

The abundances and distributions of molluscs in the southern Iberian Peninsula: A comparison of marine and terrestrial systems

A. Menez^{1,2}, D. A. Fa², J. E. Sánchez-Moyano³, I. García-Asencio³,
J. C. García-Gómez³ and J. Fa⁴

¹ The University of Wales, Cardiff, UK

² The Gibraltar Museum, 18-20 Bomb House Lane, Gibraltar, UK. E-mail: darrenfa@gibnet.gi

³ Laboratorio de Biología Marina, Departamento de Fisiología y Zoología, Facultad de Biología, Universidad de Sevilla, Avda. Reina Mercedes, 6, E-41012, Sevilla, Spain

⁴ Jersey Wildlife Preservation Trust, Jersey, Channel Islands, UK

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ABSTRACT

Molluscs are the second most diverse of all animal phyla, and occur in many habitat types. They are, therefore, a particularly good phylum with which to compare and contrast differences between ecosystems. Mollusc data from a number of sites along the southern coast of the Iberian Peninsula are analysed to study patterns of diversity and distribution using a range of multivariate techniques. Within each site, data are presented from three locations -fully terrestrial, rocky intertidal and soft bottom benthic (10 m and 20 m depths)- all in close proximity. The species are then classified in relation to morphology and size, and analysed at supraspecific levels to elucidate underlying patterns. The observed patterns are briefly discussed, with particular reference to the differential scope and importance of controlling factors in each ecosystem, such as dispersal processes. The results from the systems are compared and discussed in the context of ecological and evolutionary constraints in Mollusca.

Keywords: Terrestrial, intertidal, benthic, system comparisons.

RESUMEN

Abundancia y distribución de moluscos en el sur de la península Ibérica. Una comparación entre los sistemas terrestre y marino

Los moluscos constituyen el segundo filo animal más diverso y se encuentran en muchos tipos de hábitat, por lo que son idóneos para establecer comparaciones entre distintos ecosistemas.

Se han analizado los datos de los moluscos obtenidos en una serie de emplazamientos que cubrían el sur de la península Ibérica para determinar, empleando distintas técnicas multivariantes, los patrones de diversidad y distribución de estos organismos. Los datos se tomaron de ejemplares capturados en lugares del medio terrestre próximos a la línea de costa, de la franja intermareal rocosa y de sedimentos de fondos marinos situados a 10 y 20 m de profundidad. Las especies fueron clasificadas atendiendo a la morfología y el tamaño, y se analizaron a nivel supraespecífico para elucidar los patrones generales, que se discuten aquí, brevemente, con especial énfasis en las diferencias según la importancia de los factores que controlan cada ecosistema, como, por ejemplo, los procesos de dispersión. Los resultados de los distintos sistemas se comparan y discuten en el contexto de las tendencias ecológicas y evolutivas de los moluscos.

Palabras clave: Terrestre, intermareal, bentónico, comparación de sistemas.

INTRODUCTION

The Mollusca is a very old monophyletic lineage, dating from before the Cambrian (Barker, 2001), and is the second most diverse of all animal phyla (Morton, 1967; Russell-Hunter, 1983), occurring in many habitat types (Cain, 1983; Solem, 1984). A major constraint on land molluscs is humidity, and so the highest diversities generally occur in habitats with high humidity levels, although other factors are also important (Sacchi, 1965; Van Bruggen, 1969; Cameron and Redfern, 1976; Pflieger and Chatfield, 1988; Cameron, 1995; Emberton, 1995; Kerney, 1999). The shell, along with physiological and behavioural adaptations, contributes substantially to water conservation (Rollo *et al.*, 1983; Cook, 2001). Shell-less species (e.g., slugs), which have arisen independently on several occasions (Hausdorf, 2001), are more dependent on humidity than shelled species (Runham and Hunter, 1970), but are more mobile and faster (Wiktor, 1984).

The majority of marine species do not have the same humidity constraints that land species have. An exception to this are some intertidal species which are influenced by desiccation and temperature, but have adapted to these factors (Lewis, 1964; Underwood, 1985; Fretter and Graham, 1994). Benthic molluscs are not influenced by desiccation, although other factors, such as substratum type, availability for attachment, and water currents are important (Hartnoll, 1983; Hiscock, 1983; Russell-Hunter, 1983; Stanley, 1988).

Groups that are present in more than one major ecological system provide an opportunity for the comparison of underlying physiological and functional adaptations to environmental constraints. Some groups are extremely diverse within one system, whilst being almost absent in others. An example of this are the Insecta, with the highest diversity of all groups, yet with few truly marine species (Barnes, 1987). Additionally, general trends in ecological data can be examined using taxon groups higher than species (Sale and Guy, 1992; Brown, 1995).

In the present paper we examine molluscs' abundances and distributions in four systems: 1) terrestrial; 2) marine intertidal; 3) marine soft bottom benthic, 10 m; 4) marine soft bottom benthic, 20 m. Data from 20 sites around the southern Iberian Peninsula are analysed. The species are classified by morphology and size, and analysed at

the supraspecific level. The results are compared and briefly discussed in relation to ecological and evolutionary constraints in the Mollusca.

MATERIALS AND METHODS

Twenty sites were sampled around the southern Iberian Peninsula (table I and figure 1) for terrestrial molluscs (following the methodology in Menez, 2001), marine intertidal molluscs (following the methodology in Fa, 1998 and Fa and Fa, 2002), and marine soft bottom benthic molluscs, following the methodology in Fa *et al.*, 2003. Family-level analyses were carried out for 13 sites, and species level analyses were carried out for 20 sites (indicated in table I).

Terrestrial and intertidal specimens (20 sites) were identified to the species level; benthic specimens (13 sites) were identified to family level. Abundances were obtained in the field (intertidal) or in the laboratory after specimen collection (terrestrial and benthic).

Diversity is expressed as the Shannon index (H') (Magurran, 1988) and Pielou's evenness is calculated as: $J' = H' / \ln(s)$. The Shannon index (an in-

Table I. The sites sampled in the study, showing abbreviations used throughout the text and figures. The table indicates sites sampled for species analyses (all sites) and those used for family analyses (13 sites)

Site	Abbreviation	Species analyses	Families analyses
Punta del Estació	EST	*	
Águilas	AGU	*	*
Cabo de Gata	GAT	*	*
El Lance	LAN	*	*
Punta de la Mona	MON	*	*
Malaga	MAL	*	*
Punta de Calaburras	CBR	*	*
Puerto Banús	BAN	*	*
Puerto de la Duquesa	DUQ	*	*
Europa Point	EUR	*	*
Punta del Carnero	CAR	*	*
Tarifa	TAR	*	
Punta Camarinal	CMR	*	
Cabo de Trafalgar	TRF	*	
Cabo Roche	ROC	*	*
Rota	ROT	*	
Punta Umbría	UMB	*	*
Vila Moura	VIL	*	*
Cabo Sao Vicente	VIN	*	
Milfontes	MIL	*	

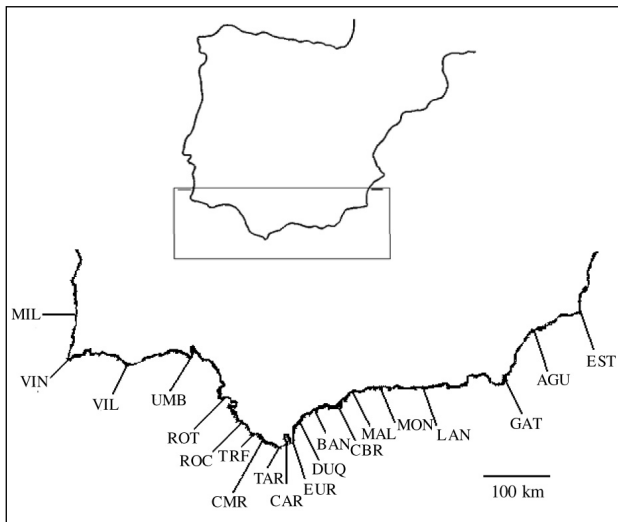


Figure 1. Iberian Peninsula (above) showing extent of 38° latitude (box) and positions of sites along the coast of the southern Iberian Peninsula (below) (see table I for site abbreviations)

formation theory index) was chosen over a dominance index (such as Simpson’s index) because dominance measures are weighted towards the abundances of the most common species. Base 2 logs were used for calculating the Shannon index.

Anova was carried out on the variables from the different systems to compare their means. Fisher’s least significance difference test was used as a post hoc test (at $p = 0.05$) to check for groups that were not significantly different.

