



Habitat type as a determinant of species range sizes: the example of lotic–lentic differences in aquatic Coleoptera

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Species differ in the size of their geographical ranges, but it is unclear how this is affected by the intrinsic properties of various habitat types. Using data on range sizes for 490 species of aquatic Coleoptera from the Iberian Peninsula we show that running-water (lotic) species have much smaller distributional ranges than those occurring in standing water (lentic). This robust association of habitat type and range size has independently arisen in at least four monophyletic coleopteran lineages, in Hydradephaga, Hydrophiloidea, Hydraenidae and Byrrhoidea, and several more times within these main groups. We propose that this pattern is due to different evolutionary dynamics of both habitat types: stagnant water bodies are more likely to completely disappear, requiring frequent migration of resident populations. Rivers and streams, on the contrary, have more temporal and spatial continuity, and therefore permit the long-term persistence of local populations. In less permanent habitats species will require a greater geographical mobility, which indirectly results in a larger size range. The less dispersive populations of running water should also have reduced gene flow, increasing the probability of allopatric speciation, and thus reducing the average range of more widespread ancestral species. These differences in population parameters, and the frequency of transitions between the two habitat types, may have strong macroevolutionary consequences, in particular regarding speciation rates and possible morphological specializations.

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INTRODUCTION

The sizes of the distributional ranges of species differ characteristically from each other, but what determines these differences is unclear. Because of the strong positive correlation between range size and local abundance observed in a wide range of organisms (Hanski, 1982; Brown, 1984; Hanski, Kouki & Halkka, 1993; Gaston, 1994, 1997, 1998; Rosenzweig, 1995; Holt, 1997; Hanski & Gyllenberg, 1997) it has been suggested that deterministic processes play a role in regulating these parameters, as proposed for other parameters of biological rarity (Rosenzweig & Lomolino, 1997). The factors that determine range size are usually linked to specific traits of organisms that also determine abundance (Gaston, 1997), e.g. those permitting wider resource use, escape from predation, or higher competitive ability. However, there is a possibility that particular qualities of the habitat itself also affect range size by imposing a physical framework that constrains the possible ecological and evolutionary strategies of the species living in it (a templet in the sense of Southwood, 1977, 1988). This possibility, although suggested before (Janzen, 1985), has not been extensively tested (but see Liebherr, 1986, 1988).

In this paper we study the correlation between range size and habitat type in aquatic Coleoptera. The most important variable determining habitat specificity for aquatic beetles is the general water flow regime, besides other characteristics such as chemical composition, pH, and oxygen and nutrient content of the water. Species tend to be restricted to either standing water bodies or to running water, both in the larval and in the more dispersive adult stage. Water flow is therefore the most important habitat characteristic determining the composition of the assemblages of aquatic Coleoptera (see Foster *et al.*, 1992 and Foster & Eyre, 1992 for Irish and British species respectively; Ribera & Isart, 1994 for Pyrenean Hydradephaga; and Larson, 1997 for Australian Hydradephaga). It is also one of the best known autecological requirements of species, being in general well defined and easy to record.

Stagnant and running water bodies may operate under different dynamics of ecological and geological turnover. Rivers and streams can be expected to persist over longer geological periods, exhibiting spatial and temporal continuity despite changes in the exact location of the river bed (which can involve changes in the drainage patterns while preserving the continuity of individual rivers or streams; Bishop, 1995). This is in contrast to small stagnant water bodies, such as those typically occupied by aquatic beetles, which are generally short-lived and discontinuous in time and space. Once a particular stagnant water body disappears there is no direct physical connection to any other similar habitat.

We propose that because of these different temporal dynamics in stagnant and running water bodies, the dynamics of dispersal and population persistence may

also be different. If running waters are indeed more persistent than small stagnant water bodies, populations living in them will be less dependent on migration and dispersal to other similar habitats and therefore should tend to be genetically isolated. Although evidence is scarce, there are some data in support of this assumption (e.g. Ponder *et al.*, 1994; Hughes *et al.*, 1995, 1996; Bunn & Hughes, 1997; but see Bilton, 1992 for a counter-example of a stagnant-water species with a complex genetic population structure). Dispersal ability of insects is inversely correlated with permanence of the habitat (Jackson, 1956; Southwood, 1962; Roff, 1990; Wagner & Liebherr, 1992; see also a simulation study in Travis & Dytham, 1999), as flight ability is frequently lost when there is no need for dispersal (Roff, 1990; Ahlroth *et al.*, 1999 and references therein). The reduced dispersal may have implications for the distributional range of species: those found in (long-term, stable) running waters will have smaller distributional ranges than the more dispersive species occurring in (long-term, unstable) stagnant waters. Thus, population parameters such as overall abundance and range size should depend on the particular habitat type.

We test this prediction with data on main habitat type and range size of the aquatic Coleoptera from the Iberian peninsula. Aquatic beetles include species from a phylogenetically heterogeneous set of 16 families and three suborders of Coleoptera, representing several independent invasions of the aquatic medium. They are also functionally diverse, with different degrees of dependency on the aquatic habitat that range from species only marginally associated with water in some of the life stages (some riparian beetles) to those that spend their whole life cycle under water without the need to come to the surface, using plastron structures to obtain oxygen (some Elmidae) (Crowson, 1981). Diet and other autecological characteristics of the main groups are also very different, including those with predatory larvae and adults (e.g. Dytiscidae), predatory larvae and phytophagous adults (e.g. Hydrophilidae), or with both detritivorous adults and larvae (e.g. Hydraenidae and Elmidae).

