



# Determinant variables of Iberian Peninsula Aphodiinae diversity (Coleoptera, Scarabaeoidea, Aphodiidae)

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## ABSTRACT

**Aim** The aims of this paper are to examine diversity–variability patterns for species of Aphodiinae (Coleoptera, Scarabaeoidea, Aphodiidae) on the Iberian Peninsula, and to determine the factors that influence their geographic distribution.

**Location** Iberian Peninsula (Spain and Portugal).

**Methods** Data from 30 studies and their bibliographies on species of Iberian Peninsula Aphodiinae were compiled. The reliability of the inventories was evaluated using parametric species richness estimators. In addition, a further 11 variables related to rarity, geographic distribution, or phylogenetic diversity were considered. Diversity variables were analysed using principal components analysis to reduce the number of dependent variables. Subsequently, the effect of differences in locality size among the 30 studies was eliminated by calculating and retaining the residuals of the curvilinear relationship of each diversity variable with the area. Generalized linear models were used to examine the relationships between diversity and 17 environmental variables. The diversity variables and their residuals were also subject to trend surface analysis in order to identify the relevance of spatially structured variables that had not been considered. The contribution of explanatory variables was determined through hierarchical variance analysis.

**Results** Principal components analysis of biodiversity variables revealed that most of the variability could be explained using three biodiversity indexes: BI1, correlated positively with species richness, widely distributed species, frequent species, abundant species, species occurring in North Africa, Europe and the Iberian Peninsula, and phylogenetic diversity; BI2, correlated positively with numbers of infrequent and African–Iberian species; and, BI3, correlated positively with numbers of endemic, non-abundant, European, and Iberian-restricted species. A latitudinal disjunction emerged in BI1, with maximum scores at the north-western and southern corners, while maximum BI2 scores were found throughout the south, and maximum BI3 scores in the north-west. For BI1, it was climate that had the greatest influence, followed by lithology, and livestock presence. Geographic variables were the most significant for BI2, followed by climate and livestock presence. Finally, for BI3, climate variables were the most important, while geography, lithology and livestock presence had some relevance.

**Main conclusions** The relevance of geographic variables indicates that other unaccounted-for factors that are spatially structured could possibly explain additional variation in Aphodiinae diversity. These factors may be historic in nature, relating to the species groups, namely the Ibero-European and the Mediterranean or Afro-Iberian. The northern pattern could reflect the fact that the Iberian Peninsula acted as a colonization route and as a refuge during the glacial/

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interglacial cycles, while the southern pattern could be a consequence of the connection between the Iberian Peninsula and North Africa during the Messinian crisis, and/or a historic relationship in common, related to human activity.

### Keywords

Aphodiinae, climatic variables, diversity patterns, dung beetles, environmental factors, historic factors, Iberian Peninsula, spatial structure.

## INTRODUCTION

Species diversity is an ambiguous term, lacks a commonly accepted definition (Whittaker, 1972; Hengeveld, 1990; Purvis & Hector, 2000) and is a difficult concept to describe using a single attribute. Nevertheless, because it often correlates with other relevant biodiversity variables (Humphries *et al.*, 1995; Gaston, 1996; Whittaker *et al.*, 2001), species richness has frequently been used as a measure of biodiversity within a group of organisms. There are, however, other attributes that can contribute to the knowledge and description of variation in biodiversity, such as demographic and geographic rarity (Rabinowitz *et al.*, 1986; Gaston, 1994), complementarity or compositional variation (Whittaker, 1972), phylogenetic diversity (May, 1990) and endemism (Jetz *et al.*, 2004).

Distribution patterns are important attributes of biodiversity, and, although they are not usually homogeneous throughout a region, it is likely that they are an emergent consequence of many influential environmental, spatial or historical factors (Ricklefs & Schluter, 1993; Brown & Lomolino, 1998; Rahbek & Graves, 2001; Whittaker *et al.*, 2001; Hawkins *et al.*, 2003). The comparative importance of these factors cannot be deduced from experimental results, but the correlation of biodiversity variables with environmental, spatial, or historical variables provides the raw material with which to construct hypotheses concerning the determinants of species diversity variation (Huston, 1994; Hengeveld, 1996). Statistical techniques such as variance partitioning (Borcard *et al.*, 1992; Legendre & Legendre, 1998), or hierarchical partitioning analysis (MacNally, 2000, 2002), can help to identify more precisely which variables are the most likely to influence distributional patterns (e.g. Birks, 1996; Lobo *et al.*, 2001).

A significant problem encountered in the determination of the comparative relevance of different types of environmental variable is the lack of reliable information on the distribution of biodiversity attributes within an area. At present, biodiversity attribute distribution is mapped reliably for only a few regions, and primarily for vertebrate taxa (Brooks *et al.*, 2004). Comprehensive mapping of the distributions of organisms is expensive, both in time and economic resources. It may be more cost effective to use data from localities that have reasonably reliable inventories, along with diverse environmental and spatial information, to build models that can be used to extrapolate the distribution of desired biodiversity attributes in localities whose inventories are poor or unknown.

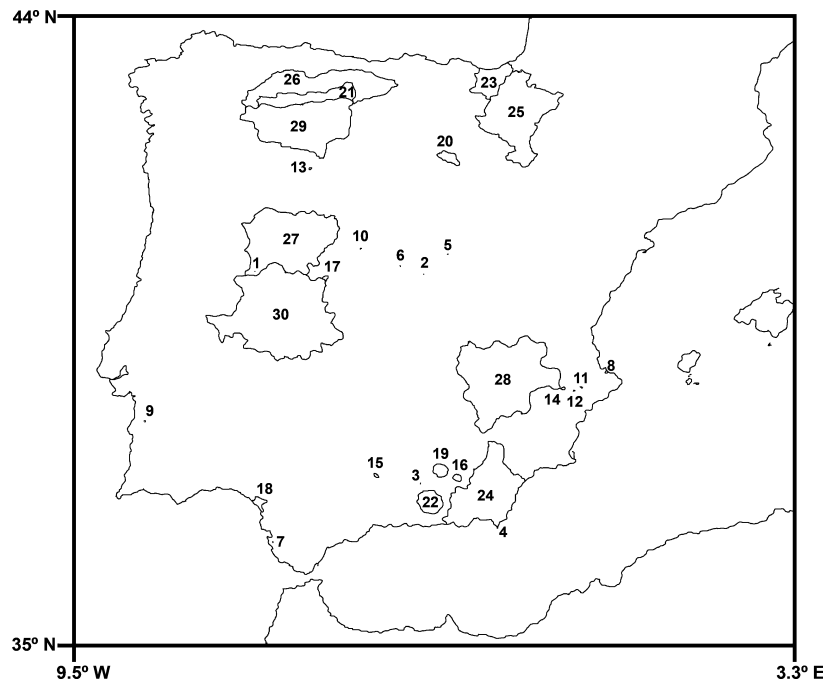
Indeed, this is the present strategy for dung beetles in some European regions, where information from faunistic Atlases (Lobo *et al.*, 2002, 2004), and exhaustive data bases are used (Hortal *et al.*, 2001; Lobo & Martín-Piera, 2002). Unfortunately, reliable sources of similar information do not exist for most taxonomic groups (Martín-Piera & Lobo, 2000). It is not necessary, however, to wait for the availability of complete distributional information to offer preliminary hypotheses concerning these questions. In this paper, the limited information in the literature on the Aphodiinae (Coleoptera: Scarabaeoidea: Aphodiidae) (Cabrero-Sañudo & Lobo, 2003) is used to examine statistically the factors that may explain the diversity and distribution of this group in the Iberian Peninsula.

Several studies have analysed the influence of environmental factors, such as temperature, humidity or precipitation, on the local distribution of some Aphodiinae species (Landin, 1961). The altitudinal (Martín-Piera *et al.*, 1992; Jay-Robert *et al.*, 1997) and seasonal variations of Aphodiinae assemblages have also been examined (Hanski & Koskela, 1979; Palmer, 1995; Sowig, 1997), as well as the influence of type and quantity of trophic resources (Lumaret *et al.*, 1992; Kadiri *et al.*, 1997; Galante & Cartagena, 1999; Finn & Giller, 2002), or habitat type (Menéndez & Gutiérrez, 1996; Romero-Alcaraz *et al.*, 2000). However, despite information on the relationship of the Aphodiinae assemblages with environmental variables in the Western Palearctic region (Lumaret, 1978; Hanski & Cambefort, 1991a,b; Sowig & Wassmer, 1994), geographic patterns of biodiversity variation and their determinant environmental factors have received little attention (Verdú & Galante, 2002; Cabrero-Sañudo & Lobo, 2003; Lobo *et al.*, 2004). This paper contributes to the understanding of these relationships by examining the effect of various environmental and spatial variables on a group of Iberian Aphodiinae diversity variables, and proposes biological mechanisms that are likely to explain these relationships.

## METHODS

### Data origin

Taxonomy and species richness data were compiled from both published and unpublished studies of 30 Iberian localities (Fig. 1) of various sizes (Table 1). Six localities were  $\leq 1$  km<sup>2</sup>, 11 were between 1 and 100 km<sup>2</sup>, and 13 were  $> 100$  km<sup>2</sup>. Although geographic coverage is diverse, data are lacking from



**Figure 1** Map of the Iberian Peninsula, showing localities in the present study. Numbers correspond to the localities in Table 1.

