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Relationships between terrestrial gastropod distribution and soil properties in Galicia (NW Spain)

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Abstract

This study investigated the influence of edaphic factors on the distribution of 17 terrestrial gastropod species over a large area of the northwest Iberian Peninsula. A total of 498 gastropod/soil samples were obtained, and a total of 19 edaphic variables determined. The resulting data matrix was analysed by detrended canonical correspondence analysis (DCCA). Our results indicate that the gastropods of the study area can be grouped on two types of criteria: first, chemical criteria (notably pH, cation exchange capacity, and Al content), and secondly physical criteria (notably texture and moisture content). In view of distribution with respect to these factors, two well-defined groups can be identified: one comprising *Acanthinula aculeata*, *Euconulus fulvus*, *Punctum pygmaeum*, *Columella aspera* and *Oxychilus alliarius* preferring coarse-textured acid soils, the other comprising *Cochlicopa lubrica*, *Vertigo pygmaea*, *Zonitoides excavatus*, *Carychium tridentatum*, *Deroceras reticulatum* and *Deroceras lombricoides* preferring wetter, finer-textured, less acid soils. *Arion intermedius* and *Ponentina subvirescens* were in general indifferent to the edaphic factors considered.

Keywords: Terrestrial gastropods; Soil factors; Community ecology; Detrended canonical correspondence analysis; Galicia; Spain

1. Introduction

Historically, research on relationships between terrestrial gastropods and soil environmental properties has passed through various phases: from early descriptive studies, to current studies in which rationalized sampling techniques and sophisticated statistical procedures are used to identify the factors influencing the distribution of species, and to assess the extent to which such factors predict a species' presence in a given location.

Although the importance of edaphic variables has been extensively documented, a number of important questions remain: notably, exactly which edaphic factors are the more important determinants of terrestrial gastropod distributions? Even the importance of pH and calcium, traditionally considered as limiting factors (Boycott, 1934; Lozec, 1962; Valovirta, 1968; Cameron, 1973; Radea and Mylonas, 1992), has been questioned by some authors, who have either not found a direct relationship or have found other factors to be more important (Burch, 1955; Newell, 1967; Bishop, 1977; Reinink, 1979).

This is perhaps due to the fact that there have been rather few numerical studies. Sample size and/or sample number have in many studies been very small. Gastropods are mostly small organisms that live in the surface layer of the soil and litter, so that quantitative sampling is difficult, and most stud-

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ies have been qualitative or semiquantitative (Curry, 1994).

Here, we report the results of a study of relationships between soil properties and gastropod distributions in the northwest Iberian Peninsula. The study was based on quantitative sampling over a large geographical area.

2. Material and methods

Samples were obtained from western Galicia (provinces of A Coruña and Pontevedra, total area 12,400 km^2). This area comprises the coastal region and a series of mountain ranges that delimit the area to the east, reaching 1180 m in altitude. Soils are predominantly cambisols (humic or dystic), mostly developed on acid granitic rocks, though this acidity is limited by the high aluminium content of these rocks. Climate is oceanic, with mild temperatures and high rainfall. Biogeographically, the area lies within the Eurosiberian Region, with major woodland species including *Quercus robur*, *Laurus nobilis* and *Crataegus monogyna*. Meadow vegetation in the study area falls in the phytosociological class *Molinio-Arrhenatheretea elatioris*. The most frequent species within this association include *Agrostis capilaris*, *Linum bienne*, *Lolium perenne*, *Trifolium dubium*, *Plantago lanceolata* and *Bellis perennis*. Riverbank vegetation, rich in ferns, is dominated by *Alnus glutinosa.*

For sampling the area was divided into a grid of 10 km × 10 km squares of the Universal Transversal Mercator (UTM) resulting in a total of 166 km^2. Within each of these three quantitative samples of surface soil/litter (0.5 m^2 to a depth of 5 cm) were collected from the three most representative vegetation types in the study area (woodland, pasture and riverbank), giving a total of 498 samples.

The sampling was conducted over three consecutive years and in each of the four seasons of the year. Sampling of adjacent squares was avoided in the same season, so that each square of 20 km × 20 km UTM was sampled in each one of the four season of the year.

In the laboratory, the samples were wet-sieved through a 7 mm mesh over a 0.5 mm mesh. Material retained by the second mesh was carefully examined under a magnifying glass, with the aim of finding all live gastropods. A more detailed description of the study area and sampling procedure is given in Ondina and Mato, 2001.

