

Geographical distribution of Adephaga and Polyphaga (Coleoptera) in the Cantabrian Mountains (Spain): Specific richness and analysis of the altitude factor

By JOSEFINA GARRIDO GONZÁLEZ¹, MARGARITA FERNÁNDEZ ALAEZ² and
JUAN A. RÉGIL CUETO³

With 9 figures and 2 tables in the text

Abstract

A detailed ecological analysis related to altitude is carried out by means of the study of the distribution of 145 species and subspecies of aquatic coleoptera (Coleoptera, Adephaga and Polyphaga), detected in 299 sampling stations disposed throughout the Cantabrian Mountains. After defining the species richness at different altitudinal levels, we point out the indicator species by establishing their ecological features profile in terms of the reciprocal species-factor information.

Introduction

The geographical distribution of aquatic insecta is greatly conditioned by the altitude factor, which directly influences the characteristics of aquatic settings and, for that matter, has an influence on the variability of its fauna.

This work intends to correlate the species distribution of aquatic coleoptera (Adephaga and Polyphaga) collected in the Cantabrian Mountains with the altitude factor, and to achieve as well an ecological analysis to show the species which are strongly conditioned by this factor.

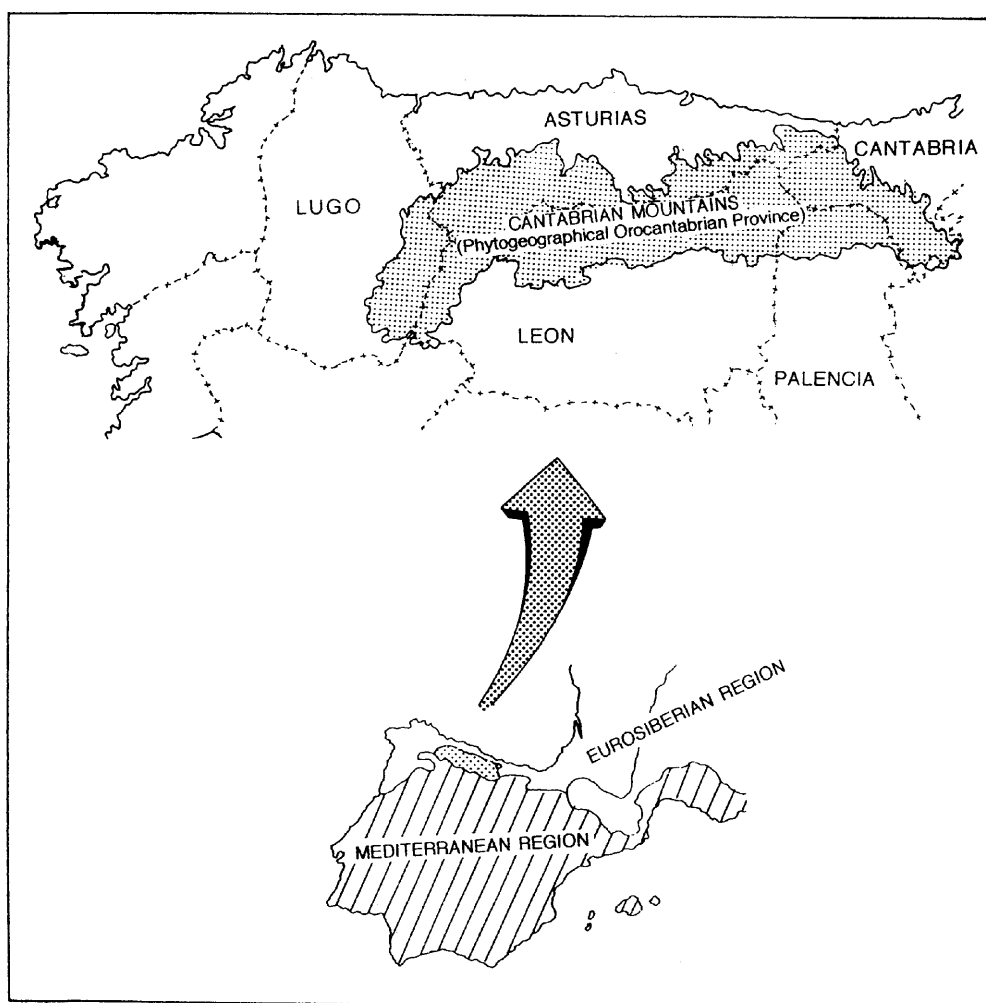
The study area is confined to the Cantabrian mountain ranges (Spain), which stretch through the northeast of the provinces of León, Palencia and Burgos, the south of Cantabria and Asturias, the northeast of the Galician provinces of Orense and Lugo, and the southwest of the Basque Country.

The Cantabrian Mountains comprise the territory that basically constitutes the phytogeographical "orocantabrian" province (RIVAS et al. 1984). Its southwestern limit is defined by the meridional spurs of the Sierras del Ce-

¹ Addresses of the authors: Departamento de Recursos Naturales y Medio Ambiente, Facultad de Ciencias, Universidad de Vigo, 32004, Orense, España.

² Departamento de Ecología Genética y Microbiología, Facultad de Biología, Universidad de León, 24071, León, España.

³ Departamento de Biología Animal, Facultad de Biología, Universidad de León, 24071, León, España.



Map 1. Situation of the Cantabrian Mountains (phytogeographic "Orocantabrian" province), Spain.

brero and the Caurel; northerly it borders on Asturian and Galician territories; easterly its limit is the Alto Campóo, the Ebro dam and the region of Valderredible; and southerly, the foot-of-the-mountain glacises in León (Map 1).

The Orocantabrian province is characterized by especially been montane and only in the northern versant of the Picos de Europa and the Navia and Narcea basins there appears a sloping ground. The subalpine ground stretches from Ancares to Mount Tres Mares, along massifs above 1,700 m; whereas the alpine ground occupies just the massifs of Curavacas, Peña Prieta and Picos de Europa, where an altitude of 2,400 m can be reached.

In the researched area analogous studies about the taxonomic groups have not been carried out, although we should make a reference to the research achieved by VALLADARES et al. (1990) on the altitudinal distribution of Hydrophiloidea in the province of León. There are other references to surveys on longitudinal zonations in watercourses but restricted to genus *Hydraena* in

Italy (BINAGHI 1958, 1959, 1960, 1961, 1965) and in the Pyrenees (BERTHELEMY 1966, TIBERGHEN 1976).

Material and methods

The collection of basic material for this study was achieved between 1986 and 1988. The specimens studied, belonging to 145 species, were collected at 299 sampling places distributed throughout the Cantabrian Mountains. The great number of places visited and their wide distribution have the basic objective of revealing as faithfully as possible the faunistic composition of the families of aquatic Adephaga and Polyphaga in the different natural areas of the Cantabrian Mountains.

The collection procedure for these families of insects varies with the kind of aquatic setting analyzed and the taxa intended to obtain. By means of usual collecting techniques for aquatic entomofauna, both stagnant and running waters have been prospected. Special care has been taken to collect species of lotic and lentic facies in running waters.

A list of 145 catalogued species and subspecies, as well as a detailed description of the places and sampling techniques can be found in GARRIDO (1990).

The altitude factor for the capture of the 145 species and subspecies of Adephaga and Polyphaga in the Cantabrian Mountains is very wide, ranging from 135 m/n.m. to 1,975 m/n.m. In order to offer an actual view of the insects altitudinal preferences the number of sampling sites for the different altitude levels, in which every species is localized, must be taken into consideration.

The 299 sampling sites were classified with respect to their corresponding height above sea level, in such a way that all of them were distributed at 7 altitudinal levels. With this aim 6 semi-open intervals were established (having the lower limit but not the superior one) from 0 up to 1,800 m/n.m., with an amplitude of 300 m. Heights above 1,800 m were included in a single class, because these levels were very homogeneous and faunistically poor (Fig. 1).

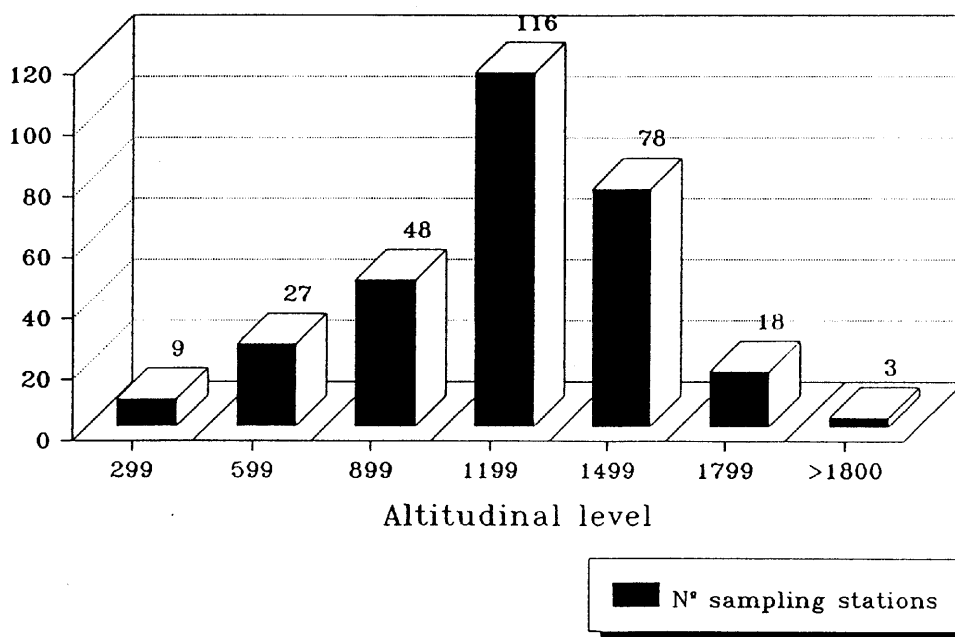


Fig. 1. Relationship between number of sampling stations and altitudinal levels taken.

Firstly the **sampling quality** has been assessed by comparing the maximum entropy of the altitude factor and the one which results from the sampling achieved. Entropy linked to altitudinal gradient has been calculated from the expression that DAGET et al. (1972) proposed:

$$H(L) = \sum_1^{Nk} \frac{R(k)}{NR} \log_2 \frac{NR}{R(k)}$$

where,

$R(k)$ = Number of sampling stations at every altitudinal level;

NR = Total number of sampling stations (299);

Nk = Number of altitudinal levels considered (7).

We arranged a species presence/absence table with respect to the 7 kinds of altitude. Therefore, the table includes a **profile of absolute frequencies** for every species.

In order to avoid, on the one hand, the problem of lack of uniformity in the distribution of sampling sites among the different kinds of altitude, and on the other hand, the problem of deviations between the features of rare and frequent species, a calculation of the **corrected frequency** for every species in relation to altitude has been made. Thus we used the expression of DAGET & GODRON (1982) which considers the median frequency $C(k)$ of the species in the sample lot:

$$C(k) = \frac{U(k)}{R(k)} : \frac{U(E)}{NR}$$

where,

$U(k)$ = Number of sampling sites at every altitudinal level in which species E is present;

$U(E)$ = Total number of sampling stations in which species E is present.

The **reciprocal information** or quantity of information provided by a species in terms of the altitude factor was estimated from the ecological features of presence and absence, and was taken as a measure of the indicator value of the species, in relation to the describer. For a species E and an altitude L, such information is expressed as $I(L;E)$ and defined from the following expression (GODRON 1968):

$$I(L;E) = \sum_1^{Nk} \frac{U(k)}{NR} \log_2 \frac{U(k)}{R(k)} \times \frac{NR}{U(E)} + \sum_1^{Nk} \frac{V(k)}{NR} \log_2 \frac{V(k)}{R(k)} \times \frac{NR}{V(E)}$$

where, besides the above notations:

$V(k)$ = Total number of sampling stations for every altitudinal level in which species E is absent;

$V(E)$ = Total number of sampling stations in which species E is absent.

Once the ecological features are prepared for every considered species, the information given by every profile was resumed by means of the calculation of **abscissa "g" of the barycentre** (DAGET & GODRON 1982), defined as follows:

$$G = \frac{\sum_1^{Nk} C(k) d(k)}{\sum_1^{Nk} C(k)}$$

where,

$C(k)$ = Index of frequencies corrected for every species and for every altitudinal level;

$d(k)$ = Number of the corresponding class for the altitude factor.

Results

The information linked to the altitudinal gradient gave a score of 2.23 bits, while maximum entropy, which only depends on the number of altitudinal levels considered, resulted to be: $H(L)_{\max} = \log N_k = \log 7 = 2.91$ bits.

The quotient between those two scores, which determines the quality of the sampling, was $Q(L) = 0.80$. Such relatively high score indicates that the altitude factor has been sufficiently sampled; however, a small piece of information is lost because of the high frequency of sampling sites placed in between the altitudes of 900 and 1,500 m (64.88 %) especially those sites within the 900–1,200 interval, which represent 38.79 %. This sampling characteristic, presents an easy justification as between those altitudinal levels there is quite a high percentage of the sampled surface.

