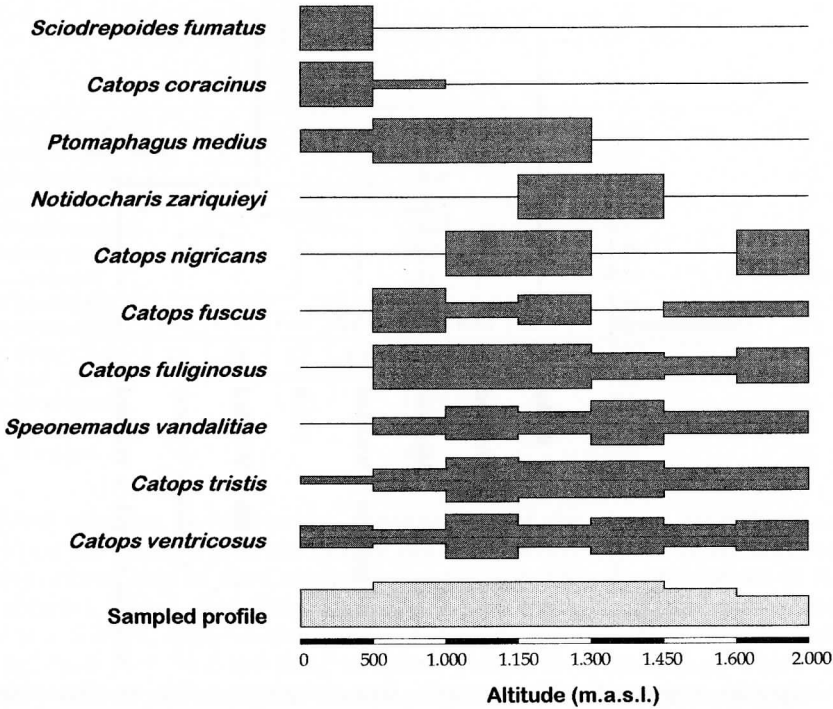


FIG. 3. – Ecological profile plot of the distribution of cholevid species by altitude class. Only those species with a species-factor mutual information value greater than 0.10 bits are shown.

containing *Ptomaphagus medius*, which extends up to 1,300 m, c) that comprising *Catops ventricosus* and *C. tristis*, which occur throughout the studied altitudinal range, and d) that comprising *Notidocharis zariquieyi*, *Speonemadus vandalitiae*, *Catops fuliginosus*, *C. fuscus* and *C. nigricans*, which show irregular distribution although occur above 500 m. However, the apparent distribution of various species with respect to altitude is far from regular; this could be due to other factors being more important determinants of distribution, or to insufficient sampling to account for the full range of habitat variability within each altitude class.

Local-scale correlates of distribution

The sampling stations were assigned to groups on the basis of the vegetation strata present (NÚÑEZ *et al.*, 1989), and these groups were then classified, again on the basis of vegetation strata present, by cluster analysis using UPGMA as agglomerative method and Motyka’s index (MOTYKA *et al.*, 1950) as distance measure. The resulting tree diagram (fig. 4) clearly illustrates the difference between rocky sites (with little or no vegetation) and vegetated sites. However, strata-combination class cannot be considered an important determinant of cholevid distribution in the study region since, although the range of strata-combination classes was sampled effectively ($Q_L=0.97$) and sampled factor entropy was high (2.9 bits), the species-factor mutual information value was very low (0.08 bits).