The western Mediterranean water beetle fauna is a suitable model to study problems related to the evolution of geographic ranges and their size: the fauna is very rich, exhibiting a high level of endemism (around 20% in the Iberian peninsula), but also with species widely distributed across the Palaearctic region (Ribera, 2000). The Iberian peninsula was less affected by the Quaternary glaciations than central and northern Europe (e.g. Suc *et al.*, 1995; Thinon, Ballouche & Reille, 1996), with permanent glaciers restricted to mountain areas above 1500 m a.s.l. and adjacent valleys (Jalut *et al.*, 1982; Guimerà, 1992). It is likely that many species with restricted distributions survived the Pleistocene without major shifts in their ranges (e.g. Ribera & Blasco-Zumeta, 1998, and references therein). This is confirmed by recent evidence that Pleistocene range shifts of animals and plants largely progressed in West–East direction across central and northern Europe, the Iberian peninsula being in a more isolated position than previously thought (Bilton *et al.*, 1998; Sinclair, Morman & Ennos, 1999).

Our findings indicate a striking correlation between range size and habitat type, with running-water species being more restricted geographically than species confined to stagnant water bodies. In an attempt to explain this observation we accept the hypothesis that running water is the more persistent habitat, and that range sizes are in some way related to the long-term survival of populations. The

TABLE 1. Number of genera, species and subspecies per family of aquatic Coleoptera presently known in the Iberian peninsula (after Ribera *et al.*, 1999 and Ribera, 2000), with the species included in the analysis. Family ordination follows Lawrence & Newton (1995) except for Hydrophiloidea, for which the family ordination of Hansen (1991a) was used

Suborder	Superfamily	Family	Genera	Species ^a	Sub-species ^b	sp & ssp studied	
Myxophaga		Microsporidae	1	2 (1)	—	1	
		Hydrosaphidae	1	1	—	1	
Adephaga		Gyrinidae	3	10	—	10	
		Haliplidae	3	19 (5)	—	16	
		Noteridae	2	3	—	3	
		Hygrobiidae	1	1	—	1	
		Dytiscidae	33	163–165 (15)	6 (4)	155	
Polyphaga	Hydrophiloidea	Helophoridae	1	35 (2)	(1)	29	
		Georissidae	1	3	—	3	
		Hydrochidae	1	9	—	9	
		Hydrophilidae	20	90–92 (3)	1	62	
	Staphylinoidea	Hydraenidae	6	138 (4)	1	135	
	Scirtoidea	Scirtidae	6	34 (4)	—	—	
	Byrrhoidea	Elmidae	10	29–30 (1)	2 (2)	32	
		Dryopidae	2	17 (2)	—	14	
		Limmichidae	3	6	—	6	
		Heteroceridae	2	17 (1)	—	13	
		Psephenidae	1	1	—	—	
		Chrysomeloidea	Chrysomelidae	2	19–20 (1)	—	—
			Donaciinae				
	Curculionoidea	Curculionidae	1	23	—	—	
		Bagoiini					
	Totals			100	627 (43)	11 (7)	490

^a When some of the species are likely to be synonyms a range is given. In brackets, species in need of confirmation (included in the total number).

^b Subspecies other than the nominate form of the species. Number of endemic subspecies in brackets (included in the total). Doubtful subspecies are excluded.

observed correlation also may have interesting effects on the rates of speciation under low and high habitat stability.

MATERIAL AND METHODS

Groups included in the analysis

The relationship between range size and habitat was tested on 490 of the 627 species of aquatic Coleoptera from Iberia listed in Ribera *et al.* (1999). Aquatic species and generally accepted subspecies from all families of Myxophaga, Adephaga, Hydrophiloidea, Staphylinoidea and Byrrhoidea (except Psephenidae, with only one species) were included in the analysis (Table 1 and Appendix; see Ribera, 2000, for a biogeographical analysis of Iberian water beetles). Terrestrial species of Helophoridae and Hydrophilidae were excluded, as well as aquatic species of Curculionidae and Chrysomelidae (the latter for lack of detailed distributional data within the Iberian peninsula).

Comparisons of stagnant-water and running-water species were made for the pooled sets of all aquatic species combined, and separately for monophyletic groups

of species lineages. It is clear that aquatic habits arose at least four times: once in the suborder Adephaga (monophyly of all aquatic families, or 'Hydradephaga' following Shull *et al.*, in press); and three times in the suborder Polyphaga, in particular in the Staphylinoidea (family Hydraenidae only; Hansen, 1991a, 1997; Perkins, 1997), in Hydrophiloidea (Hansen, 1991b, 1997; Archangelsky, 1998); and in Byrrhoidea (Crowson, 1978; Beutel, 1997). We follow Hansen (1991a, 1997) and Archangelsky (1998) in considering Hydraenidae within the Staphylinoidea and not the sister group of Hydrophiloidea, as suggested by Beutel (1997) and Beutel & Molenda (1997). In the Byrrhoidea, not all of the families are aquatic; we treat all families included in the study as monophyletic (following Costa, Vanin & Ide, 1999), although this is currently not well established, and it is possible that several independent invasions of the aquatic medium had taken place in this clade, at least once in Elmidae and a second time in Dryopidae, Limnichidae and Heteroceridae (Kasap & Crowson, 1975; Lawrence, Nikitsky & Kirejtshuk, 1995; Beutel, 1997).

To analyse the taxonomic distribution of habitat type *within* these four aquatic clades it was useful to test the relationships between range size and habitat at lower levels of hierarchy. Monophyletic groups of lower hierarchical rank were based on phylogenetic hypotheses obtained from the literature. At an intermediate level of hierarchy, family-level taxa were used in the analysis, limiting the selection to those that had sufficient numbers of species for the statistical analysis (see below). These intermediate-level categories were: Dytiscidae (monophyly following Beutel, 1997), Helophoridae, Hydrochidae and Hydrophilidae (Hansen, 1991b, 1997). At the lowest phylogenetic level, categories within the Dytiscidae were the *Deronectes* group of genera (monophyly following Nilsson & Angus, 1992 and Alarie, Nilsson & Hendrich, 1999), *Agabus* plus *Ilybius* (Fery & Nilsson, 1993; Alarie, 1998) and *Hydroporus* (unpublished results). In Hydraenidae, lowest level groups include *Hydraena*, *Limnebius* and the subfamily Ochthebiinae (Hansen, 1991a; Perkins, 1997) (see Appendix for the genera included in these groups).

