Evolutionary Ecology Research, 2004, **6**: 1–18

Comparative analysis of range sizes in Helicidae *s.l.* (Pulmonata, Gastropoda)

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ABSTRACT

I analysed the importance of shell size, shell shape, habitat preferences and availability, experienced climate, active dispersal and influence of Pleistocene glaciations for the range sizes of 37 Western Palaearctic Helicidae *s.l.* species for which a phylogeny was available. In both cross-species and phylogenetically controlled analyses, the range sizes were positively correlated to climatic tolerance, shell size, active dispersal and influence of Pleistocene glaciations. In addition, range sizes increased significantly with latitude. Multiple regression suggested that, predominantly, the influence of Pleistocene glaciations, tolerance to large annual temperature ranges and shell size influenced the distributional range sizes. Habitat preference, range and availability, active dispersal and shell shape explained no additional variance. The results suggest that the processes influencing species range size of the Helicidae *s.l.* are mainly related to the climatic shifts after the Pleistocene.

Keywords: land snails, macroecology, Rapoport effect.

INTRODUCTION

Understanding the processes governing the range size distribution of taxonomic assemblages is one of the major goals in macroecology (Gaston, 1996). Despite the growing number of studies during the last decade, the accumulating knowledge is based on a restricted choice of animal taxa, mainly vertebrates and insects (Gaston and Blackburn, 2000). Taxa with less capacity for active dispersal have not yet been studied. Land snails are notorious for their rather sedentary habits and may therefore serve as a good example for other taxa with little vagility. The distance between adjacent habitat patches often exceeds the active lifetime dispersal of land snails, effectively isolating local populations even on very small scales (e.g. Pfenninger, 2002). Additionally, many species are restricted to a particular type of habitat, resulting in a usually patchy distribution on the landscape level (e.g. Magnin and Tatoni, 1995). Yet many species have attained large geographic ranges. It is therefore assumed that land snails rely mainly on passive dispersal mechanisms for

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the colonization of unoccupied habitat on a scale larger than a few hundred metres (Dörge *et al.*, 1999).

In this study, I used species of the Western Palaearctic Helicidae *s.l.* to examine the following processes that may play a role in shaping their range sizes on an ecologic time-scale:

1. *Dispersal*. Due to the restricted dispersal capabilities and the ubiquitous presence of insurmountable barriers, active dispersal is presumably a minor factor in determining the geographic range size of land snails. However, the outward shape of an organism can influence the effectiveness of its passive dispersal (e.g. Venable *et al.*, 1998; Fryer, 1991). This may also be true for land snails, if certain shell shapes favour, for example, the attachment to dispersal vectors. Presence in certain habitat types may also enhance the chance for passive dispersal. It has been shown that land snails are passively dispersed by livestock from pastures or with seeds from agricultural fields (Dörge *et al.*, 1999). Finally, the attractiveness to birds or large mammals (including mankind) as prey or food, which is positively correlated to shell size, may favour large-scale displacement by accidental release of specimens captured elsewhere (Godan, 1996). Any of these processes leading to effective passive dispersal can result in a comparatively larger species range.
2. *Habitat availability*. Different habitat types are unevenly distributed in the landscape. Species associated with more widespread habitat should therefore be more widespread themselves (Gaston, 1994). Additionally, species that can utilize a larger range of habitat types should be able to cover larger geographical ranges (Brown, 1984). This should be true in particular for mainly passive dispersed organisms, because the chance to reach suitable habitat is increased compared with habitat specialists. Therefore, Helicidae *s.l.* species that occur in a larger number of habitat types and/or whose preferred habitat types cover a larger area should have larger ranges.
3. *Climatic and environmental tolerances*. Studies have shown that land snails are restricted by physiological constraints related to environmental conditions (e.g. Arad *et al.*, 1998). In particular, their resistance to drought appears to limit their distribution (Kadmon and Heller, 1998). This may restrict the southern distribution of species from temperate regions. However, sensitivity to cold could also limit the species range. Species with a greater tolerance against climatic variation should therefore attain larger ranges.
4. *Historical changes of habitat distribution*. Species ranges may shift in space because of changes in habitat distribution (Gaston, 1996). The post-glacial warming in the Holocene resulted in large-scale expansions in particular of woodland habitat types in the Western Palaearctic, making previously uninhabitable areas available for colonization by species able to cope with the emerging conditions. The spread of human agricultural activity diversified the post-glacial landscape further, creating additional habitat types (Küster, 1999). As a consequence, snail species that at present occur in habitats that profited most from the retreat of the glaciers (woods and agricultural areas) should have attained larger ranges.