Fig. 2 shows a histogram of frequencies which represent the variation of **specific richness** at different altitudinal levels, and proves that areas with altitudes between 900 and 1,200 m are the ones with the greatest specific abundance. There is an increase in the number of species with the altitude, maximum scores being reached between 900 and 1,500 m since above and below these heights the richness of species decreases. Table 1 indicates the distribution of species within the studied families of Adephaga and Polyphaga, with respect to the altitudinal levels considered.

The ecological profile of absolute and corrected frequencies for every taxon is shown in Table 2.

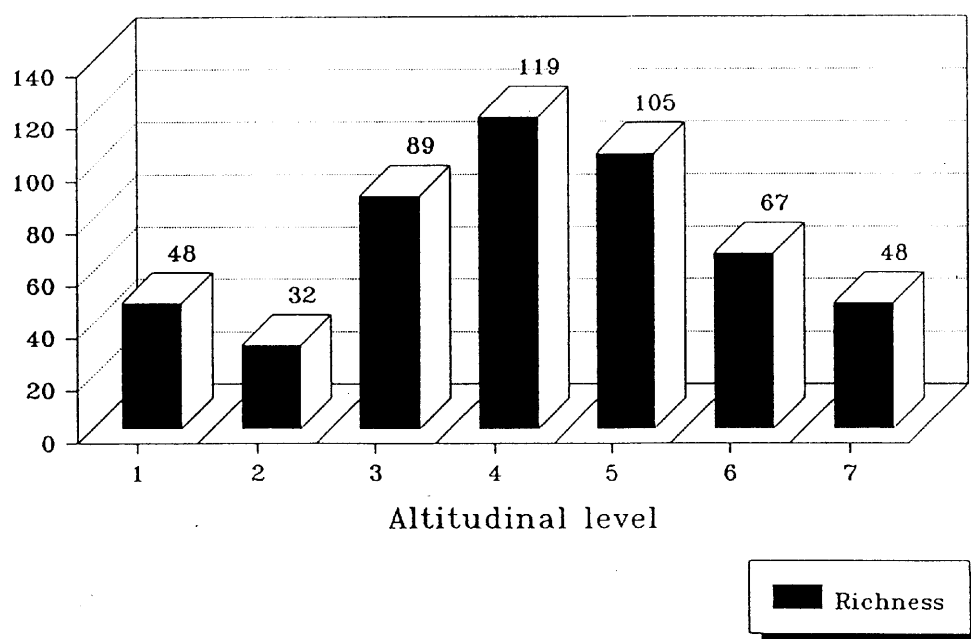


Fig. 2. Relationship between number of sampling stations and specific richness.

Table 1. Values of specific richness for every family and every altitudinal level here dealt with.

Families	Altitudinal level						
	0–300	300–600	600–900	900–1200	1200–1500	500–1800	> 1800
Haliplidae	3	2	3	9	5	4	2
Hygrobiidae				1	1		1
Gyrinidae	1	2	2	5	3	1	40
Dytiscidae	29	30	47	63	63	40	31
Hydraenidae	11	16	25	28	21	10	5
Elmidae	12	12	12	14	13	12	8
Total	48	32	89	119	105	67	48

In an overall regional survey like the one we are attempting in which sampling stations are distributed over a very wide extension it is not interesting to analyze the ecological features of all species, the basic reasons being two: first of all, because it would not be expedient to analyze features of species not having any “useful information” and secondly because it would be difficult to handle such an increased level of features. Therefore it is of interest to attribute as great an indicator value to every ecological feature as high is the information that it gives.

In this way we have been able to identify the indicator species, which are those strongly linked to altitude. Taxa with highest I (L;E) scores are most sensitive to this factor (Table 2). The highest the number of sensitive species, the most important the role of this ecological parameter in the biotope.

From the species whose reciprocal species-altitude information exceeds the score 0.04, those having more significant features from the corrected frequencies and comprising the variability spectrum of the parameter in the biotope, have been selected for being representative. As to their altitudinal preferences, the 24 represented species can be distributed in 3 groups: a) species present along the whole altitudinal gradient (ubiquitous in terms of altitude); b) those species present at high altitudes, and c) those present at low altitudes (Figs. 3, 4 and 5).

To represent a series of species characteristic of intermediate heights and on a local basis (Fig. 6) scores of reciprocal information below 0.04 had to be considered. We selected some of them, which are evidently less linked to the studied parameter (altitude factor).

1. Species present along the whole altitudinal gradient

Most of the species of Elmidae are included. Half of the 16 species of Elmidae studied have a profile of corrected frequencies which places them as ubiquitous species. The profile of 3 of them has been represented, as well as 4 of Dytiscidae and one of Hydraenidae (Fig. 3 a–h).

Table 2. Values of absolutes and corrected frequencies, mutual information I (L; E) and "G" value of the barycentre for every species. The asterisk indicates species whose reciprocal information species-factor exceed value 0.04.

Species	Absolute frequencies							I (L; E)	Corrected frequencies							"G"
	1	2	3	4	5	6	7		1	2	3	4	5	6	7	
<i>Peltodytes (P.) caesus</i>			1	1			2	0.006745	0	0	3.11	1.28	0	0	0	3.291571
<i>Peltodytes (P.) rotundatus rotundatus</i>				3		1	4	0.016607	0	0	0	1.93	0	4.15	0	5.365131
<i>Peltodytes (P.) rotundatus conifer</i>				1			1	0.004581	0	0	0	2.57	0	0	0	4
<i>Brychius elevatus</i>	1		1	5			7	0.022135	4.74	0	0.88	1.84	0	0	0	1.975871
<i>Haliplus (H.) obliquus</i>				2	1		1	0.018655	0	0	0	1.28	0.95	0	24.9	6.788426
<i>Haliplus (Neohaliplus) lineaticollis</i>	7	9	14	36	17	4	87	0.034242	2.67	1.14	1.00	1.06	0.74	0.76	0	2.774762
<i>Haliplus (Haliplus) immaculatus</i>	1				1	2	4	0.031174	8.30	0	0	0	0.95	8.30	0	3.581196
<i>Haliplus (Haliplus) beydeni*</i>				2	5	2	11	0.049498	0	0	0	0.46	1.74	3.02	18.1	6.662092
<i>Haliplus (Liaphlus) mucronatus</i>	1			2			3	0.011627	0	3.69	0	1.71	0	0	0	2.633333
<i>Haliplus (Liaphlus) fulvus</i>				1			1	0.004581	0	0	0	2.57	0	0	0	4
<i>Haliplus (Liaphlus) andalusicus</i>					1		1	0.006506	0	0	0	0	3.83	0	0	5
<i>Hygrobia hermanni</i>				6	4		11	0.028097	0	0	0	1.40	1.39	0	9.06	6.410970
<i>Aulonogyrus (A.) striatus</i>				1			1	0.004581	0	0	0	2.57	0	0	0	4
<i>Gyrinus (G.) dejeani</i>				1	2		3	0.008394	0	0	0	0.85	2.55	0	0	4.75
<i>Gyrinus (G.) distinctus</i>				1			1	0.004581	0	0	0	2.57	0	0	0	4
<i>Gyrinus (G.) substriatus</i>	1	3	12	8	3	2	29	0.025642	0	0.38	0.64	1.06	1.05	1.71	6.87	6.022203
<i>Orectochilus (O.) villosus*</i>	4	4	2	4	2		16	0.047703	8.30	2.76	0.77	0.64	0.47	0	0	1.625965
<i>Hyphydrus (H.) aubei</i>			2	7	1		10	0.017887	0	0	1.24	1.80	0.38	0	0	3.748538
<i>Yola (Y.) bicarinata</i>	1	1	2	2			4	0.009594	0	2.76	1.55	1.28	0	0	0	2.735241
<i>Bidessus minutissimus</i>	4	1	1	2	1		9	0.046406	14.76	1.23	0.69	0.57	0.42	0	0	1.339558
<i>Bidessus goudoti</i>	1		1	1		2	4	0.033536	8.305	0	1.55	0	0	8.30	0	3.456623
<i>Hydroglyphus pusillus</i>		1	1	9	1	1	13	0.016770	0	0.85	0.47	1.78	0.29	1.27	0	4.141630
<i>Coelambus impressopunctatus</i>				1			1	0.004581	0	0	0	2.57	0	0	0	4
<i>Coelambus marklini</i>	1			1		3	5	0.035109	0	2.21	0	0.51	0	9.96	0	5.222397
<i>Coelambus confluent</i>				2	1		3	0.006449	0	0	0	1.71	1.27	0	0	4.426174
<i>Hygrobia inaequatus</i>			1	4	2	1	9	0.014760	0	0	0.69	1.14	0.85	1.84	11.0	6.375241
<i>Hydroporus (H.) marginatus</i>			1	4	5	1	11	0.021138	0	0	0.56	0.93	1.74	0	9.06	6.307567
<i>Hydroporus (H.) foveolatus</i>			1	1	1	1	4	0.016211	0	0	1.55	0.64	0.95	0	24.9	6.642653

Table 2. Continued.

Species	Absolute frequencies							I (L; E)	Corrected frequencies							“G”	
	1	2	3	4	5	6	7		Total	1	2	3	4	5	6		7
<i>Hydroporus (H.) pubescens</i>	3	5	9	23	23	5	2	70	0.015773	1.423	0.79	0.80	0.84	1.25	1.18	2.84	4.600789
<i>Hydroporus (H.) limbatus</i>					1			1	0.006506	0	0	0	0	3.83	0	0	5
<i>Hydroporus (H.) planus</i>	2	4	4	11	12	3	1	33	0.026160	2.013	0	0.75	0.85	1.39	1.51	3.02	4.700828
<i>Hydroporus (H.) lucasi</i>					3	1		4	0.022445	0	0	0	0	2.87	4.15	0	5.591168
<i>Hydroporus (H.) discretus</i>					2	1		3	0.017500	0	0	0	0	2.55	5.53	0	5.684405
<i>Hydroporus (H.) analis</i>	1			2	2	3		8	0.029942	4.152	0	0	0.64	0.95	6.22	0	4.078080
<i>Hydroporus (H.) obscurus</i>				1	3	2	1	7	0.031582	0	0	0	0.36	1.64	4.74	14.2	6.565425
<i>Hydroporus (H.) vespertinus*</i>				2		4	1	7	0.056218	0	0	0	0.73	0	9.49	14.2	6.521703
<i>Hydroporus (H.) palustris</i>							1	1	0.023108	0	0	0	0	0	0	99.6	7
<i>Hydroporus (H.) vagipictus</i>	4	2	8	14	19	5	2	54	0.037195	2.460	0.41	0.92	0.66	1.34	1.53	3.69	4.576748
<i>Hydroporus (H.) tessellatus*</i>	2	1	4	7	18	5	3	40	0.075450	1.661	0.27	0.62	0.45	1.72	2.07	7.47	5.551574
<i>Hydroporus (H.) nigrita*</i>	3	2	4	7	14	6	2	38	0.051750	2.622	0.58	0.65	0.47	1.41	2.62	5.24	4.933931
<i>Hydroporus (H.) nivalis</i>			1	7	3	3		14	0.021237	0	0	0.44	1.28	0.82	3.55	0	5.228243
<i>Hydroporus (H.) obsoletus</i>				1				1	0.004581	0	0	0	2.57	0	0	0	4
<i>Hydroporus (H.) cantabricus</i>					2	1		3	0.017500	0	0	0	0	2.55	5.53	0	5.676395
<i>Hydroporus (H.) gyllenhalii</i>			1	1	5	1		8	0.018409	0	0	0.77	0.32	2.39	2.07	0	5.037837
<i>Hydroporus (Sternoporus) brancoi</i>					2			2	0.013059	0	0	0	0	3.83	0	0	5
<i>Hydroporus (Sternoporus) longulus</i>	1			2	2	1		6	0.014403	5.537	0	0	0.85	1.27	2.76	0	3.057214
<i>Rhythrodites bimaculatus</i>				1	2			3	0.008394	0	0	0	0.85	2.55	0	0	4.75
<i>Graptodytes ignotus</i>			3	2				5	0.019722	0	0	3.73	1.03	0	0	0	3.216386
<i>Graptodytes fractus*</i>					1	1	2	4	0.048771	0	0	0	0	0.95	4.15	49.8	6.889799
<i>Graptodytes flavipes</i>	1	1	4	4	5			15	0.011322	2.214	0.73	1.66	0.68	1.27	0	0	2.704302
<i>Scarodytes balensis balensis</i>		1	1	11	3			16	0.020179	0	0.69	0.38	1.77	0.71	0	0	3.704225
<i>Stictonectes lepidus</i>		2	7	10	5			24	0.018525	0	0.92	1.81	1.07	0.79	0	0	3.376906
<i>Stictonectes epipleuricus*</i>	8	4	3	7	7	1		30	0.086271	8.859	1.47	0.62	0.60	0.89	0.55	0	1.833012
<i>Deronectes latus</i>		1					1	2	0.028087	0	5.53	0	0	0	0	49.8	6.500271
<i>Deronectes aubei</i>		2			1			3	0.020799	0	7.38	0	0	1.27	0	0	2.440462
<i>Deronectes bertrandi</i>	1	2	1	1				5	0.021877	6.644	4.42	1.24	0.51	0	0	0	1.657874
<i>Deronectes costipennis gignouxii</i>			2	8	5	2		17	0.014350	0	0	0.73	1.21	1.12	1.95	0	4.856287
<i>Deronectes ferrugineus</i>		2	1	1				4	0.016841	0	5.53	1.55	0.64	0	0	0	2.366580

Table 2. Continued.