Table 1
Maximum, minimum and mean values of the different edaphic factors determined in the 498 samples

Soil factors	Maximum	Minimum	χ^2	σ
Moisture	82.98	5.50	37.17	13.91
Porosity	94.46	6.21	69.03	10.30
Aeration	69.21	2.77	31.93	10.61
F > 2 mm	59.35	0.06	11.72	11.11
Coarse sand	92.94	0.77	35.99	20.32
Fine sand	77.53	3.25	35.91	12.61
Silt	44.26	0.01	15.94	9.38
Clay	32.58	0.20	12.11	6.52
C/N	22.83	5.33	12.04	2.32
Carbon	19.04	0.29	4.80	2.72
Nitrogen	1.43	0.03	0.40	0.22
Sodium	3.55	0.00	0.36	0.43
Potassium	1.90	0.05	0.33	0.23
Calcium	25.70	0.11	3.18	3.79
Magnesium	11.90	0.04	1.34	1.56
Aluminium	10.88	0.00	1.72	1.84
pH in H_2O	8.1	3.6	5.1	0.6
pH in KCl	7.8	2.8	4.3	0.6
pH litter	7.6	3.6	4.9	0.6

Standard deviations are also shown.

At each sampling site, we also took a soil sample for analysis of 19 physicochemical variables, namely soil moisture content (Mois), soil porosity (Por), soil aeration (Aer), proportion of gravel fraction [F > 2 mm], proportion of coarse sand fraction (Coa), proportion of fine sand fraction (Fin), proportion of silt fraction (Silt), proportion of clay fraction (Clay), C/N ratio (C/N), carbon content (C), nitrogen content (N), sodium content (Na), potassium content (K), calcium content (Ca), magnesium content (Mg), aluminium content (Al), soil pH in water (pHW), soil pH in KCl (pHK), and litter pH (pHL). Maximum, minimum and mean values of each variable are listed in Table 1.

To investigate relationships between gastropods and edaphic factors we performed a multivariate gradient analysis, detrended canonical correspondence analysis (DCCA; see Ter Braak, 1986, 1988, 1990). DCCA is a combined ordination and regression technique (Ter Braak, 1994) which evaluates community composition in terms of response to environmental gradients (Whittaker, 1956). Analyses of this type are based on the idea that species occur in a characteristic range of habitats, and tend to be most abundant around an optimum, so that community composition changes along gradients. This approach contrasts with classical approaches based on linear models, such as canonical correlation, principal components analysis and multiple regression (Gauch and Whittaker, 1972; Ellenberg, 1979). The results of DCCA are conventionally represented by plots in which species are represented by points and environmental factors by straight lines with low–high direction indicated by an arrow. The length of each line is proportional to the strength of the correlation between that factor and the axes of the plot; in other words, longer lines indicate more important determinants of distribution. The distribution of a given species with respect to a given factor is determined by the length of the perpendicular between the point representing that species and the line representing that factor: species close to the line are more strongly influenced by the factor in question, and species far from the coordinate origin show stronger preference for the critical values of that factor. The coordinate origin of the plot represents the mean value of all factors.

Percentage variance explained is not a reliable indicator of the goodness of fit of DCCA models (Gauch, 1982), and we therefore used a Monte Carlo permutation test (Briones et al., 1992; Verdonschot and Ter Braak, 1994).

To avoid distortion introduced by infrequent species (Briones et al., 1994; Hermida et al., 2000), only species present in 10% or more of samples were included in the analysis. Species abundance values were log-transformed ($n \rightarrow \log[n + 1]$, where n is number of individuals) to achieve better approximation to the normal distribution.

Additionally, we constructed corrected frequency profiles (Daget and Godron, 1982), which facilitate assessment of the extent to which species abundances vary among classes of a given environmental factor. Statistical significances were tested by χ^2 tests.

3. Results

A total of 47 species was detected, but only 17 were present in 10% or more of samples. Table 2 lists these species, with species codes and total number of individuals detected in the 498 samples.