Hierarchical agglomerative clustering and non-metric multidimensional scaling (Digby and Kempton, 1987; Clarke and Warwick, 1994; Van Tongeren, 1995) were done using the software package Primer for Windows (Clarke and Warwick, 1994). The data were 4th-root transformed, which retains quantitative information but downplays the species dominants. Cluster groups were assigned dependent on similarity levels on the cluster analyses, and groups on multidimensional scaling were compared to cluster groups (Clarke and Warwick, 1994).

The distances between individuals and their positions in the habitat, as well as size, colour and shell shape, were obtained from field observations and specimen analyses in the laboratory. These data are used to give an indication of species’ tendencies for these variables. In some species, there may be more variation in values than indicated here, where the most frequent observations for the species are used. Slugs are excluded from these analyses (except for

position in the habitat). Species with abundances of less than five from any site are excluded from the distance between individuals analyses, and bivalves are excluded from the shape analyses. For each of these variables, a simple scale is used to score values; these are shown in table II.

Table II. The scales used for scoring distance, position, size, colour and shape. For size, colour and shape, an example of a terrestrial species is given for each score value

Scale for distance between individuals (distance)	
Score	Distance (mm)
1	0 - 5
2	5.1 - 10
3	10.1 - 15
4	15.1 - 20
5	> 20
Scale for position in habitat (position)	
Score	Position
1	Under substratum
2	On ground surface
3	On substratum at < 25 cm height from ground
4	On substratum at > 25 cm height from ground
5	On substratum both at < 25 cm and > 25 cm height from ground
6	On plants at < 25 cm height from ground
7	On plants at > 25 cm height from ground
8	On plants both at < 25 cm and > 25 cm height from ground
Scale for shell size (size)	
Score	Size
1	Minute (e.g. <i>Truncatellina cylindrica</i>)
2	Small (e.g. <i>Ferussacia follicula</i>)
3	Medium (e.g. <i>Theba pisana</i>)
4	Large (e.g. <i>Otala punctata</i>)
Scale for shell colour (colour)	
Score	Colour
1	Colourless (e.g. <i>Ceciloides jani</i>)
2	White (e.g. <i>Helicella stiparum</i>)
3	Brown (e.g. <i>Cantareus aspersus</i>)
4	White-brown (e.g. <i>Otala lactea</i>)
5	Red-brown
6	Green-brown
7	Red-white
8	Blue-black
Scale for shell shape (shape)	
Score	Shape
1	Cylindrical (e.g. <i>Truncatellina cylindrica</i>)
2	Conical (e.g. <i>Cochlicella acuta</i>)
3	Discoidal (e.g. <i>Caracollina lenticula</i>)
4	Spherical (e.g. <i>Cantareus aspersus</i>)
5	Fusiform

RESULTS

The first part of this section deals with family level data from 13 sites (table I). Terrestrial, intertidal, benthic 10 m and benthic 20 m data are analysed. In the second part, species data from 20 sites (terrestrial and intertidal) are analysed.

Family data from 13 sites (terrestrial, intertidal, benthic 10 m, benthic 20 m)

Figure 2 shows the number of families, abundances, Shannon diversity (\log_2), and Pielou's evenness for all sites. Significant differences were found between the systems for number of families, Shannon diversity (\log_2), and Pielou's evenness at $p = 0.001$ or less. Table III shows the results of anova and post-hoc testing. Abundance does not achieve statistical significance for differences between the systems (although it almost does at $p = 0.06$) and is not considered further here. Results of Fisher's least significance difference tests, which identifies which groups in the anova analyses differ, show that the terrestrial and intertidal systems are not significantly different for number of families, Shannon diversity (\log_2) and Pielou's even-

ness. Other system groups are all significantly different from each other.

Families present at more sites have higher abundance than families present at fewer sites, even when we correct for the number of sites at which they occur (by dividing total abundance by number of sites). This applies to all systems (terrestrial: $\rho = 0.645$, $p < 0.001$; intertidal: $\rho = 0.660$, $p = 0.014$; benthic 10 m: $\rho = 0.642$, $p < 0.001$; benthic 20 m: $\rho = 0.768$, $p < 0.001$), see figure 3 for graphs. Most families are represented by low numbers of individuals, although a few families have high numbers of individuals (figure 4).

Figure 5 shows the percentages of abundance for each of the families out of the total abundance, in each of the systems. The number of families in the systems ranges from 13 (intertidal) to 46 (benthic, 20 m), and the number of families representing greater than 1% of the total abundance ranges from 3 (intertidal) to 12 (benthic, 20 m). When the number of families representing greater than 1% of the total abundance are considered as a percentage of the total number of families, for each system, there is no significant difference in number (Kolmogorov-Smirnov $Z = 0.500$, $p = 0.964$).

The numbers of families in each class are shown in table IV. Molluscs are represented in the terrestrial

Table III. Anova results for terrestrial (TER); intertidal (INT); benthic, 10 m (10 m); and benthic, 20 m (20 m) systems. Degrees of freedom (df), mean square, F ratio and significance for the variables, both between groups and within groups, are also shown. Results of post-hoc testing are shown in the lower part of the table. Fisher's least significant difference test is used (at $p = 0.05$) to test for groups that are not significantly different. These groups are shown underlined. Groups that are significantly different are shown in bold, and are not underlined. In each case, the groups are arranged into ascending order of the mean

Parameter	Df	Mean square	F ratio	Significance
N. families (between groups)	3	255.763	36.929	< 0.001
N. families (within groups)	48	7.119		
Abundance (between groups)	3	25 630 589.59	2.600	0.063
Abundance (within groups)	48	9 857 560.19		
Shannon (\log_2) (between groups)	3	8.537	21.134	< 0.001
Shannon (\log_2) (within groups)	48	0.404		
Pielou's evenness (between groups)	3	0.258	6.688	0.001
Pielou's evenness (within groups)	48	0.039		

Number of families	Abundance	Shannon (\log_2)	Pielou's evenness
<u>TER INT</u>	TER INT	<u>TER INT</u>	<u>INT TER</u>
TER 10 m	<u>TER 10 m</u>	TER 10 m	TER 10 m
TER 20 m	<u>TER 20 m</u>	TER 20 m	TER 20 m
INT 10 m	<u>INT 10 m</u>	INT 10 m	INT 10 m
INT 20 m	<u>INT 20 m</u>	INT 20 m	INT 20 m
10 m 20 m	<u>10 m 20 m</u>	10 m 20 m	20 m 10 m