Species	Absolute frequencies							I (L; E)	Corrected frequencies							“G”
	1	2	3	4	5	6	7		1	2	3	4	5	6	7	
<i>Deronectes opatrinus</i>				1				1	0.004581	0	0	2.57	0	0	0	4
<i>Deronectes bicostatus</i>			1	7	3			11	0.014998	0	0	1.64	1.04	0	0	4.148148
<i>Stictotarsus duodecimpustulatus*</i>	3	2	1	1		1		8	0.045982	12.45	2.76	0.77	0.32	0	2.07	1.849755
<i>Potamonectes (P.) canaliculatus</i>	3	3	5	14	18	5	1	49	0.023059	2.034	0.67	0.63	0.73	1.40	1.69	4.304660
<i>Potamonectes (P.) ceresyi</i>			1	1	1			3	0.004005	0	0	2.07	0.85	1.27	0	3.809069
<i>Potamonectes (P.) griseostriatus</i>		1	2	2	3	3	1	12	0.023702	0	0.92	1.03	0.42	0.95	4.15	5.983512
<i>Potamonectes (P.) carinatus*</i>	7	3	8	19	19	3	2	61	0.050214	3.812	0.54	0.81	0.80	1.19	0.81	3.93414
<i>Potamonectes (P.) luctuosus</i>			1					1	0.008868	0	0	6.22	0	0	0	3
<i>Potamonectes (P.) sansi</i>					1			1	0.006506	0	0	0	0	3.83	0	5
<i>Potamonectes (P.) depressus elegans</i>	3	2	1	3	1		1	11	0.039656	9.060	2.01	0.56	0.70	0.34	0	3.804878
<i>Oreodytes sanmarkii</i>	4	3	6	18	17	3	1	52	0.016815	2.555	0.63	0.71	0.89	1.25	0.95	3.915120
<i>Oreodytes septentrionalis*</i>	4		1	1	3		1	10	0.059789	13.28	0	0.62	0.25	1.15	0	3.626682
<i>Noterus laevis</i>				6	2			8	0.019038	0	0	1.93	0.95	0	0	4.329861
<i>Laccophilus minutus</i>		1	2	12	8	2		25	0.013122	0	0.44	0.49	1.23	1.22	1.32	4.529787
<i>Laccophilus byalinus</i>	1	1	1	9	2			14	0.015918	2.373	0.79	0.44	1.65	0.54	0	2.515622
<i>Platambus maculatus</i>	4		1	13	8	1		27	0.044744	4.921	0	0.23	1.24	1.13	0.61	2.445086
<i>Agabus (Agabinectes) brunneus</i>		1	2	7	3			13	0.008345	0	0.85	0.95	1.38	0.88	0	3.564039
<i>Agabus (Agabinectes) didymus</i>			4	10	4			18	0.021311	0	0	1.38	1.43	0.85	0	3.855191
<i>Agabus (Dichonectes) biguttatus</i>			1	5	1			7	0.011467	0	0	0.88	1.84	0.54	0	3.895705
<i>Agabus (Dichonectes) nitidus</i>				1	1			2	0.004382	0	0	1.28	1.91	0	0	4.598746
<i>Agabus (Dichonectes) guttatus</i>	1		3	5	2		1	12	0.020065	2.768	0	1.55	1.07	0.63	0	5.094845
<i>Agabus (Gaurodytes) bipustulatus*</i>	3	3	11	33	30	8	3	91	0.044147	1.095	0.36	0.75	0.93	1.26	1.46	5.014230
<i>Agabus (Gaurodytes) paludosus</i>	1	2	5	5	3	1	1	18	0.012649	1.845	1.23	0.71	0.63	0.92	5.53	4.741167
<i>Agabus (Gaurodytes) nebulosus*</i>				9	7	5	1	22	0.052263	0	0	1.05	1.21	3.77	4.53	6.115530
<i>Agabus (Gaurodytes) chalconotus*</i>	1		2	3	8	7	2	23	0.077082	1.444	0	0.54	0.33	1.33	5.05	5.874956
<i>Agabus (Gaurodytes) congener</i>					1	1		2	0.013488	0	0	0	0	1.91	8.30	5.812928
<i>Agabus (Gaurodytes) neglectus</i>					2	2	1	5	0.038230	0	0	0	0	1.53	6.64	6.654435
<i>Agabus (Gaurodytes) albarracinensis*</i>					1	3	1	5	0.048458	0	0	0	0	0.76	9.96	6.625081
<i>Agabus (Gaurodytes) melanocornis</i>					1			1	0.006506	0	0	0	0	3.83	0	5

Table 2. Continued.

Species	Absolute frequencies							I (L; E)	Corrected frequencies							“G”	
	1	2	3	4	5	6	7		Total	1	2	3	4	5	6		7
<i>Ilybius (I.) meridionalis</i>	1	2	4	17	12	1	1	37	0.020041	0.897	0.59	0.67	1.18	1.24	0	2.69	4.656254
<i>Rhantus (R.) pulverosus</i>				5	3			8	0.017045	0	0	0	1.61	1.43	0	0	4.470394
<i>Rhantus (R.) hispanicus</i>				2	1	2	1	6	0.027740	0	0	0	0.85	0.63	5.53	16.6	6.604404
<i>Colymbetes fuscus*</i>	3		1	16	7	1	1	29	0.042250	3.436	0	0.21	1.42	0.92	0.57	3.43	4.183456
<i>Acilius (A.) sulcatus*</i>				2	1	2	2	7	0.046112	0	0	0	0.73	0.54	4.74	28.4	6.767218
<i>Dytiscus (Macrodytes) semisulcatus</i>	1	1	3	9	4	3		21	0.008898	1.582	0.52	0.88	1.10	0.73	2.37	0	3.833472
<i>Dytiscus (Macrodytes) marginalis</i>	1	2	1	7	10	2	1	24	0.018914	1.384	0.92	0.25	0.75	1.59	1.38	4.15	5.012854
<i>Dytiscus (Macrodytes) pisanus</i>				6	2			8	0.019038	0	0	0	1.93	0.95	0	0	4.329861
<i>Hydraena (Photobydraena) testacea*</i>	3	1	2	2				8	0.040708	12.4	1.38	1.55	0.64	0	0	0	1.400751
<i>Hydraena (H.) affusa</i>			1	6	9	1		17	0.024219	0	0	0.36	0.90	2.02	0.97	0	4.847058
<i>Hydraena (H.) barrosa</i>	4	5	11	1	1			21	0.033437	0	2.10	1.48	1.35	0.18	0	0	2.923679
<i>Hydraena (H.) brachymera</i>	4	7	12	25	17	2		67	0.013597	1.98	1.15	1.11	0.96	0.97	0.49	0	2.88888
<i>Hydraena (H.) unca</i>				1				1	0.004581	0	0	0	2.57	0	0	0	4
<i>Hydraena (H.) cordata</i>			2	7				9	0.027213	0	0	1.38	2.00	0	0	0	3.591715
<i>Hydraena (H.) corinna</i>	4	8	7	5				24	0.026941	0	1.84	2.07	0.75	0.79	0	0	3.089908
<i>Hydraena (H.) corrugis</i>			4	9	3			16	0.020636	0	0	1.55	1.44	0.71	0	0	3.772972
<i>Hydraena (H.) inapicipalpis</i>	5	4	9	4				22	0.021448	0	2.51	1.13	1.05	0.69	0	0	2.985130
<i>Hydraena (H.) nigrita</i>			1					1	0.008868	0	0	6.22	0	0	0	0	3
<i>Hydraena (H.) sharpi</i>			1	1	1			3	0.004382	0	0	0	1.28	1.91	0	0	4.598746
<i>Hydraena (H.) stussineri</i>	3	10	11	22	9	3	1	59	0.023563	1.68	1.87	1.16	0.96	0.58	0.84	1.68	3.698973
<i>Hydraena (H.) reyi</i>			2					2	0.017823	0	0	6.22	0	0	0	0	3
<i>Hydraena (H.) minutissima</i>			5	2	1	1	1	10	0.036653	0	5.53	1.24	0.25	0.38	1.66	0	3.050772
<i>Hydraena (Haenydra) emarginata</i>	4	8	23	36	32	9		112	0.023146	1.18	0.79	1.27	0.82	1.09	1.33	0	3.592592
<i>Hydraena (Haenydra) exasperata</i>	2	8	9	30	10	4		63	0.018816	1.05	1.40	0.88	1.22	0.60	1.05	0	3.333870
<i>Hydraena (Haenydra) gracilis*</i>	6	6	8	25	11		1	57	0.047769	3.49	1.16	0.87	1.13	0.73	0	1.74	3.154605
<i>Hydraena (Haenydra) hispanica</i>					2			2	0.013059	0	0	0	0	3.83	0	0	5
<i>Hydraena (Haenydra) iberica</i>	4	2	13	5				24	0.022387	0	1.84	0.51	1.39	0.79	0	0	3.249448
<i>Hydraena (Haenydra) truncata</i>	5	7	12	20	11	4		59	0.025510	2.81	1.31	1.26	0.87	0.71	1.12	0	2.841584
<i>Hydraena (Haenydra) monstruosipes</i>			2	2	2	1		5	0.010355	0	0	0	1.03	1.53	3.32	0	5.389455

Table 2. Continued.

Species	Absolute frequencies							I (L; E)	Corrected frequencies							“G”
	1	2	3	4	5	6	7		1	2	3	4	5	6	7	
<i>Hydraena (Haenydra) polita</i>			1					1	0.00868	0	6.22	0	0	0	0	3
<i>Ochthebius (Enicocerus) exsculptus*</i>	4	6	6	5	1			22	0.06770	6.04	3.02	1.69	0.58	0.17	0	1.766956
<i>Ochthebius (Enicocerus) legionensis</i>	2	4	4	4	3	1		18	0.020214	3.69	2.46	1.38	0.57	0.63	0.92	2.455958
<i>Ochthebius (Aulacochthebius) exaratus</i>	1							1	0.017173	33.2	0	0	0	0	0	1
<i>Ochthebius (Asiobates) beydeni</i>	2	7	7	5	2			16	0.026189	0	1.38	2.72	0.80	0.47	0	3.067039
<i>Ochthebius (Asiobates) figueroi</i>			1	1				2	0.006745	0	0	3.11	1.28	0	0	3.291571
<i>Ochthebius (Homalochthebius) minimus</i>				1				1	0.004581	0	0	0	2.57	0	0	4
<i>Ochthebius (Hymenodes) nanus</i>			1					1	0.008868	0	6.22	0	0	0	0	3
<i>Ochthebius (Hymenodes) socius</i>				1				1	0.004581	0	0	0	2.57	0	0	4
<i>Limnebius (L.) gerhardti</i>	1	3	2	5	3		1	15	0.016379	2.21	2.21	0.83	0.85	0.76	0	4.651851
<i>Limnebius (L.) papposus</i>				3			1	4	0.026028	0	0	0	1.93	0	6.64	6.784196
<i>Limnebius (L.) truncatellus</i>			2	8	7	2		19	0.016848	0	0	0.65	1.08	1.41	1.74	4.868852
<i>Limnebius (Bilimneus) myrmidon</i>				1				1	0.004581	0	0	0	2.57	0	0	4
<i>Dupophilus brevis</i>	6	7	12	31	17	3	1	77	0.019977	2.58	1.00	0.97	1.03	0.84	0.64	3.434730
<i>Elmis aenea</i>	5	8	15	31	20	8	3	90	0.030849	1.84	0.98	1.03	0.88	0.85	1.47	4.505303
<i>Elmis maugetii maugetii*</i>	9	12	16	29	17	4	1	88	0.070030	3.39	1.51	1.13	0.84	0.74	0.75	3.084299
<i>Elmis obscura</i>			1	6	1	1		9	0.013056	0	0	0.69	1.71	0.42	1.84	4.731759
<i>Elmis rioloides*</i>	9	13	16	25	16	5	1	85	0.080379	3.51	1.69	1.17	0.75	0.72	0.97	3.107214
<i>Esolus angustatus</i>	2	5	17	45	29	9	1	108	0.016158	0.61	0.51	0.98	1.07	1.02	1.38	4.417565
<i>Esolus parallelepipetus</i>	8	11	23	38	25	5	1	111	0.037490	2.39	1.09	1.29	0.88	0.86	0.74	3.308353
<i>Limnius opacus*</i>	8	7	18	25	12	4	2	76	0.066410	3.49	1.01	1.47	0.84	0.60	0.87	3.655045
<i>Limnius perrisi subcarinatus</i>	5	14	24	24	16	4		63	0.018267	0	0.87	1.38	0.98	0.97	1.05	3.990476
<i>Limnius wolckemari*</i>	6	9	12	16	9	3		55	0.049556	3.62	1.81	1.35	0.74	0.62	0.90	2.516592
<i>Normandia nitens</i>	1							1	0.011684	0	11.0	0	0	0	0	1
<i>Oulimnius troglodytes*</i>	4	1		6	2	1		14	0.044826	9.49	0.79	0	1.10	0.54	1.18	1.927480
<i>Oulimnius tuberculatus perezii</i>	2		1	6	4	1	1	15	0.022741	4.42	0	0.41	1.03	1.02	1.10	4.647742
<i>Riolus subviolaceus</i>				4	2			6	0.012983	0	0	0	1.71	1.27	0	4.426174
<i>Riolus illiesi</i>	2	1	1	1				5	0.027785	13.2	2.21	1.24	0.51	0	0	1.362470
<i>Stenelmis canaliculata</i>	1							1	0.017173	33.2	0	0	0	0	0	1