Fig. 1 shows the species and factor positions on the first two axes extracted by DCCA. These axes explained 42.8 and 14.3% of inertia respectively (total

Table 2
List of species, species code (e.g. Aa) and number of individuals detected

Family	Species name and code	No. of individuals
Valloniidae	*Acanthinula aculeata* (Müller, 1774) Aa	191
Arionidae	*Arion intermedius* (Normand, 1852) Ai	1220
Vertiginidae	*Vertigo pygmaea* (Draparnaud, 1801) Vp	77
	Columella aspera (Waldén, 1966) Ca	175
Cochlicopidae	*Cochlicopa lubrica* (Müller, 1774) Cl	3167
Carichiidae	*Carychium tridentatum* (Risso, 1826) Ct	2713
Agriolimacidae	*Deroceras reticulatum* (Müller, 1774) De	108
	Deroceras lombricoides (Morelet, 1845) Do	63
Discidae	*Discus rotundatus* (Müller, 1774) Dr	1723
Euconulidae	*Euconulus fulvus* (Müller, 1774) Ef	84
Zonitidae	*Aegopinella nitidula* (Draparnaud, 1805) An	1024
	Vitrea contracta (Westerlund, 1871) Vc	391
	Nesovitrea hammonis (Ström, 1765) Nh	3223
	Zonitoides excavatus (Alder, 1830) Ze	1024
	Oxychilus alliarius (Miller, 1822) Oa	371
Punctoidea	*Punctum pygmaeum* (Draparnaud, 1801) Pp	95
Hygromiidae	*Ponentina subvirescens* (Bellamy, 1839) Ps	208
	Total	15857

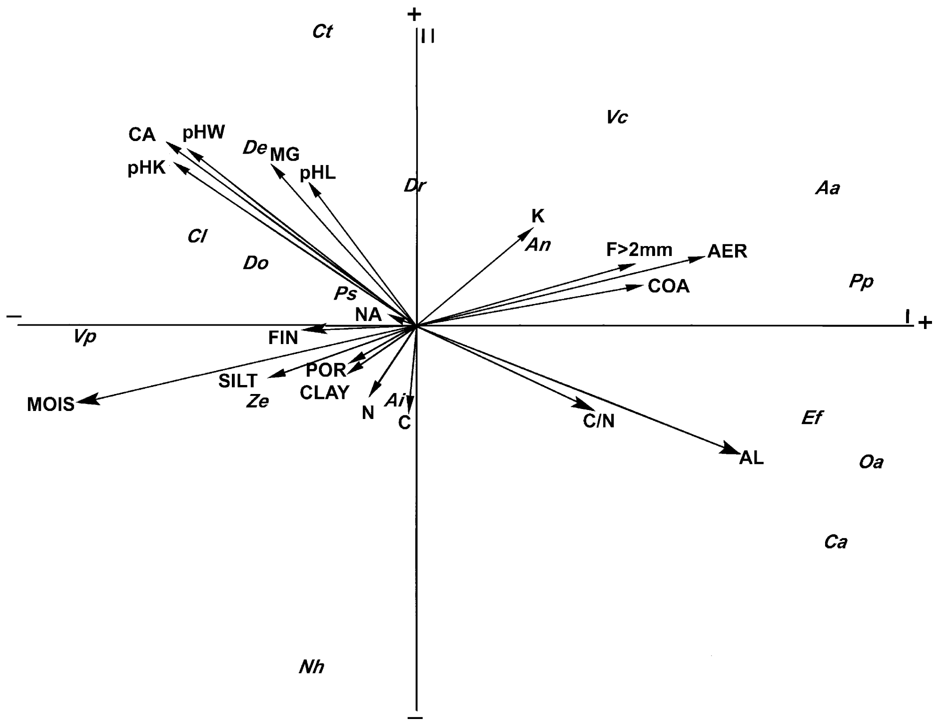

Fig. 1. Plot of species and factors on the first two axes extracted by detrended canonical correspondence analysis. Species are expressed by points (see Table 1 for key to abbreviations) and environmental factors by arrows (see Section 2 for key to abbreviations). The greater the influence of the factor, the longer the arrow will be. The projections of the species on this axis will show the preference gradient for high or low values of the factor.

57.1%). Monte Carlo permutation testing indicated an F-ratio of 27.21 ($P < 0.01$).

Table 3 shows correlations between these axes and the different environmental factors. As can be seen, the factors that best explain species distribution are: soil moisture content, Ca content, soil pH in water, soil pH in KCl, Al content, soil aeration, coarse sand, gravel, Mg content and litter pH. Table 3 lists variance inflation factors indicating which factors are most strongly cross-correlated, with both soil C and soil N contents informationally redundant (inflation factors >20).