To test the hypotheses outlined above, I addressed the following question: Are there correlations between the range sizes in Western Palaearctic Helicidae *s.l.* species and measures of shell size, shell shape, habitat preferences and availability, experienced climate and influence of Pleistocene glaciations?

MATERIALS AND METHODS

Geographic range size measures of species

Distributional data were obtained for 37 species of the families Helicidae and Hygromiidae, referred to hereafter as Western Palaearctic Helicidae *s.l.* Species were included in the analysis if: (1) phylogenetic information was available; (2) the species status was considered as unequivocal; (3) they are present in Western Europe; and (4) reliable information about the geographic distribution was available.

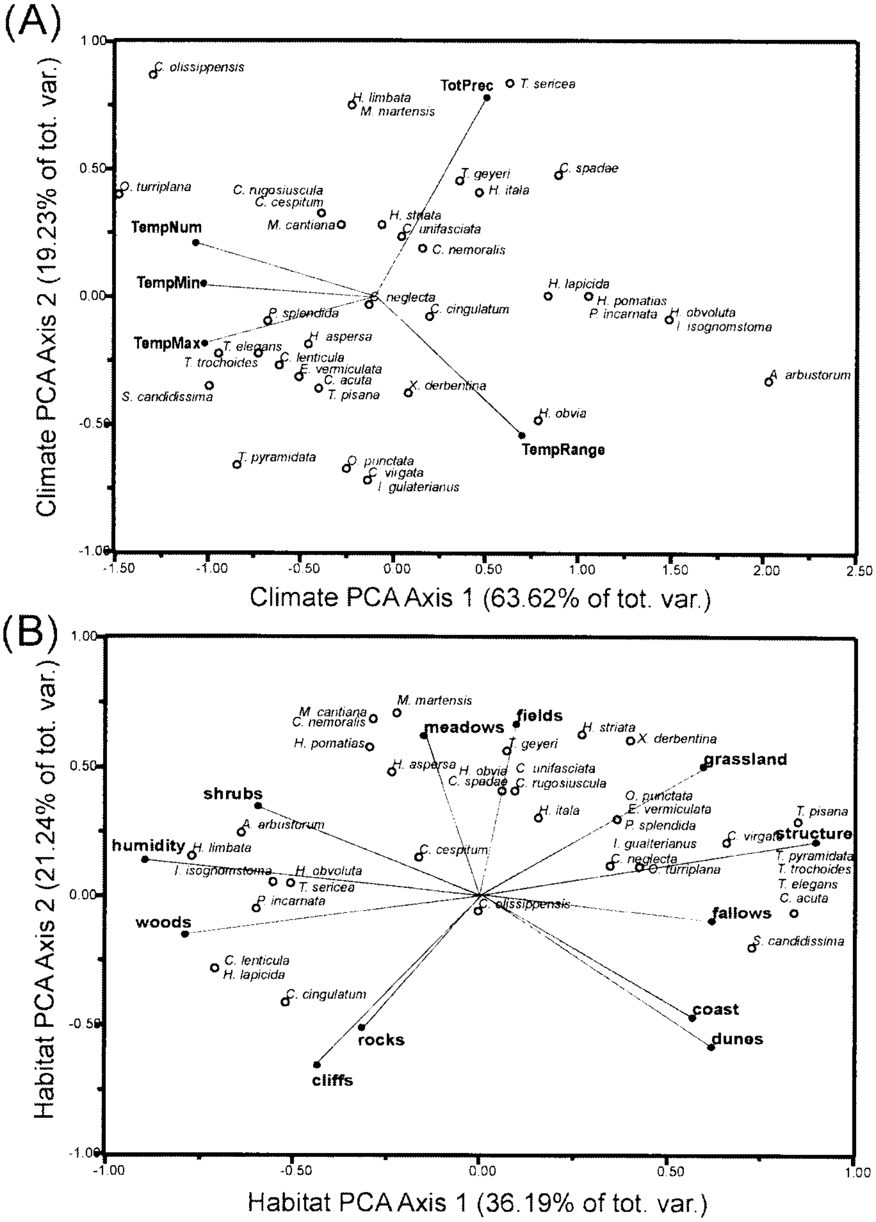
The area of distribution was marked on an electronic equal area projection map of Europe and the circummediterranean area, according to the distribution maps published in Cossigniani and Cossigniani (1995) and Kerney *et al.* (1983) and from my own observations. From these maps, the geographic species ranges were extracted as the log-transformed surface of the land area where populations of the respective species can be found (variable LOGAREA). This is a measure of extend of occurrence (Gaston, 1996). The surface areas were estimated from the electronic images using Scion Image for Windows beta 4.0.2. The latitudinal centre of the distribution range (LATITUDE) was determined as the latitude splitting the distribution range into equally sized halves.