Range size

The analysis requires a measure of range size for each species. The distribution of many species within the Iberian peninsula and in the south Mediterranean area is not known with enough detail to allow a precise quantification of their ranges by the use of equal sized grid squares, and consequently a semiquantitative scale of range size was used based on presence/absence in major biogeographic areas.

The Iberian peninsula (including the north side of the Pyrenees and some areas in the extreme south of France) was divided into five major areas according to established main geological domains and present topography (Fig. 1, see Friend & Dabrio, 1996 for a more detailed geological characterization). Previous results demonstrated that these areas had a good correspondence with the distributional patterns of Iberian water beetles, particularly for species with the most restricted ranges (Ribera, 2000).

Presence/absence data for each species in those areas were used to produce a contingency table grouping species into a total of 11 categories in a semiquantitative scale of increasing range size. These eleven categories were defined as follows: categories 1–5, species limited to between 1 and 5 geographical areas within the Iberian peninsula; categories 6–10, species which also occur in one of the adjacent

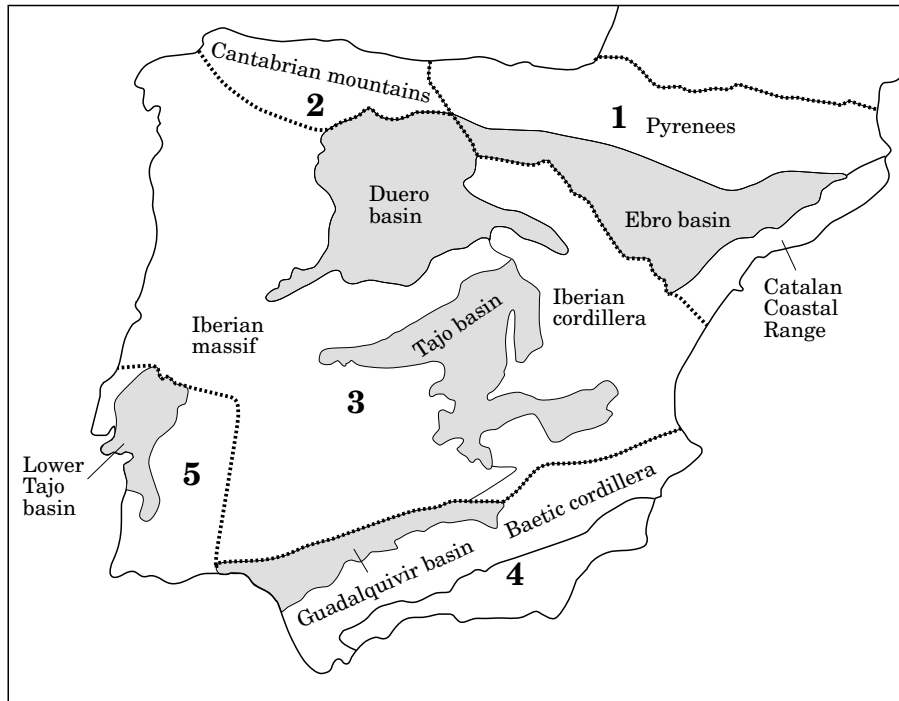


Figure 1. Geographical areas defined within the Iberian peninsula (from Ribera, 2000). (1) Pyrenean: the area north of the river Ebro valley up to the Pyrenees, including the eastern areas of the Basque country mountains. This area corresponds to the Tertiary basin of the Ebro river, the south side of the Pyrenean thrust belt, and the Catalan coastal ranges (Anadón & Roca, 1996). (2) Cantabrian: the Cantabrian mountains, from the eastern parts of the Basque Country to Galicia. The southern boundary of this region is well delimited by the plains of the Tertiary basin of the river Duero (Santisteban *et al.*, 1996). Its eastern and western limits are less clear, as they intermix with the Pyrenees and the northernmost mountain systems of the Hercynian Iberian massifs. (3) Hercynian Iberia: this area includes the Iberian cordillera, all the Hercynian mountain systems of the Iberian massif, and the Tertiary basins of the Duero and the upper Tajo rivers. (4) SE Iberia: this area includes the Tertiary basin of the Guadalquivir river, with all the Baetic cordilleras (including Sierra de Alcaraz in Albacete) and the Baetic and Rif internal zones (Sanz de Galdeano, 1996). (5) SW Iberia: the area south of the Sistema Central and the river Tajo (the limit of the Hercynian zone), and west of the Guadalquivir basin. This is a lowland area including the Tertiary basin of the lower Tajo river, plus some lowland areas and some isolated mountain massifs in the Algarve (south Portugal). Geologically it is linked to the Iberian Massif, but because of the abrupt end of the mountain systems of the Sistema Central and related mountains in Spain and Portugal, it forms a well-defined area.

areas (either France north of the Pyrenees, Morocco, or the eastern or central Mediterranean); category 11, widespread species with a trans-Iberian distribution (i.e. occurring in any, but not necessarily all, biogeographic regions in Spain and in both France north of the Pyrenees and northern Africa).

The definition of a large number of categories to describe range sizes resulted in small sample sizes in the individual cells of the contingency tables of some species. Therefore, categories were merged to form three main range types: (1) Iberian endemics (groups 1–5 above); (2) eastern, northern or southern species (groups 6–10 above); and (3) trans-Iberian species (group 11 above). A further contraction of these categories at a lower level of resolution distinguishes only Iberian endemics (1–5)

from those species with distribution in at least one area outside of the Iberian peninsula (6–11). By pooling categories we also assessed the possible effect of the dissimilar size of the five specified biogeographic regions within Iberia.