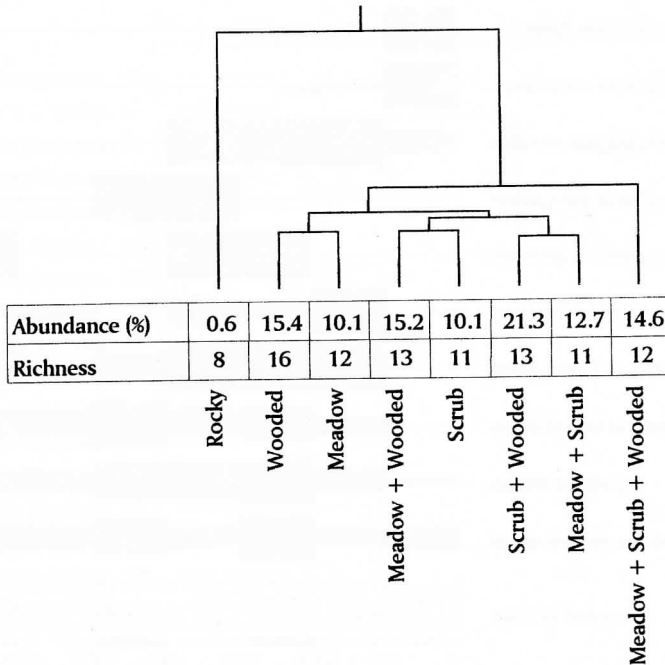


FIG. 4. – Tree diagram showing the results of clustering the eight vegetation types on the basis of vegetation strata combinations. Motyka's index was used as distance measure. Clustering was by UPGMA agglomerative method. Also shown is cholevid species richness and abundance for each vegetation type.

In other groups of detritivorous coleoptera such as the Silphidae (TIZADO *et al.*, 1992), the presence of a herb layer significantly increases the probability of occurrence. In contrast, our data suggest that the presence/absence of different vegetation strata has little effect on the probability of occurrence of cholevids (although species of this group clearly occur less frequently in sites with no vegetation).

With the aim of identifying other factors correlated with the distribution of cholevids, we used correspondence analysis to analyse a reduced 65×14 data matrix (the 65 sites at which more than 5 specimens had been caught, and the 14 most abundant species of cholevid, i.e. excluding *Choleva punctata*, *C. cisteloides*, *C. jeannelli*, *Catops nigriclavis*, *Nargus velox* and the unidentified *Nargus* species). The first three axes extracted explained 52.1% of total variance (20.9%, 17.7% and 13.5% of variance explained by axes I, II and III, respectively; table I).

A biplot of sites and species on these three axes is shown in figure 5. The first axis clearly separates wet sites on the positive side (as meadow at Candín or willow scrub at La Hermita) from dry sites on the negative side (as juniper scrub at Mirantes de Luna), both of them with vegetal cover; as expected given that the study area is in the Eurosiberian Region, most sites are plotted at the wet end of the axis. This axis thus probably reflects soil water content.

TABLE I. – Coordinates of 14 most frequent species of cholevid on the first three axes extracted by correspondence analysis.

	Factor 1	Factor 2	Factor 3
<i>Notidocharis zariquieyi</i>	.743	–1.030	1.086
<i>Ptomaphagus tenuicornis</i>	.748	–.026	–1.435
<i>Ptomaphagus medius</i>	–2.804	.561	.718
<i>Speonemadus vandalitiae</i>	.300	–.671	–1.617
<i>Sciodrepoides watsoni</i>	.340	.182	–.141
<i>Sciodrepodes fumatus</i>	1.340	4.470	.396
<i>Catops coracinus</i>	.834	1.929	–.040
<i>Catops grandicollis</i>	–.757	–.256	–3.747
<i>Catops ventricosus</i>	.389	–.502	.455
<i>Catops tristis</i>	.607	–1.027	.893
<i>Catops quadraticollis</i>	.481	–.292	.352
<i>Catops fuliginosus</i>	–1.012	–.236	.375
<i>Catops fuscus</i>	.022	–.377	.557
<i>Catops nigricans</i>	.042	–.656	.402

Most sites are plotted on the negative side of the second axis; the few sites plotted on the positive side are largely heavily wooded sites in steep-sided valleys on the northern side of the Cantabrian Range (as oakwood with chesnut at Arenas de Cabrales). These sites differ from the rest in that they are in near-continuous shade at soil level; even wooded sites on the southern slopes have higher insolation. This axis can thus be considered to reflect ground-level insolation, which in turn probably reflects soil temperature and, more specifically, extent of variation in soil temperature.

Most sites are plotted on the positive side of the third axis; those plotted on the negative side are mostly habitats such as heathland, meadow, willow scrub and juniper scrub (as both of Crémenes). In general, these sites are on steep slopes or are very close to rivers, so that soil organic matter is low or inaccessible due to waterlogging or leaching. This axis may thus reflect the influence of detritus availability on the distribution of cholevids.