Climatic tolerance

Because land snails are, to varying degrees, sensitive to desiccation and frost and require a certain minimum temperature and humidity for activity, the following available climate variables are most relevant for the climatic tolerance of land snail species: minimum average monthly precipitation; maximum annual temperature range between hottest and coldest month; minimum number of months with average daily temperatures above 10°C; maximum monthly average daily temperature; and minimum monthly average daily temperature. However, direct data on the climatic tolerances of land snail species were not available. The respective minimum or maximum values occurring within the species range were therefore used. The values were extracted for each species from global climate maps made available by the Food and Agriculture Organization of the United Nations at http://www.fao.org/waicent/faoinfo/sustdev/eidirect/climate/eisptext.htm. The maps provide mean monthly data, gained by spatial extrapolation of neighbouring weather stations for grid cells of 0.5° assembled over the period 1961–1990 and thus represent the long-term climate in this area (Leemans and Cramer, 1991).

This procedure harbours the potential for circular reasoning, because a larger species range has *per se* a greater chance to encompass more extreme values in some part of the range. To avoid potentially artificially inflated correlations and to make sure that a significant proportion of populations are affected by these extremes, I adopted a conservative approach. The most extreme climatic values were recorded only if they occurred in at least 15% of the species range. This percentage is the proportion of a single climate grid cell of the smallest species range. The variables were subjected to a principal components analysis (PCA) using Ntsys-pc vers. 2.0.

The PCA on the measures of climatic extremes experienced by the species yielded two relevant axes (larger eigenvalues than expected), summarizing 63.6% and 19.2% of the total variation, respectively (Fig. 1A). Axis 1 (CLIM1) was a gradient of species exposed to thermal extremes, while axis 2 (CLIM2) compared species experiencing little thermal variation throughout the year with a high amount of total annual precipitation with species exposed to high annual thermal variation and little rainfall. The factor scores of the species on the axes were used as measures of climatic variation experienced in subsequent analyses. Besides reducing the number of variables by summing the major trends in multivariate data, the use of principal components scores in subsequent correlation analyses has the additional advantage that the axes are not intercorrelated.



Habitat preference and habitat potential

The habitat preference of the species was characterized as presence/absence (1/0) in ten habitat types, according to Cossigniani and Cossigniani (1995), Kerney *et al.* (1983) and my own observations: (1) woods, (2) scrub, (3) intensely used agricultural areas like fields, gardens and vineyards, (4) extensively used agricultural areas like meadows and pastures, (5) dry grassland, (6) fallows or barren land, (7) coastal habitats, (8) sand dunes, (9) rock debris and (10) cliffs. To include estimates of microclimatic and structural differences not accounted for by the large-scale climatic variables into habitat preference, meristic descriptors of habitat structure and locally available humidity were recorded. The vegetation structure of the habitat was categorized as open (score 2), half open (1) or closed (0). The available humidity was categorized as very humid (3), humid (2), dry (1) and very dry (0). Principal components analysis was used to condense information on habitat preference. The PCA on habitat variables resulted in two meaningful PCA axes (Fig. 1B). The first axis, which accounted for 36.2% of total variance (HAB1), compared species from open, dry habitats on grasslands, coasts and dunes with species from humid, closed woods and shrubs. The second axis (HAB2, 21.2%) was a gradient of anthropogenization, with species associated with agriculturally used areas at one extreme and cliff dwelling species at the other. The number of habitat types utilized by a species was considered as a measure of habitat range (HABRANGE). The habitat area potentially available for each species (HABPOT) was estimated from the Pan European Land Cover Monitoring (PELCOM) map, published by the PELCOM Project (2000). This map provides colour-coded land