Main habitat type

The main habitat type of the studied species was defined according to the general water flow regime. Information for all the species included in the study was compiled from various published and unpublished sources (see Acknowledgements) (Appendix; data on each species available on request). Three categories were distinguished: (1) lotic (strictly running water); (2) both running and stagnant water; and (3) lentic (strictly stagnant water). All species occurring in association with springs, streams or rivers were included under 'lotic', irrespective of their microhabitat (e.g. the calmest areas of rivers, or the inundated areas surrounding some springs, were also considered to be running water). 'Lentic' includes all kind of isolated water bodies, or, if associated with running water, those large enough to make the effect of the possible inlets and outlets negligible. According to this classification, residual pools left when a temporary stream has no water flow are still considered to be running waters. This has the drawback of assigning opportunistic species to the 'both' category even though they have strong habitat affinity to stagnant water only, but was necessary due to the high number of species which are mainly found in running water, but of which adults can also be found in the residual pools of streams when the water flow is minimal or nil. Trying to avoid that, when an otherwise stagnant water species is found in residual pools only very occasionally, it was classified as lentic.

It could be argued that the lotic–lentic distinction made in this paper in fact reflects short-term differences in the permanence of the habitat, as small stagnant water bodies are usually considered to be more temporary than running waters. This is not the case in the Iberian peninsula, where many streams and rivers in the Mediterranean area are temporary, and many stagnant water bodies in the north-west and in the mountainous areas are permanent or quasi-permanent (i.e. not drying seasonally).

Analysis of the data

The relationship between range size and habitat was analysed with a Chi-square test on the contingency table of the absolute frequencies of species in each category. Contingency tables were constructed successively for all pooled species, for the main four clades of aquatic Coleoptera, and for less inclusive groups within these four main clades, at the 'intermediate level' equivalent to families and at the 'lower level' equivalent to genera or groups of genera. The data were further subdivided for the analysis by applying different levels of resolution of the range data distinguishing either 11 categories of range sizes, 3 categories, or 2 categories only. Columns of the contingency tables were the number of species in each habitat type (running, stagnant or both), and rows were the number of species in each category of range size.

The Spearman non-parametric correlation coefficient between range size (as measured with the semiquantitative scale of 11 categories) and the percentage of

species in a habitat type was also calculated, and this was repeated for the three habitat types. To avoid the bias introduced by categories with a very low number of species, categories were merged whenever they contained less than four species (one more than habitat types). This analysis was done with the most species-rich groups only, i.e. all aquatic species combined, the four main aquatic lineages separately, and the family Dytiscidae. The Spearman correlation was used because it is less sensitive to uncertainties in the position of closely related categories than other non-parametric correlation coefficients (Sokal & Rohlf, 1995), which is desirable because of the possible uncertainties in the exact range within Iberia for some species.

RESULTS

When all aquatic Coleoptera were pooled for a combined analysis the size of the range was found to be strongly dependent on the main habitat type, regardless of the level of resolution applied to the range data (Table 2). Lotic species were predominant among the lower range sizes, with increasing numbers of lentic species especially among those with trans-Iberian range (Fig. 2, Appendix). A similar relationship was observed in each of the four main aquatic lineages of the Coleoptera when tested separately (Table 2, Fig. 2): endemic Iberian species predominated among the running-water species, whereas stagnant and stagnant-and-running water species predominated in the trans-Iberian category. In the extreme case of Byrrhoidea all narrowly distributed species occur exclusively in running water, and in Hydraenidae all except one of the narrowly distributed species are found exclusively in running water.

The Spearman non-parametric rank correlation between range size (as measured with the highest resolution) and the proportion of lotic species was highly significant for all pooled species and for two of the main lineages (Hydradephaga and Hydraenidae) (Table 3). In all cases the proportion of lotic species was negatively correlated with range size. The correlation between range size and the proportion of lentic species, and of the species in both habitat types, was either positive or non-significant. The relationship between range size and habitat type was not significant in Hydrophiloidea and Byrrhoidea, but it has to be considered that in these two groups the number of species and categories of range size were lower than in Hydradephaga and Hydraenidae, thus decreasing the power of the test (see below).

While these findings suggest that the correlation of range size and habitat type originated separately in each of the large groups of aquatic beetles, we were also interested in the taxonomic distribution of this relationship *within* the four major groups. In almost all less inclusive groups tested ('intermediate' and 'lower' hierarchical levels in Table 1) the same trend as seen for higher level groups was observed, with the highest proportion of Iberian endemics always among the lotic species, decreasing values in species distributed in an adjoining area outside Iberia, and the lowest in species with the largest range category (Table 2, Appendix). Within the Hydraenidae the correlation of habitat type and range size was highly significant for all lower hierarchical levels (*Hydraena*, *Limnebius* and *Ochtebiinae*) and at all levels of resolution of the range size (Table 2). In other cases the relationship was significant only when ranges were pooled in three categories (Iberia, Iberia plus one adjacent area, and trans-Iberian distribution). These data suffered from the low number of comparisons or species in some of the

TABLE 2. Chi-square test on the contingency tables of the number of species of aquatic Coleoptera occurring in running or stagnant waters, sorted according to their range size measured with three levels of resolution (high: 11 categories, intermediate: 3 categories, low: 2 categories, see Methods). df: degrees of freedom of the contrast