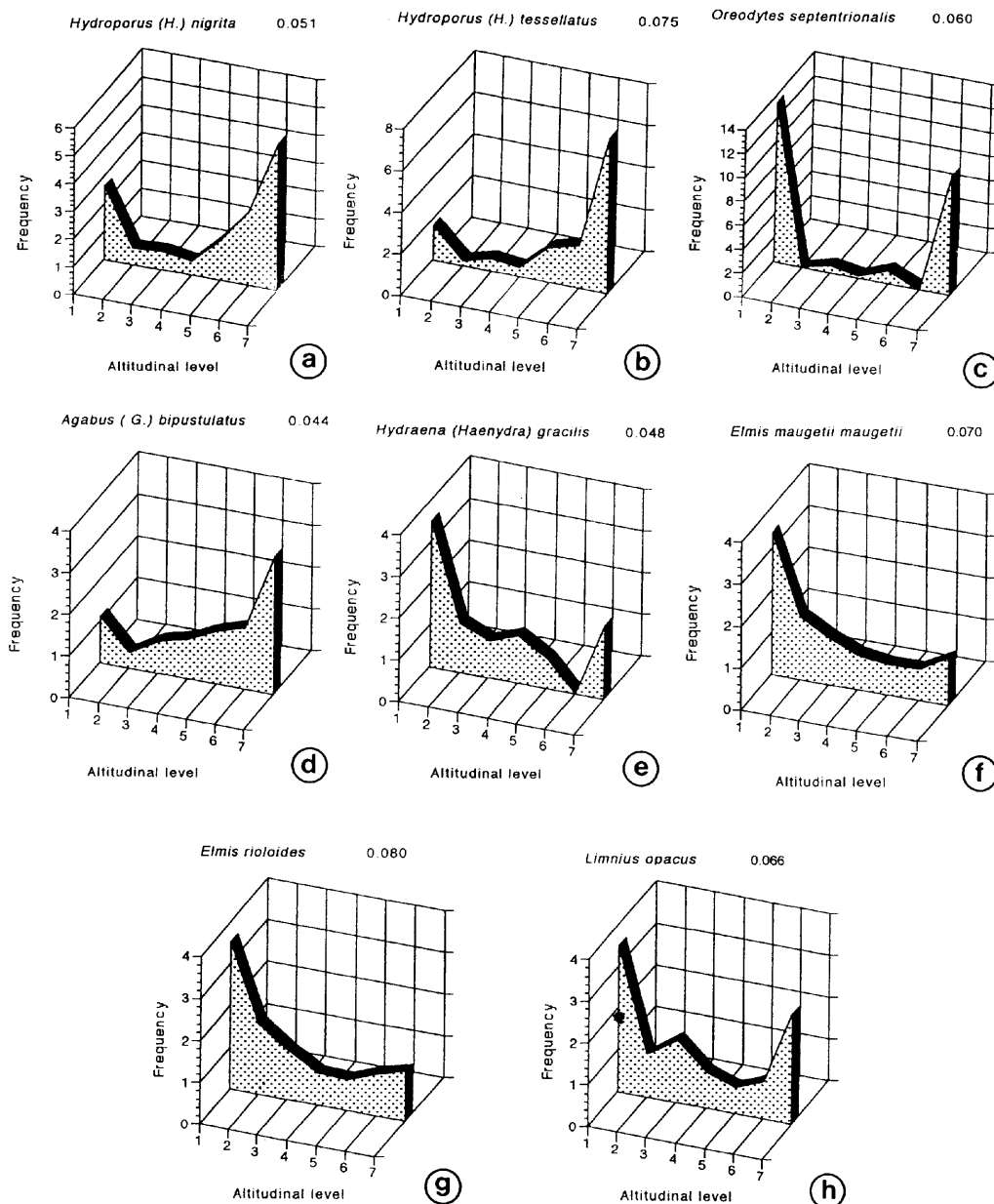


Fig. 3. a–h. Ecological features of corrected frequencies for the wide-distribution species providing a major mutual information in terms of altitude.

Hydroporus (Hydroporus) nigrita (FABRICIUS, 1792) (Fig. 3 a). It can be taken as a subalpine species, collected in hillside areas and low mountain where it occupies very quiet, nearly stagnant, water streams. Also in pools with slimy bottom and abundant vegetation, irrigation canals and river banks. More abundant above 1,200 m but also present at lower altitude levels. Less abundant at intermediate heights and again highly present at low heights.

Hydroporus (Hydroporus) tessellatus DRAPIEZ, 1819 (Fig. 3 b). It is typical of subalpine levels, like the above species, with which it appears at numerous

aquatic settings. It has a wide ecological valence, as it has been located in nearly all biotopes, either in lotic (streams and rivers) or lentic media (pools, tarns, lakes, irrigation canals), temporal or permanently; in every kind of substrata (gravel, sand, sludge) and in a great variety of vegetation: algae, mosses, macrophytes, etc. It has been recorded from 150 m to 1,975 m, at altitudes lower than 300 m being relatively abundant, and increasing considerably its occurrence above 1,200 m up to 1,800 m.

Oreodytes septentrionalis (GYLLENHAL, 1827) (Fig. 3 c). It shows a wide profile with a strong occurrence above 1,800 m reaching its highest level at 1,834 m in a subalpine pond, as well as below 300 m. Most of the captures were made in the east side of the studied territory, precisely in the area of the Picos de Europa with a substratum predominantly of gravel and sand. FRANCISCOLO (1979) defines this species as less orophylic than *Oreodytes rivalis*.

Agabus (Gaurodytes) bipustulatus (LINNAEUS, 1767) (Fig. 3 d). It is a ubiquitous species likely to be found in very different aquatic media (RIBERA et al. 1988) either lotic or lentic (FOCARILE 1960, ANGELINI 1973). It has been captured in nearly all the sampled biotopes: muddy-bottom stagnant waters, crystal-clear mountain waters, banks of rivers and streams, well basins, and mountain lakes and tarns. Its highest altitude places at 1,975 m and the minimum at 325 m.

Hydraena (Haenydra) gracilis GERMAR, 1823 (Fig. 3 e). Its profile classifies it as an abundant species at altitudes below 900 m, although remains widely distributed. As VALLADARES (1989) points out, it is one of *Haenydra* species with a major longitudinal amplitude, as it is the only species which can be captured from river sources to the potamon area. It has been collected from as high as 1,890 m at a river source, down to 135 m (minimum sampled height). BERTHELEMY & WHYTON DA TERRA (1977) labelled this species as tolerant and euritherm when captured it along the different water courses or in large stretches.

Elmis maugetii maugetii LATREILLE, 1978 (Fig. 3 f). Its profile covers all the altitudinal gradient, with a greater abundance at altitudes below 300 m. From this height up, its occurrence decreases, but increases above 1,200 m. Most of the captures belong to places from the west side of the territory, which presents a strong altitudinal slope, from high-altitude mountains to areas of river mouths.

Elmis rioloides (KUWERT, 1890) (Fig. 3 g). This is a species with a profile similar to the one before as it shows preference for lower heights, generally below 900 m.

Limnius opacus MÜLLER, 1806 (Fig. 3 h). This species has an analogous profile to the two previous species, although as it is shown in the figure it presents important preference peaks. It is well represented in the lower areas below 900 m, and above 1,800 m, its occurrence being very scarce in montane areas.

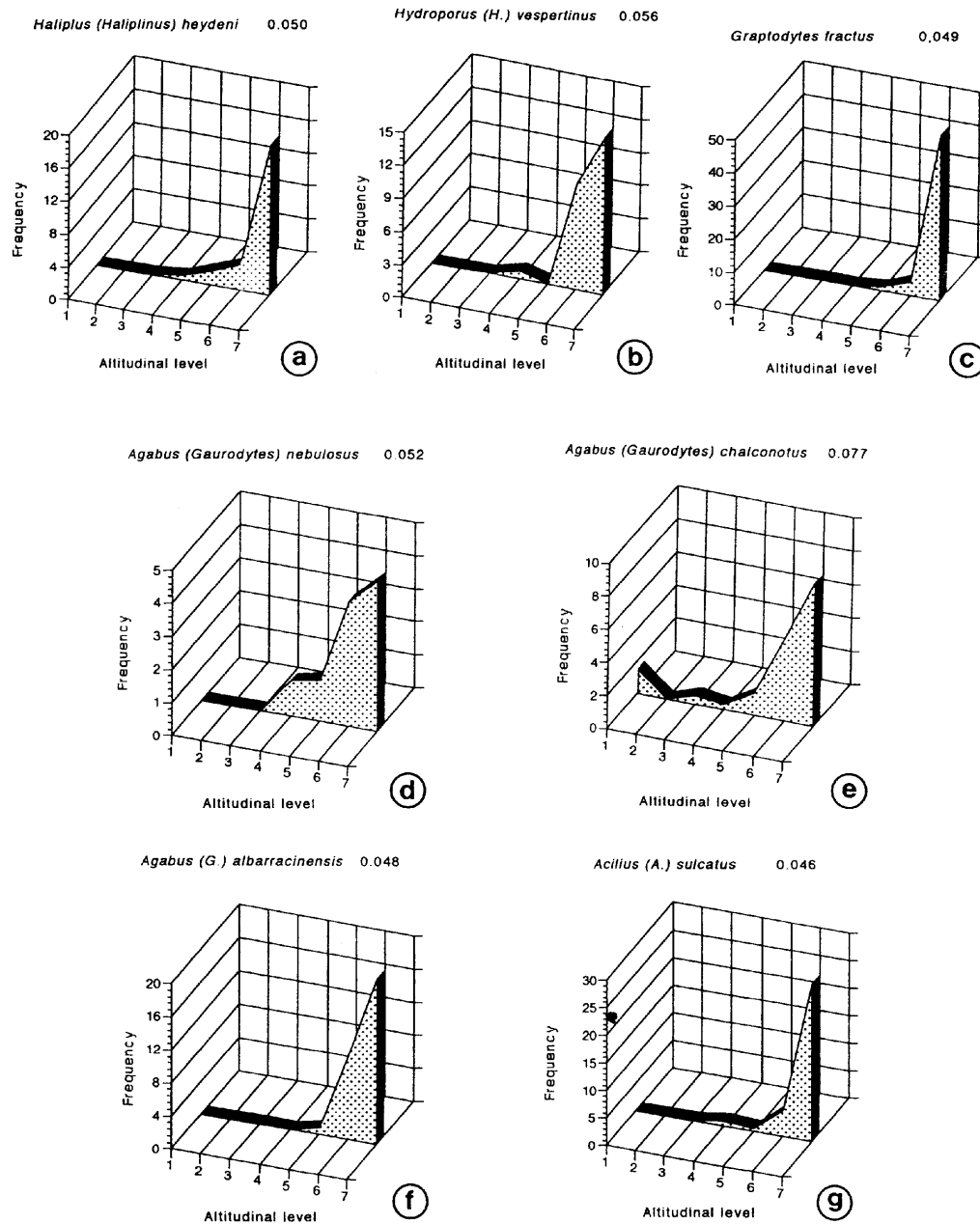


Fig. 4. a–g. Ecological features of corrected frequencies for highland species providing a major mutual information in terms of altitude.

2. Species of high altitudes

They are species of the Dytiscidae family, typical of subalpine tarns and ponds, and high mountain watercourses.