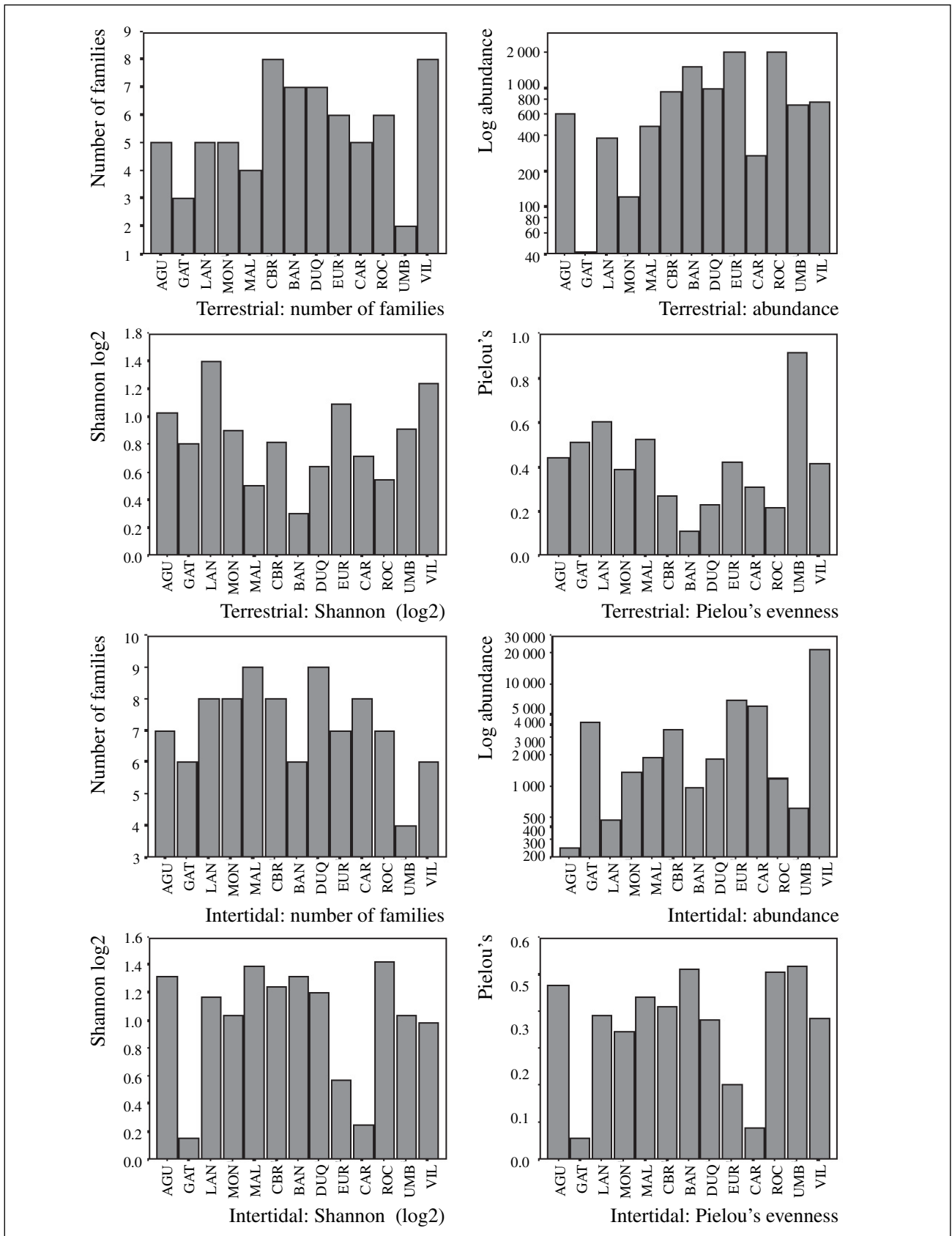


Figure 2. The number of families, total abundances of all families, Shannon diversity and Pielou's evenness, for all systems at all sites (see table I for site abbreviations)

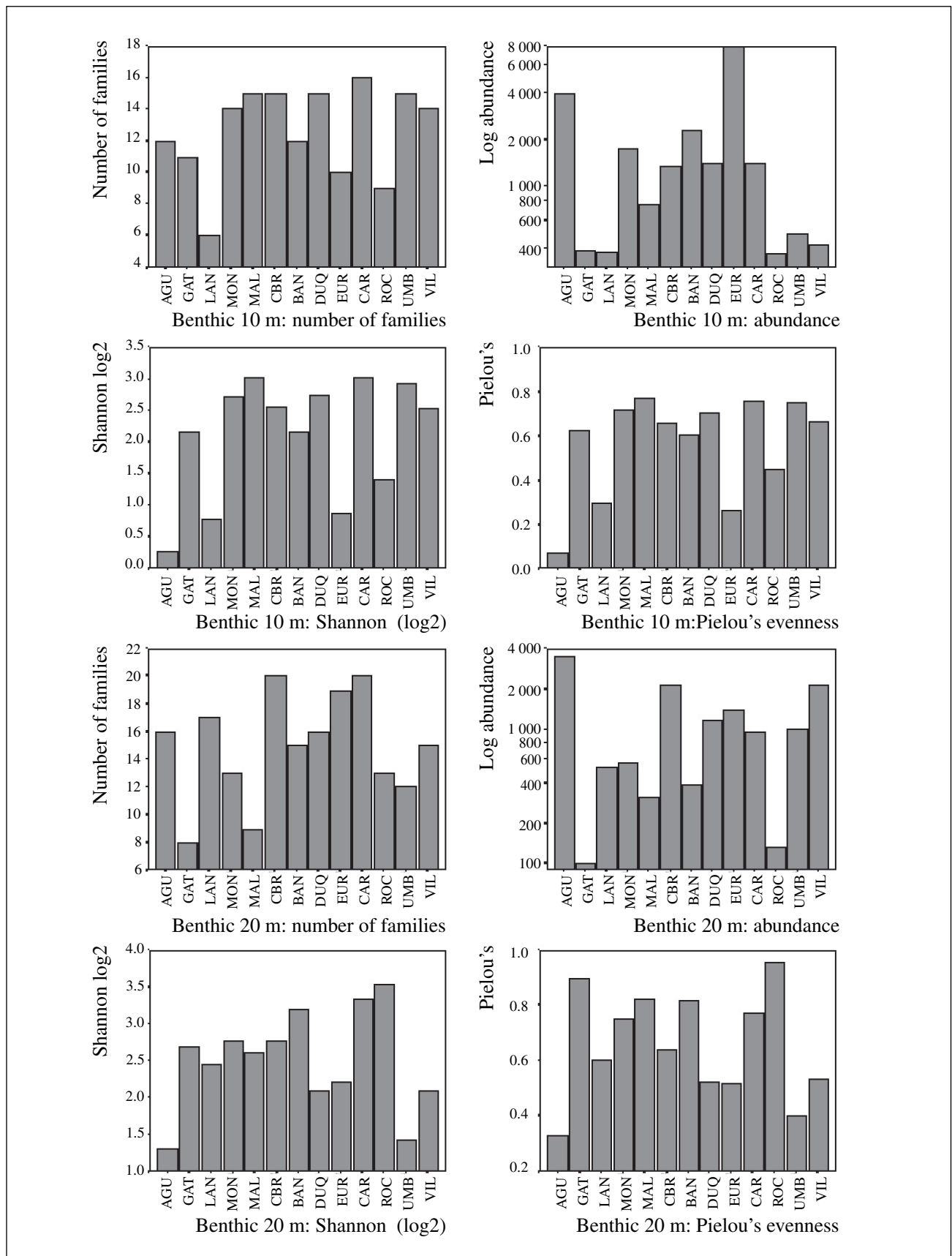


Figure 2 (continuation)

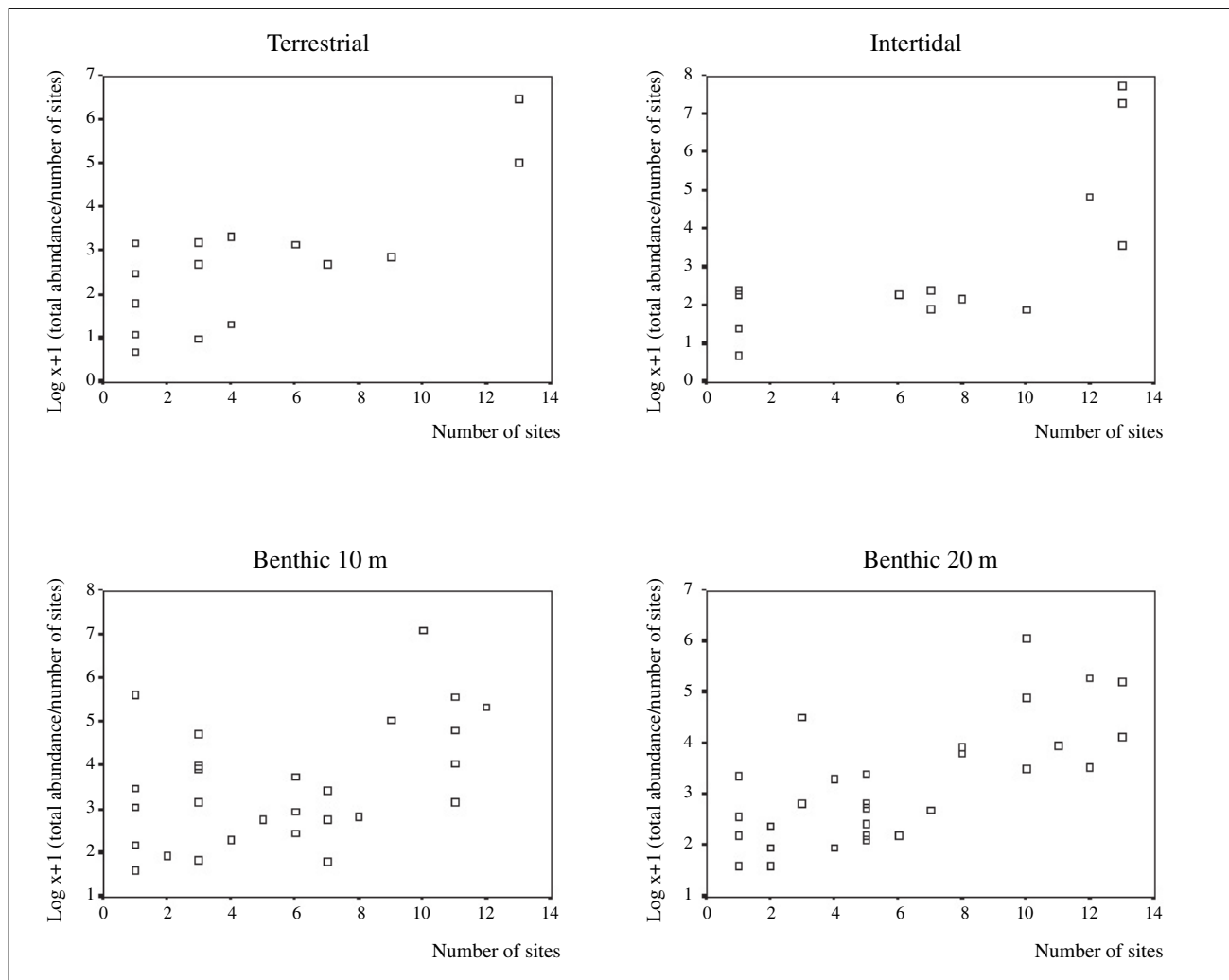


Figure 3. Families present at more sites have higher abundances than families present at fewer sites, even when the number of sites at which they occur is corrected for (terrestrial: $\rho = 0.645$, $p < 0.001$; intertidal: $\rho = 0.660$, $p = 0.014$; benthic 10 m: $\rho = 0.642$, $p < 0.001$; benthic 20 m: $\rho = 0.768$, $p < 0.001$)