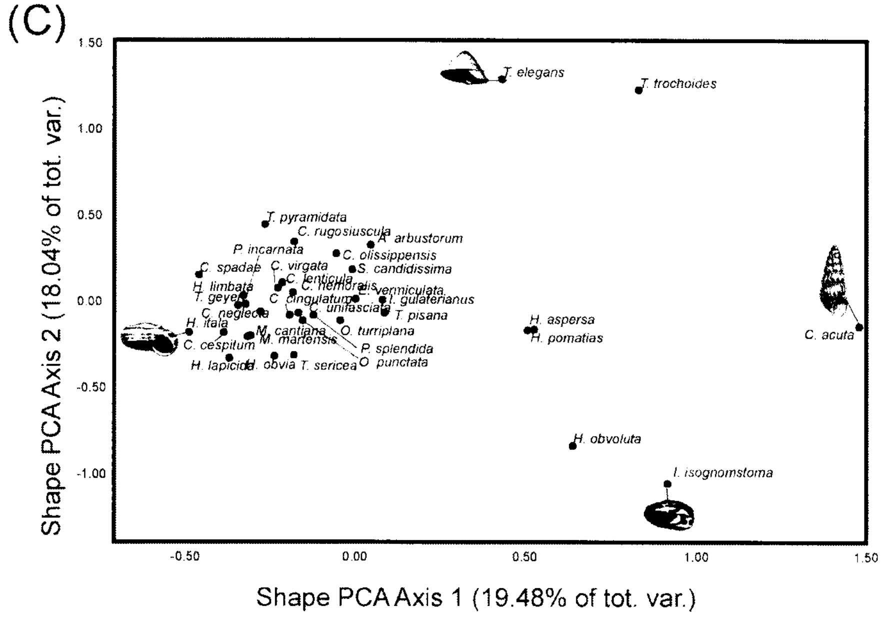


Fig. 1. Plots of Helicidae *s.l.* species component scores on the first two PCA axes of (A) climate variables, (B) habitat variables and (C) shape variables. In the first two plots, the contribution of the original variables (bold type) to the PCA axes is indicated. For details, see text.

cover information, derived from remote sensing with a resolution of 1 km. The potential habitat area for each species was calculated by adding up the land cover areas for all habitat types used by the respective species.

Shell shape and size

The shell of an adult specimen of each species was photographed with a digital camera from the front, with a ruler included on the image. The program tpsDIG (Rohlf, 1999) was used to apply 300 equidistantly spaced points on the outline. These points were used to produce a closed outline curve. The shape of the shells was quantified by elliptic Fourier approximation as described by Kuhl and Giardana (1982). This technique consists of decomposing a closed contour curve in a two-dimensional plane into a sum of harmonically related sequences. Fourier decompositions are sensitive to location, size and orientation of objects. Consequently, the horizontal and vertical axes of the shells were used to rotate them into the same orientation. The images were then centred and normalized for size. These operations and the decomposition into Fourier series were computed with EFAWin (Isaev and Denisova, 1995), using the algorithms of Ferson *et al.* (1985). The application of eight harmonics was sufficient to reproduce the outline of the shells with high accuracy. This resulted in 29 non-trivial Fourier variables. The Fourier variables were subjected to a PCA to summarize the shape information. The area enclosed by a two-dimensional projection of the shell front view before normalization for size was employed as an estimator for the shell volume. The variable was log-transformed prior to statistical treatment. Given the great variation in shell shape, this measure, provided by EFAWin, is more reliable than conventionally used shell height and width. Principal components analysis of the Fourier variables summarized variation in shape on two meaningful axes (Fig. 1C). The axis containing most shape information (SHAPE1, 19.5%) contrasted slim, high-spired shells against globulose, depressed shells. The second gradient (SHAPE2, 18.0%) separated trochoid from cylindrical shells.

Historic factors

For each species, the percentage of the present-day geographic species range covered by the maximum Pleistocene glaciation was recorded (GLACIATION) and arcsine-transformed for statistical analyses.

Active dispersal

For a subset of 12 species, data on active dispersal were extracted from the literature. Because of the heterogeneity of measurements, the average dispersal for 7 days was calculated (DISPERSAL) from the studies and log-transformed for statistical analyses.

Phylogeny and statistical analyses

The characters of species are not independent of their phylogeny (Felsenstein, 1985; Harvey and Pagel, 1991). This increases the potential for Type I error and biases results towards higher significance than is warranted. If the phylogeny of the species in question is known, this information can be used to remove phylogenetic non-independence from the data

(Felsenstein, 1985). For this study, I used the well-supported phylogeny of the Helicidae *s.l.* inferred by Steinke *et al.* (in press). However, the branch lengths reported therein did not conform to the molecular clock hypothesis, which was a necessary prerequisite for the intended analyses. Therefore, I enforced the topology of this tree on a mitochondrial data set (906 bp of COI and 16S), for which the molecular clock hypothesis was not rejected (likelihood ratio test, $P = 0.32$, under a GTR+G+I model of sequence evolution). The resulting phylogeny was fully resolved, even if some of the branch lengths were close to zero (Fig. 2). These calculations were carried out in PAUP 4.0 10b (Swofford, 1998).