Species included	Level of resolution of range size	χ^2	df	<i>P</i>
All species	high	103.79	20	0.0001
	intermediate	370.60	4	0.0001
	low	72.70	2	0.0001
Higher level groups				
Hydradephaga	high	58.10	20	0.0001
	intermediate	103.62	4	0.0001
	low	30.99	2	0.0001
Hydrophiloidea	high	26.03	20	n.s.
	intermediate	24.00	4	0.0001
	low	6.56	2	0.038
Hydraenidae	high	68.35	18	0.0001
	intermediate	169.37	4	0.0001
	low	29.24	2	0.0001
Byrrhoidea	high	12.57	16	n.s.
	intermediate	1337.13	4	0.0001
	low	2.16	2	n.s.
Intermediate level groups				
Dytiscidae	high	55.09	20	0.0001
	intermediate	63.26	4	0.0001
	low	26.18	2	0.0001
Helophoridae	high	11.10	14	n.s.
	intermediate	90.51	4	0.0001
	low	4.83	2	(0.089)
Hydrochidae	intermediate	82.13	4	0.0001
	low	2.93	2	n.s.
Hydrophilidae	high	13.58	14	n.s.
	intermediate	51.80	4	0.0001
	low	7.05	2	0.03
Lower level groups				
<i>Hydroporus</i>	high	22.91	18	n.s.
	intermediate	9.58	4	0.048
	low	3.01	2	n.s.
<i>Deronectes</i> gr	high	14.71	10	n.s.
	intermediate	47.02	4	0.0001
	low	5.58	2	(0.06)
<i>Agabus</i> + <i>Ilybius</i>	high	13.60	18	n.s.
	intermediate	26.28	4	0.0001
	low	1.78	2	n.s.
<i>Hydraena</i>	high	38.64	9	0.0001
	intermediate	38.64	2	0.0001
	low	439.90	1	0.0001
<i>Limnebius</i>	high	12.80	6	0.046
	intermediate	8.88	2	0.012
	low	13.77	1	0.0002
Ochthebiinae	high	34.27	14	0.002
	intermediate	49.62	4	0.0001
	low	11.42	2	0.003

analyses, as in the case of the *Deronectes* group of genera. Seventeen out of 31 species in this clade are only found in one or two areas within the Iberian peninsula, and all of them occur exclusively in running water. Only two species are exclusively found in stagnant water, both of them trans-Iberian species. Despite this clear trend, the analysis

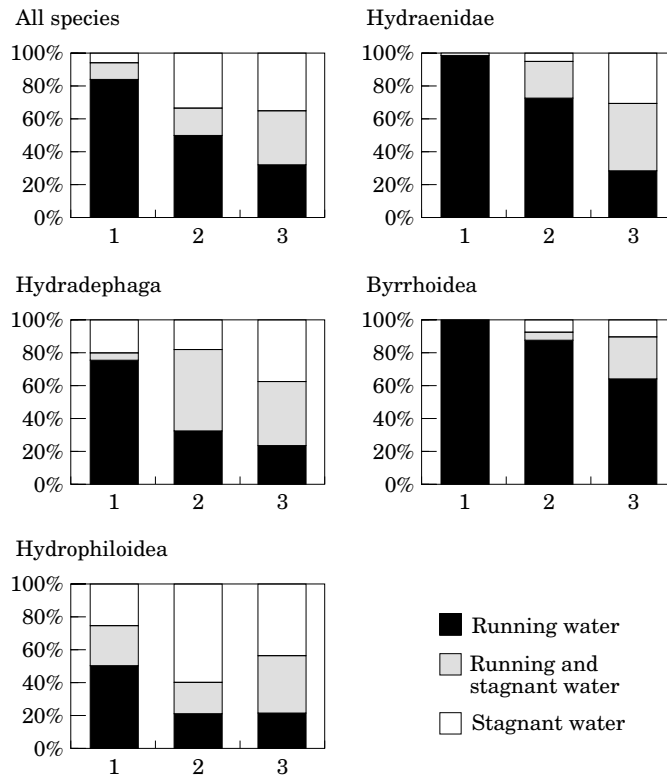


Figure 2. Relationship between range size and main habitat for all pooled species and the four independent aquatic lineages of the Coleoptera. The columns represent the percentage of species in each of the main habitat types. Data are presented for the case where range data were separated into three categories (see Material and Methods for details): (1) Iberian endemics (categories 1–5); (2) northern, southern or eastern species (categories 6–10); (3) trans-Iberian species (category 11).

at the lowest level of resolution (Iberian endemics *vs.* non-endemics) was only marginally significant ($P < 0.6$), and that at the highest resolution of range sizes (with 6 categories) was not significant (Table 3). If species living in stagnant water are pooled with those living on both types of habitats, thus reducing the number of cells and increasing the number of species in some cells, the contrast using the lowest level of resolution of range sizes becomes highly significant ($P < 0.001$), and that using the highest marginally significant ($P < 0.08$).

Within Hydradephaga, the Spearman non-parametric rank correlation between range size and proportion of lotic species was negative and significant for family Dytiscidae (Table 3). No other groups had enough species and range size categories to apply this type of statistical test.

DISCUSSION

Relationship between habitat and range size

The association of smaller range sizes with running water appears to be very strong, and was statistically most strongly supported when range size was measured

TABLE 3. Spearman non-parametric rank correlation (r_s) between range size (as measured with the highest resolution, i.e. a maximum of 11 categories) and percentage of species in each of the main habitats. n : number of final categories of range size; pooled ranges: initial categories of range size pooled to amount at least four species (see Methods and Appendix). Only groups with at least $n=6$ were studied. Significant correlations at a $P<0.05$ level are marked with two asterisks, and at $P<0.1$ level with one (one-tailed values)

Species included	n	Pooled ranges	Habitat	r_s
All species	11	none	lotic	-0.59**
			both	n.s.
			lentic	0.63**
Higher level groups				
Hydradephaga	8	3+4+5; 9+10	lotic	-0.74**
			both	0.53*
			lentic	n.s.
Hydrophiloidea	7	2+3+4+5; 9+10	lotic	n.s.
			both	n.s.
			lentic	n.s.
Hydraenidae	9	4+5	lotic	-0.83**
			both	0.88**
			lentic	n.s.
Byrrhoidea	6	1+2+3; 8+9	lotic	n.s.
			both	n.s.
			lentic	n.s.
Intermediate level groups				
Dytiscidae	8	3+4+5; 9+10	lotic	-0.76**
			both	n.s.
			lentic	n.s.

at intermediate resolution (with three categories). Less significant results were obtained when range sizes were analysed with higher (up to 11 categories) or lower (two categories) resolution. This may in part be explained by the low number of species in some cells of the contingency tables in the first case, and the lower number of cells in the second, as described above.