The distribution in the space defined by the three axes reveals a central cluster (group E) corresponding to the main vegetation types of the study region and characterized (on the basis of the above interpretation of the results of correspondence analysis) by relatively high soil water content (due either to high rainfall or frequent mists), moderate insolation leading to relatively high soil temperature variation, and sufficient detritus availability.

This central cluster (E) grades into other vegetation types (fig. 5), four of which constitute clearly defined groups. The first group (A) comprises dry wooded sites – including the holm oak wood at Llanos de Alba, the juniper scrub at Mirantes de Luna and the oakwoods at Morgovejo and Vada – characterized by low soil water content, high soil temperature variation and high soil organic matter content. The second group (B) comprises wet wooded sites – including the willow scrubs at La Hermida and Ceneya, the ashwood at Ceneya and the oakwood with chestnut at Arenas de Cabrales – which are characteristically shaded, with relatively low soil temperature variation and abundant detritus. The third group (C) comprises solely the meadow at Candín, which has very high soil water content (due to frequent flooding), relatively high insolation at soil level and low soil organic matter content.

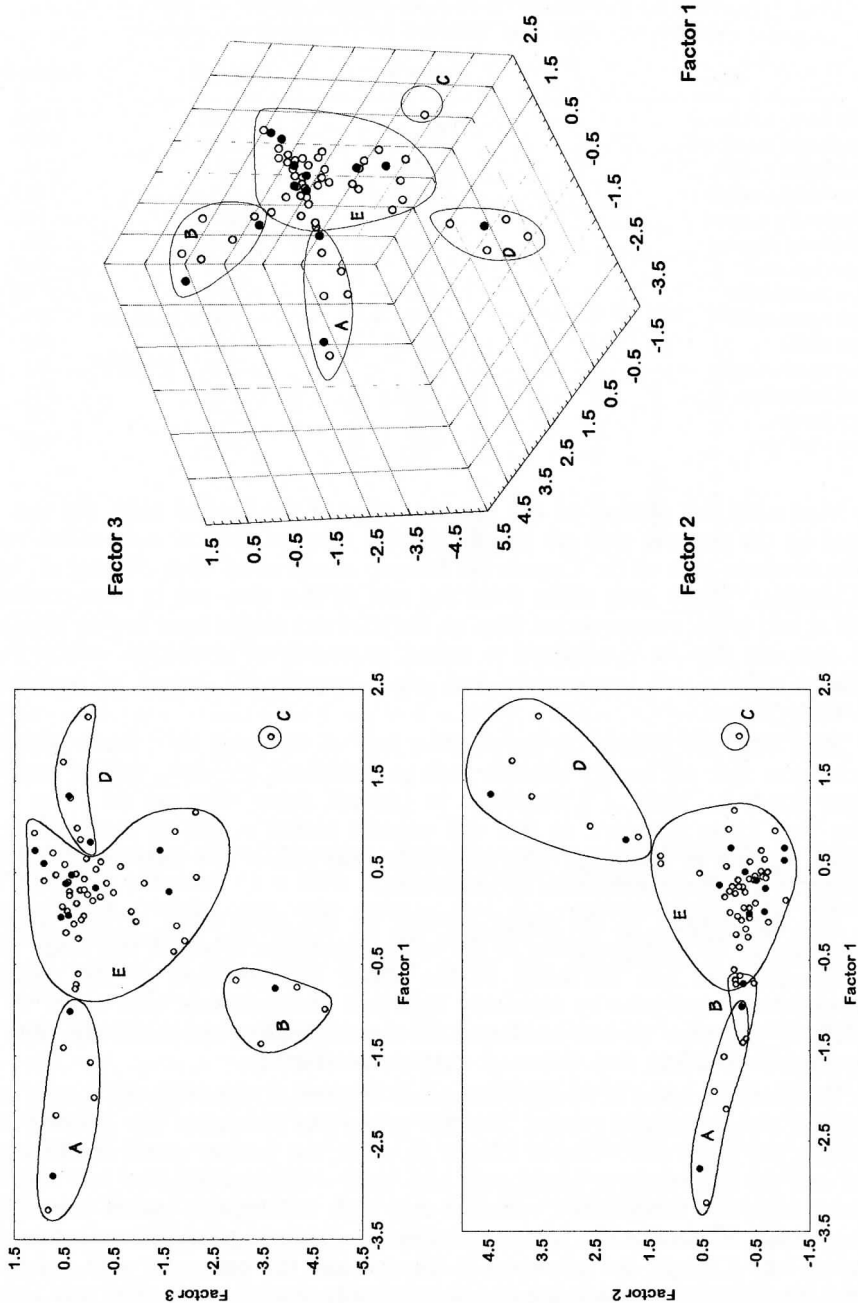


FIG. 5. – Biplots of sampling sites (white circles) and species (black circles) on the first three axes extracted by correspondence analysis of the 65-sites-by-14-species data matrix (see text); the coordinates of each species on each axis are listed in table I.

The fourth group (D) comprises impoverished formations – such as the willow scrub and juniper scrub at Crémenes, the heath at Villamanín and the subalpine meadow by the San Glorio Pass – with moderate soil water content and insolation but with relatively low soil organic matter content (due to intense leaching).

Ecological characteristics of species

The position of the different cholevid species in the space defined by correspondence analysis (fig. 5) permits conclusions to be drawn about their ecological affinities. Most of the species studied were plotted close to the central cluster of vegetation types, indicating either that they are adapted to mean study-region conditions or that they have broad niches. However, some species show clear affinity for specific habitat types, as follows.

Ptomaphagus medius is generally considered to be a common species of the woodland-floor litter layer. The results of this study indicate that this species is characteristic of dry sites such as the juniper scrub at Mirantes de Luna and the oakwood at Morgovejo (where 93% of specimens were caught).