**Table 1** List of the 30 Iberian localities used in the study. Area in km<sup>2</sup> (A), latitude (Lat), longitude (Lon), and Aphodiinae species richness (S). Locality numbers correspond to those in Fig. 1

Code	Locality	A	Lat	Lon	S	References
1	Nava de Francia	0.06	40°25'	6°23'	25	Gutiérrez-García (2000)
2	Colmenar Viejo	0.2	40°40'	3°45'	21	Veiga (1982)
3	Sierra de Alfacar	1	37°20'	3°30'	20	Fernández-Sigler (1986)
4	Cabo de Gata	1	36°45'	2°10'	12	Rozas & Ávila (1990)
5	La Hiruela	1	41°00'	3°30'	20	Baz (1988)
6	El Ventorrillo	1	40°45'	4°00'	27	Martín-Piera <i>et al.</i> (1986)
7	Chiclana de la Frontera	4	36°25'	6°10'	26	Ávila & Sánchez-Piñero (1990)
8	Pego-Oliva	9	38°52'	0°05'	6	Micó <i>et al.</i> (1998)
9	Serra de Grândola	14	38°00'	8°42'	13	Serrano <i>et al.</i> (1999)
10	Valle del Alberche	25	40°42'	4°40'	25	Lobo (1982)
11	Parque Natural de la Font Roja	25	38°40'	0°32'	10	Verdú (1994)
12	Sierra de Onil	25	38°38'	0°41'	3	Galante & Cartagena (1999)
13	Villafáfila	28	41°50'	5°40'	21	Salgado (1983)
14	Sierra de Salinas	48	38°39'	0°51'	3	Cartagena & Galante (1998), Galante & Cartagena (1999)
15	Sierras Subbéticas	50	37°25'	4°20'	20	Hidalgo & Cárdenas (1994)
16	Sierra de Baza	91	37°23'	2°53'	14	Romero-Alcaraz <i>et al.</i> (2000)
17	Macizo Central de Gredos	100	40°15'	5°20'	31	Lobo (1992)
18	Doñana	300	37°00'	6°22'	32	Lobo <i>et al.</i> (1997)
19	Depresión Guadix-Baza	400	37°30'	3°10'	29	Sánchez-Piñero (1994)
20	Sierra de Urbión	489	42°03'	2°53'	39	De la Villa (1992)
21	Picos de Europa	866	43°05'	5°05'	34	Galante & Stebnicka (1994), Menéndez (1997)
22	Sierra Nevada	1250	37°05'	3°30'	28	Ávila & Pascual (1988)
23	Vizcaya	2217	43°10'	2°50'	27	Bahillo <i>et al.</i> (1988)
24	Almería	8774	37°17'	2°24'	21	Carrión (1961)
25	Navarra	10,421	42°40'	1°40'	21	Herrera-Mesa & Rey-Escalera (1985)
26	Cordillera Cantábrica	10,569	43°00'	5°35'	45	Galante & Stebnicka (1994)
27	Salamanca	12,336	40°45'	6°00'	38	Galante (1983)
28	Albacete	14,858	38°45'	1°50'	35	Ruano <i>et al.</i> (1988), Sánchez-Ruiz <i>et al.</i> (1994)
29	León	15,468	42°40'	5°55'	55	Salgado & Delgado (1979, 1982), Delgado & Salgado (1982), Salgado & Galante (1987)
30	Cáceres	19,945	39°50'	6°20'	37	Galante & Stebnicka (1993)

the western and north-eastern Iberian Peninsula, as are data from the southern plateau (Fig. 1). Most studies are concentrated in regions near population centres or the universities from which dung-beetle researchers operate. Cited faunistic studies were carried out using basic taxonomic information on the Aphodiinae and Scarabaeoidea (Báguena, 1967; Dellacasa, 1983; Baraud, 1992; Veiga, 1998; Dellacasa *et al.*, 2000; Martín-Piera & López-Colón, 2000). These studies contain the only available species distribution information for the Iberian Peninsula. Species nomenclature followed the taxonomic criteria of Dellacasa (1983), Baraud (1985, 1992), Ádám (1994), Veiga (1998), and Dellacasa *et al.* (2000).

Localities that have been sampled for at least one complete year were selected for analysis. Their catalogues were compiled over long time periods, and are either inventories of all available information on a region, or are ecological studies based on standardized samplings from excrement or baited pitfall traps (Lobo *et al.*, 1988). To avoid the effect of insularity (MacArthur & Wilson, 1963) on group diversity, Balearic archipelago faunistic information (Español, 1950; Compte, 1968; Martín-Piera & Lobo, 1992) was not used.

Inventory reliability was evaluated using Chao2 and abundance-based coverage estimator (ACE) nonparametric species richness estimators (Chao, 1987; Colwell & Coddington, 1994; Chazdon *et al.*, 1998) that yield estimates of the total number of species in each locality, assuming optimal sampling effort. The values were calculated using *EstimateS* version 7 (Colwell, 2004). With the exception of four localities (Sierra de Alfacar, Pego-Oliva, Serra de Gràndola, and Depresión Guadix-Baza), observed species richness values were similar to those estimated (see Cabrero-Sañudo & Lobo, 2003). The four exceptions, in the arid south-east or south-west of the Iberian Peninsula, are species- and individual-impoverished. Owing to the considerable effort in collection that had been expended (at least a complete year of sampling, with several collection methods or trap types), information from these impoverished localities was included in the later analyses. However, as a result of the great discrepancy between estimated and observed species richness values and the lack of information on collection effort, inventories from Los Monegros (López-Colón, 1999; Melic & Blasco-Zumeta, 1999) and Montseny (Español & Viñolas, 1986), previously used by Verdú & Galante (2002), and an inventory from Catalonia (Mesa, 1985) were not included.

### Biodiversity variables

Species richness was calculated for each of the 30 selected localities (Table 1). Eleven additional variables related to rarity, geographic distribution, or phylogenetic diversity were also considered, termed biodiversity variables from this point on.

To quantify rarity, the geographic range size (GR) of each species (Rabinowitz *et al.*, 1986) was estimated. We also summed the number of endemic (Ed) and widely distributed species (Wd) present in each locality. These variables were

defined by considering the six classes of geographic range size suggested by Lumaret & Lobo (1996), which were used to calculate each species' distribution area as a percentage of the total western Palaearctic region area ( $12 \times 106 \text{ km}^2$ ). Those species of range-size classes 1–4 (with an area approximately that of the Iberian Peninsula) were considered to be 'endemic', and those of classes 5 and 6 were classed as widely distributed. The geographic range size information not given by Lumaret & Lobo (1996) was extracted from bibliographic sources (Baraud, 1985, 1992; Dellacasa, 1987, 1988a,b, 1991, 1995; Hollande & Thérond, 1998; Veiga, 1998). The distribution of the number of Iberian species with different range sizes is biased, and for most species the geographic range size is large. The numbers of endemic and widely distributed species are shown in Table 2.

Regional rarity (Reg), the proportion of localities in which each species occurred, was calculated as follows. As the areas of the 30 localities considered differ, the inverse of the sum of the decimal logarithm of the area (+1) of all localities in which the species occurred was calculated for each species, so that

$$\text{Reg}_i = \frac{1}{\log(a+1) + \log(b+1) + \log(c+1) + \dots + \log(n+1)},$$

where  $i$  is each species, and  $a, b, c, \dots, n$  are the areas of each of the localities where the species occurred. Species in the upper and lower quartiles of this measure of Iberian Aphodiinae regional species rarity were classified as frequent (Fr), or infrequent (Infr), respectively. The number of species in each of these two categories was recorded for each locality (Table 2). The last type of rarity considered, local population rarity (LPR), takes abundance scores estimated for each species in the 30 localities as an indirect measure of population size (Rabinowitz *et al.*, 1986). To obtain these rarity scores, the abundance of each species as a proportion of the estimated total abundance from a locality was calculated, and the local population rarity for each species was derived as the inverse of the mean of these proportions. Iberian Aphodiinae species in the upper and lower quartiles of these scores were classified as abundant (Ab) or less abundant (LAb), and their numbers tabulated for each locality (Table 2).

Four geographic distribution categories were defined from the Palaearctic region in which each species occurs. Iberian Aphodiinae species were subdivided biogeographically into species restricted to the Iberian Peninsula (I species), those present in the western Palaearctic region including North Africa (Africa + Europe + Iberian Peninsula: AEI species), species whose distribution is restricted to North Africa and the Iberian Peninsula (Africa + Iberian Peninsula: AI species), and Iberian species present in Europe but absent in North Africa (Europe + Iberian Peninsula: EI species). Thus, the total Iberian fauna is the sum of the four groups (I + AEI + AI + EI), the fauna shared between the Iberian Peninsula and North Africa is AEI + AI, and fauna that the Iberian Peninsula shares with Europe is AEI + EI. The

**Table 2** List of the biodiversity variables for the 30 Iberian localities. Geographic range rarity (GR): endemic species (Ed), widely distributed species (Wd); regional rarity (Reg): infrequent species (Infr), frequent species (Fr); local population rarity (LPR): less abundant species (LAb), abundant species (Ab); geographic distribution categories: species present in North Africa, Europe and the Iberian Peninsula (AEI), species restricted to North Africa and the Iberian Peninsula (AI), species restricted to Europe and the Iberian Peninsula (EI), species restricted to the Iberian Peninsula (I); phylogenetic diversity (PD). Values refer to the number of species for each category, except for PD, where the p-median diversity index values are given (Faith & Walker, 1993; Faith, 1995)

Code	Localities	Rarity						Geographic distribution categories				Phylogenetic diversity (PD)
		GR		Reg		LPR		AEI	AI	EI	I	
		Ed	Wd	Infr	Fr	LAb	Ab					
1	Nava de Francia	1	24	0	20	1	11	15	0	9	1	65
2	Colmenar Viejo	0	21	0	12	0	9	15	1	5	0	47
3	Sierra de Alfacar	3	17	2	13	2	9	12	3	3	2	54
4	Cabo de Gata	1	11	2	1	0	5	7	5	0	0	17
5	La Hiruela	1	19	0	16	1	10	12	1	6	1	56
6	El Ventorrillo	4	23	0	17	0	9	13	0	10	4	75
7	Chiclana de la Frontera	2	24	3	11	1	10	20	6	0	0	70
8	Pego-Oliva	0	6	0	4	0	4	4	1	1	0	24
9	Serra de Grândola	0	13	0	8	1	7	11	1	1	0	34
10	Valle del Alberche	1	24	1	15	3	11	14	1	9	1	63
11	Parque Natural de la Font Roja	1	9	2	6	0	8	4	2	4	0	31
12	Sierra de Onil	0	3	0	3	0	3	2	0	1	0	8
13	Villafáfila	1	20	0	15	1	11	15	0	5	1	60
14	Sierra de Salinas	1	2	0	2	0	3	1	1	1	0	21
15	Sierras Subbéticas	2	18	2	10	2	9	14	5	0	1	61
16	Sierra de Baza	3	11	1	8	0	8	7	3	2	2	39
17	Macizo Central de Gredos	4	27	1	19	4	14	15	1	11	4	73
18	Doñana	4	28	5	11	2	12	21	9	1	1	75
19	Depresión Guadix-Baza	2	27	4	14	1	12	17	8	3	1	65
20	Sierra de Urbión	3	36	4	21	5	13	17	0	19	3	82
21	Picos de Europa	4	30	2	16	6	12	12	0	20	2	81
22	Sierra Nevada	2	26	0	17	1	11	20	4	3	1	76
23	Vizcaya	1	26	1	14	4	7	12	0	14	1	64
24	Almería	0	21	0	10	0	7	15	2	4	0	52
25	Navarra	2	19	0	12	0	9	9	2	9	1	65
26	Cordillera Cantábrica	7	38	3	19	10	14	16	1	23	5	91
27	Salamanca	2	36	0	21	3	14	24	1	11	2	81
28	Albacete	5	30	2	19	1	15	19	6	8	2	79
29	León	6	49	1	23	8	14	25	0	24	6	95
30	Cáceres	3	34	1	19	4	13	21	1	12	3	94

numbers of species with these four distributional types for each locality are recorded in Table 2.