Fig. 1 shows a group of species on the positive part of axis I, with preference for high values of aeration, gravel, coarse sand and Al content, and low values of soil moisture, calcium and pH. This group comprises *Acanthinula aculeata, Punctum pygmaeum, Euconulus fulvus, Oxychilus alliarius* and *Columella aspera*, together with *Vitrea contracta* and *Aegopinella nitidula*, which appear to be strongly influenced by potassium.

On the negative part of axis I is a group of species showing the opposite behaviour. This group comprises *Cochlicopa lubrica, Deroceras lombricoides, Deroceras reticulatum* and *Carychium tridentatum*. *Vertigo pygmaea* and *Zonitoides excavatus* are also located on the negative part of axis I, and appear to be strongly influenced by high humidity values.

Arion intermedius and *Ponentina subvirescens* are located close to the origin, and thus can be considered indifferent to the environmental gradient represented by axis I. *Discus rotundatus* and *Nesovitrea hammonis* do not show clear behavior with respect to this axis.

Corrected frequency profiles allow a more detailed analysis of the preferences of individual species for the different values of each factor. Table 4 shows the upper limits of the six classes into which each edaphic variable was divided for this analysis, and the number of sites in each class. Fig. 2 summarizes the results obtained for each species with respect to the most important edaphic factors as identified by DCCA. As

Table 3
Correlations between each factor and the first two axes extracted by DCCA

Factor	Axis I	Axis II	Inflation factor
Moisture	−0.438	−0.125	4.8187
Porosity	−0.085	−0.059	2.2560
Aeration	0.372	0.112	2.9497
$F > 2$ mm	0.283	0.100	1.4762
Coarse sand	0.293	0.066	3.9993
Fine sand	−0.138	−0.008	1.7846
Silt	−0.189	−0.84	3.3958
Clay	−0.087	−0.076	3.3467
C/N	0.229	−0.131	2.6630
Carbon	−0.010	−0.139	23.2595
Nitrogen	−0.059	−0.112	21.5949
Sodium	−0.034	0.018	1.4484
Potassium	0.152	0.156	1.2456
Calcium	−0.322	0.287	2.4034
Magnesium	−0.186	0.252	2.7682
Aluminium	0.417	−0.198	2.4191
pH in H_2O	−0.295	0.276	18.6334
pH in KCl	−0.310	0.253	18.3392
pH litter	−0.139	0.226	1.6381

The rightmost column shows variance inflation factors.

can be seen, these results support those obtained by DCCA, and help elucidate the behaviour of *N. hammonis* and *D. rotundatus*. As shown in Fig. 2, *N. hammonis* is indifferent to factors like Mg, Ca and pH (important determinants for the other species located on the negative side of axis I, Fig. 1), but shows apparent preference for fine soil texture and for high soil moisture contents, as well as high soil porosity, a factor not identified as an important determinant by DCCA (Fig. 3). Similarly, *D. rotundatus* shows preference for the conditions represented by the top left quadrant of axis I, namely pH, magnesium and calcium, but also a clear preference for high potassium levels (see Fig. 4), which explains its intermediate position on this axis, close to the origin. The same occurs with *A. nitidula* and *V. contracta*, which as noted show preference for high potassium levels (Fig. 4).

Taken together, our results suggest that, as regards gastropod distribution, the soils of our study area can be usefully classified on the basis of chemical and physical criteria. The major chemical criteria are pH, cation exchange capacity, and aluminium, and as regards gastropod distributions, the soils can be divided into acid soils with low pH, Ca and Mg, and high Al and less acid soils with higher pH, Ca and Mg and lower Al. The major physical criteria are textual factors, soil aeration and soil moisture content. Again on the basis of these factors and gastropod distribution, the soils can be divided into two categories, namely well-drained coarse-textured soils (high proportions

Table 4
Class limits used for construction of corrected frequency profiles (LC1–LC6, upper limits of each class; NC1–NC6, number of samples in each class)