To determine whether the overall evolution of the traits deviates from the expectations of a Brownian motion model of evolution, a two-tailed permutation test was employed (Wilke *et al.*, 2002). In this test, the coefficient of variation (CV = standard deviation/mean) is used as the test statistic on the untransformed variables to assess the probability that a continuously valued trait shows more or less variation than expected from an empirical null distribution of CVs for a given phylogeny. This null distribution is generated by simulating the evolution of a large number of traits (in this case 2000) along the branches of the phylogeny in question, according to a Brownian motion model of phenotypic evolution. It is assumed that the branches of the phylogeny are proportional to the divergence time. If the observed CV is larger than, say, 95% of the simulated CVs, one can assume that forces other than random divergence governed the overall evolution of the respective trait, for example directed evolution in at least one branch of the phylogeny. An observed CV smaller than expected may indicate constrained evolution. The advantage of the test, compared with the *K*-statistics proposed by Blomberg *et al.* (2003), is the statistical assessment of the significance of deviation from Brownian expectations.

To establish whether the traits studied contain phylogenetic signal, I conducted the permutation test on the variance of independent contrasts proposed by Blomberg *et al.* (2003). I permuted the trait values 100 times over the phylogeny; the calculation of the resulting independent contrasts was performed with COMPARE 4.5 (Martins, 2003).

To remove the phylogenetic non-independence from the data, I employed an independent-contrast approach, suggested by Felsenstein (1985), as implemented in the software COMPARE 4.5. This method assumes that the branch lengths of the phylogeny are known and proportional to the amount of evolutionary change.

Relationships among species traits and geographic range size distributions were explored for cross-species and independent contrast analyses using correlation analyses. To account for the usually complex interrelationships of independent variables, multiple regressions were computed (all effects, P to enter = 0.05). For phylogenetically independent contrasts, the regression was forced through the origin (Garland *et al.*, 1992). All analyses were carried out with the largest possible data set.

RESULTS

Geographic range size distribution

The species *Candidula rugosiuscula* had the smallest range, with an estimated area of 8500 km^2; *Arianta arbustorum* had the largest range, with an area of 2.9 million km^2. The mean range size of all species was 84,000 km^2. The frequency distribution was strongly right skewed (Fig. 3). The log-transformed range sizes showed no significant deviation from a