The last biodiversity variable considered was phylogenetic diversity (PD; Vane-Wright *et al.*, 1991; Faith, 1992; Humphries *et al.*, 1995; Walker & Faith, 1995), a measure of character diversity (Vane-Wright *et al.*, 1991) that takes into account phylogenetic relationships among the species present in a locality. PD is the p-median diversity index (Faith & Walker, 1993; Faith, 1995) calculated from the character distance between species, which is derived from a 50% majority-rule consensus phylogenetic tree obtained from morphological characters (Cabrero-Sañudo, 2004). As some species were not considered in that phylogenetic study ( $n = 8$ ), the phylogenetic distance between all Aphodiinae species was established

from the values for other presumably phylogenetically related species according to standard taxonomic criteria (Dellacasa, 1983; Baraud, 1992; Veiga, 1998). Thus, the phylogenetic positions of *Agrilinus ater* (Degeer, 1774), *Calamosternus algiricus* (Pittino & Mariani, 1983), *Chilothorax conspurcatus* (Linnaeus, 1758), *Chilothorax pictus* (Sturm, 1805), *Heptaaulacus brancoi* Baraud, 1976, *Heptaaulacus gadetinus* Baraud, 1973, *Melinopterus dellacasai* (Ávila, 1986), and *Pseudacrossus sharpi* (Harold, 1874) were established from those of *Agrilinus constans* (Duftschmid, 1805), *Calamosternus granarius* (Linnaeus, 1767), *Chilothorax cervorum* (Fairmaire, 1871), *Chilothorax melanostictus* (W. Schmidt, 1840), *Heptaaulacus testudinarius* (Fabricius, 1775), *Melinopterus tingens* (Reitter, 1892), and *Amidorus thermicola* (Sturm, 1800), respectively.

Phylogenetic diversity for each locality followed Barker (2002) and is presented in Table 2.

### Explanatory variables

The values of 17 environmental continuous variables were estimated for each locality (Table 3). Nine of these variables are climatic: annual mean temperature ( $t_m$ ), mean minimum temperature ( $t$ ), mean maximum temperature ( $T$ ), annual mean precipitation ( $P$ ), summer total precipitation ( $P_s$ ), daily hours of sunshine ( $H_s$ ), thermicity index ( $It$ ), mediterraneity index ( $Im$ ), and aridity index ( $Ia$ ), with the last three variables taken from Rivas-Martínez (1987). Three variables related to environmental diversity were also used: altitude range ( $a_r$ ), temperature range ( $t_r$ ), and precipitation range ( $P_r$ ). Two additional elevational variables were also considered: the mean ( $am$ ) and the maximum ( $A$ ) altitude, together with three geographic variables, namely the distance from each locality to the Pyrenees ( $Dp$ ), to the Strait of Gibraltar ( $Dg$ ), and to the sea ( $Ds$ ). Also included for each locality were three ordinal lithology variables: the presence of calcareous ( $Sca$ ), clay ( $Sc$ ), and siliceous ( $Ss$ ) soils. Their values range according to the presence of the respective soils as a proportion of the total area of each locality: up to 33.3% (1), between 33.4 and 66.6% (2), and above 66.7% (3). Finally, two variables representing the size of bovine ( $Lb$ ) and ovine ( $Lo$ ) herds were included. Their ranges are based on data from provincial livestock censuses (Ministerio de Agricultura Pesca y Alimentación, 2000): for bovines, up to 50,000 head (1), between 50,001 and 100,000 head (2), and more than 100,000 head (3); for ovine livestock, up to 200,000 head (1), between 200,001 and 400,000 head (2), and more than 400,000 head (3). For each of the localities, the range corresponding to that of their county was assigned, except in the case of the Serra of Grândola (Portugal), to which the mean value of the adjacent Spanish provinces was assigned because of a lack of precise data.

All explanatory variable scores were extracted using a Geographic Information System (Idrisi 32: Eastman, 2001). Maps of thermicity, mediterraneity, and aridity indexes were interpolated to a resolution of 10 km by means of a distance-weighted averaging of climatic information from 314 meteorological stations (see Verdú & Galante, 2002). Elevation variables were extracted from a digital elevation model with a 1-km resolution. The remaining climate maps were interpolations at a resolution of 1 km, provided by the Instituto Nacional de Meteorología in Spain and the Portuguese Instituto de Meteorologia. The scores for each locality were extracted by superimposing digital maps and polygons that represent each locality. For the geographic variables, a distance map was created so that the minimum distance between the polygon of each locality and the geographic attribute could be calculated. The lithology categories were estimated by digitizing a lithology map (Instituto Geográfico Nacional, 1995) and superimposing the polygons of each locality onto the digitized map. All continuous variables were standardized to a

mean of 0 and a standard deviation of 1, in order to eliminate the effect of measurement scale.

### Data analysis

As the 12 biodiversity variables considered can be highly correlated, the 30 locality scores were first examined using principal components analysis (PCA; Legendre & Legendre, 1998). The dependent biodiversity variables were reduced to three non-correlated biodiversity indexes (BI). Subsequently, the effect of differences in size among the areas of each locality was eliminated by calculating and retaining the residuals of the curvilinear relationship between the area of each biodiversity variable. That is, after the biodiversity variables and the area of their corresponding locality were quasi-Newton fitted to the curvilinear function  $S = cA^z$  (Table 1;  $c$  and  $z$  constants) (Connor & McCoy, 1979; Rosenzweig, 1995), the residuals became an area-independent measure of the value of each biodiversity variable.

Generalized linear models (GLM; McCullagh & Nelder, 1989; Crawley, 1993) were used to analyse the relationship of each biodiversity variable with the explanatory variables considered. The species-number relationship with the explanatory variables (link function) was assumed to be logarithmic, with a normal or Poisson biodiversity variable error distribution, depending on the statistical significance (or lack thereof) of the species-number relationship with locality area. Model goodness-of-fit was measured by the deviance statistic, and the change in deviance  $F$ -ratio tested (McCullagh & Nelder, 1989; Dobson, 1999) with a 5% significance level. The percentage of deviance explained was also calculated for each model (see Dobson, 1999), in order to estimate the percentage of explained variation. Curvilinear relationships between explanatory and predictor variables were also examined (Austin, 1980) for significant linear ( $y = a + bx$ ), quadratic ( $y = a + bx + cx^2$ ) or cubic ( $y = a + bx + cx^2 + dx^3$ ) components, as well as for the possible explanatory power of independent variable interactions (Margules *et al.*, 1987).

After examining the individual relationships between biodiversity variables and each of the independent explanatory variables, a general model was built using a stepwise procedure. First the linear, quadratic, or cubic component of the variable that had caused the most significant change in deviance was included, then the next most significant component, and so on, until the last statistically significant explanatory variable was included. After each forward inclusion step, the complete model was backward-selected, to remove terms that had become non-significant.

As environmental variables do not usually explain the variation in biodiversity variables completely, the dependent variables were also fitted, stepwise, to a third-degree polynomial of the central latitude and longitude of each locality (trend surface analysis: see Legendre & Legendre, 1998):  $b_1LAT + b_2LON + b_3LAT^2 + b_4LAT \times LON + b_5LON^2 + b_6LAT^3 + b_7LAT^2 \times LON + b_8LAT \times LON^2 + b_9LON^3$ . Latitude and longitude were centred on their respective means prior to

**Table 3** List of observed values for the explanatory variables for the 30 Iberian localities. Mean altitude ( $a_m$ ), maximum altitude ( $A$ ), distance to the Pyrenees ( $Dp$ ), distance to the Strait of Gibraltar ( $Dg$ ), distance to the sea ( $Ds$ ), and altitude range ( $a_r$ ) in metres; annual mean temperature ( $t_m$ ), mean minimum temperature ( $t$ ), mean maximum temperature ( $T$ ), and temperature range ( $t_r$ ) in degrees centigrade; mean annual precipitation ( $P$ ), summer precipitation ( $P_s$ ), and precipitation range ( $P_r$ ) in millimetres; daily hours of sunshine ( $Hs$ ) as a percentage; indexes of thermicity ( $It$ ), mediterraneity ( $Im$ ), and aridity ( $Ia$ ) as in Rivas-Martínez (1987); calcareous ( $Sc$ ), clay ( $Sc$ ), and siliceous ( $Ss$ ) soils; and numbers of bovine ( $Lb$ ) and ovine ( $Lo$ ) livestock in three classes, as given in the text. Locality numbers correspond to those in Fig. 1