Factor	LC1	LC2	LC3	LC4	LC5	LC6	NC1	NC2	NC3	NC4	NC5	NC6
Moisture	23.31	31.34	36.83	41.57	49.75	83.00	83	83	83	83	83	83
Porosity	59.14	65.19	69.52	73.45	78.71	95.00	83	83	83	83	83	83
Aeration	22.33	27.06	31.01	35.99	42.48	70.00	83	83	83	83	83	83
$F > 2$ mm	1.82	4.68	8.3	14.00	21.48	59.50	83	83	83	83	83	83
Coarse sand	14.66	24.15	32.86	44.58	56.42	93.00	83	83	84	82	83	83
Fine sand	23.97	29.16	35.06	41.50	47.51	78.00	83	83	84	82	83	83
Silt	6.91	11.16	14.75	18.11	25.31	45.00	83	83	83	83	83	83
Clay	5.04	8.69	11.42	14.62	19.15	33.00	83	83	84	82	83	83
C/N	10.37	10.89	11.55	12.41	13.70	23.00	83	82	83	85	82	83
Carbon	2.35	3.45	4.36	5.42	6.93	19.50	83	84	81	84	83	83
Nitrogen	0.19	0.28	0.36	0.45	0.58	1.50	82	81	86	81	89	79
Sodium	0.07	0.12	0.20	0.37	0.67	4.00	82	80	96	77	80	83
Potassium	0.15	0.21	0.28	0.35	0.49	2.00	80	89	90	67	92	80
Calcium	0.62	1.18	1.92	3.00	5.33	26.00	82	84	83	83	83	83
Magnesium	0.34	0.57	0.81	1.21	2.21	12.00	81	85	83	81	86	82
Aluminium	0.08	0.61	1.08	1.91	3.41	11.00	81	86	81	84	84	82
pH in H_2O	4.50	4.80	5.00	5.20	5.60	8.50	82	93	74	79	91	79
pH in KCl	3.80	4.00	4.20	4.40	4.90	8.00	82	70	79	97	99	71
pH litter	4.30	4.60	4.80	5.10	5.50	7.80	82	93	59	85	104	75

	MOIS	AER	>2mm	COA	Ca	Mg	Al	pH	pHK	pHL
A.aculeata	↓	↑	↑	↔	↔	↔	↑	↔	↕	↕
E. fulvus	↓	↑	↑	↔	↔	↕	↑	↔	↔	↓
C. aspera	↓	↑	↑	↑	↓	↓	↑	↓	↓	↓
O. alliarius	↓	↑	↓	↑	↓	↓	↑	↓	↓	↓
V. contracta	↓	↑	↕	↔	↑	↕	↓	↑	↑	↑
C. lubrica	↑	↓	↓	↓	↑	↑	↓	↑	↑	↑
D. reticulatum	↔	↓	↔	↓	↑	↔	↓	↑	↑	↑
D.lombricoides	↑	↓	↓	↓	↑	↑	↓	↑	↑	↑
C. tridentatum	↑	↓	↓	↕	↑	↑	↓	↑	↑	↑
V. pygmaea	↑	↓	↓	↓	↑	↑	↓	↑	↑	↑
Z. excavatus	↑	↓	↓	↓	↑	↕	↓	↑	↑	↑
A. nitidula	↕	↑	↔	↑	↔	↕	↕	↕	↕	↕
A. intermedius	↕	↕	↕	↓	↕	↑	↓	↕	↕	↕
D. rotundatus	↑	↕	↕	↓	↑	↑	↓	↑	↑	↑
N. hammonis	↑	↓	↓	↓	↕	↕	↕	↕	↔	↔
P. pygmaeum	↓	↑	↔	↔	↓	↓	↑	↔	↔	→
P.subvirescens	↕	↕	↕	↔	↑	↔	↓	↑	↑	↑

Fig. 2. Summarized results of corrected frequency profiles analysis. (↑) preference for high values. (↓) preference for low values. (↔) preference for intermediate values. (↕) indifference.

of gravel and sand, high aeration, low proportions of silt and clay, low soil moisture content) and wet fine-textured soils (higher proportions of silt and clay, higher soil moisture content). The remaining factors did not have significant effects on species distribution, and will not be considered further.

Fig. 5 shows a schematic representation of species distributions with respect to these four categories. *A.*

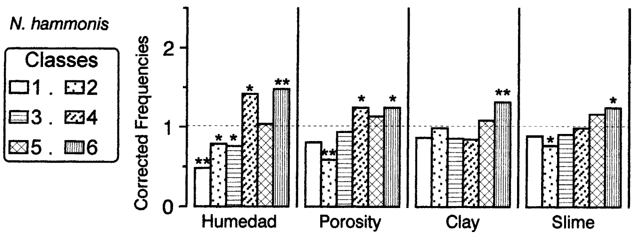

Fig. 3. Corrected frequency profiles for *N. hammonis* with respect to soil moisture content, soil porosity, and fine texture. Profile values of 1 indicates a uniform distribution (i.e. indifference); values greater than 1 indicate preference. Asterisks indicate significant departures from uniformity ($^{*}P < 0.05$; $^{**}P < 0.01$).