Table IV. Numbers of families in each class, total number of families and Bivalve:Gastropod (B:G) ratio for each system

Sites / system	Polyplacophora	Gastropoda	Bivalvia	Total	B:G
20 Sites terrestrial (species)	0	18	0	18	0
20 Sites intertidal (species)	2	13	4	19	0.31
13 Sites terrestrial (families)	0	16	0	16	0
13 Sites intertidal (families)	2	8	3	13	0.38
13 Sites benthic 10 m (families)	0	16	22	38	1.38
13 Sites benthic 20 m (families)	3	15	28	46	1.87

system by gastropods only. The intertidal system has more gastropod families than bivalve families, whereas the opposite is true for both benthic systems; this is clearly indicated by the bivalve:gastropod ratio.

The results of hierarchical clustering and MDS ordination compare well. Figure 6 shows the dendro-

grams and two-dimensional ordinations for all systems. The stress function for all MDS analyses was < 0.2 , indicating acceptable ordinations in two dimensions (Clarke and Warwick, 1994). For the present paper, a new system for illustrating group membership was used (table V) which enabled us to rapidly

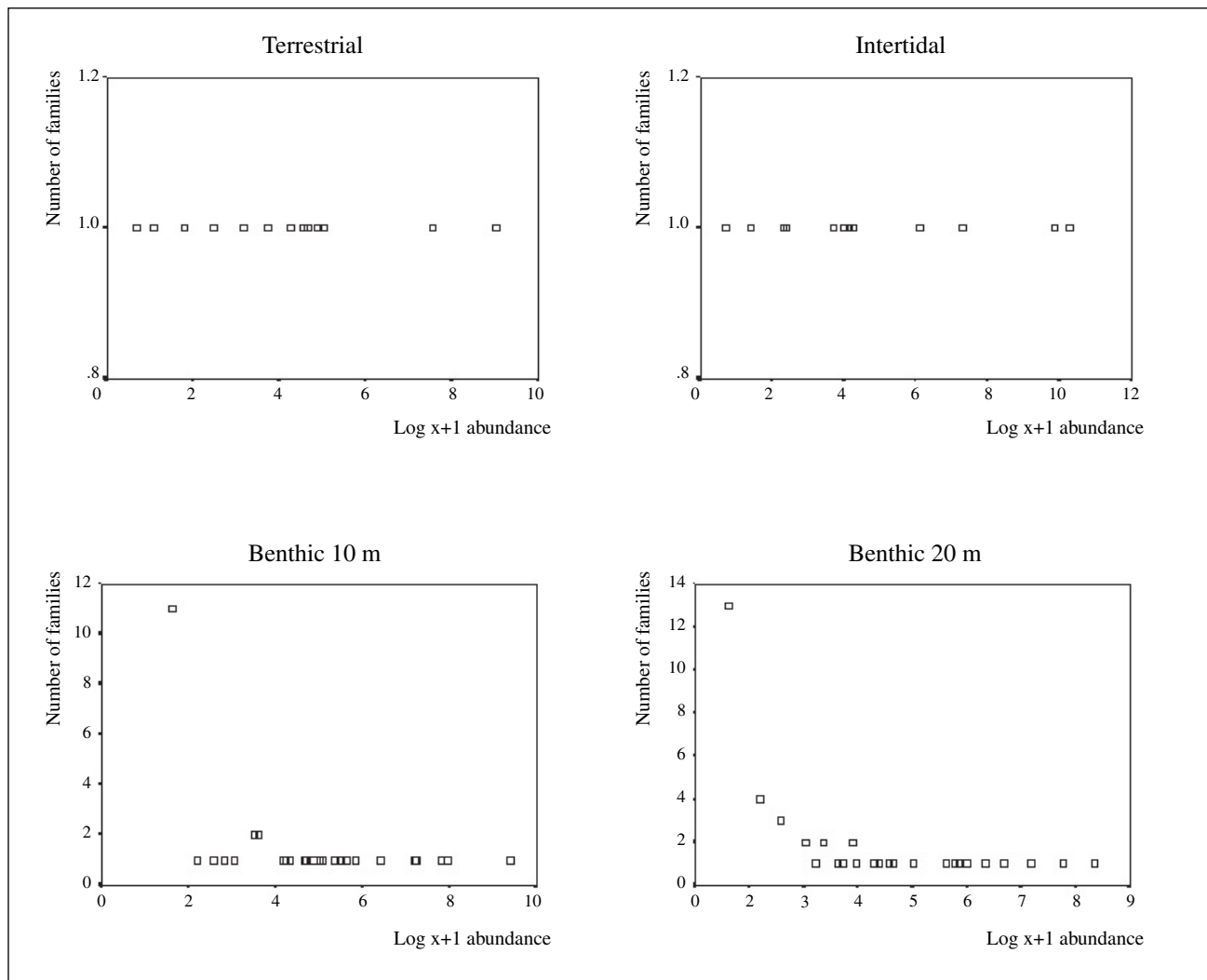


Figure 4. The majority of families are represented by low numbers of individuals, whereas a few families have high numbers of individuals

visualise memberships. For the terrestrial system, there is a weak longitudinal effect, with most site groupings approximating actual site positions on the coast (figure 1). The intertidal system has a major group along most of the east coast between Malaga and Punta del Carnero. Groupings for the two benthic systems differ markedly from each other, suggesting differences in these systems. A large group in the benthic 10 m system approximates the extent of grouping on the east coast for the intertidal system.

Species data from 20 sites (terrestrial and intertidal)

Figure 7 shows the number of species, abundances, Shannon diversity (\log_2) and Pielou's even-

ness for all sites. There were significant differences between the two systems for abundance, Shannon diversity (\log_2) and Pielou's evenness, but not for number of species (table VI).

Species present at more sites have higher abundances than species present at fewer sites, even when we correct for the number of sites at which they occur (by dividing total abundance by number of sites). This applies to both terrestrial and intertidal systems (terrestrial: $\rho = 0.492$, $p < 0.001$; intertidal: $\rho = 0.598$, $p < 0.001$), see figure 8 for graphs. Most species are represented by low numbers of individuals, while a few species have high numbers of individuals (figure 9).

As in the previous section, the results of hierarchical clustering and MDS ordination compare well.