Code	Localities	$a_m$	$A$	$Dp$	$Dg$	$Ds$	$t_m$	$t$	$T$	$P$	$P_s$	$Hs$	$It$	$Im$	$Ia$	$a_r$	$t_r$	$P_r$	$Sc$	$Ss$	$Lb$	$Lo$
1	Nava de Francia	1	1	517	514	211	11.3	5.0	23.0	62	134	59	250	6	4	15	18.0	49	1	1	3	3
2	Colmenar Viejo	900	900	332	584	312	12.4	3.0	22.0	46	90	58	129	4	3	0	19.0	46	1	1	3	2
3	Sierra de Alfacar	1	2	636	250	68	11.3	3.0	21.0	79	127	59	302	19	6	30	18.0	80	1	1	3	1
4	Cabo de Gata	10	260	654	352	3	17.8	11.0	24.0	32	25	64	377	25	9	0	13.0	50	3	1	1	2
5	La Hiruela	1	1	290	630	271	10.0	4.0	24.0	58	114	56	170	4	3	0	20.0	53	1	3	1	2
6	El Ventorrillo	1	1	340	584	299	9.6	3.0	22.0	48	97	57	42	3	1	40	19.0	46	1	1	3	2
7	Chiclana de la Frontera	17	17	841	72	5	18.1	10.0	22.0	66	68	66	401	19	4	5	12.0	98	1	3	1	3
8	Pego-Oliva	20	93	378	621	4	17.8	8.0	25.0	42	68	60	390	12	5	10	17.0	49	1	3	1	2
9	Serra de Gràndola	200	252	828	376	20	17.1	10.0	22.0	55	19	66	351	21	4	100	12.0	101	1	3	1	3
10	Valle del Alberche	1	1	384	556	302	10.8	2.6	21.0	44	85	58	160	5	5	650	18.4	45	1	1	3	2
11	Parque Natural de la Font Roja	1	1	412	572	31	13.7	7.0	25.0	41	75	61	271	8	5	652	18.0	40	3	1	1	2
12	Sierra de Onil	1	1	420	558	35	14.4	6.0	24.0	42	75	61	288	9	5	100	18.0	42	3	1	1	2
13	Villafáfila	650	714	390	650	194	12.0	5.0	23.0	64	59	57	176	6	5	50	18.0	100	1	3	1	3
14	Sierra de Salinas	640	699	423	544	48	15.4	5.3	23.0	42	78	61	262	7	7	280	17.7	40	3	1	1	2
15	Sierras Subbéticas	781	1	661	201	79	14.8	6.5	24.0	48	46	60	315	15	4	550	17.5	65	3	1	1	3
16	Sierra de Baza	2	2	606	312	72	10.5	2.0	19.0	89	156	60	321	25	8	1	17.0	85	3	1	1	3
17	Macizo Central de Gredos	2	2	459	484	302	8.4	3.0	20.0	74	119	60	184	6	2	500	17.0	74	1	1	3	2
18	Doñana	10	49	799	134	9	17.8	9.0	23.0	68	97	65	382	20	5	50	14.0	85	1	3	1	2
19	Depresión Guadix-Baza	917	1	605	288	84	14.0	2.7	20.3	84	144	60	284	16	6	350	17.6	81	1	3	1	3
20	Sierra de Urbión	2	2	179	764	148	7.9	4.0	23.9	50	121	52	149	3	3	1	19.9	33	3	1	1	3
21	Picos de Europa	1	2	318	810	44	7.4	6.1	20.2	77	97	49	172	3	2	2	14.1	107	3	1	1	3
22	Sierra Nevada	2	3	659	250	35	9.9	3.4	21.6	74	115	59	296	18	5	2	18.2	76	1	1	3	1
23	Vizcaya	303	1	861	918	20	12.3	7.8	23.3	104	198	44	269	2	2	856	15.5	98	3	1	1	2
24	Almería	607	3	611	331	31	18.4	5.9	21.8	59	92	62	345	22	8	2	15.9	64	1	2	1	2
25	Navarra	1	2	58	878	83	9.4	6.0	22.5	67	110	48	228	3	3	2	16.5	77	1	3	1	3
26	Cordillera Cantábrica	1	2	360	803	54	8.1	6.2	21.1	85	119	49	182	3	2	1	14.9	108	1	1	3	2
27	Salamanca	842	2	472	550	226	7.8	3.9	21.8	61	96	58	204	6	4	900	17.9	66	1	2	2	3
28	Albacete	912	2	431	460	139	13.9	3.8	22.1	46	82	61	256	8	6	2	18.3	45	2	2	1	3
29	León	917	2	384	751	103	9.3	5.1	21.4	79	106	53	171	4	3	1	16.3	106	1	2	2	3
30	Cáceres	505	2	553	433	247	15.1	6.9	23.5	60	80	62	277	9	3	1	16.6	70	1	1	3	3

backward-selecting the nine terms of the equation, to remove the non-significant spatial terms. As spatial structure can indicate the relevance of historical, biotic, or environmental variables not otherwise taken into consideration (Legendre & Legendre, 1998), the residuals of the regression analysis between explanatory and biodiversity variables were also submitted to a trend surface analysis and mapped in order to identify which factors had not been considered.

To compare the contribution of each type of explanatory variable, the percentage of deviance explained by each of the possible  $2^k$  functions was calculated, and the weight of each group of independent variables estimated as the average effect of including this type of variable in all possible models built with the remaining variables (MacNally, 2000, 2002).

The correlation between variables was examined using a nonparametric Spearman rank correlation test, and the significance level corrected according to the number of pairwise comparisons (Siegel & Castellan, 1988). All the analyses were carried out using *Statistica* (Statsoft, 2001).

## RESULTS

### The biodiversity variables

As most of the 12 biodiversity variables considered are significantly correlated (Table 4), the biological diversity of Iberian Aphodiinae could be represented by fewer variables. PCA revealed that only three factors or BI explain almost 92% of the total variability in these variables (Table 5, Fig. 2). BI1 alone accounts for almost two-thirds of the variability. Its scores relate positively to the number of widely distributed species (Wd), frequent (Fr) or abundant (Ab) species, species present in North Africa, Europe and the Iberian Peninsula (AEI species), and with species richness (S) and phylogenetic diversity (PD) (Table 5, Fig. 2). BI2 correlates positively with the number of infrequent species (Infr) and of species

restricted to North Africa and the Iberian Peninsula (AI species) (Table 5, Fig. 2). Finally, BI3 correlates positively with the number of Iberian endemic species (Ed), less abundant species (LAb), European-distribution species (EI species), and the number of species restricted to the Iberian Peninsula (I species).

### Species–area relationships

The  $z$  parameters obtained from the species–area relationships for the 12 original biodiversity variables differ. They are low for the variables positively correlated with BI1, non-significant in the case of the variables correlated with BI2, and significantly higher for the variables correlated with BI3 (Table 6). Variables associated with BI1 seem to be characterized by a small increase in species number with area, and the general presence of higher local species richness scores represented by the  $c$  value (Rosenzweig, 1995). The number of demographically rare and endemic species related to BI3 seems to increase more quickly with increased area, suggesting that these types of species can make important contributions to the spatial turnover of these assemblages (see Lobo & Martín-Piera, 1999). The biodiversity variables related to BI2 do not figure in a significant species–area relationship.

The percentage of explained variability for biodiversity variables ranges from 19% to 36% (Table 6), and the residuals of their variability not due to area effects were retained for subsequent analysis.

### The Iberian distribution of Aphodiinae biodiversity

Maps interpolated by distance-weighted averaging represent the Iberian variation in the residuals of the area relationship with the Iberian biodiversity variables (Fig. 3), and so display the main geographic patterns of the variables influencing Iberian Aphodiinae biodiversity variation. There is a latitudinal

**Table 4** Spearman rank correlation coefficients among all the biodiversity variables considered. Significant correlations are shown in bold after correcting for multiple statistical significance tests on the same data (Bonferroni adjustment) [species richness (S), endemic species (Ed), widely distributed species (Wd), infrequent species (Infr), frequent species (Fr), less abundant species (LAb), abundant species (Ab), species present in North Africa, Europe and the Iberian Peninsula (AEI), species restricted to North Africa and the Iberian Peninsula (AI), species restricted to Europe and the Iberian Peninsula (EI), species restricted to the Iberian Peninsula (I), phylogenetic diversity (PD)]

	S	Ed	Wd	Infr	Fr	LAb	Ab	AEI	AI	EI	I	PD
S	–	<b>0.73</b>	<b>0.99</b>	0.39	<b>0.86</b>	<b>0.76</b>	<b>0.90</b>	<b>0.85</b>	–0.12	<b>0.72</b>	<b>0.75</b>	<b>0.96</b>
Ed		–	<b>0.67</b>	<b>0.56</b>	<b>0.59</b>	<b>0.58</b>	<b>0.73</b>	0.51	0.11	0.47	<b>0.86</b>	<b>0.78</b>
Wd			–	0.39	<b>0.85</b>	<b>0.79</b>	<b>0.89</b>	<b>0.85</b>	–0.13	<b>0.72</b>	<b>0.70</b>	<b>0.94</b>
Infr				–	0.08	0.47	0.39	0.29	0.43	0.01	0.28	0.34
Fr					–	<b>0.69</b>	<b>0.86</b>	<b>0.72</b>	–0.37	<b>0.82</b>	<b>0.80</b>	<b>0.87</b>
LAb						–	<b>0.72</b>	<b>0.58</b>	–0.24	<b>0.62</b>	<b>0.68</b>	<b>0.74</b>
Ab							–	<b>0.82</b>	–0.01	<b>0.62</b>	<b>0.75</b>	<b>0.88</b>
AEI								–	0.13	0.38	0.48	<b>0.81</b>
AI									–	<b>–0.60</b>	–0.25	–0.13
EI										–	<b>0.73</b>	<b>0.70</b>
I											–	<b>0.79</b>
PD												–



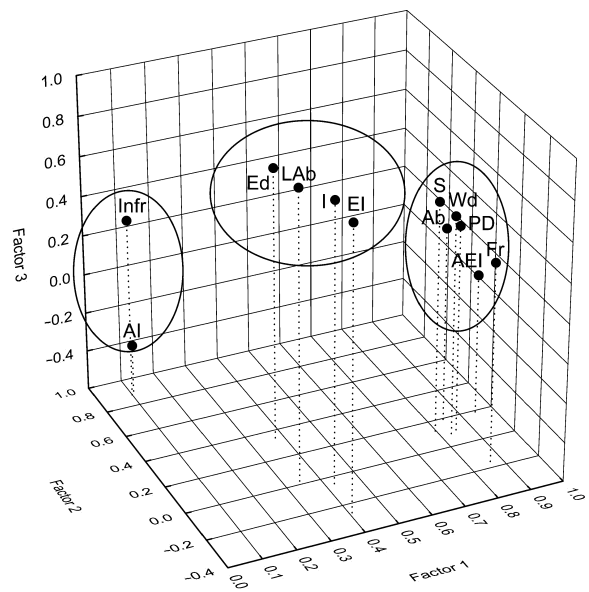
**Table 5** Results of principal components analysis of the 12 biodiversity variables. Factor loadings higher than 0.70 are emboldened. According to the factor loadings, three biodiversity indexes (BI) can be extracted. AEI species: species present in North Africa, Europe and the Iberian Peninsula; AI species: species restricted to North Africa and the Iberian Peninsula; EI species: species restricted to Europe and the Iberian Peninsula; I species: species restricted to the Iberian Peninsula

	Factor loadings			BI
	Factor 1	Factor 2	Factor 3	
AEI species	<b>0.9459</b>	0.1906	0.1129	BI1
Frequent species	<b>0.8648</b>	-0.1599	0.4124	
Phylogenetic diversity	<b>0.8533</b>	0.1023	0.4477	
Abundant species	<b>0.8452</b>	0.1930	0.3865	
Widely distributed species	<b>0.8326</b>	0.0848	0.5132	
Species richness	<b>0.7977</b>	0.1277	0.5726	
AI species	0.1112	<b>0.9037</b>	-0.3565	BI2
Infrequent species	0.0996	<b>0.8833</b>	0.3093	
Less abundant species	0.3459	0.0232	<b>0.8622</b>	BI3
EI species	0.4087	-0.2605	<b>0.8342</b>	
I species	0.4263	-0.0500	<b>0.8145</b>	
Endemic distribution species	0.3762	0.3460	<b>0.7672</b>	
Eigenvalue	7.96	1.97	1.07	
Accumulated eigenvalue	7.96	9.93	11.00	
% Total variance	66.38	16.41	8.88	
% Accumulated variance	66.38	82.78	91.67	

disjunction (north–south) in the pattern of biodiversity variables related to BI1, with maximum scores in the north-western and southern corners, and, to a lesser extent, around the centre of the Iberian Peninsula. Minimum scores occurred at the south-western and eastern boundaries. Scores of the two biodiversity variables related to BI2 reach a maximum throughout the southern Iberian Peninsula, and a minimum in the north-eastern and north-western corners. Finally, the maximum scores of the biodiversity variables related to BI3 occur in the northern Iberian Peninsula, principally in the north-western corner.