Haliphus (Haliplinus) heydeni WEHNCKE, 1875 (Fig. 4 a). It is clearly a highland species as it is found occupying montane and subalpine ground. All collections were carried out above 1,050 m, and permanently from high mountain ponds, tarns and streams, with a substratum of slime, sand and gravel.

These new captures lead us to reassert the theory that their geonemy is confined to the northern half of the Peninsula, having a tendency to be located in regions with a major Atlantic influence, although its occurrence in Portugal is not known.

Hydroporus (Hydroporus) vespertinus (FERY & HENDRICH, 1988) (Fig. 4b). This species occupies both lentic and lotic biotopes. Most of the specimens were collected at high altitude, reaching the subalpine ground at 1,975 m. Collections belong to two mountain streams with well-oxygenated fast-flowing waters and abundant vegetation. The lowest altitude was detected in a pond at 910 m.

Graptodytes fractus (SHARP, 1880–82) (Fig. 4c). This species preference for the highest areas is perfectly defined by its growing profile. It is frequent along the banks of high-mountain watercourses. It was collected in 4 settings, 3 of them in subalpine ground (1,340 m–1,975 m) with a sand- and gravel substratum and aquatic vegetation-bryophytes and mosses. The fourth setting is placed at 1,648 m and belongs to a peat bog swamping.

Agabus (Gaurodytes) nebulosus (FORSTER, 1771) (Fig. 4d). It has been captured in two kinds of biotopes, one lentic (pond and irrigation canal) and the other lotic (river and high mountain streams); although some authors (FOCARILE 1960, BILARDO 1969 and ANGELINI 1978) label it as typical of slow current media. It reached its highest altitude at 1,835 m in a high mountain pond, which is indicative of a subalpine species although it was located in a setting with abundant vegetation and a great quantity of vegetal remains.

Agabus (Gaurodytes) chalconotus (PANZER, 1976) (Fig. 4e). In spite of being a species with a great ecological valence, present along the whole altitudinal gradient, it has been classified as a high-altitude species for having a minimal frequency, almost uniform, at low altitude levels and because from 1,800 m upwards it becomes more abundant. It has been collected in all kinds of media, both lotic and lentic, especially in small stony-bottom puddles along the banks of rivers and streams, as well as in well basins, pools, irrigation canals, mountain lakes and tarns, with muddy and gravelly bottoms, occasionally with scarce water but very rich in organic matter.

Agabus (Gaurodytes) albarracinensis FERRY, 1986 (Fig. 4f). It has been collected in a subalpine pond in the company of *A. neglectus*, *A. nebulosus* and *A. bipustulatus*, and in a stream with a stony bottom of sand and gravel, with sediments of vegetal remains, surrounded by abundant riverside vegetation.

Acilius (Acilius) sulcatus (LINNAEUS, 1758) (Fig. 4g). Collected at the highest sampled altitudes and almost exclusively in lentic media, ponds and tarns, getting to occupy the subalpine ground. It shows an altitudinal range between 1,040 m and 1,975 m. All of the settings presented a sandy and gravelly bottom, or hard rock with slimy sediments. A lonely local capture in a lotic medium at 1,250 m is to be indicated.

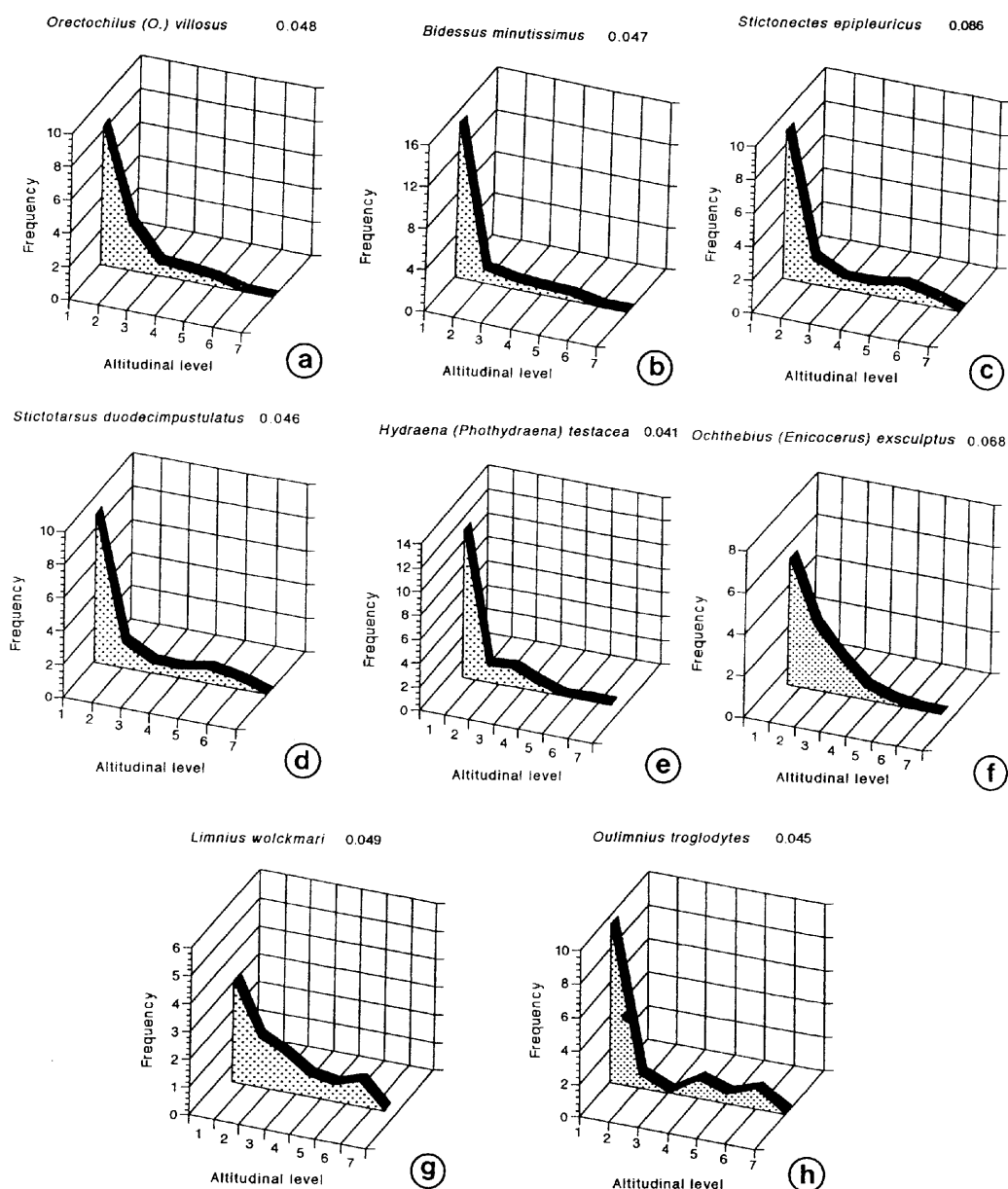


Fig. 5. a–h. Ecological features of corrected frequencies for lowland species providing a major mutual information in relation to altitude.

3. Low altitude species

The species assigned to this group live in stagnant water media or in the cre-non or potamon of rivers or torrents of the Cantabrian Mountains valleys.

Orectochillus (Orectochillus) villosus MÜLLER, 1776 (Fig. 5a). As it can be seen from the values of corrected frequencies, its occurrence increases greatly by the lower altitude levels, reaching a very high value in class 1 (0–300 m). Most of this species specimens have been collected in running watercourses, mountain streams and rivers flowing through very stony riverbeds with plenty of trees, which makes it possible for the waters to be shady.

This kind of biotope seems to be characteristic of this species (ANGELINI 1978) because unlike other gyrids, they present nocturnal habits (FOCARILE 1960, LAGAR 1967, REGIL 1982, 1983; HOLMEN 1987) whereas its activity during the day decreases, this species taking refuge under submerged stones or among vegetal remains, always in scarcely or partly illuminated areas.

Bidessus minutissimus (GERMAR, 1824) (Fig. 5 b). Most of the specimens were collected in irrigation canals, quiet puddles of torrents and river banks, with little current and scarcely deep; such conditions are similar to those observed by GUIGNOT (1931–1933) and FRANCISCOLO (1979), and the species were located within the masses of abundant green filamentous algae; the association with algae seems a relatively frequent fact and ANGELINI (1978) indicates this situation too. Its altitudinal level is very low as most captures were made at 135 m and at 150 m in rivers. The highest altitude belongs to a local capture at 1,340 m in a montane pond.

Stictonectes epiplauricus (SEIDLITZ, 1887) (Fig. 5 c). It was collected at many different places, but most of them were picked up in lotic-type biotopes. Most of the collection places are situated at very low altitude, 150 m, and the highest altitude recorded, almost sporadic, reaches 1,525 m in a mountain stream. The different biotopes, both temporal and permanent, had in common a stony substratum of sand and gravel, on which there is an abundant vegetation composed of aquatic riverside macrophytes and occasionally green filamentous algae with plentiful vegetal organic remains.

Stictotarsus duodecimpustulatus (FABRICIUS, 1792) (Fig. 5 d). The major occurrence of specimens belongs to lotic settings, particularly rivers deeply incised by great mountains and at very low altitude, with abundant water flow, clear waters and swift current, as well as a hard substratum of pebbles and stones. It is also important to mention a local capture at 1,525 m in a stream, and another one as well at 1,100 m, in a very eutrophicated and temporal pond.

Hydraena (Phothydraena) testacea CURTIS, 1830 (Fig. 5 e). As other authors have already pointed out, it lives in scarcely flowing or stagnant waters, at times invaded by algae (DERENNE 1952) or strongly eutrophicated (PIRISINU 1981). Its dispersion seems to be affected by the existence of characteristic biotopes, preferably placed at low altitude; therefore its profile is typical of lowlands and its occurrence diminishes considerably above 900 m.

Ochthebius (Enicocerus) exsculptus GERMAR, 1824 (Fig. 5 f). It lives at places with flowing water, locating preferably on stones which keep directly in contact with the water surface. Not only does it occupy the air-water interface but in many occasions it was collected totally on the outside, on top of rocks occupying small holes, most of the times in the company of *O. legionensis*. Its altitudinal range is quite wide, having the highest altitude at 1,330 m and the lowest at 135 m.

Limnius wolckmari (PANZER, 1793) (Fig. 5 g). Our collections match the observations by ILLIES (1953) who labels it as a species of streams and rivers in lowlands and valleys, as well as those by (BERTHELEMY 1979) who points out its association with stones, shingle, and sometimes mosses. It can be seen associated with *Elmis maugetii* and cohabiting in the rhithron and the potamon with *Limnius opacus*, *L. intermedius* and *L. perrisi*. It has been collected in between altitudes of 135 m and 1,650 m, but judging from its profile it clearly prefers low altitude areas.

Oulimnius troglodytes (GYLLENHAL, 1827) (Fig. 5 h). A eurytherm and euryoic species, with muscicolous preferences (BEYER 1932), able to live even in the mud. It is typical of median and inferior watercourses, and also of the breaking part of lakes and tarns (HEBAUER 1980). This coincides with the captures carried out, nearly all of them in the rhithron and the potamon of rivers. It was collected in media of a temporal nature, having a highest altitude at 1,650 m, but as it may be seen from its profile it shows preference for lowlands.

4. Species of intermediate altitude

Scarodytes halensis halensis (FABRICIUS, 1787) (Fig. 6 a). It has been isolated as much in lotic as in lentic media, clearly being a montane-ground species. Its capture range has been from 325 m up to 1,250 m although most of the specimens belonging both to the type form and the var. *fuscitarsis* and *ibericus*, were collected in a stream at 1,100 m. It has been captured as well in ponds, usually temporal with sandy and slimy bottom, the great majority of collections belonging to var. *somocencis*.

Agabus (*Agabinectes*) *didymus* (OLIVIER, 1795) (Fig. 6 b). A montane species in terms of its altitudinal level since it is distributed from 645 m in height up to 1,295 m. Its greatest affinity is shown for an altitude between 900 and 1,200 m, where it is more abundant. It is located either in lotic or in lentic media (mainly in the latter ones), since although considered as rheophilic, proper of clear and well oxygenated waters, it may as well occupy other media with more or less stagnant waters (GUIGNOT 1947, MALADORA & FRANCISCOLO 1976, FRANCISCOLO 1979, ANGELINI 1978) especially during winter and spring, whereas with the arrival of temperature rises it deserts these media (BILARDO 1965). In general it was collected in ponds receiving a weak current, although its occurrence was not rare in the periphery of more or less stagnant and lightly muddy areas.