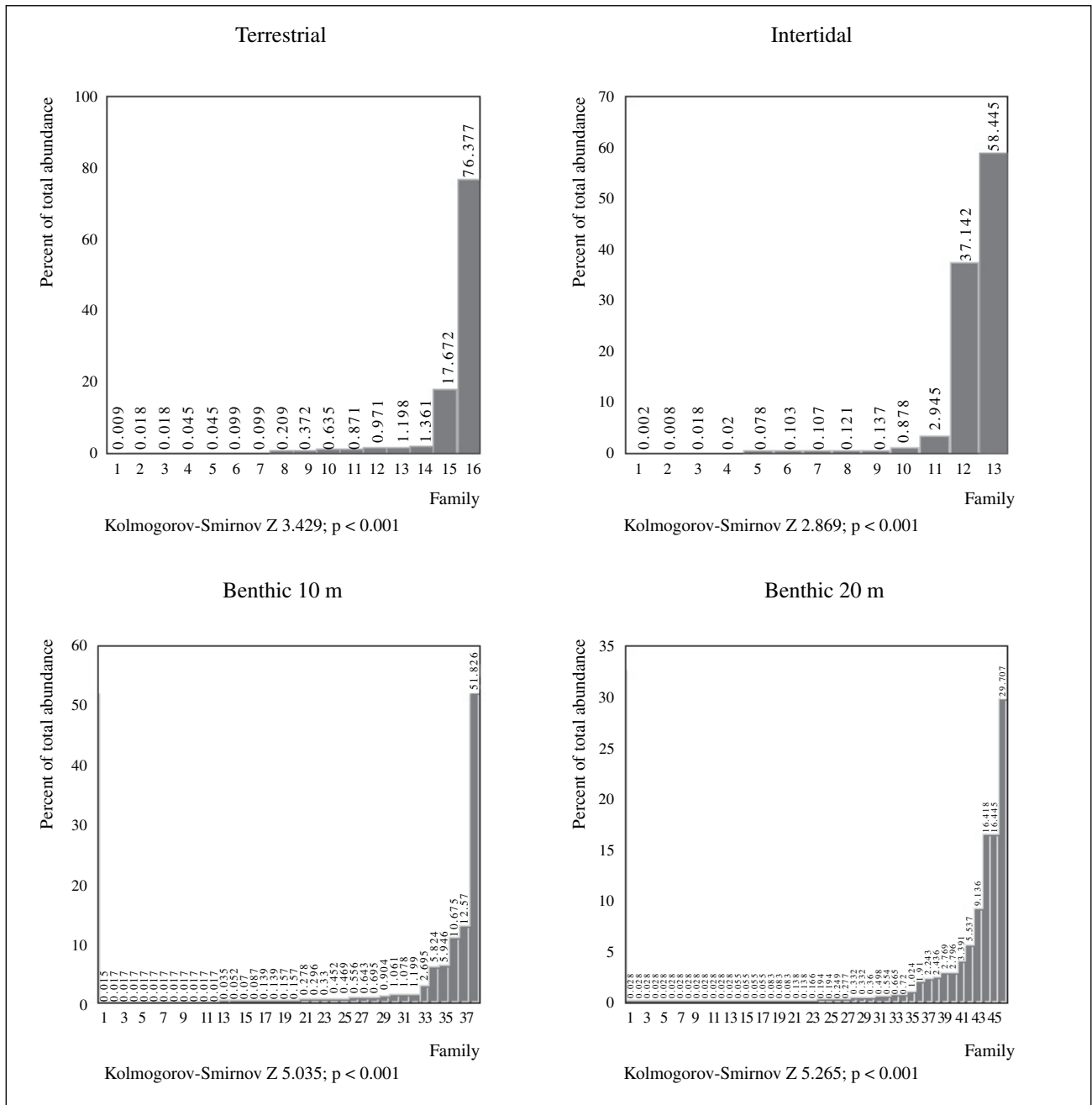


Figure 5. Percentages of abundance that each of the families comprises within the total abundance, in each of the systems (see text for details)

Figure 10 shows the dendrograms and two-dimensional ordinations for the two systems. The stress function for the MDS analyses was < 0.2 , indicating acceptable ordinations in two dimensions (Clarke and Warwick, 1994). The weak longitudinal effect present for the terrestrial system with the family analyses at 13 sites (see previous section) is not present with the species data. One of the groups (group 3, see table VII) includes sites from the east and west

coasts. However there is a marked longitudinal effect for the intertidal system, which is clearly apparent in table VII, where the close site fidelity of coastal positioning in relation to groups obtained from the analyses is represented by the diagonal arrangement of site groupings.

Scoring criteria for distances between individuals, position in habitat, shell size, colour and shape are shown in table II. Data for these variables,

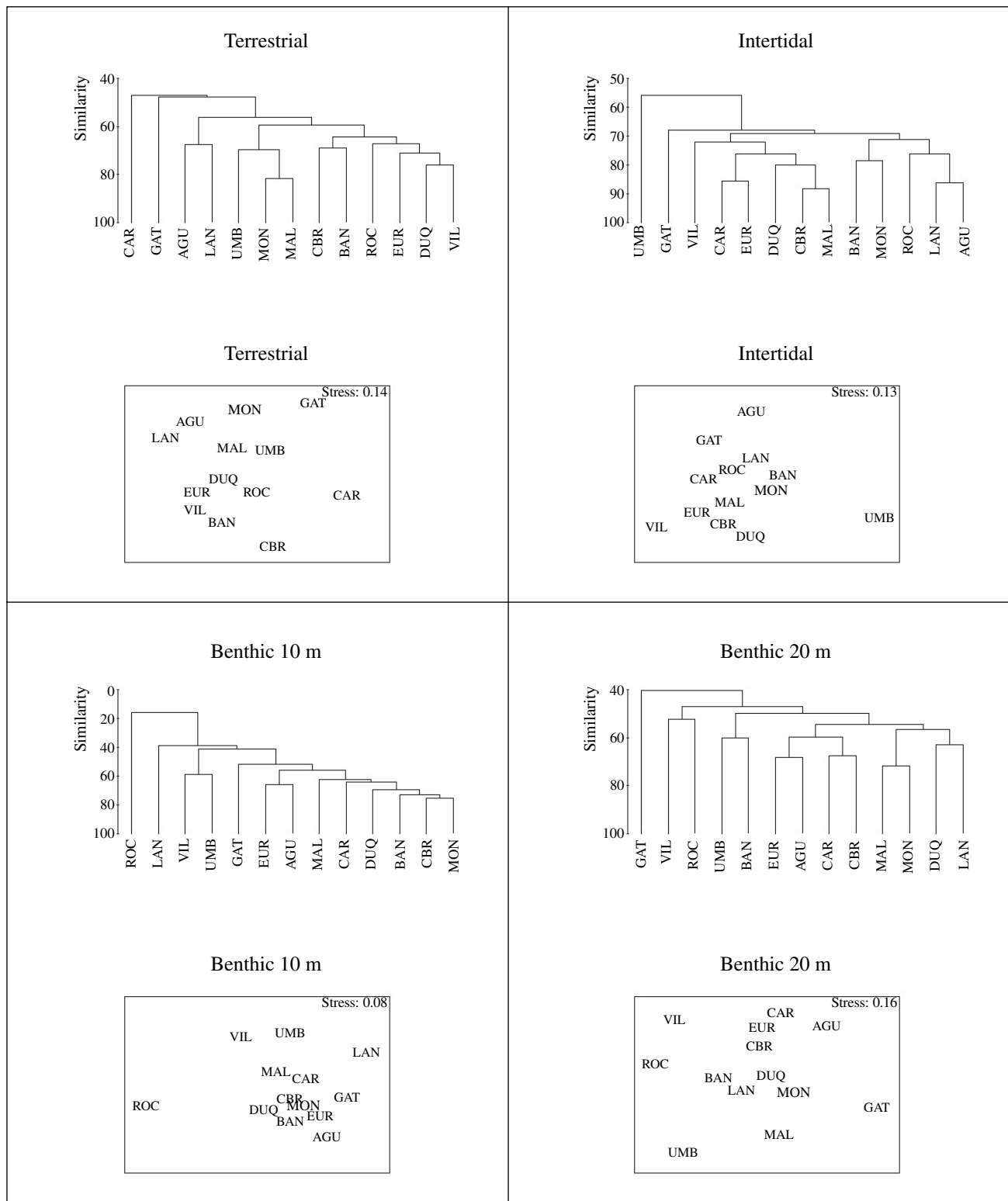


Figure 6. Cluster and MDS plots for all systems (13 sites) (see table I for site abbreviations)

shown in figure 11, indicate that there are general differences between molluscs from the two systems. In the terrestrial system, most species have distances

between individuals of either 0-5 mm or > 20 mm, whereas in the intertidal system most species have distances between individuals of 5-10 mm. The ma-