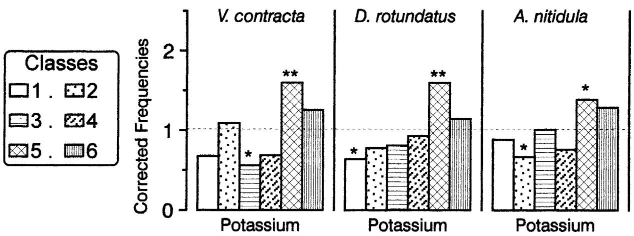

Fig. 4. Corrected frequency profiles for *V. contracta*, *D. rotundatus* and *A. nitidula* with respect to soil potassium content. Profile values of 1 indicates a uniform distribution (i.e. indifference); values greater than 1 indicate preference. Asterisks indicate significant departures from uniformity ($^{*}P < 0.05$; $^{**}P < 0.01$).

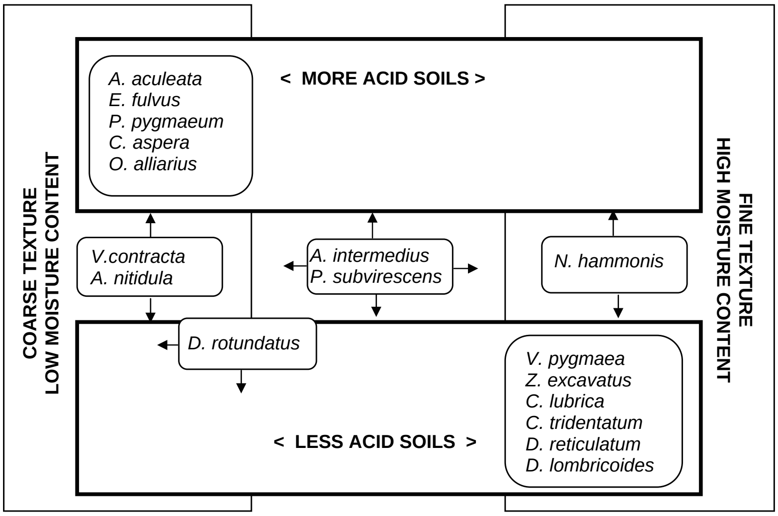

Fig. 5. Schematic summary of the results showing the distribution of the common gastropod species with respect to edaphic factors.

aculeata, *E. fulvus*, *P. pygmaeum*, *C. aspera* and *O. alliarius* typically occur in acid soils with coarse texture. By contrast *V. pygmaea*, *Z. excavatus*, *C. lubrica*, *C. tridentatum*, *D. reticulatum* and *D. lombricoides* typically occur in less acid soils with finer texture. *V. contracta* and *A. nitidula* typically occur in soils with coarse texture, whether acid or less acid; this explains their frequent association with the *A. aculeata* group. *N. hammonis* typically occurs in soils with fine texture, whether acid or less acid; similarly, this explains this species' frequent association with the *V. pygmaea* group. *D. rotundatus* shows a slight preference for more basic soils and coarser textures, while *A. intermedius* and *P. subvirescens* appear to be indifferent to the factors considered.

4. Discussion

Previous reports on the distribution of gastropods with respect to soil characteristics have been rather contradictory. Thus, some authors, such as Bruijns et al., 1959 and Evans (1972), have suggested that soil characteristics are the principal determinants of gastropod species distributions. By contrast, other authors (e.g. Bishop, 1977) have suggested that the most important determinants are first litter characteristics, second soil characteristics, and third vegetation type. Subsequent studies have confirmed the importance of soil characteristics as determinants of gastropod distribution (André, 1982; Gärderforns et al., 1995; Ondina et al., 1998), although climatic factors (Hermida et al., 1994) and vegetation (Štamol, 1992; Ondina and Mato, 2001; Nekola, 2003) are also known to be significant.

The factors identified as important in the present study coincide in part with those identified by authors like Wäreborn (1992); Gärdenfors (1992); Johannessen and Solshøy (2001), and especially by Outeiro (1988); Riballo (1990); Outeiro et al. (1993); Hermida et al. (1995, 2000) and Ondina et al. (1998), who focussed on textural characteristics and, as in the present study, used a multivariate statistical approach. Some of these factors have also been identified as important determinants of the distribution of other soil invertebrates (Mascato et al., 1987).