**Significant explanatory variables**

BI1 biodiversity variables relate similarly and significantly to some explanatory variables (Table 7). Of the geographic variables, only the distance to the sea is positively and linearly related with these variables, accounting for 17–48% of deviance. Higher scores occur in localities farther from the coast. Topographic and environmental diversity variables are not related to these variables. However, five climate variables (tm, T, It, Ia, and P) are significantly related (Table 7). The first four (tm, T, It, Ia) are negatively related to these biodiversity variables, accounting for mean percentages of total deviance of 40%, 29%, 40% and 41%, respectively. The annual mean precipitation (P) is positively related to these variables, explaining 32% of the deviance. Thus, low diversity-variable scores are associated with increases in temperature, mediter-

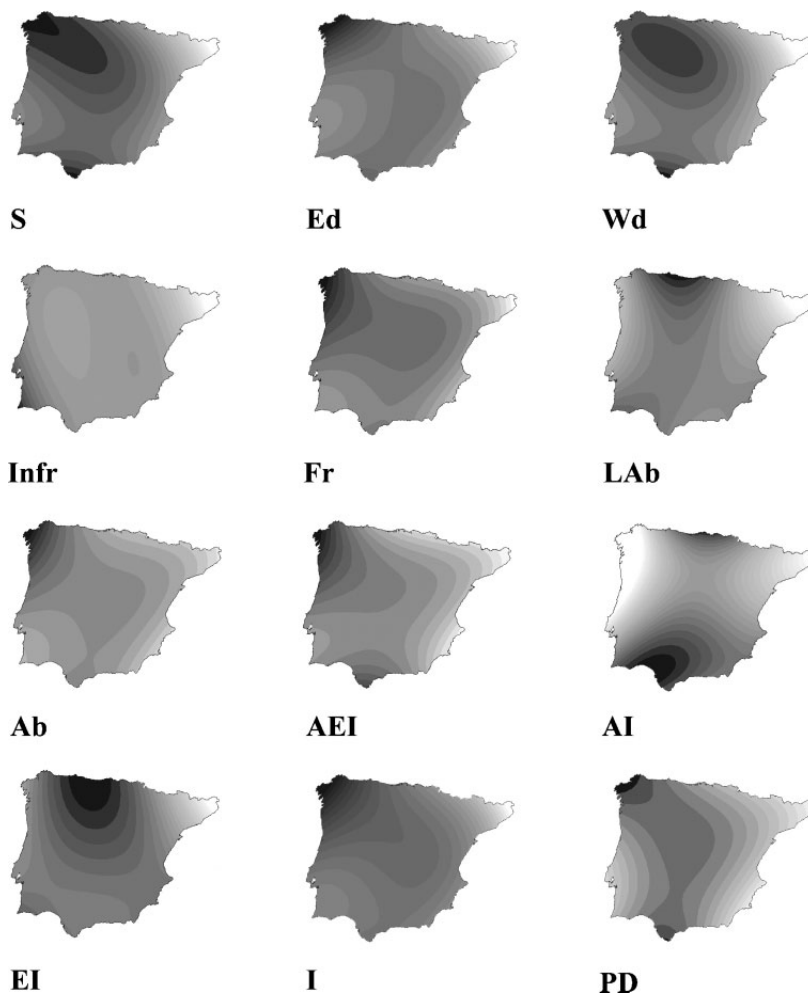


**Figure 2** Factor loadings or factor coordinates that represent the 12 biodiversity variable correlations with the three factor axes (all eigenvalues higher than 1) extracted using principal components analysis. Aphodiinae species richness (S), endemic species (Ed), widely distributed species (Wd), infrequent species (Infr), frequent species (Fr), less abundant species (LAb), abundant species (Ab), species present in North Africa, Europe and the Iberian Peninsula (AEI), species restricted to North Africa and the Iberian Peninsula (AI), species restricted to Europe and the Iberian Peninsula (EI), species restricted to the Iberian Peninsula (I), phylogenetic diversity (PD).

**Table 6** Species–area parameters adjusting each one of the 12 biodiversity variables to the function  $S = cA^z$  through a curvilinear fit (quasi-Newton method). BIs are the new biodiversity indexes extracted using principal components analysis (see Table 5). AEI, AI, EI and I as in Table 2

	<i>c</i>	<i>z</i>	% of explained variance	BI
Abundant species	8.55	0.03	19.14	BI1
AEI species	10.70	0.05	19.11	
Frequent species	10.00	0.06	15.83	
Phylogenetic diversity	43.83	0.06	30.53	
Species richness	15.58	0.09	35.96	
Widely distributed species	14.30	0.09	34.84	
Infrequent species	–	–	–	BI2
AI species	–	–	–	
Endemic distribution species	1.17	0.12	23.74	BI3
EI species	3.18	0.15	29.78	
I species	0.64	0.15	20.18	
Less abundant species	0.62	0.20	25.41	

raneity and aridity, and high diversity scores occur with an increase in mean precipitation (Fig. 4). Among the lithology variables, the linear components of calcareous and siliceous soils are significantly related to BI1 biodiversity variables



**Figure 3** Iberian distribution patterns of the 12 Aphodiinae biodiversity variables obtained by distance-weighted average interpolation, taking into account the residuals of the relationship between the scores of each biodiversity variable and the area, or the data of the biological variable when the relationship with the area was not significant (number of infrequent and AI species; see Table 6). The darker curves correspond to higher residual values (or higher values for infrequent and AI species richness), and the lighter curves correspond to lower residual values (or lower values for infrequent and AI species richness).

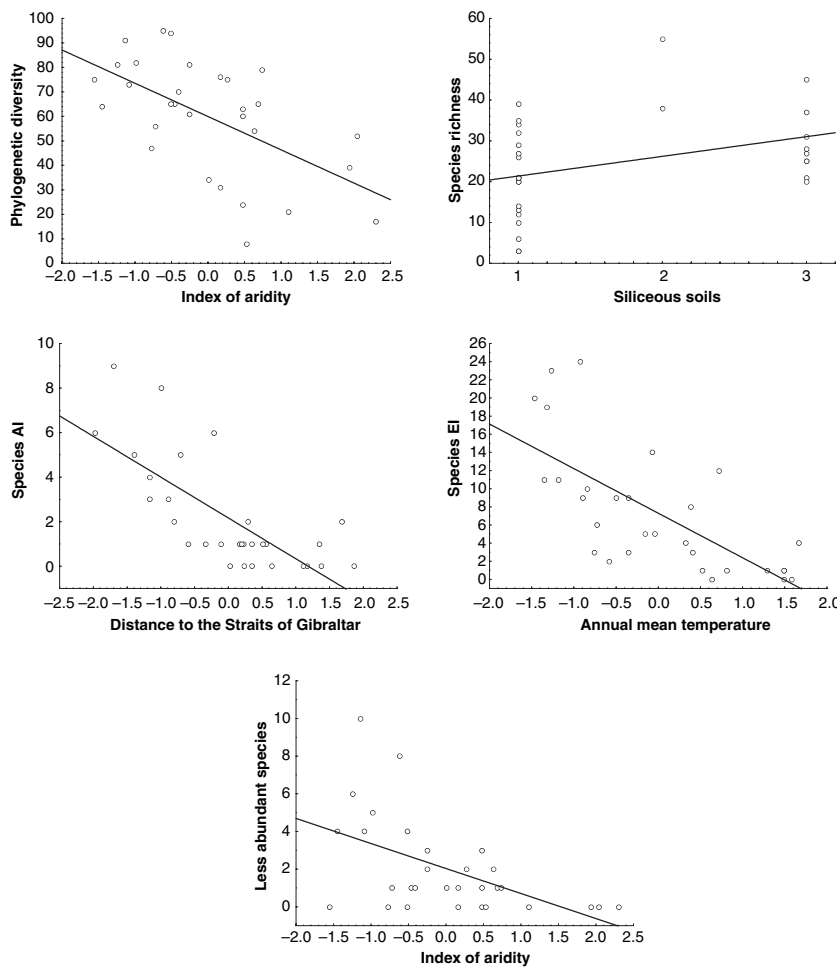
(Table 7), accounting for around 14–34% and 22–36% of the total deviance, respectively. The BI1 variable scores are inversely related to the proportion of calcareous soils, and positively related to the proportion of siliceous soils (Fig. 4). Of the livestock-presence variables, the number of bovine livestock is positively and significantly related with these biodiversity variables, accounting for 18–28% of the total deviance, with higher scores indicating greater bovine abundance. A backward stepwise analysis of all the above-mentioned significant BI1 biodiversity variables together indicates that only the linear terms of the aridity index and the area of siliceous soils are significant, accounting for between 33% and 73% of the total deviance, depending on the variable considered (Table 8). The success of the third-degree polynomial of latitude and longitude in explaining more than 30% of this function's residual variability would seem to indicate spatial structuring (Table 8). It is likely, therefore, that undetected variables could considerably increase the explanatory power of the models. These variables are likely to be spatially structured, as spatial terms can explain a great deal (between 71% and 80%; Table 8), and when added to environmental variables increase their predictive power substantially. Interpolation of the residuals for the complete

environmental model leads to a description of the general Iberian distribution of these undetected variables (Fig. 5), showing that a greater number of observed species occur in the north-west and south of the Iberian Peninsula, and a smaller number in the extreme north-east.