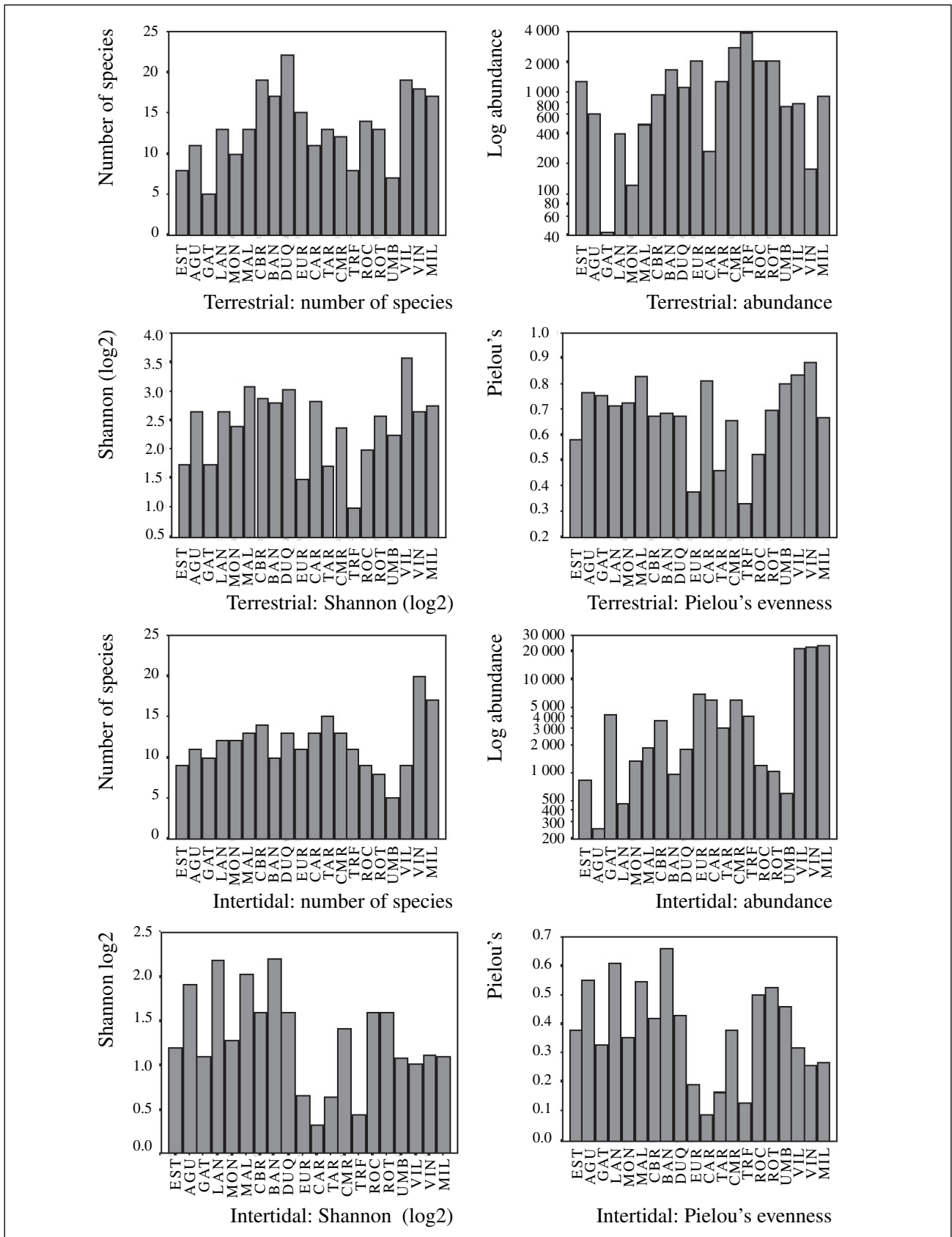


Figure 7. The number of species, total abundances of all species, Shannon diversity and Pielou's evenness, for terrestrial and intertidal systems at all sites (see table I for site abbreviations)

Table V. Summary of hierarchical clustering and MDS ordination of sites for all systems for family data. For each system the number of groups resulting from analyses are shown, with the sites that belong to each group indicated with a solid square. The total number of sites in each of the groups is also shown. The sites are arranged in descending order from the eastern-most site (Águilas) to the western-most site (Vila Moura) (see text for details)

Site	Terrestrial						Intertidal						Benthic 10 m					Benthic 20 m					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	1	2	3	4	5	6
Águilas			■									■					■					■	
Cabo de Gata		■						■								■						■	
El Lance			■									■		■									■
Punta de la Mona				■							■											■	
Malaga				■						■							■					■	
Punta de Calaburras					■					■							■					■	
Puerto Banús					■						■						■				■		
Puerto de la Duquesa						■				■							■					■	
Europa Point						■				■							■					■	
Punta del Carnero	■									■							■					■	
Cabo Roche						■					■			■								■	
Punta Umbría			■					■								■					■		
Vila Moura						■			■						■					■			
Total in group	1	1	2	3	2	4	1	1	1	5	2	3	1	1	2	1	8	1	2	2	4	2	2

Table VI. Anova results for terrestrial and intertidal systems showing degrees of freedom (df), mean square, F ratio and significance for the variables both between groups and within groups. Post hoc testing was not possible because there are only two groups

Parameter	Df	Mean square	F ratio	Significance
N. species (between groups)	1	22.500	1.450	0.236
N. species (within groups)	38	15.513		
Abundance (between groups)	1	199 281 888.1	6.640	0.014
Abundance (within groups)	38	30 010 266.9		
Shannon (log2) (between groups)	1	12.204	35.403	< 0.001
Shannon (log2) (within groups)	38	0.345		
Pielou's evenness (between groups)	1	0.731	27.499	< 0.001
Pielou's evenness (within groups)	38	0.027		

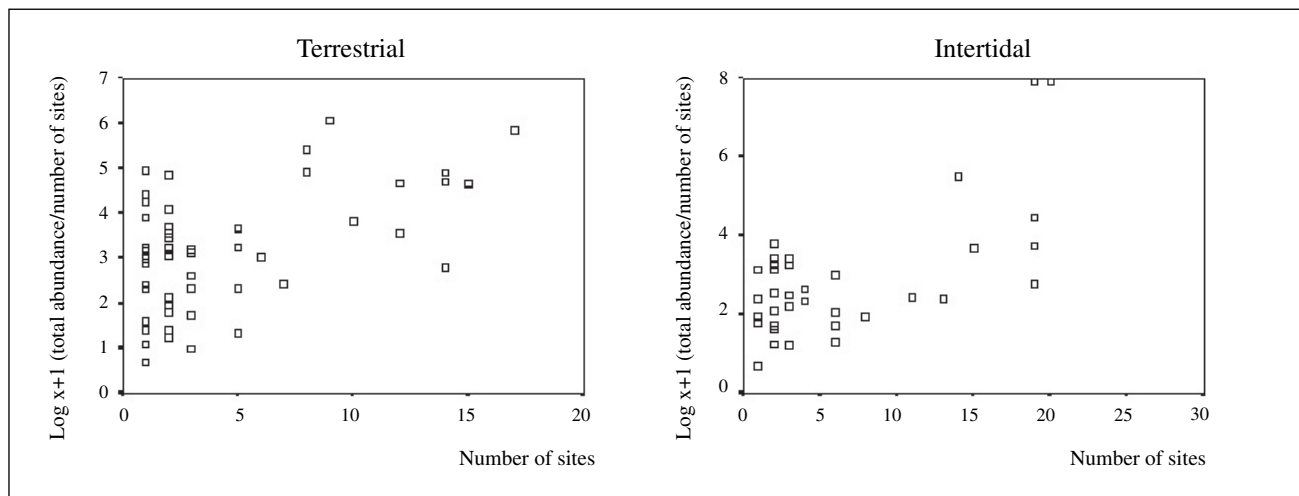


Figure 8. Species present at more sites have higher abundances than species present at fewer sites, even when the number of sites at which they occur is corrected for (terrestrial: $\rho = 0.492$; $p < 0.001$; intertidal: $\rho = 0.598$, $p < 0.001$)