Hydraena (*Hydraena*) *affusa* D'ORCHYMONT, 1936 (Fig. 6 c). It lives in the lotic facies of the crenon and rhithron of Cantabrian watercourses, therefore it does not appear at altitudes below 600 m. It is clearly a highland species as it is strongly represented between the altitudes of 1,200 and 1,500 m. Our collec-

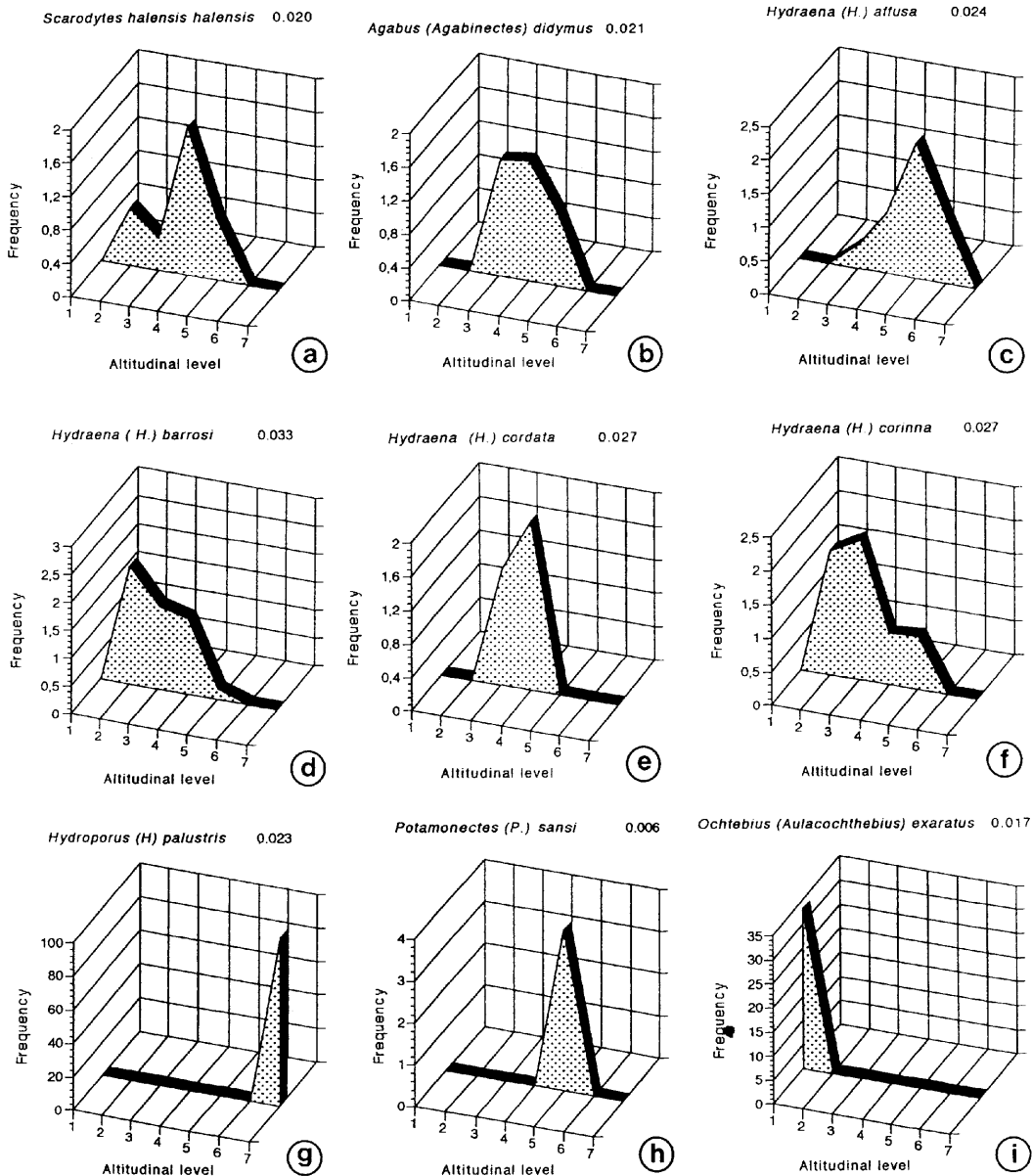


Fig. 6. a–i. Ecological features of corrected frequencies for species of intermediate and punctual heights providing a major mutual information in terms of altitude.

tions belong to little-flow high-mountain torrents and streams with clear running waters. The substratum was stony with sand and gravel, and mosses on the banks.

Hydraena (Hydraena) barrosi D'ORCHYMONT, 1936 (Fig. 6 d). It lives almost exclusively in the lotic facies of running water courses of mountain streams and torrents. It has been captured from the riverhead zone at 1,425 m high, to purely potamic areas at 385 m. The substratum was in general slate and siliceous materials, what tallies with this species preferences for acid waters, as BALFOUR-BROWNE (1978) points out.

Hydraena (Hydraena) cordata SCHAUFUSS, 1833 (Fig. 6 e). This species lives in mountain streams and rivers having little current and a stony substratum with rocks and gravel. These settings lie at altitudes between 685 and 1,100 m. This habitat does not differ much from that one pointed out by HERRANZ & TANAGO (1985) with respect to the river Tagus or from the collection of VAL-LADARES (1989) in the province of León.

Hydraena (Hydraena) corinna D'ORCHYMONT, 1936 (Fig. 6 f).

All the captures were achieved in mountain rivers and rivulets with clear waters, a weak current and usually a slate substratum. They have been collected especially in running sites, associated with submerged mosses. Its altitudinal level ranges from 385 m up to 1,400 m.

5. Species of punctual heights

In this group species occurring at a single height, either low, median or high, have been joined together; the features of three of them have been studied.

Hydroporus (Hydroporus) palustris (LINNAEUS, 1761) (Fig. 6 g). According to FRANCISCOLO (1979) it lives in limpid preferably stagnant waters, occasionally in torrents (in that case, in drought periods) usually collectable at high altitudes reaching the alpine ground. These observations fully coincide with our captures, as all the specimens were obtained at 1,874 m in a subalpine permanent tarn in the Picos de Europa (Fuente Dé). The substratum was sand, gravel and slime, with plentiful macrophytic vegetation. This fact is indicated by GUIGNOT (1931–33) who also captured this species in the same place.

Potamonectes (Potamonectes) sansi (AUBÉ, 1836) (Fig. 6 h). This species lives in the most calm places of streams, where vegetation is more abundant and thick. The collecting site corresponds to a temporal mountain pond at 1,250 m with a stony substratum and sludge accumulation in some areas; the vegetation, composed of aquatic macrophytes and green algae, is very abundant.

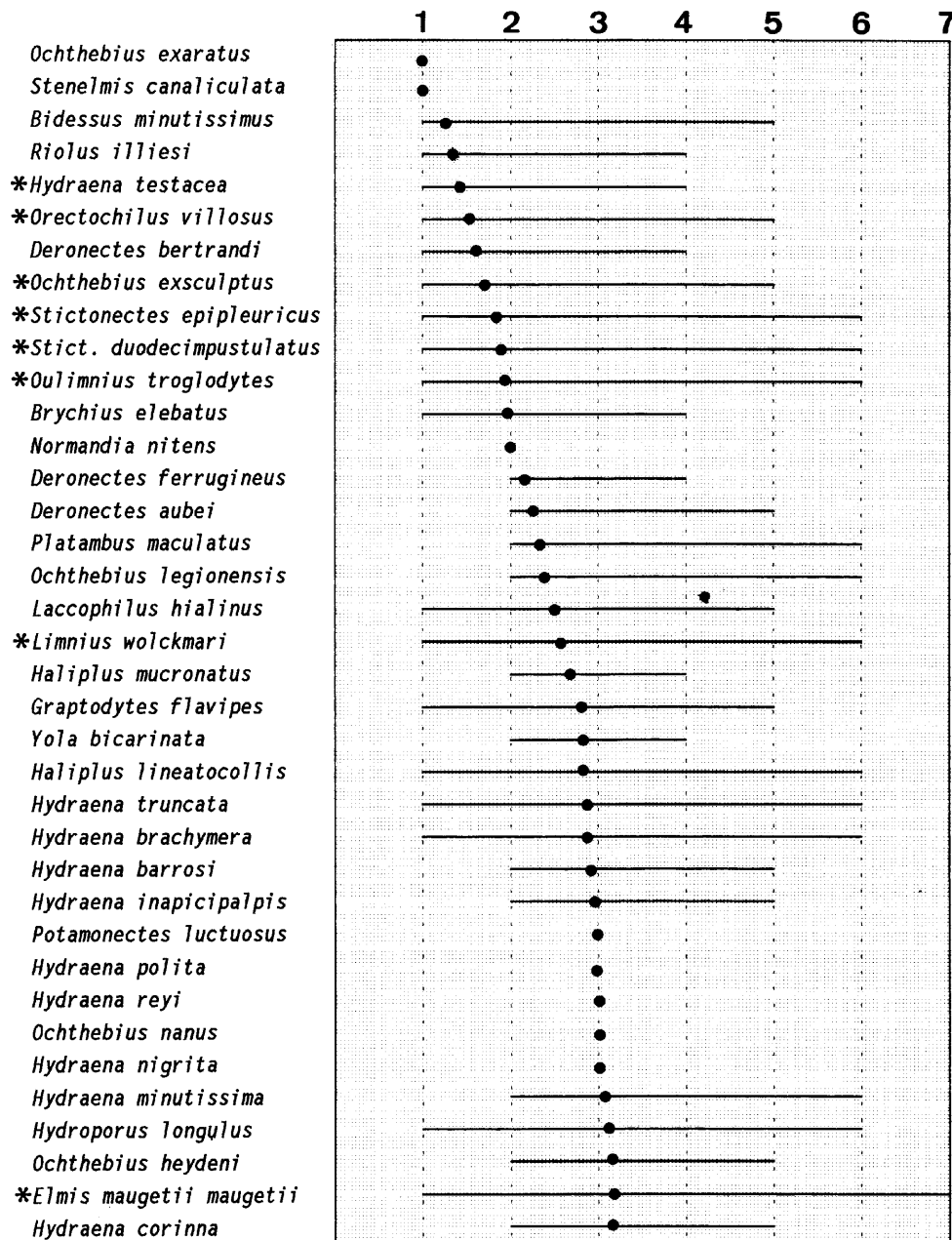
Ochthebius (Aulacochthebius) exaratus MULSANT, 1834 (Fig. 6 i). Its profile is restricted to a single low altitude placed in a river at 265 m in a small inlet with rich vegetation (algae and mosses) on the banks, and a substratum of gravel and sand.

Discussion

The ecological importance of the altitude factor in the distribution of aquatic coleoptera has been clearly demonstrated by means of the identification of a set of indicator species. This result was in a way predictable since VAL-LADARES et al. (1990) in a similar ecological study, although applied to a more restricted geographical area, made evident the existence of species with a high indicator value.

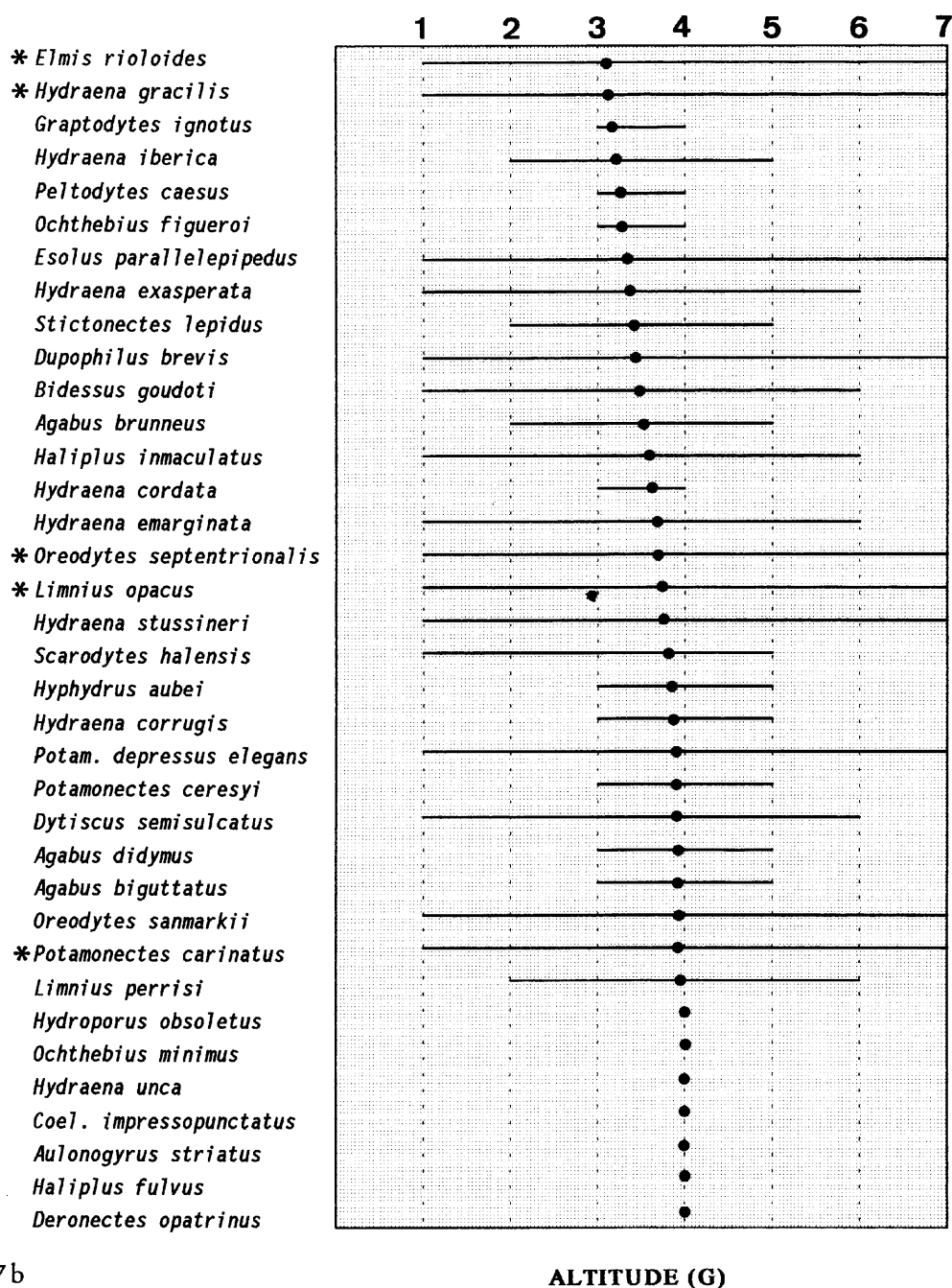
The information provided by the species ecological features was summed up in the calculation of the barycentre. Table 2 shows the barycentre abscissa