Of the BI2 biodiversity variables, only the number of species restricted to North Africa and the Iberian Peninsula (AI species) is significantly related to the explanatory variables (Table 7). None of these variables is significantly related to the size of the locality (see Table 6). The geographic variables seem to be especially relevant in explaining the number of AI species. Distance to the Pyrenees accounts for 28% of the deviance, distance to the Strait of Gibraltar, 62% (see Fig. 4), and distance to the sea, 17%, showing that AI species occur in localities far from the Pyrenees, but near the Strait of Gibraltar and the sea. Five climate variables are significantly related to the number of AI species (tm, Hs, It, Im, and Ia) and account for 26%, 31%, 40%, 53%, and 26% of the total deviance, respectively. Thus, more AI species coincide with increased mean temperature, number of hours of sunshine, or aridity. The only other significant variable is the number of ovine livestock, which explained 13% of the total deviance and is positively related to AI species richness.

**Table 7** Statistically significant explanatory variables related to the 12 biodiversity variables (see Table 2). Signs represent the general trend of the relationship, for linear, quadratic and cubic functions (\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$ ). Abbreviations as in Table 2

Explanatory variables	BI1					BI2					BI3				
	AEI	Fr	PD	Ab	Wd	S	AI	Infr	LAb	EI	I	Ed			
<b>Geography</b>															
Distance to the Pyrenees	-	-	-	-	-	-	(+)**	-	-	(-)*	-	-			
Distance to the Strait of Gibraltar	-	-	-	-	-	-	(-)**	-	-	(+)**	-	-			
Distance to the sea coast	(+)*	(+)*	(+)**	(+)**	(+)**	(+)**	(-)*	-	-	(+)*	(+)*	-			
<b>Topography</b>															
Mean altitude	-	-	-	(+)*	-	-	-	-	-	(+)*	(+)**	(+)*			
Maximum altitude	-	-	-	-	-	-	-	-	-	-	-	-			
<b>Environmental diversity</b>															
Altitude range	-	-	-	-	-	-	-	-	-	-	-	-			
Medium temperature range	-	(+)*	-	-	-	-	-	-	-	-	-	-			
Precipitation range	-	-	-	-	-	-	-	-	(+)*	-	-	-			
<b>Climate</b>															
Annual mean temperature	-	(-)**	(-)**	(-)*	(-)*	(-)**	(+)**	-	(-)**	(-)**	(-)**	(-)*			
Mean minimum temperature	-	(-)**	-	(-)*	-	-	-	-	-	-	(-)*	(-)*			
Mean maximum temperature	(- -)**	-	(- -)**	(-)*	-	-	-	-	-	-	-	-			
Annual mean precipitation	(+ -)**	(+ -)*	(+ -)**	(+ -)**	-	-	-	-	-	-	-	-			
Summer precipitation	-	-	-	-	-	-	-	-	-	-	-	-			
Daily hours of sunshine	-	(- -)**	-	-	-	-	(+)**	-	(-)*	(-)**	(- -)**	-			
Thermicity index	-	(-)**	(-)**	(-)*	(- + +)**	(- + +)**	(+)**	-	(-)*	(-)**	(-)**	-			
Mediterranean index	-	(-)*	-	-	-	-	(+ -)**	-	(-)**	(- +)**	(-)**	-			
Aridity index	-	(-)**	(-)**	(-)*	(-)**	(-)**	(+ -)**	-	(-)**	(- +)**	(-)**	-			
<b>Lithology</b>															
Calcareous soils	(-)**	(-)*	(-)*	(-)*	(-)*	(-)*	-	-	-	-	-	-			
Clay soils	-	-	-	-	-	-	-	-	-	-	-	-			
Siliceous soils	(+ -)**	(+)**	(+)**	(+)**	(+)**	(+)**	-	-	-	(+)*	(+)**	-			
<b>Cattle use</b>															
Bovine	(+)*	(+)*	(+)**	(+)**	(+)**	(+)*	-	-	(+)*	(+)*	-	-			
Ovine	(+)*	-	-	-	-	-	(+)*	-	-	-	-	-			



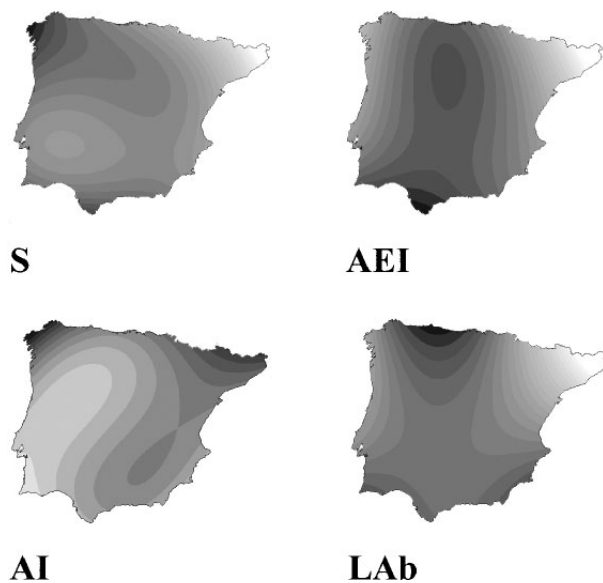
**Figure 4** Relationships between some significant environmental explanatory variables and Aphodiinae biodiversity variables (see Table 7). The effect of area size on biodiversity variables was extracted using the residuals of the relationship between them and the area of each locality. The broken line represents the linear, quadratic or cubic fit of the relationship. Index of aridity as the division of Ps by P (Rivas-Martínez, 1987), no units; siliceous soils in three classes, as given in the text; distance to the Straits of Gibraltar in meters; annual mean temperature in degrees centigrade. Continuous variables were standardized to a mean of 0 and a standard deviation of 1.

**Table 8** *F*-test and percentage of explained deviance (% Dev) of the third-degree polynomial of latitude and longitude (trend surface analysis, TSA) for the residuals from the area and biodiversity variables, and for the model residuals with the explanatory variables considered (complete environmental model). The last column shows the supplementary explanatory capacity of the spatial terms (TSA) on the full environmental model (\**P* ≤ 0.05; \*\**P* ≤ 0.01; \*\*\**P* ≤ 0.001). AEI, AI, EI and I as in Table 2

Biodiversity variables	Full spatial model			Full environmental model (% Dev)	Added spatial variability (% Dev)
	Selected terms	<i>F</i>	% Dev		
BI1 AEI species	Lon + Lon <sup>2</sup> + Lat + Lat <sup>3</sup> + Lon*Lat <sup>2</sup>	77.71***	79.53	33.65	57.93
Frequent species	Lon <sup>2</sup> + Lon <sup>3</sup> + Lat + Lat <sup>2</sup> + Lon*Lat <sup>2</sup>	1.20***	77.04	73.71	34.07
Phylogenetic Diversity	Lon + Lon <sup>2</sup> + Lat <sup>2</sup> + Lon*Lat + Lon*Lat <sup>2</sup> + Lon <sup>2</sup> *Lat	94.63***	80.45	52.85	35.61
Abundant species	Lon <sup>2</sup> + Lon <sup>3</sup> + Lat <sup>2</sup> + Lon*Lat <sup>2</sup> + Lon <sup>2</sup> *Lat	50.39***	71.59	54.73	–
Widely distributed species	Lon <sup>2</sup> + Lon <sup>3</sup> + Lat + Lat <sup>3</sup> + Lon*Lat <sup>2</sup>	61.28***	74.27	53.90	35.09
Species richness	Lon + Lon <sup>2</sup> + Lat + Lat <sup>3</sup> + Lon*Lat <sup>2</sup>	69.27***	74.27	43.04	40.73
BI2 AI species	Lat	40.86***	59.34	62.34	–
Infrequent species	Lat <sup>2</sup>	5.42*	16.22	–	16.22
BI3 Less abundant species	Lon + Lon <sup>2</sup> + Lon <sup>3</sup> + Lat <sup>3</sup> + Lon*Lat <sup>2</sup>	39.11***	62.97	29.14	55.52
EI species	Lon <sup>2</sup> + Lat + Lon*Lat + Lon <sup>2</sup> *Lat	60.61***	75.19	72.63	40.48
I species	Lon <sup>2</sup> + Lat + Lon*Lat <sup>2</sup>	16.63***	45.40	35.66	–
Endemic species	Lon <sup>2</sup> + Lon*Lat <sup>2</sup>	16.14***	44.65	17.60	42.06

A backward selection of the above-mentioned significant variables generates a complete model in which the distance to the Strait of Gibraltar remains as the only significant variable

for the AI species. The residuals of this function cannot be explained by spatial variables and, therefore, do not show an undetected spatial pattern (Table 8 and Fig. 5). The quadratic



**Figure 5** Iberian distribution patterns of the residuals of the scores of four Aphodiinae biodiversity variables and the explanatory environmental variables (complete environmental model). These residuals have a spatial structure and can be explained by spatial variables to different degrees (see Table 8). Interpolations were obtained by distance-weighted averaging. Darker and lighter curves correspond to higher and lower residual values, respectively. S: species richness; AEI: species present in North Africa, Europe and the Iberian Peninsula; AI: species restricted to North Africa and the Iberian Peninsula; LAB = less abundant species.

component of latitude is the only variable significantly related to the number of infrequent species (Infr). This suggests that the two BI2 biodiversity variables seem to be related to spatial or geographically related variables.

The BI3 biodiversity variables also show many coincident relationships with the explanatory variables. Geographic variables seem to have some relevance (Table 7): distance to the sea best explains total deviance (around 9%). In general, the highest scores of these variables can be found far from the coast. Mean altitude is the only significant topographic variable (around 4% of total deviance), with more species at higher elevations (Table 7). Four climate variables are significantly related to the BI3 biodiversity variables: *tm*, *Hs*, *It*, and *Ia* (49%, 40%, 52%, and 56% of the total deviance, respectively), with higher scores occurring with lower aridity and temperature, or fewer sunshine hours (Table 7 and Fig. 4). The proportion of siliceous soils (around 13% of total deviance) and the number of bovine livestock (3%) are the other significant variables positively related to BI3 biodiversity variables.

A backward stepwise analysis of all the above-mentioned significant BI3 biodiversity variables together leaves only the mean minimum temperature (*t*) and the aridity index (*Ia*), accounting for 17% to 72% of the deviance of the various biodiversity variables (Table 8). As the residuals of this complete environmental model can generally be explained by

spatial variables, an influential spatial structure remains hidden in these variables. The considerable influence of spatial variables on BI3 variables (from 44% to 75% of total deviance), and the permanence of spatial structure regardless of the introduction of environmental variables suggest that an unknown variable that greatly influences the biodiversity variables remains unaccounted for. Interpolation of the residuals of the complete environmental model (Fig. 5) indicates that a greater number of species occur in the north of the Iberian Peninsula, and a smaller number in the north-eastern corner.