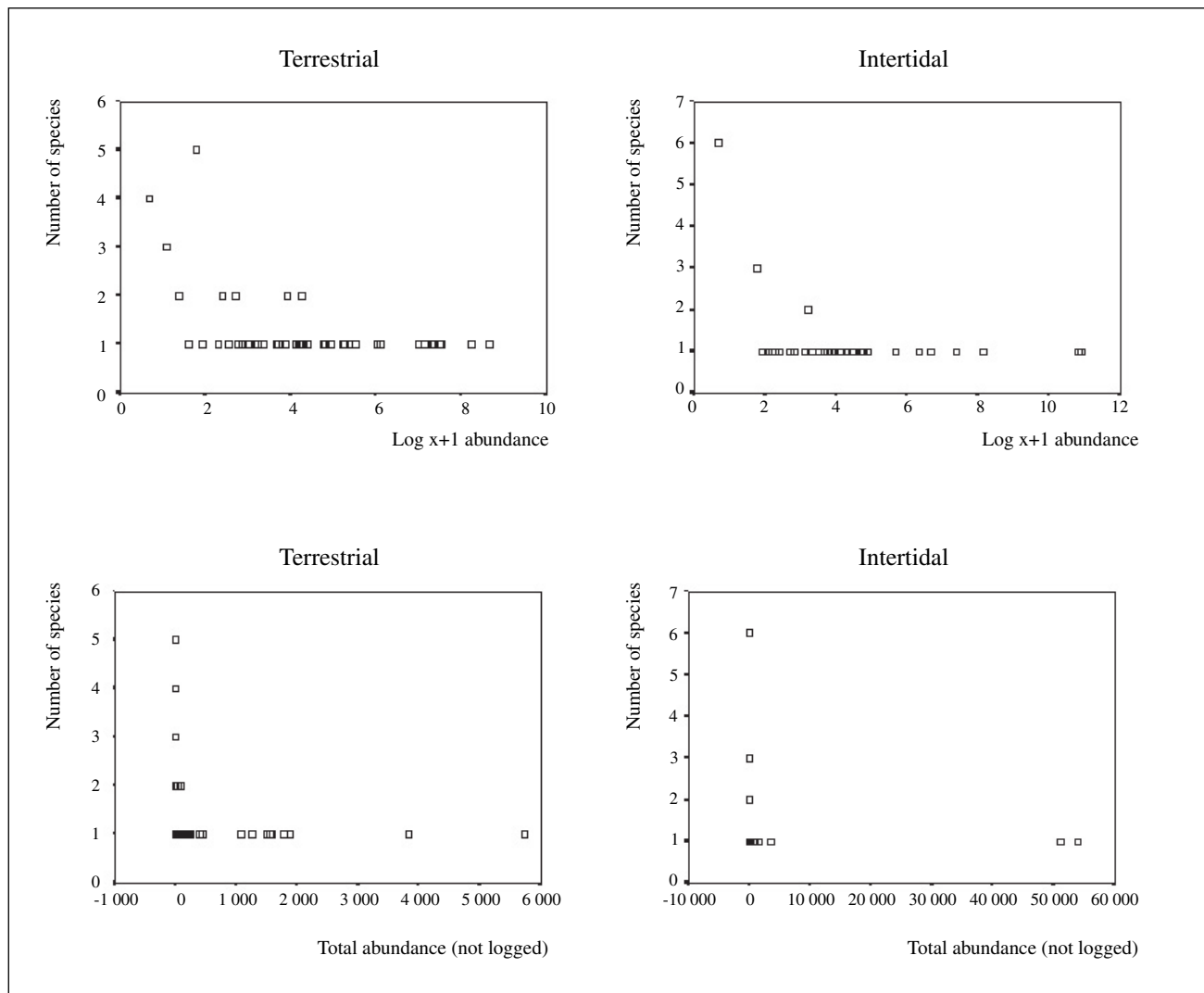


Figure 9. The majority of species are represented by low numbers of individuals, whereas a few species have high numbers of individuals. This is clearly evident in the untransformed total abundances plots

majority of terrestrial species are found either under the substratum, or on the substratum at < 25 cm from the ground; most intertidal species are on the ground surface. Both systems have mostly intermediate sized species, with more minute species in the terrestrial system than in the intertidal system.

The majority of terrestrial species are brown, or white-brown. Most intertidal species are white-brown, but there are other colour combinations, such as red-brown, green-brown, red-white and blue-black, none of which are present in the terrestrial system. The majority of terrestrial species are spherical, whereas the majority of intertidal species are conical. There are cylindrical and discoidal terrestrial species; both of these shapes be-

ing absent in the intertidal system. Fusiform species are only present in the intertidal system.

DISCUSSION

Molluscs living in different places: emergent properties of the systems

The benthic systems may be hypothesized as having less environmental variability (in relation to abiotic factors) and less habitat heterogeneity than the intertidal and terrestrial systems. This may partly explain the higher number of families in the benthic systems, as well as their higher evenness.

Table VII. Summary of hierarchical clustering and MDS ordination of terrestrial and intertidal systems for species data. For each system, the number of groups resulting from analyses are shown, with the sites that belong to each group indicated by a solid square. The total number of sites in each of the groups is also shown. The sites are arranged in descending order, from the easternmost site (Punta Estació) to the westernmost site (Milfontes) (see text for details)

Site	Terrestrial										Intertidal										
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11
Punta del Estació					■																■
Águilas			■																		■
Cabo de Gata	■																				■
El Lance										■											■
Punta de la Mona										■											■
Malaga								■													■
Punta de Calaburras								■													■
Puerto Banús								■													■
Puerto de la Duquesa						■															■
Europa Point				■																	■
Punta del Carnero		■																			■
Tarifa								■						■							■
Punta Camarinal							■									■					■
Cabo Trafalgar									■												■
Cabo Roche						■										■					■
Rota								■								■					■
Punta Umbría			■							■											■
Vila Moura						■															■
Cabo Sao Vicente									■												■
Milfontes			■																		■
Total in group	1	1	3	1	1	3	1	5	2	2	1	3	2	1	1	3	1	2	3	1	2

However, it does not satisfy the conditions of most diversity models, which predict higher diversities at middle to high levels of disturbance and heterogeneity (Hurlbert, 1971; Connell, 1978; Huston, 1979; Hughes, 1984, 1986). The success of the class Bivalvia in the benthic systems may explain these results just as well, or even better. This success is also indicated by the higher ratio of bivalves to gastropods in the two benthic systems.

There are fewer families present in the terrestrial system. Two factors that could possibly account for this are 1) molluscs are represented in terrestrial systems only by the single class Gastropoda (possibly as a result of evolutionary and ecological constraints on molluscan physiology); and 2) more than 75 % of species belong to one family (Hygromiidae).

The families present at a higher number of sites had higher abundances. Species present at a higher number of sites also had higher abundances. This relationship has been reported for many taxa (Brown, 1995). Recent work on Gibraltar subtidal molluscs has also demonstrated such a relationship (Menez, 1996). There are a few families with high abundances, and many families with low abundances. Similarly, there are a few species with high

abundances, and many species with low abundances. This pattern was described by Fisher, Corbet and Williams (1943) and has been reported by others, as well (Williams, 1964; Krebs, 1985; Hughes, 1986; Magurran, 1988). Our findings here, from several systems, substantiate the possibility that these relationships may be underlying trends in many ecological systems.

Of particular interest is our finding that there is no difference in the proportion of families representing more than 1 % of the total abundance, in any of the systems studied. This has many potential explanations, especially because the systems have different numbers of species, families, and even representative classes. The finding may indicate an assembly rule for these systems for molluscs, which may apply to other phyla.

Latitude and longitude can be considered to be surrogate variables for a range of other variables, such as temperature or climatic variables. They have been used in this context in studies of intertidal macrofauna in the area under study here (Fa, 1998). The results from the present study indicate a marked longitudinal effect for the intertidal. This may be indicative of differential structuring

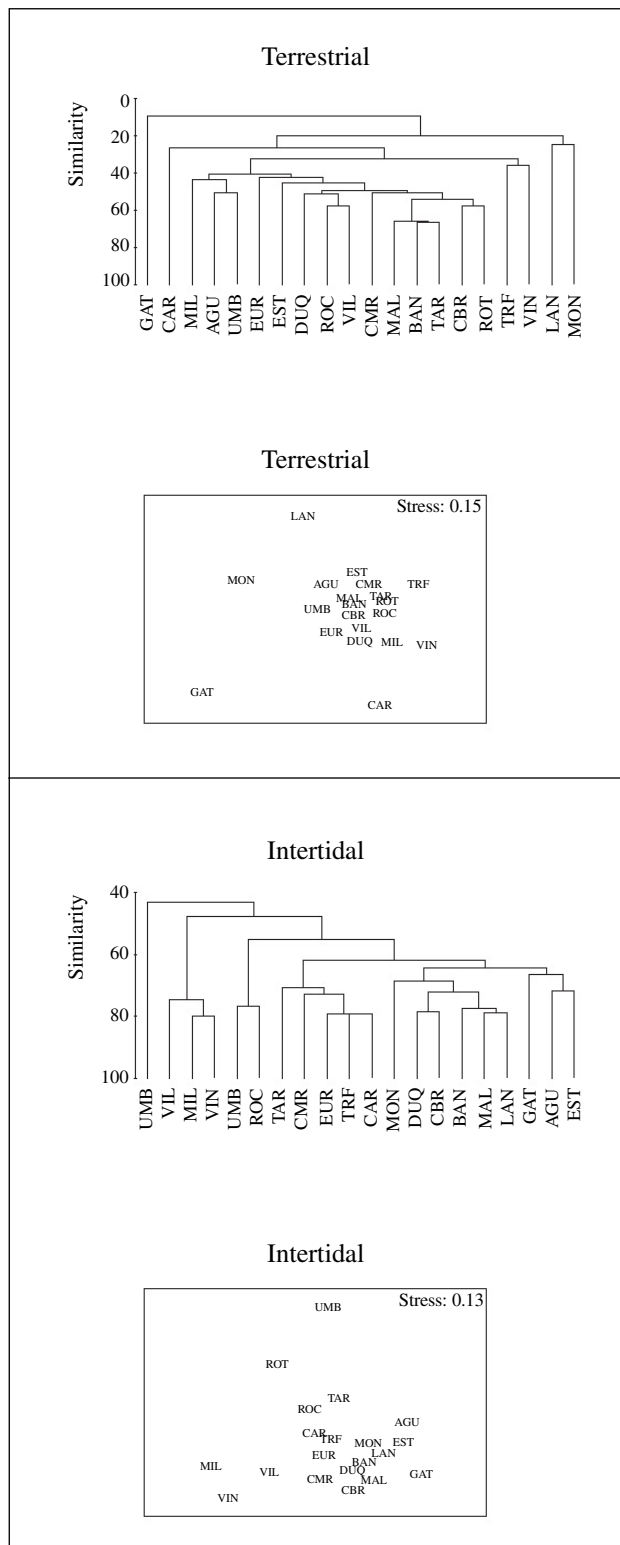


Figure 10. Cluster and MDS plots for terrestrial and intertidal systems (20 sites) (see table I)