While soil factors are clearly not the only factors associated with the distribution of terrestrial gastropods, these previous studies and the present results clearly indicate that they are usually important. Two questions arise: first, which soil factors are important, and to what extent, and second, which species are most strongly dependent on soil characteristics? As regards the first question, most authors have concluded—as in the present study—that the most important edaphic factors are calcium, pH and texture. Thus, André (1982) and Hermida et al., 1994, 2000) have noted that pH and calcium are the most important factors, while Johannessen and Solshøy (2001) additionally reported cation exchange capacity to be important. Outeiro (1988); Riballo (1990) and Outeiro et al. (1993) concluded that texture is the most important factor, while Outeiro (1988) found that pH and cation levels were likewise important.

However, the fact that the presence of a species in a given location is determined by its range of tolerance for particular factors, and that species groups reflect overlapping tolerance ranges, makes it more difficult to answer our second question above. This is because the study areas where the various previous studies were conducted include different ranges of the different soil factors, and often different species; for example, Outeiro et al., 1993 used a procedure similar to that used in this study, but found entirely different species. Thus, it is difficult to extrapolate from the conclusions of individual studies. For example, André (1982) suggests that *V. pygmaea* and *C. lubrica* are closely linked to calcium-poor soils, in contrast with our results. This discrepancy is attributable to the fact that this author studied an area with limestone substrates, in which certain sites were subject to intense leaching leading to reduced calcium levels, but nevertheless still had basic pH. It certainly does not seem reasonable to consider these species as calciphobes in any general sense. We would also add that André's study does not include the observed ranges of the factors considered, making comparison even more difficult.

Our results are basically in agreement with those of Outeiro (1988) as regards species groupings, though he found textural factors to be more important. Outeiro's conclusions differ in some respects from ours: specifically, Outeiro found that the distribution of *P. subvirescens* correlates with edaphic factors (notably texture), and that the distribution of *C. tridentatum* is correlates with textural factors only.Our results coincide most closely-as regards both important environmental factors and species groupings with those of Hermida et al. (1995). These authors obtained samples over a wide area, covering sites with a wide range of environmental conditions. As in the present study they found two major groups (one comprising *A. aculeata*, *A. nitidula* and *P. pygmaeum*, the other *C. lubrica*, *N. hammonis*, *V. pygmaea* and *C. tridentatum*), and concluded that the most important environmental factors were cation exchange capacity, pH and texture. Likewise *N. hammonis* was found to show a preference for soils with high porosity.

Humidity is an important factor affecting the distribution of gastropods (Cameron, 1973; Nekola, 2003). However, it is necessary to point out the limitations of soil moisture data based on measurements at particular points in time, since this parameter can vary considerably over time and is strongly influenced by weather conditions.

In conclusion: in view of our results and previous findings, it is clear that gastropod distributions are correlated with soil properties (Peake, 1978; Gärderforns et al., 1995; Nekola and Smith, 1999; Johannessen and Solshøy, 2001), although clearly other environmental factors may also be important. The influence of soil properties reflects above all soil acidity and basicity, since the most important determinants are pH and cation exchange capacity, particularly in studies which have covered a large area covering a wide range of values. The second most important property is texture, which appears to have major effects on gastropod distribution in studies of small areas, in which species number is lower, and environmental factor ranges are narrower (see for example Outeiro, 1988; Riballo, 1990; Outeiro et al., 1993).

In view of the above, in studies of malacofauna–soil relations, we consider it very important to consider the environment not as a single entity, but as a multifactorial grouping whose effects on the fauna and vegetation are in continuous interaction. Starting from this assumption, if we compare the present results with our previous study focussed on the relationship between gastropod distributions and vegetation type (Ondina and Mato, 2001), we can see that the species showing the strongest correlation with edaphic factors (such as *C. lubrica* and *Z. excavatus*) are those defined by these authors as characteristic of pasture vegetation, while those showing the least correlation (such as *A. aculeata*, *O. alliarius* and *C. aspera*) are those defined as characteristic of woodland vegetation. This suggests that the woodland species may be rather less dependent on edaphic conditions, since they typically live in the litter layer and at the litter/soil interface, where they are less exposed to insolation and to brusque changes in temperature and moisture. Pasture species, by contrast, show little mobility, and live in the soil itself, typically in spaces between roots and in earthworm holes.

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