### Relative importance of explanatory variables

As is normal in natural systems, most environmental variables are correlated. This collinearity disguises the causal mechanisms that determine the spatial distribution of biodiversity variables. Hierarchical variance analysis (Table 9) showed that, among the environmental variables, climatic ones had the greatest effect on the Iberian Aphodiinae distribution (contribution between 0% for infrequent species number and 17% for phylogenetic diversity). Climate appears to be a key limiting factor for the more generalist group of species, as they have wider distribution areas or occur frequently in Iberian localities. The considerable influence of these species on species richness or phylogenetic diversity contributes to the explanation of climate-variable influence on the Iberian distribution of these biodiversity variables. In all cases, higher diversity scores are associated with low temperature and high precipitation (Table 7).

Although less important than climate variables, lithology and livestock presence can occasionally be influential (Table 9). All BI1 biodiversity variables are related to these variables (contributions between 3% and 12%, and 3% and 8%, respectively), and the correlation scores are always positive: species richness increases with increased proportion of siliceous soils and bovine livestock abundance (Table 7). On the other hand, environmental diversity and topographic variables, the least relevant environmental variables (Table 9), exert only a minor influence on BI3 biodiversity variables, characterized by the presence of endemic and Iberian species. Interestingly, geographic variables seem to be relatively important in explaining species richness, but their effect, although regular, is low for BI1 biodiversity variables (between 3% and 6%; Table 9). Thus, species richness increases with increased distance to the coast (Table 7). However, geographic variables (especially the distance to the Strait of Gibraltar, Table 7) seem to be particularly influential on the AI distributional pattern of species richness (Table 9). Finally, the effect of geographic variables on BI3 biodiversity variables seems to be more important (between 8% and 10%; Table 9); generally, more species occur farther from the coast and nearer to the Pyrenean mountains (Table 7).

The effect of geographic variables is probably linked to spatial issues (Table 9). A high proportion of variation, in nearly all the biodiversity variables considered, can be

**Table 9** Average percentage of explained deviance for each biodiversity variable by independent factors obtained by a hierarchical variance analysis. The confidence interval is set at 0.05 (in brackets, %). AEI, AI, EI and I as in Table 2

Biodiversity indexes	Biodiversity variables	Geography	Topography	Environmental diversity	Climate	Lithology	Cattle use	Spatial terms
BI1	AEI species	3.75 (1.12–6.37)	–	–	7.91 (3.41–12.41)	6.23 (2.04–10.42)	7.80 (3.82–11.78)	46.64 (41.23–52.05)
	Frequent species	6.29 (4.01–8.57)	3.95 (1.08–6.82)	2.54 (1.38–3.71)	14.78 (11.61–17.96)	3.65 (2.03–5.27)	3.50 (1.79–5.22)	19.78 (16.46–23.10)
	Phylogenetic diversity	3.93 (0.09–7.78)	–	–	16.97 (8.62–25.32)	5.43 (1.38–9.48)	5.34 (1.27–9.41)	38.78 (30.43–47.13)
	Abundant species	4.29 (1.83–6.75)	2.21 (0.66–3.76)	–	1.94 (0.30–3.59)	12.42 (8.16–16.69)	4.43 (2.21–6.65)	29.55 (25.11–33.99)
	Widely distributed species	3.36 (0–6.71)	–	–	15.43 (8.24–22.44)	6.55 (3.20–9.95)	4.70 (1.81–7.64)	39.86 (32.29–47.28)
	Species richness	2.60 (0–5.59)	–	–	11.54 (5.30–17.78)	7.30 (3.54–11.06)	6.20 (3.94–8.46)	42.54 (35.60–49.47)
BI2	AI species	18.21 (0–38.24)	–	–	12.36 (0–30.49)	–	4.00 (0.65–7.35)	17.23 (0–37.01)
	Infrequent species	–	–	–	–	–	–	16.22 (–)
BI3	Less abundant species	–	–	4.19 (0–8.63)	10.97 (2.30–19.65)	–	3.81 (0–9.29)	40.69 (31.18–50.21)
	EI species	10.21 (4.44–15.99)	3.88 (2.31–5.45)	–	3.73 (2.64–4.83)	18.79 (11.91–25.66)	2.30 (0.69–3.92)	25.66 (19.02–32.21)
	I species	8.31 (4.96–11.66)	2.70 (0.22–5.18)	–	9.47 (4.58–14.36)	6.99 (3.02–10.97)	–	18.24 (14.55–21.94)
	Endemic species	–	6.87 (0–16.76)	–	7.00 (0–19.30)	–	–	33.00 (23.73–43.14)

explained by spatial variables, which are the most relevant to the Iberian distribution of Aphodiinae diversity. Spatial variables account for 20–47% of the variability for BI1, c. 16% for BI2, and 18–41% for BI3. As the relevance of these spatial terms is generally unaffected by significant environmental variables (Table 8), one or several important spatially structured explanatory variables have probably not been accounted for, and their effect on the biodiversity variable distribution probably conforms to the pattern displayed in Fig. 5.

## DISCUSSION

Our results demonstrate that the influence of diverse variables on the geographic biodiversity distribution of a species group can be explored by using a few available sources of faunistic information.

Using these limited data, it is possible to create diverse dependent variables that represent geographic biodiversity-attribute variation to delimit some new independent factors that are able to express the primary biodiversity distributional patterns of a group of organisms. In the case of the Iberian Aphodiinae, three biodiversity indexes were delimited. BI1 represents the geographic variation in some of the most common biodiversity variables, namely species richness, phylogenetic diversity, and the numbers of widely distributed, abundant and frequent species. Species richness and phylogenetic diversity are often positively correlated (Williams & Humphries, 1996; Tôrres & Diniz-Filho, 2004), and the numbers of abundant and widely distributed generalist species usually contribute strongly to variation in species richness (Lennon *et al.*, 2004; Vázquez & Gaston, 2004). This first biodiversity index seems to conform to the main pattern of Aphodiinae biodiversity variation throughout the Iberian Peninsula, characterized principally by the presence of the most common and widely distributed species. Whereas the other two biodiversity indexes are related to Iberian and North African species richness, and the number of Iberian endemic species, a significant fraction of Aphodiinae Iberian biodiversity results from rare species with both southern and northern distribution patterns.

### Environment–biodiversity relationships

Climate factors seem to be especially relevant for BI1 and BI3, with aridity, thermicity, and mean temperature explaining most of their variability. As in the case of other small insects, the relevance of these temperature-related factors is based on the lack of physiological temperature control mechanisms (Heinrich, 1993). Landin (1961) has suggested that higher-temperature localities would generally be inhospitable for most Aphodiinae species. However, for the North African group of Iberian Aphodiinae species, the number of species increases positively with aridity, mean temperature, and hours of sunlight. This pattern has also been observed for the Mediterranean Scarabaeidae (Lobo *et al.*, 2002; Lobo & Martín-Piera,

2002). In general, the climate and geographic patterns of Scarabaeidae and Aphodiinae do not overlap. Scarabaeidae species, adapted to higher temperatures, occur in southern and lowland localities, while Aphodiinae species, adapted to lower temperatures, occur in northern and high-mountain assemblages (Hanski & Cambefort, 1991b; Hanski, 1991; Lumaret & Kirk, 1991; Jay-Robert *et al.*, 1997; Lobo & Martín-Piera, 1999; Lobo & Halffter, 2000). A similar turnover also seems to occur within the Iberian Aphodiinae. Preliminary phylogenetic analyses (Cabrero-Sañudo, 2004) suggest that these general climate adaptations could be reflected in phylogeny (the first branches of Aphodiinae genera are generally those adapted to colder environments).

Surprisingly, precipitation does not seem especially relevant to Iberian Aphodiinae species patterns. Only some BI1 biodiversity variables are curvilinearly related to total annual precipitation (more species with intermediate rainfall scores), while summer precipitation is not significantly related to any of the diversity variables. The lifestyle of Aphodiinae larvae and their ability to exploit Scarabaeidae dung beetle nests under most arid conditions (Sánchez-Piñero, 1994) could be decisive factors in making Aphodiinae species independent of regional hydrological processes.

As with the Scarabaeidae (Lobo *et al.*, 2002; Lobo & Martín-Piera, 2002) and French Aphodiinae (Lobo *et al.*, 2004), topographical variables are not especially important descriptors of the diversity of Iberian Aphodiinae. The number of Aphodiinae species neither varies with altitude nor increases in the west Palaearctic region, as a result of the gradual compositional turnover of species adapted to higher and lower temperatures (Jay-Robert *et al.*, 1997). Thus, BI1 biodiversity variables are not influenced by altitude, owing to the mixture of species with different climate adaptations present in the diverse Iberian Aphodiinae assemblages. However, the endemic or Iberian species with a northern distribution pattern (BI3 biodiversity variables) seem to be uniquely influenced by mean altitude, with more species in this category occurring at higher elevations. As in other European regions (Balletto, 1995), the numbers of endemic species of Iberian taxonomic groups are highest in mountain areas (Martín *et al.*, 2000; Baquero & Tellería, 2001; García-Barros *et al.*, 2002). This pattern has been associated with the demonstrated role of the Iberian Peninsula as a refuge during Pleistocene climate cycles (Bennet *et al.*, 1991; Hewitt, 1996; Taberlet *et al.*, 1998; Brewer *et al.*, 2002). In the specific case of the Aphodiinae, some fossil evidence clearly suggests large dispersal distances, a reflection of the flexibility of these species' distributions in response to Pleistocene climate change (Coope & Angus, 1975; Coope, 1979, 1990; Foddari, 1994). Thus, highly environmentally heterogeneous mountainous areas must have been especially important as faunistic corridors and even as refuges for some species (Fjeldså *et al.*, 1999; Jansson, 2003). What happened in the Alps to cause the accumulation of endemic Aphodiinae species (Jay-Robert *et al.*, 1997) could have been repeated in the northern Iberian mountain ranges. This fact would be observed for some typical endemic Aphodiinae

species present high in the Iberian mountains that are phylogenetically closely related to species in northern latitudes (genera *Acrossus* Mulsant, 1842, *Agolius* Mulsant & King, 1870, *Neagolius* W. Koshantschikov, 1912, and *Planolinus* Mulsant & King, 1870). An interesting characteristic of these genera is their apparent placement among the first branching lineages of all Iberian Aphodiinae (Cabrero-Sañudo, 2004). This could suggest that the Aphodiinae, or at least those of the western Palaearctic distribution, are possibly of Laurasic origin, although more phylogenetic studies would be necessary to confirm this.