Sciodrepoides fumatus occurred with high abundance in wet wooded sites; if this vegetation type is taken to include the ashwood at Arenas de Cabrales, 90% of specimens of this species were from such sites.

Catops grandicollis is, according to JEANNEL (1936), basically a “hole-in-the-ground” species (being found, for example, at the entries to caves and animal burrows). In the present study, *C. grandicollis* was found principally at impoverished woodland sites (47% of specimens, or 82% if other sites with a deep dry litter layer – such as the pinewood at Prioro or the oakwoods at Morgovejo and Vada – are included in this vegetation category).

Catops fuliginosus can be considered as a common species of the litter layer. We found it at 46% of areas, none of which were wet woodland sites; 55% of specimens of this species were from dry woodland sites.

Catops coracinus showed clear affinity for wet woodland sites (56% of specimens), although it possibly tolerates soil temperature variation somewhat better than *Sciodrepoides fumatus*, enabling it to colonize holm oak woodland and riparian communities (which are typically relatively open and have a well-developed herb layer).

Notidocharis zariquieyi was found in well-established beechwoods and open birchwoods, and is clearly the characteristic species of the montane woodlands of the Cantabrian Range.

CONCLUSIONS

The distribution of cholevid species within the Orocantabrian Province appears to be more strongly influenced by local variation in environmental factors than by regional variation. Only *Sciodrepoides fumatus* and *Catops coracinus* appear to be restricted to low altitudes (below 500 m).

In general, the species of this family occur most frequently at wooded sites. In the cases of *Notidocharis zariquieyi* and *Sciodrepoides fumatus*, this can probably be attributed to the high rates of input of organic matter to the soil due to leaf fall.

Other species – such as *Ptomaphagus medius*, *Catops coracinus*, *C. grandicollis* and *C. quadraticollis* – likewise show affinity for wooded sites, though they also occur in non-wooded habitats. *Speonemadus vandalitiae*, *Ptomaphagus tenuicornis*, *Sciodreporides watsoni*, *Catops ventricosus* and *Catops tristis* do not occur any more frequently in wooded than non-wooded sites, and appear to show affinity for sites with a well-developed shrub and/or herb layer.

The results of this study suggest that the most important environmental factors governing the distribution of cholevid species within the study region are soil water content, extent of soil temperature variation and detritus availability. Particularly marked affinities are shown by *Ptomaphagus medius* (for dry woodland sites), *Sciodreporides fumatus* (for low-altitude wet woodland sites) and *Catops grandicollis* (for sites with a well-developed litter layer and relatively low detritus availability).

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