The general trend of a negative correlation between range size and water flow is further supported by the fact that the proportion of small range sizes among running water species is even higher when only the species with the most restricted distributions are considered. For example, of the 29 Iberian endemic species considered to be scarce or geographically restricted by Ribera (2000), only two are not exclusively found in running water, although the range of these two species is still uncertain.

The correlation between habitat type and range size, however, is probably not linear: our hypothesis precludes the existence of narrow local endemics among lentic species, but there still exists the possibility of lotic species with large ranges. Lentic species depend on effective dispersal mechanisms to persist by colonization of new habitats. Lotic species, in contrast, do not require good dispersal abilities for persistence but they may still exhibit these abilities. This asymmetry is best exemplified by the existence of some running water species with widespread distributions, such as the dytiscids *Platambus maculatus* (Linnaeus), *Agabus biguttatus* (Olivier) and *Hydroporus obsoletus* Aubé, or the elmid *Stenelmis canaliculata* (Gyllenhal). In contrast, no true local endemic of stagnant waters is known from the Iberian peninsula: the few species with restricted ranges are likely to be relicts of a formerly wider distribution (Ribera, 2000).

Many of these widespread lotic species are riparian, particularly among the families of Byrrhoidea. In fact, there are no presently recognized Iberian endemics among Limnichidae or Heteroceridae, and only one in Dryopidae, most of which are considered riparian (Appendix). Riparian species may have different dispersal dynamics, possibly determined by the changes of the water level rather than by the permanence of the water body *per se*, and therefore their habitat requirements may depend on different factors than those affecting true aquatic species. Most of them are good fliers, with very good dispersal abilities. The low number of species in these groups did not allow a separate analysis, but, in any case, the possible bias that the inclusion of riparian species could introduce would be contrary to the general trend, as they are running water species with large size ranges.

Given that the four main lineages of aquatic water beetles are unrelated, the association of running water and narrow range size originated at least four times independently in Hydradephaga, Hydrophiloidea, Hydraenidae and Byrrhoidea. The analysis of significance on lower hierarchical levels also suggests that the pattern has originated many times independently. Even in the groups at the lowest hierarchical level, comparable to the level of genera in taxonomic classifications, when the number of species is sufficient to allow statistical analysis the same correlation of range size and habitat is observed as in the more inclusive groups. This clearly argues against the possibility that the correlation is produced by combining phylogenetically highly conserved lineages of either standing or running water species with an equally conserved distribution of traits affecting their range size. Only in a few cases was a whole clade of species found to have very low or no variation in habitat type, such as in the genus *Deronectes* (with all species living in running water) or in the family Elmidae (with all species but two living exclusively in running water; Appendix). Both groups of species have morphological modifications that have been associated with water flow, in relation to swimming behaviour in the former (Ribera & Nilsson, 1995; Ribera, Foster & Holt, 1997), and to respiration and fixation to substrata in the later (Olmi, 1976).

Relationship between morphological specialization and habitat type

Shifts in habitat type seem to be more common in lineages which retain a more 'generalist' morphology, i.e. those that occupy the central area of the multivariate morphospace defined by the group (Ribera & Nilsson, 1995). In these lineages, several cases are found in which close species of a very similar morphology have different habitat types. This is the case for the closely related lotic-lentic species-pairs *Hydroporus discretus* Fairmairei & Brisout and *H. pubescens* (Gyllenhal), *Nebrioporus baeticus* (Schaum) and *N. cersyi* (Aubé), and *Agabus hozgargantae* Burmeister and *A. chalconatus* (Panzer). Closely related species pairs with similar morphology but different habitat type can also be found in other families, although at present it is not possible to assess the degree of specialization of their morphology in relation to other genera of the same families (e.g. *Hydrochus ibericus* Valladares, Díaz-Pazos & Delgado and *H. angustatus* Germar, *Ochthebius glaber* Montes & Soler and *O. notabilis* Rosenhauer, *Hydraena hernandoi* Fresneda & Lagar and *H. testacea* Curtis, *Limnebius ordunyai* Fresneda & Ribera and *L. nitidus* (Marsham)).

Morphological specialization in running water species seems thus likely to have limited the probability of habitat change. Once a running-water type morphology

is established, the possibility of a transition to stagnant water appears to be greatly reduced, if not, however, eliminated entirely. For example, some species of *Oulimnius* with the typical morphology of the family Elmidae can be found both in running and in stagnant waters. In a different ecological domain, Ribera *et al.* (1999) found that some species of ground beetles, despite retaining the plesiomorphic morphology of the genus, may change habits (e.g. from nocturnal to diurnal) or habitat (from digger to superficial) without any apparent disadvantage. In fact, the species that showed this shift in habit or habitat while retaining their supposed specialized ancestral morphology were the most common and widespread species of their respective genera in the studied area (Ribera *et al.*, 1999).

Long-term habitat stability explains range size

Our hypothesis is that the time scale over which populations of water beetles can persist in the two main habitat types is very different, and this fact ultimately results in different range sizes. Stagnant-water habitats are in general spatially and temporally unconnected to other water bodies, and in case of their disappearance the population is required to migrate. Running-water habitats, in contrast, may provide spatial and temporal continuity, even in times of climatic and geological change, as populations can move up and down a river to track the changes of the habitat. Persistence is not measured on an ecological time scale here, because species do not need to migrate when the habitat temporarily dries up, as they have multiple strategies to overcome short dry periods in place (Wiggins, Mackay & Smith, 1980).