Lithology variables are relatively important to the distribution of Aphodiinae species. Both BI1 and BI3 biodiversity variables are positively related to the proportion of siliceous soils, while calcareous soils do not seem to favour the survival of a large number of Iberian Aphodiinae species. Perhaps larval survival is a result of the greater water retention of siliceous soils, and of the fact that they are colder and less compact when drying (Lumaret, 1983; Hanski & Cambefort, 1991a; Lumaret & Kirk, 1991; Osberg *et al.*, 1994). BI2 biodiversity variables, which are related to southern Iberian species also present in North Africa, are unique in not relating to lithology, perhaps because of the capacity of these species to survive in more extreme or diverse edaphic conditions.

Livestock presence seems to be relevant to the number of species of almost all biodiversity variables, although it does not explain very much. The number of bovine herds is generally positively related to BI1 and BI3 biodiversity variables, while ovine herd number is positively related to BI2. The abundance and biomass of dung beetles depend on the quantity of trophic resources; assemblages that inhabit localities with bovine livestock are richer in species (Lumaret *et al.*, 1992). The available data on Mediterranean Aphodiinae dung preference shows that, in general, these species usually prefer dung with a high moisture content, such as that of bovine origin (Martín-Piera & Lobo, 1996). Unlike Scarabaeidae and Geotrupidae, Aphodiinae usually live and feed inside relatively fresh dung (endocoprids) and need this type of excrement to reproduce. As a result, sheep or goat pellets could be selected less frequently by Aphodiinae because of their rapid drying, which impedes both nidification and feeding. However, Iberian species also present in North Africa are positively influenced by ovine livestock presence; these species seem to be especially adapted to survive in the arid conditions of some southern Iberian localities with calcareous soils, feeding and nesting on small, dehydrated trophic resources (Verdú & Galante, 2002).

### Biogeographical patterns and their significance

Three primary patterns can be deduced from the analyses presented in this paper. The principal pattern brings together the greatest proportion of Aphodiinae diversity, and includes the dominant and more widely distributed species. Maximum scores of the pattern occur in the north-western and southern corners of the Iberian Peninsula, and are related to a

low-temperature and high-rainfall climate, as well as to siliceous soils and the presence of bovine livestock. The second pattern is related to the presence of infrequent species and species present in both North Africa and the Iberian Peninsula, with a distribution restricted to southern Iberian localities near the Strait of Gibraltar in which ovine herds dominate. The third pattern is associated with less abundant and endemic or European high-altitude species in the north-western corner, where a cold climate, siliceous soils and bovine livestock dominate.

Biological diversity can, however, be explained by factors other than environmental variables. Geographic variables, such as distance to the sea, provided a slightly positive influence on both BI1 and BI3 biodiversity variables, which suggests a preference for continental conditions. This general pattern is reversed for the number of species present in both the Iberian Peninsula and North Africa (AI species), for which a geographic variable directly related to latitude (distance to the Pyrenees) accounts for higher variability. Traditionally, distance to the Pyrenees has been considered important in explaining the Iberian Lepidoptera distribution (historically entering from northern latitudes) (Martín & Gurrea, 1990). Similarly, the importance of distance to the Strait of Gibraltar would suggest dispersion from North Africa, or the proximity of southern Pleistocene refuges.

In the case of Iberian Aphodiinae, spatial variables predictive power is very high for almost all the biodiversity variables considered. The relevance of spatial variables is manifest not only in the generally high percentage of variability explained in all the possible combinations of explanatory variables considered (Table 9), but also in the enhancement of their explanatory power when taking climate, topographic, lithology, or livestock-presence variables into consideration (Table 8). This means that the final models obtained from the environmental variables leave an important percentage of variability unexplained and indicates that, even after considering a large number of relevant environmental variables, other factors could improve measures of the influence of geography on the variability of Aphodiinae biodiversity. The relevance of spatial variables indicates that these unaccounted-for factors are spatially structured (Legendre & Legendre, 1998). Unquestionably, other environmental factors could help to explain the variation in the Aphodiinae Iberian biodiversity variables, such as quantity and type of trophic resources (Lumaret *et al.*, 1992; Kadiri *et al.*, 1997), the relative density of rabbits (Verdú & Galante, 2002), or the biotic interactions with other scarabs. In our opinion, however, historical factors would best explain this unknown fraction of biodiversity variation.

### Historical considerations

The biological variables that reflect Aphodiinae biodiversity (such as total species richness or other BI1 variables) are arranged in a disjunct latitudinal pattern that corresponds to two groups of species with different origins and physioclimatic adaptations: an Ibero-European group in the north and

north-west of the peninsula, and a Mediterranean or Ibero-North African group in the south. Such a disjunction also appears in the patterns of the other two groups of biodiversity variables: BI3 distributed in the north or north-western Iberian corner, and BI2 present in the south. High species richness not explained by environmental variables in the north-western Iberian corner could be a result of the role played by this territory as a corridor and a refuge during glacial–interglacial cycles (Taberlet *et al.*, 1998). The Alps would have acted as a barrier to the dispersion of eastern and central European fauna (Hewitt, 2001), blocking access of the northern species to the Iberian Peninsula through the eastern Pyrenees, and so favouring the arrival of species along the French Atlantic coast and through the western Pyrenees (Brewer *et al.*, 2002; Cottrell *et al.*, 2002; Petit *et al.*, 2002a,b; Lobo *et al.*, 2004). Accordingly, if Eurosiberian or European Aphodiinae elements entered the Iberian Peninsula mainly through the western Pyrenees, the Cantabrian mountain range in the north-west would have acted as a corridor and a refuge. Evidence indicates that many western Iberian populations are phylogenetically related to other European populations (Lunt *et al.*, 1998; Branco *et al.*, 2000; Olalde *et al.*, 2002), and that Cantabrian–Atlantic areas have repeatedly acted as a refuge for the European or Eurosiberian species (Hewitt, 2001; Brewer *et al.*, 2002). The current high species richness in the north-western Iberian corner could, therefore, be a consequence of the repeated accumulation of species that would have entered after successive glacial and interglacial periods. For example, species such as *Acrossus carpetanus* (Graëlls, 1847), *Agolius bonvouloiri* (Harold, 1860), *Ammoecius frigidus* Brisout, 1866, and *Neagolius heydeni* (Harold, 1871), among others, are currently present only in the Cantabrian mountain range, some of them reaching the Iberian Central System and the Pyrenees.

To understand the southern pattern of distribution it is necessary to consider both the geographic and historical relationships between North Africa and the south of the Iberian Peninsula. Europe and Africa are now separated by the Strait of Gibraltar (14 km), but exchange of terrestrial animals in the western part of the Mediterranean basin was possible during the Baetic crisis (14–16 Ma), and during the Alboran plate uplift (*c.* 5.6 Ma; Blondel & Aronson, 1999; Krijgsman, 2002; Duggen *et al.*, 2003; Veith *et al.*, 2004). At 5.3 Ma, the Strait of Gibraltar reopened, separating Africa from Europe (Steininger *et al.*, 1985), long before the establishment of the seasonal Mediterranean-type climate, *c.* 3 Ma (Suc, 1984). Since then, the Strait seems to have acted as an insurmountable barrier for various animal groups (Boursot *et al.*, 1985; Filippucci, 1992; Castella *et al.*, 2002; Gantenbein & Largiadèr, 2003), although anthropogenic activity may have led to passive dispersal on occasions (Paulo *et al.*, 2002; Veith *et al.*, 2004). The dispersal of some Aphodiinae taxa coming from Africa would have potentially marooned these taxa on the Iberian Peninsula, generating Iberian endemic species phylogenetically related to North African relatives (e.g. species of the genera *Anomius* Mulsant & King, 1870, *Ahermodontus* Báguena, 1930,



*Erytus* Mulsant & King, 1870, *Nobius* Mulsant & King, 1870, and *Pseudacrossus* Reitter, 1892). In other animal groups, some phylogenetically related species currently show an allopatric distributional pattern between North Africa and the south of the Iberian Peninsula (see also Martín-Piera & Zunino, 1983, 1985; Busack, 1986; Doadrio, 1990; Caputo, 1993; Doadrio *et al.*, 1998; Zardoya & Doadrio, 1998, 1999; Castella *et al.*, 2002; Sanmartín, 2003).

The available data for other taxa (Filippucci, 1992; Castella *et al.*, 2002; Gantenbein & Largiadèr, 2003) and the known dispersal power of Aphodiinae species (Roslin, 2000; Roslin & Koivunen, 2001) suggest that these species are unlikely to have crossed the Strait of Gibraltar under their own power. It is possible, however, that the recent human history that links the Iberian Peninsula to North Africa could have favoured the exchange of Aphodiinae species, as has been confirmed for other animal groups (Paulo *et al.*, 2002; Veith *et al.*, 2004). The Muslim influence over eight centuries is especially interesting, as Muslims introduced bovine, equine and ovine livestock from North Africa (Waterbolk, 1968; Rodríguez-Gallardo *et al.*, 1992; Payne & Hodges, 1997; Cymbron *et al.*, 1999). The comparative importance of ancient and recent historical factors will be elucidated only by future phylogeographic studies.

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## BIOSKETCHES

**Francisco J. Cabrero-Sañudo** obtained his PhD at the Universidad Complutense de Madrid, working at the Museo Nacional de Ciencias Naturales de Madrid (Spain) and using phylogenetic and biogeographical analyses to describe Iberian Aphodiinae diversity. He is interested in the evolutionary biology, biogeography, and ecology of dung beetles (Coleoptera, Scarabaeoidea), especially Aphodiidae. This work formed part of his doctoral research.

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## Corrections

- **Page 1035, 2<sup>nd</sup> column, 3<sup>rd</sup> line:** *Mulsant & King* must be changed to *Mulsant & Rey*
- **Page 1035, 2<sup>nd</sup> column, 4<sup>th</sup>-5<sup>th</sup> lines:** *Mulsant & King* must be changed to *Mulsant & Rey*
- **Page 1036, 2<sup>nd</sup> column, last line:** *Mulsant & King* must be changed to *Mulsant & Rey*
- **Page 1037, 1<sup>st</sup> column, 1<sup>st</sup> line:** *Mulsant & King* must be changed to *Mulsant & Rey*