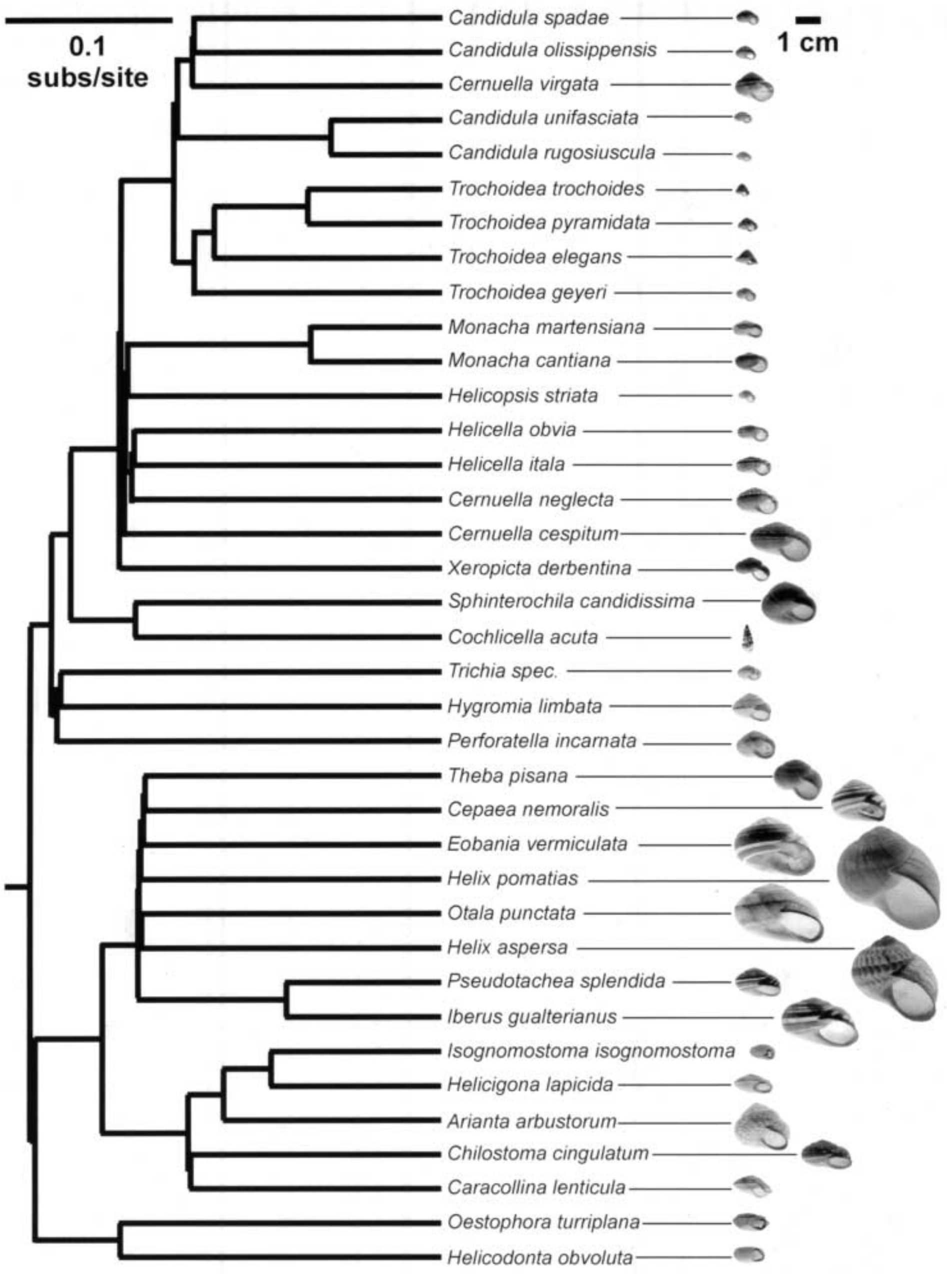


Fig. 2. Phylogeny used for independent contrast analyses. The branch lengths, derived from mitochondrial gene sequences (COI and 16S), conform to the assumptions of a molecular clock. The topology corresponds to the phylogeny in Steinke *et al.* (in press). The scaled images of the taxa were used in morphological analyses.

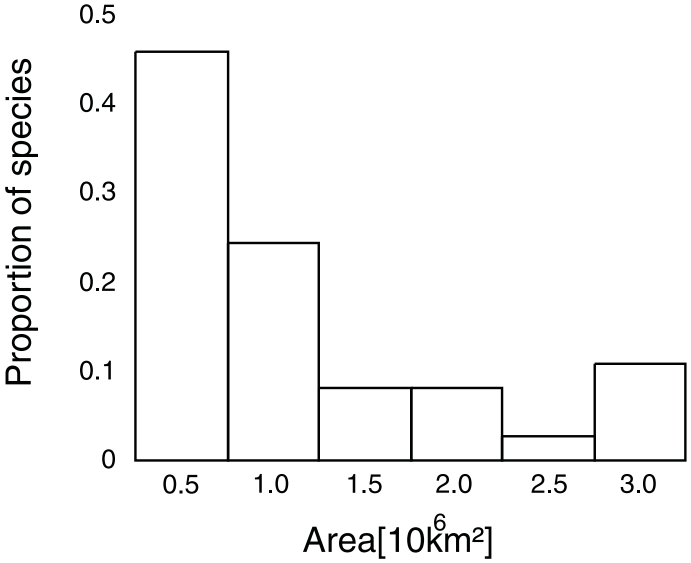


Fig. 3. Frequency distribution of range sizes in the Helicidae *s.l.*

normal distribution (Komogorov-Smirnov test, $n = 37$, $D = 0.11$, $P = 0.73$). The size of the ranges increased significantly with latitude in cross-species and phylogenetically controlled analyses ($r_{\text{raw}} = 0.431$, $P = 0.005$; $r_{\text{phyl}} = 0.284$, $P = 0.021$).

Phylogenetic signal and mode of evolution

The trait HABRANGE was slightly less differentiated than expected by a Brownian motion model of phenotypic evolution. However, this may be an artificial effect due to the relatively crude resolution of habitat categorization. SHAPE1 showed considerably more differentiation, owing to the skewed distribution of the shells along this PCA axis (Fig. 1). Note that these deviations may lead to undesirable statistical properties of the resulting independent contrasts (Felsenstein, 1985). The other traits did not deviate from expectations and conform, therefore, to the assumptions of independent contrasts.

There was no significant correlation between the standard deviation of the contrasts and the contrasts themselves, indicating the adequacy of the branch lengths used (Garland *et al.*, 1992). The presence of significant phylogenetic signal was detected in the traits LATITUDE, LOGSIZE, HAB1 and DISPERSAL (Table 1). Additionally, the variables CLIM1, HAB2 and HABRANGE were close to significance ($P < 0.10$), suggesting that common phylogenetic history may have reduced variance in these traits, too. The use of phylogenetically informed statistical methods in addition to cross-species analyses was thus indicated.