Molluscs living in different places: emergent properties of the Mollusca

Molluscs from the intertidal and terrestrial systems (for which data are available from the present study) show differences. Most terrestrial species have distances between individuals of 0-5 mm (closely aggregating species) or > 20 mm, whereas intertidal species mostly have distances of 5-10 mm. A major difference in strategies between closely aggregating molluscs in the two systems is the time period of aggregation. Closely aggregating intertidal species, such as *Mytilus*, generally maintain close proximity throughout the life of the individuals (dependent on removal by wave action and predation, and growth speed). Closely aggregating terrestrial genera, such as *Theba*, tend to maintain closest proximity during prolonged periods of inactivity (in Mediterranean habitats, this is typically 20-25 % of the year). Most terrestrial species are present under substratum or on it at less than 25 cm from the ground. In the more flattened intertidal space, where the vertical element is not as pronounced as in most terrestrial situations, the majority of species are present on the ground surface.

Most terrestrial and intertidal species are of intermediate size, which is in agreement with the pattern originally reported by Hutchinson and MacArthur (1959). May (1978) showed this pattern for beetles, butterflies, birds, and mammals. Lawton (1991) also showed that species of intermediate size are more abundant than others (see also Fenchel, 1993). Some authors have considered the number of species, abundance, and body size as a three-dimensional pattern (Lawton, 1991; Nee and Lawton, 1996; Siemann, Tilman and Haarstad, 1996; Fa and Fa, 2002). The size-species number pattern seems to be widely applicable across many taxa, but there is no consensus regarding its explanation (Rosenzweig, 1995).

Colour in molluscs shells is dependent on many factors, such as dietary components, excretory function, predation pressures and abiotic variables (Morton, 1967; Cain, 1983; Vermeij, 1993; Claassen, 1998). Our terrestrial and intertidal systems both had mollusc that were white-brown, but only the intertidal had species with colours such as red-brown and blue-black. Further research is required to determine which of the above factors may be acting to produce this marked difference in colour schemes. It is interesting to note, however, that many of these

processes in the systems, as well as varying mollusc dispersal strategies and mechanisms.

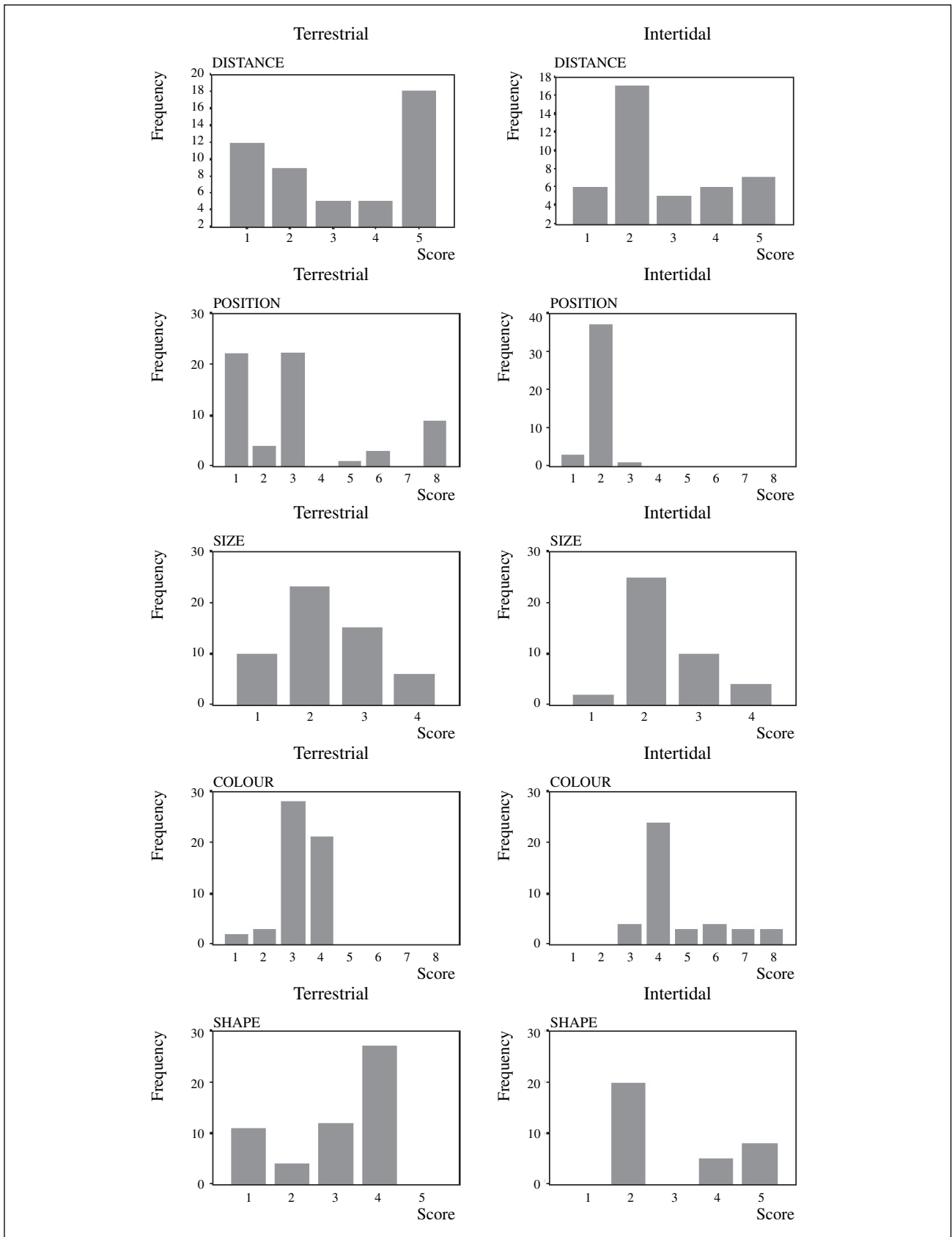


Figure 11. Frequencies for distance between individuals (distance), position in habitat (position), shell size (size), shell colour (colour) and shell shape (shape), for species from all sites (see table II for scale values and text for details)

colour combinations are present in other intertidal taxa (Riedl, 1986).

The diversity of shell shape in molluscs has been reviewed several times in the literature (Vermeij, 1971, 1993; Stanley, 1988), although shapes can be described with a small number of geometric variables (Vermeij, 1993). Morphology has been related to predation, abiotic variables and evolutionary constraints (Currey, 1988; Stanley, 1988; Vermeij, 1982, 1993; Faller-Fritsch and Emson, 1985; Barker, 2001). Cain (1977, 1981) and Cook (1984) considered shell size/shape in groups of taxa in relation to preferred surface angles. Data from the present study show that most terrestrial species are spherical, and that most intertidal species are conical. The spherical shape may represent an optimal shape in relation to apertural area/shell volume as well as surface area/volume ratio (heat exchange relations) in addition to providing increased stability on many surfaces during movement. In the intertidal, where wave action is a prime component of dislodgement of individuals, a conical shell may represent an optimal shape to minimise this effect (Branch, 1985; Stanley, 1988). It may be hypothesised that any shell shape increasing the probability of dislodgement from the substratum as a result of wave action (or other mechanism) would either be absent from the intertidal or minimally represented. Some evidence for this may be provided by the lack of both cylindrical and discoidal shapes from this system, both shapes being less resistant to removal from the substratum. In the terrestrial system, where dislodgement from the substratum is not as important, both of these shapes are present.

A preliminary study of several systems, such as this one, raises many more questions than it can possibly answer. Our findings suggest several avenues of research which may elucidate some of the ecological and evolutionary factors that constrain molluscs.

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