In the search for an explanation of the observed relationship between range size and habitat type we considered—and discarded—some alternative hypotheses. It could be argued that the prevalence of mountainous areas in the Iberian peninsula is responsible for the observed small range sizes of running water species. Populations in mountains tend to be more genetically subdivided, presumably because of habitat fragmentation (Liebherr, 1988) or the increased harshness of the climate with altitude, as the development of the flight apparatus requires an extra investment which may be prohibitive under extreme climatic conditions (Ahlroth *et al.*, 1999). Finally, mountain areas are likely to be ecologically more stable over evolutionary time because of the possibility of tracking suitable environmental conditions by altitudinal shifts with small horizontal displacements (Darlington, 1943; Noonan, 1990). If running waters were more frequent in mountainous areas, these three factors, singly or in combination, could result in a spurious correlation between running water and elevated levels of endemism in the Iberian peninsula. These factors should be most influential at the summits, the mountain areas which are also the most rich in stagnant water bodies. However, the alpine zone in the Iberian mountain ranges is extremely poor in endemic species, despite the generally high rate of endemism among other groups of Coleoptera. (The few lentic species with restricted distributions are likely to be relicts of former wider ranges [Ribera, 2000]). This clearly argues against the possibility that the particular topography of the Iberian peninsula is the primary cause for the restricted range of lotic species.

While searching for the same pattern in other faunas with different geological history, or in other taxonomic groups, is the only way to completely overcome these objections, we think that there is sufficient evidence to accept that long habitat persistence results in a smaller range size of the species living in them.

There are two possible mechanisms by which this relationship can be established. In habitats that lack temporal and spatial continuity, the survival of populations is only made possible by frequent dispersal, while long-term persistence of the habitats makes dispersal unnecessary. The consequences of this difference in dispersal ability on range size would be indirect—only populations which can migrate are in a position to persist long term in stagnant-water (unstable) habitats, so this propensity to disperse will also lead to the colonization of a wide geographic area. Their larger range size would therefore be an incidental result of being able to persist in a spatially and temporally unstable habitat.

On the other hand, in running water the long-term persistence of populations is possible without the need to migrate. It is expected that this would lead to a reduction of gene flow between populations, with a greater level of genetic subdivision between them. The increased genetic subdivision of species in the more persistent running-water habitats will result in separation of groups of populations that, on a larger geographical scale, are recognized as different species. What could have been a single widespread species becomes a set of closely related, allopatrically distributed species. By contrast, in temporally and spatially discontinuous environments, such as small stagnant water bodies, the need for frequent dispersal would lead to a higher rate of gene flow, and a decreased probability of speciation. In this case, the differences in range size would be a consequence of the lower probability of speciation of lineages living in stagnant water, when compared to the lineages of species living in running water.

These two mechanisms—differential dispersal capabilities and different rates of speciation—are not incompatible, and both result in a smaller range size for species living in more persistent habitats. But both mechanisms are effective at different temporal scales, and they differ in their consequences for the evolutionary history of the group. The first mechanism is dependent only on the different dispersal ability of the species in continuous or discontinuous habitats, and thus is dependent on a trait of a given species. Its consequences can be manifest on shorter time scales, affecting mostly population dynamics and ecology. The second process invokes an effect on speciation rates and can act only over longer time scales, with clear consequences for the macroevolutionary history of the clades.

Macroevolutionary consequences of habitat changes

The presumed differences in the dispersal strategies and speciation rates in both habitat types have interesting consequences for clade evolution in either group. Accepting that genetically subdivided running-water species exhibit higher speciation rates, lineages in which these species predominate should have higher species richness, with a high proportion of ‘young’ species at any given time, and with allopatric ranges between closely related species. But as small ranges also favour higher extinction rates (e.g. Rosenzweig, 1995), the net result of these elevated speciation and extinction rates is a higher species turnover. Depending on the relative effect of the speciation and extinction processes the total numbers of species in the clade will increase or decrease. If extinction is comparatively low, the resulting species-rich clades should consist largely of narrowly allopatric or parapatric species; if extinction is high, the few surviving lineages should be widely allopatric.

Clades with predominantly stagnant-water species will have a lower speciation

rate, and because larger ranges decrease the probability of extinction, the species turnover will be lower. Species will be 'older', and with overlap in their ranges. The increased geographical mobility of the species living in stagnant water should be particularly evident in periods of climatic change, such as the Pleistocene glacial cycles. We hypothesize that range shifts should have been more extensive and frequent in stagnant than in running water species. Therefore, areas with a younger fauna (such as those that were fully glaciated in the last cycle) should have a higher proportion of stagnant water species than areas that may have acted as refugia (such as the Iberian peninsula or other Mediterranean zones).

Depending on the frequency of switches between running and stagnant water habitats these two basic evolutionary modes could affect the evolution of a clade in a complex way. The total species richness and the pattern of geographical distribution in a clade will depend on the frequency of character transitions between the two types of habitat, with their corresponding modes of cladogenesis. Prerequisite for testing these effects, however, are species-level phylogenies, which are not available currently.

CONCLUSIONS

The robust correlation between range size and habitat type, and its repeated origin in different groups of aquatic beetles, provides a unique opportunity to study the constraints the physical environment imposes on biologically important parameters such as rarity and species richness. Here we propose an explanation that focuses on the effects of long-term habitat permanence, which is in turn a correlated measure of dispersal ability and gene flow between populations. These processes can also be expected to have an effect on the mode and rate of evolution of entire clades, thus establishing a connection between microevolutionary processes and clade evolution. This analysis ultimately requires measurement of variables such as gene flow and dispersal ability for species in a comparative context, and to test the phylogenetic conservation of population genetic parameters.

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APPENDIX

Number of species per genus in each of the three categories of range size (as measured with the intermediate resolution level) and habitat type. Family ordination follows Lawrence & Newton (1995) except for Hydrophiloidea, for which the family ordination of Hansen (1991a) was used. Lo: lotic species; both: species present in both running and stagnant water; Le: lentic species. The data sets used in the analysis (14 monophyletic groups plus the total number of species) are marked with stars.