Factors explaining geographic range size

In cross-species analysis, the geographical range size was significantly correlated with the variables CLIM2, LOGSIZE, GLACIATION, HABPOT, HABRANGE, CLIM1 and

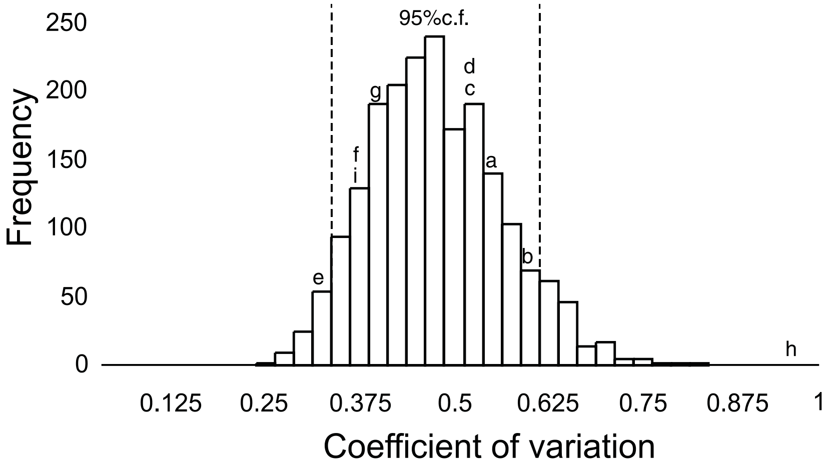


Fig. 4. Null distribution of coefficients of variation (CV) of 2000 continuous phenotypic traits simulated along the branches of the phylogeny in Fig. 2, according to a Brownian motion model of phenotypic evolution. The 95% confidence limits are indicated. Observed CVs are denoted for traits: (a) CLIM1, (b) CLIM2, (c) HAB1, (d) HAB2, (e) HABRANGE, (f) HABPOT, (g) SIZE, (h) SHAPE1 and (i) SHAPE2.

Table 1. Test on phylogenetic signal

Variable	VAR	*P*
LATITUDE	122.64	0.02*
LOGAREA	13.37	0.31
CLIM1	3.51	0.07
CLIM2	1.17	0.22
GLACIATION	1.61	0.29
HAB1	1.43	<0.01*
HAB2	1.53	0.08
HABRANGE	11.53	0.07
HABPOT	0.25	0.32
LOGSIZE	0.89	<0.01*
SHAPE1	0.96	0.35
SHAPE2	0.97	0.11
DISPERSAL	10.02	0.04*

Note: VAR = observed variance of standardized independent contrasts of traits, P = probability of these variances to be smaller than expected from a random distribution of trait values on the phylogeny, inferred from 100 random permutations.

DISPERSAL, in decreasing order (Table 2). After correction for phylogenetic non-independence, this picture altered somewhat; the variables HABPOT and HABRANGE failed to reach the 5% significance level and the correlation coefficients changed (Table 2).

Table 2. Cross-species (below diagonal, $n = 37$) and phylogenetically controlled (above diagonal, $n = 36$) correlation coefficients between Helicidae *s.l.* species range size and independent variables (n for DISPERSAL is 12 and 11, respectively)

Variable	LOGAREA	CLIM1	CLIM2	GLACIATION	HAB1	HAB2	HABRANGE	HABPOT	LOGSIZE	SHAPE1	SHAPE2	DISPERSAL
LOGAREA		0.333*	−0.557***	0.464**	0.022	0.103	0.261	−0.002	0.373*	0.084	−0.074	0.552*
CLIM1	0.194*		−0.051	0.608***	−0.526***	0.551***	−0.203	0.237	0.086	−0.047	−0.420**	0.334
CLIM2	−0.620**	0.000		0.148	−0.425**	0.267	−0.105	−0.085	−0.220	−0.129	−0.116	−0.209
GLACIATION	0.421**	0.637***	0.148		−0.458**	0.644***	−0.069	−0.127	−0.131	0.161	−0.406**	−0.115
HAB1	−0.113	−0.640***	−0.348*	−0.489***		−0.211	0.327*	−0.097	0.027	0.351*	0.421**	0.018
HAB2	0.003	0.332*	0.271	0.517***	0.000		−0.074	0.040	−0.084	0.000	−0.396**	−0.338
HABRANGE	0.283*	−0.243	−0.160	−0.113	0.365*	0.033		0.471**	0.387**	0.131	0.311*	0.657*
HABPOT	0.408**	0.231	−0.133	0.033	−0.142	0.193	0.579***		0.291*	−0.146	−0.005	0.557*
LOGSIZE	0.513***	0.110	−0.327*	−0.045	−0.138	−0.039	0.365*	0.523***		−0.236	−0.011	0.562*
SHAPE1	0.138	−0.182	−0.255	0.115	0.398**	−0.068	0.227	−0.091	−0.061		0.352*	0.103
SHAPE2	−0.159	−0.490***	−0.135	−0.453**	0.534***	−0.289*	0.295*	−0.190	−0.243	0.000		0.160
DISPERSAL	0.597*	0.376	−0.159	0.023	−0.186	−0.273	0.712**	0.470	0.587*	0.329	0.192	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3. Results of multiple regression on cross-species values for selecting an optimal subset of explanatory variables for Helicidae *s.l.* species range sizes ($n = 37$)