values of ecological features for the 145 studied species, highlighting those that provide more information in relation to altitude [$I(L,E) > 0.04$]. In this way an order structure could be established in the set of species based on the increasing G values (Figs. 7 a–d) what is equivalent to classifying species along an altitudinal gradient. We have chosen to consider in this ordination all the recorded species in order to reveal the ecological preferences of the different families of aquatic coleoptera. Nevertheless, the only consideration of indicator species, highlighted with an asterisk in Figures 7 a–d, shows with



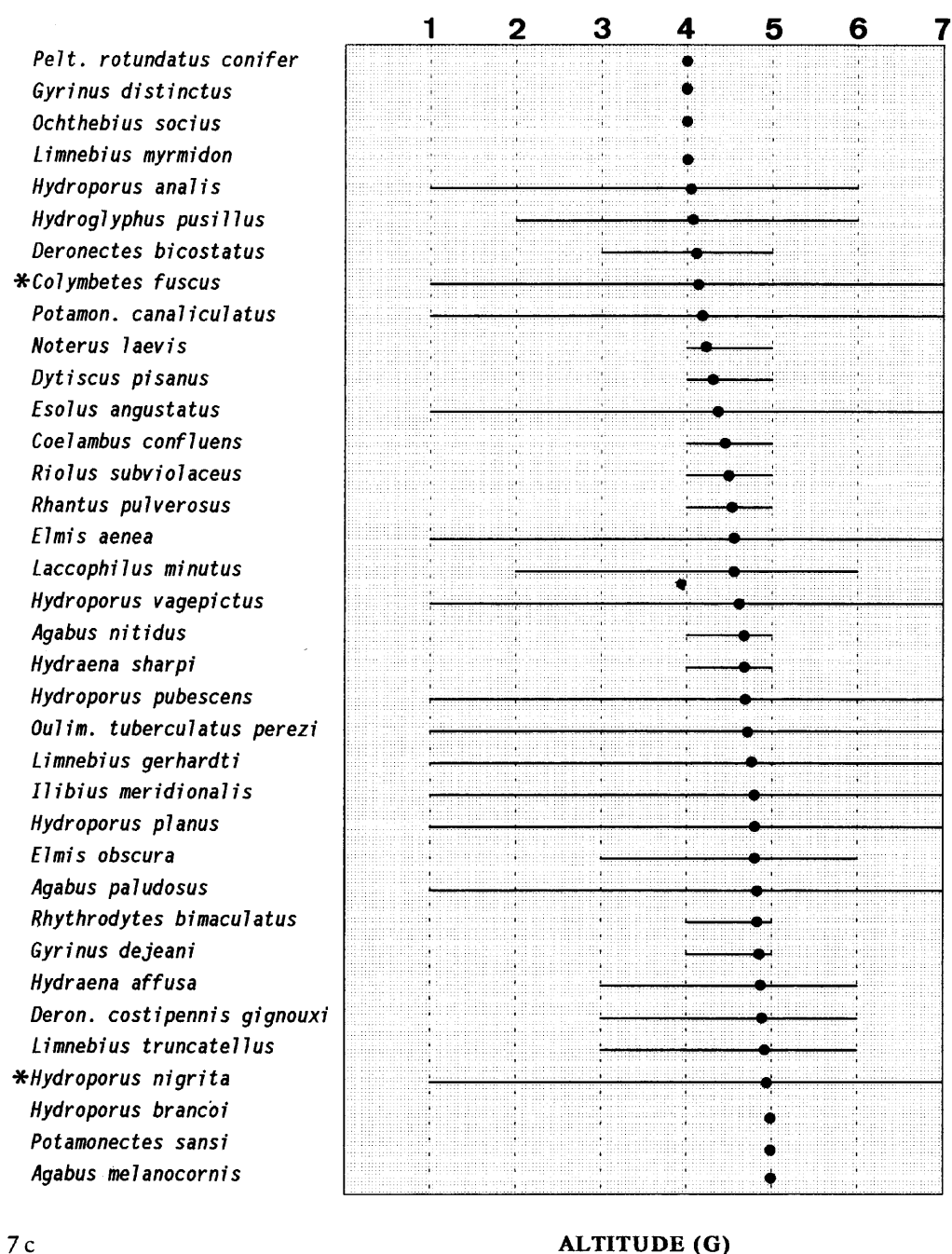
major significance the configuration of the species gradient in terms of altitude.

Species having similar barycentres are expected to possess ecological reactions alike, and the abscissa of the profile barycentre can be taken as a measure of its ecological optimum (DAJOZ 1971). However, the ecological amplitude of the frequency profile, shown in Figures 7 a–d for 145 species, also needs to be taken into account. Considering only the 24 indicator species, we observe that the species having a low barycentre abscissa are of scarce regional ecological amplitude, and it is even lower when the barycentre is high. On the contrary,



species whose profile shows an average barycentre, have greater amplitude. This phenomenon is often very significant and has been revealed in similar ecological surveys (DAGET & GODRON 1982).

For indicator species, variation of median ecological amplitude among the classes of ecological preference was considered by grouping those less frequent classes (1–2 and 4–5). We deduced a curvilinear relationship (Fig. 8) which reflects how ecological amplitude of species having a G value smaller than 3 does not exceed value 6, and when G is higher than 6, amplitude is not above 4. This has led us to adopt such values as limits for the discrimination of species



in ecological groups in terms of altitude, considering the average 4.5 between both extremes. In this way 4 groups are established: lowland species ($G < 3$), lowland-midland species ($3 < G < 4.5$), midland-highland species ($4.5 < G < 6$), and highland species ($G > 6$).

Biotope-indicator species located at lower altitudes belong to different families, of which *Stictonectes epipleuricus* and *Ochthebius exsculptus* stand out.

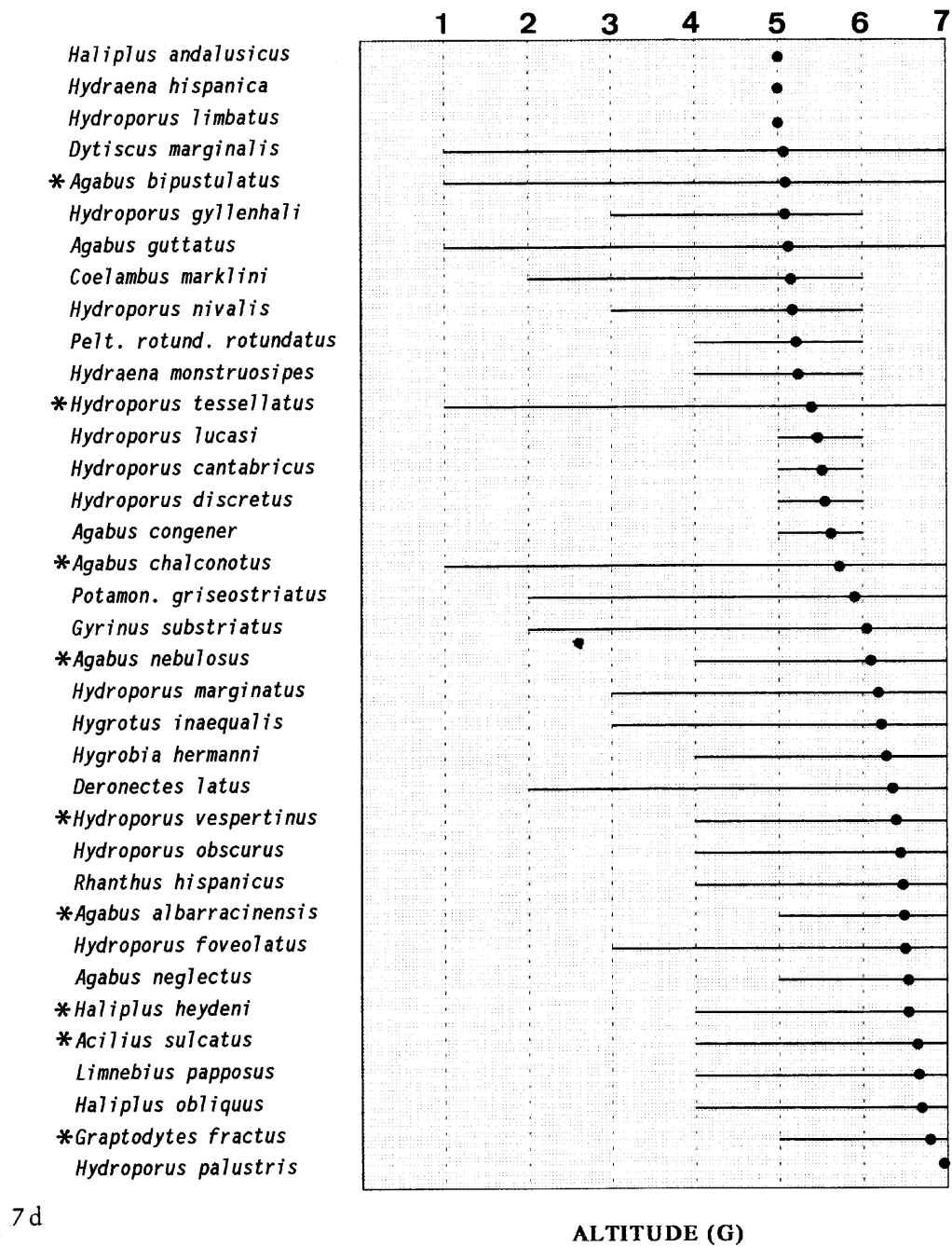


Fig. 7. a–d. Species ordination according to their ecological preference for the altitude factor, indicating regional ecological amplitude.

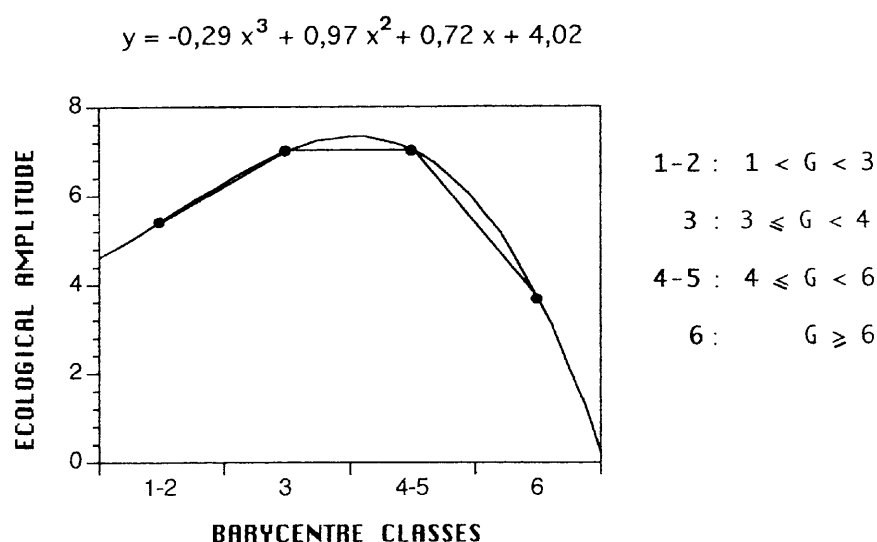


Fig. 8. Variation of average ecological amplitude for the ecological preference classes indicated in Fig. 7 a-b.