	Iberian endemics			Iberian + 1 adjacent area			Trans-Iberian			Total
	Lo	both	Le	Lo	both	Le	Lo	both	Le	
MYXOPHAGA										
Hydroscaphidae										
1 <i>Hydroscapha</i>				1						1
Microsporidae										
2 <i>Microsporus</i>							1			1
ADEPHAGA										
HYDRADEPHAGA	27	7	2	19	11	32	21	32	34	185*
Gyrinidae										
3 <i>Aulonogyrus</i>							2			2
4 <i>Gyrinus</i>						2		4	1	7
5 <i>Orectochilus</i>							1			1
Haliplidae										
6 <i>Brychius</i>				1						1
7 <i>Haliphilus</i>				1	3	1	1	2	5	13
8 <i>Peltodytes</i>									2	2
Noteridae										
9 <i>Canthydrus</i>						1				1
10 <i>Noterus</i>						1			1	2
Hygrobiidae										
11 <i>Hygrobia</i>	27	7	2	17	8	27	17	26	24	155*
16 <i>Acilius</i>									2	2
18 <i>Bidessus</i>							1	1	2	4
19 <i>Colymbetes</i>					1			1		2
20 <i>Copelatus</i>									2	2
21 <i>Cybister</i>						2			1	3
22 <i>Dytiscus</i>								2	2	4
23 <i>Eretes</i>									1	1
24 <i>Graphoderus</i>						1				1
25 <i>Graptodytes</i>		1			1	2	2	2		8
26 <i>Herophydrus</i>					1					1
27 <i>Hydaticus</i>						2			1	3
28 <i>Hydroglyphus</i>					1			1		2
30 <i>Hydrovatus</i>									2	2
31 <i>Hygrotus</i>			1			3		2	1	7
32 <i>Hyphydrus</i>								1		1
34 <i>Laccophilus</i>							1	1	1	3
35 <i>Meladema</i>							1			1
36 <i>Metaporus</i>									1	1
37 <i>Methles</i>						1				1
38 <i>Oreodytes</i>				3						3
39 <i>Platambus</i>				1						1
40 <i>Porhydrus</i>						2			1	3
41 <i>Rhantus</i>								1	1	2
42 <i>Rhithrodytes</i>	3									3
43 <i>Stictonectes</i>	2			2			2			6
44 <i>Tola</i>								1		1
29 <i>Hydroporus</i>	3	5	1	3	2	8	2	6	2	32*
<i>Agabus + Ilybius</i>	2	1		4	1	5	3	6	2	24*
17 <i>Agabus</i>	2	1		4		3	3	5	2	20
33 <i>Ilybius</i>					1	2		1		4
<i>Deronectes</i> gr	17			4	1	1	5	1	2	31*

continued

APPENDIX—*Continued*

	Iberian endemics			Iberian + 1 adjacent area			Trans-Iberian			Total
	Lo	both	Le	Lo	both	Le	Lo	both	Le	
12 <i>Deronectes</i>	11						4			15
13 <i>Nebrioporus</i>	5			3	1			1	1	11
14 <i>Scarodytes</i>							1			1
15 <i>Stictotarsus</i>	1			1		1			1	4
POLYPHAGA										
HYDROPHILOIDEA										
Helophoridae	7	4	3	9	8	24	10	17	21	103*
45 <i>Helophorus</i>	1	3	3		3	11		2	6	29*
Georissidae										
46 <i>Georissus</i>				1			2			3
Hydrochidae										
47 <i>Hydrochus</i>	3	1		1				3	1	9*
Hydrophilidae										
48 <i>Anacaena</i>	3			7	5	13	8	12	14	62*
49 <i>Berosus</i>						3	1	1	1	3
50 <i>Chaetarthria</i>							2	2	2	7
51 <i>Chasmogenus</i>						1				2
52 <i>Coelostoma</i>					1			1		2
53 <i>Cymbiodyta</i>						1				1
54 <i>Enochrus</i>	1			2		3	1	1	6	14
55 <i>Helochares</i>					1			1		2
56 <i>Hemishpaera</i>	1						1			2
57 <i>Hydrobius</i>									2	2
58 <i>Hydrochara</i>						1			1	2
59 <i>Hydrophilus</i>						1			1	2
60 <i>Laccobius</i>	1			5	3	1	3	4		17
61 <i>Limnoxenus</i>						2				2
62 <i>Paracymus</i>								2	1	3
STAPHYLINOIDEA										
Hydraenidae										
67 <i>Hydraena</i>	59		1	38	12	3	6	9	7	135*
68 <i>Limnebius</i>	34			22			1	2		59*
69 <i>Ochtebiinae</i>	12			4	5		1	1		23*
63 <i>Aulacothelbius</i>	13		1	12	7	3	4	6	7	53*
64 <i>Calobius</i>								1		1
65 <i>Enicocerus</i>	1						1			2
66 <i>Ochthebius</i>	12		1	12	7	3	3	5	6	49
BYRRHOIDEA										
Elmidae										
69 <i>Dupophilus</i>				1						1
70 <i>Elmis</i>	1			5						6
71 <i>Esolus</i>				1			2			3
72 <i>Limnius</i>	1			2			2			5
73 <i>Macronychus</i>							1			1
74 <i>Normandia</i>				1			1			2
75 <i>Oulimnius</i>	3			4				1		8
76 <i>Potamophilus</i>							1			1
77 <i>Riolus</i>				3						3
78 <i>Stenelmis</i>				2						2
Dryopidae										
79 <i>Dryops</i>	1			1	1	1	7	1	1	13
80 <i>Pomatimus</i>							1			1
Limnichidae										
81 <i>Botriophorus</i>						1				1
82 <i>Limnichus</i>							4			4
83 <i>Pelochares</i>							1			1
Heteroceridae										
84 <i>Augyles</i>				1			2	3	1	7
85 <i>Heterocerus</i>								4	2	6
Total	99	11	6	88	32	61	60	67	66	490*