Their preferences for lower altitudes is explained by the fact that they live in Cantabrian watercourse valleys.

Species with a G value between 3 and 6 have a high ecological amplitude, which is why they were designated in the previous paragraph as present in all of the altitudinal gradient. Most of Elmidae possess a wide ecological profile (Table 2), and the most significant ones are *Elmis maugetii* and *Elmis rioloides* (Fig. 3). Both species share very similar ecological behaviours and although they are ubiquitous, they preferably have a liking for areas classified into low-mid altitude. *Hydroporus tessellatus* and *Hydroporus nigrata*, belonging to Dytiscidae, also have similar ecological spectra. They are found along the whole altitudinal gradient but prefer mid-high altitudes (Fig. 3).

The highland species have a greater ecological amplitude than lowland indicators. They are almost exclusively *Agabus chalconotus*, *Hydroporus vespertinus* and *Agabus nebulosus* (Fig. 4).

Summary

A detailed ecological analysis related to altitude is carried out by means of the study of the distribution of 145 species and subspecies of aquatic coleoptera (Coleoptera, Adephaga and Polyphaga), detected in 299 sampling stations disposed throughout the Cantabrian Mountains.

The 299 sampling sites were classified with respect to their corresponding height above sea level, in such a way that all of them were distributed at 7 altitudinal levels (Fig. 1). The variation of specific richness at different altitudinal levels shows that areas with altitudes between 900 and 1,200 m are the ones with the greatest specific abundance (Fig. 2). Table 1 indicates the distribution of species within the studied families of Adephaga and Polyphaga, with respect to the altitudinal levels considered.

Ecological profiles of absolute and corrected frequencies for every taxon were carried out, and an indicator value to ecological feature was attributed (Table 2). The ecological importance of the altitude factor in the distribution of aquatic coleoptera has been clearly demonstrated by means of the identification of a set of indicator species. These species were distributed in 3 groups: a) species present along the whole altitudinal gradient (ubiquitous in terms of altitude) (Fig. 3); b) those species present at high altitudes (Fig. 4); c) those present at low altitudes (Fig. 5). With lower indicator value were recognized species present at intermediate heights and on a local basis (Fig. 6).

The information provided by the species ecological features was summed up in the calculation of the baricentre (G) (Table 2). In this way an order structure could be established in the set of species based on the increasing G values (Fig. 7 a–d) what is equivalent to classifying species along an altitudinal gradient. For indicator species, the relationship between the median ecological amplitude and the barycentre class was curvilinear (Fig. 8).

Résumé

En utilisant la distribution des fréquences de 145 espèces et sous-espèces de coléoptères aquatiques collectées dans 299 points d'échantillonnage répartis pour la Cordillère Cantabrique (Carte 1) nous avons réalisé une analyse écologique du facteur altitude.

Nous avons classifié les 299 point d'échantillonnage dans 7 niveaux d'altitude (Fig. 1). La variation de la richesse spécifique dans les différents niveaux indique que les régions situées entre 900 et 1200 m d'altitude ont la plus grande abondance spécifique (Fig. 2). Dans le tableau 1 nous montrons pour chaque niveau d'altitude le nombre d'espèces des différents familles des ordres Adephaga et Poliphaga étudiées.

Nous avons fait pour chaque taxon les profils écologiques des fréquences absolues et des fréquences corrigées et on a attaché à chaque profil écologique une valeur indicatrice d'autant plus grande que son pouvoir informatif est élevé. L'importance du facteur altitude dans la distribution des coléoptères aquatiques on a été mise en évidence au milieu de la reconnaissance d'un ensemble d'espèces indicatrices. Ces espèces ont été réparties en trois groupes: a) espèces ubiquistes par rapport à le facteur altitude (Fig. 3); b) espèces caractéristiques d'altitude élevée (Fig. 4); et c) espèces caractéristiques d'altitude basse. Avec moindre valeur indicatrice, nous avons identifié des espèces ponctuelles et espèces situés dans altitudes moyennes (Fig. 6).

L'information apportée par les profils écologiques est résumé dans le calcul du barycentre (G) (Tableau 2). De cette manière il se peut établir une structure d'ordre dans l'ensemble des espèces selon les valeurs croissantes de G (Fig. 7 a–d), ce qui revient à les classer dans un gradient d'altitude. En considérant les espèces indicatrices, la relation entre l'amplitude écologique moyenne et la préférence écologique est curvilinéaire (Fig. 8).

Acknowledgements

This work has benefited from research projects financed by the C.A.I.C.Y.T. n. PR84-0921-C02-01 and D.G.I.C.Y.T. n. PB89/0081. Help has also been received from the Mixed Committee County Council-University of León in the 1987–1991 convocation notice.

References

- ANGELINI, F. (1973): Hydroadephaga nuovi per Calabria e Sila (Col., Haliplidae, Dytiscidae, Gyrinidae). – *Bol. Soc. ent. Ital.* 105: 7–12.

- (1978): Haliplidae, Dytiscidae e Gyrinidae della Lucania. XII nota sulla entomofauna acquatica. – *Entomol. Bari* **XIV**: 63–135.
- BALFOUR-BROWNE, F. (1978): Studies on the Hydraenidae (Coleoptera) of the Iberian Peninsula. – *Ciencia Biologica* **4**: 53–107.
- BERTHELEMY, C. (1966): Recherches écologiques et biogéographiques sur les Pléocoptères et Coléoptères d'eau courante (Hydraena et Elminthidae) des Pyrénées. – *Annls. Limnol.* t. 2, fas. **2**: 224–458.
- (1979): Elmidae de la région palearctique occidentale: Systematique et repartition (Coleoptera Dryopoidea). – *Annls. Limnol.* **15**: 1–102.
- BERTHELEMY, C. & WHYTTON DA TERRA, L. S. (1977): Hydraenidae et Elmidae du Portugal (Coleoptera). – *Annls. Limnol.* **13**: 29–45.
- BEYER, H. (1932): Die Tierwelt der Quellen und Bäche des Baumbergegebietes. – *Abh. Westf. Prov. Mus. Naturr.* **3**: 1–187.
- BILARDO, A. (1965): Ricerchi sugli hydroadephaga nella provincia di Varese (Coleoptera). – *Mem. Soc. ent. Ital.* **49**: 109–153.
- (1969): Contributo alla conoscenza degli Hydroadephaga delle Alpi (Alpi Maritime ed Alpi Cozie). – *Bol. Soc. ent. Ital.* **XCIX-CI**: 17–43.
- BINAGHI, G. (1958): Materiali per lo studio delle Hydraena italiane (1° Contributo). – *Bol. Soc. ent. Ital.* **88**: 70–83.
- (1959): Materiali per lo studio delle Hydraena italiane (2° Contributo). – *Bol. Soc. ent. Ital.* **89**: 68–84.
- (1960): Materiali per lo studio delle Hydraena italiane et notizie su alcune specie della coleotterofauna acquatica viventi in associazione. (3° Contributo). – *Bol. Soc. ent. Ital.* **90**: 15–41.
- (1961): Materiali per lo studio delle Hydraena italiane. Le Hydraena dell'Isole d'Elbs e notizie sulla coleotterofauna aequatica – associata. (4° Contributo). – *Bol. Soc. ent. Ital.* **91**: 66–77.
- (1965): Materiali per lo studio delle Hydraene italiane (6° contributo). – *Mem. Soc. ent. Ital.* **44**: 12–22. •
- DAGET, P. & GODRON, M. (1982): Analyse de l'Écologie des espèces dans les communautés. – *Coll. d'Ecologie*. Masson, Paris, pp. 1–163.
- DAGET, P., GODRON, M. & GUILLERM, J. L. (1972): Profils écologiques et information mutuelle entre espèces et facteurs écologiques. – In: *Grundfragen um Methoden in der Pflanzensoziologie*. – Junk Publ. La Haya, pp. 121–149.
- DAJOZ, R. (1971): Précis d'écologie. – Dunod, Paris, pp. 1–434.
- DERENNE, E. (1952): Les Hydraena de Belgique. – *Bull. Annls Soc. ent. Bel.* **88**: 195–218.
- FOCARILE, A. (1960): Ricerche coleotterologiche sur litorale jonico della Puglia, Lucania y Calabria campagne 1956–57–58. III. Coleoptera: Haliplidae, Dytiscidae, Gyrinidae. – *Mem. Soc. ent. Ital.* **38**: 41–114. 30 figs.
- FRANCISCOLO, M. E. (1979): Fauna d'Italia. XIV: Coleoptera: Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae. – *Calderini Ed. Bologna*, pp. 1–806.
- GARRIDO, J. (1990): Adephaga y Polyphaga acuáticos (Coleoptera) en la provincia fitogeográfica Orocantábrica (Cordillera Cantábrica, España). – *Servicio de Publicaciones Universidad de León. Microficha n° 59*, pp. 1–432.
- GODRON, M. (1968): Quelques applications de la notion de fréquence en écologie végétale (recouvrement, information mutuelle entre espèces et factures écologiques, échantillonnage). – *Oecol. Plant.* **3**: 185–212.

- GUIGNOT, F. (1931–33): Les Hydrocanthares de France, Hygrobiidae, Haliplidae, Dytiscidae et Gyrinidae de la France continentale, avec notes sur les espèces de la Corse et de l'Afrique du Nord Française. – Ed. Misc. Zool. Toulouse, pp. 1–558.
- (1947): Faune de France. Coléoptères hydrocanthares. PAUL LECHEVALIER (ed.); Paris. Vol. 48: 1–286.
- HEBAUER, F. (1980): Beitrag zur Faunistik und Ökologie der Elminthidae und Hydraenidae in Ostbayern (Coleoptera). – Mitt. Münchner Ent. Ges. 69: 29–80.
- HERRANZ, J. M. & GONZALEZ DEL TANAGO, M. (1985): Efemerópteros, Plecópteros y Tricópteros de la cuenca del alto Tajo (Guadalajara). – Bol. Asoc. esp. Entomol. 9: 35–53.
- HOLMEN, M. (1987): The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark I. Gyrinidae, Haliplidae, Hygrobiidae and Noteridae. – Fauna Entomol. Scand. 20: 1–168.
- ILLIES, J. (1953): Beitrag zur Verbreitungsgeschichte der europäischen Plecopteren. – Arch. Hydrobiol. 48: 35–74.
- LAGAR, A. (1967): Los Gyrinidae (Coleoptera) de Cataluña. – Misc. Zool. II: 75–80.
- MALADORA, P. & FRANCISCOLO, M. E. (1976): Coleoptera Hydroadephaga e Hydrophiloidea del lago di Doderdo presso Dorizia. – Atti Mus. Civ. Stor. nat. Trieste 29: 123–162, 54 figs., 2 tabs.
- PIRISINU, Q. (1981): Palpicorni (Coleoptera: Hydraenidae, Helophoridae, Spercheidae, Hydrochidae, Hydrophilidae, Sphaeridiidae). Guide per il riconoscimento delle species animali delle acque interne italiane. – 13 Consiglio Nazionale delle ricerche. AQ/1/128, Verona, 97 pp.
- REGIL, J. A. (1982): Coleópteros adéfagos acuáticos de la Provincia de León. – Tesis doctoral, Universidad de León, pp. 1–255, 101 láms. (Inédita).
- (1983): Los Gyrinidae Thomson, 1860 (Col. Adephaga) de la provincia de León. – Bol. Asoc. Esp. Entom. 7: 265–276.
- RIBERA, I., ISART, J. & VALLE, M. A. N. (1988): Contribución al conocimiento de los coleópteros acuáticos (Adephaga) de la Cerdeña. – Actas II Congr. Ibér. Entomol., 637–650.
- RIVAS MARTINEZ, S., DIAZ, T. E., PRIETO, J. F., LOIDI, J. & PENAS, A. (1984): La vegetación de la alta montaña. Los Picos de Europa. – Ediciones Leonesas, S. A. 1–295.
- TIBERGHEN, G. (1976): Ecologie des Helodidae, Elminthidae et Hydraenidae d'un cours d'eau des Pyrénées atlantiques: Le Lissurage. – Thèse. Univ. P. Sabatier de Toulouse. T. I.: 1–444. T. II.: 102 figs.
- VALLADARES, L. F. (1989): Los Palpicornia acuáticos de la provincia de León. II. Hydraena Kugelann, 1794 y Limnebius Leach, 1815 (Coleoptera, Hydraenidae). – Bol. Asoc. Esp. Entom. 13: 313–330.
- VALLADARES, L. F., FERNANDEZ, M. C. & FERNANDEZ, M. (1990): Influence of altitude in the distribution of the aquatic Hydrophiloidea (Coleoptera) in the province of Leon (NW Spain). – Limnética 6: 79–86.