	Independent variables	Dependent variable cross-species	
		Beta	R^2
Variables in the model	GLACIATION	0.64***	
	CLIM2	−0.56***	
	LOGSIZE	0.31**	
			0.81***
Variables not in the model	HABRANGE	0.22	
	HAB2	−0.18	
	SHAPE1	−0.16	
	CLIM1	0.10	
	HABPOT	−0.09	
	SHAPE2	0.08	
	HAB1	0.04	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Multiple regression on the cross-species data retained the variables GLACIATION, LOGSIZE and CLIM2 in the model, accounting in decreasing order for 81% of the total variation (Table 3). Using the phylogenetically independent contrasts, the same variables significantly explained 77% of the total variance (Table 4). All other variables failed to reach the significance level.

No additional variance was explained by adding the variable DISPERSAL in subsequent multiple regression on both the cross-species and independent contrast data, using only the variables previously retained as significant (data not shown). This was because most of the variance in dispersal is explained by differences in size.

DISCUSSION

Species range size distributions are the product of speciation and transformations (Gaston, 1998). In the analysed phylogeny, the youngest divergence event is among the sister species *Candidula unifasciata* and *C. rugosiuscula* (Fig. 2). This speciation was estimated to have occurred in the late Pliocene (Pfenninger *et al.*, 2003a). Recent speciation events are therefore unlikely to have shaped the range size distribution in the present data set.

Divergence events were nevertheless not spatially independent of geographic clade distributions, as the significant phylogenetic signal of the variable latitude indicates (Table 1). However, this effect appears to be independent of range sizes, because related species do not tend to have similar range sizes, as evidenced by the absence of phylogenetic signal (Table 1). A correlation between range size and phylogenetic relatedness, however, was found for fossil molluscs, but could not be confirmed in extant avian species (Webb and

Table 4. Results of multiple regression on independent contrasts for selecting an optimal subset of explanatory variables for Helicidae *s.l.* species range sizes ($n = 36$)

	Independent variables	Dependent variable independent contrasts	
		Beta	R^2
Variables in the model	GLACIATION	0.70***	
	CLIM2	−0.54***	
	LOGSIZE	0.26*	
			0.77***
Variables not in the model	HABRANGE	0.21	
	HAB2	−0.16	
	HABPOT	−0.16	
	SHAPE1	−0.13	
	SHAPE2	0.08	
	CLIM2	0.07	
	HAB1	0.04	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Gaston, 2003). It can be assumed that speciation in land snails usually takes place in a single or geographically restricted set of populations (e.g. Douris *et al.*, 1998). Therefore, the geographic species ranges observed here are most probably the product of dynamical transformations since the emergence of the species, even though they may not be independent from the evolutionary age of the respective species (Webb and Gaston, 2000). It seems thus justified to consider only processes in ecological time as relevant for the present-day range size distribution (Gaston and He, 2002).

The shape of the log-transformed range size distribution in the subset of Helicidae *s.l.* species does not deviate significantly from a log-normal distribution. The empirical expectation from many other taxa is a slightly left skewed distribution (Gaston, 1998). However, even though the sample size was too low to detect slight deviations from normality, a stronger bias would have been detected. This suggests that the studied subset of species is a representative or only slightly biased sample of the entire taxon. The range sizes increased with latitude (Table 2), an observation made for many taxa and termed the Rapoport effect or rule (Stevens, 1989), but whose general applicability was questioned (Gaston *et al.*, 1998). The Rapoport effect decreased considerably after the correlation of related species tending to have their centre of distribution on similar latitudes (Table 2) was removed, but remained significant. In the study area as part of the Palaearctic, this is not an artificial effect due to decreasing land area at lower latitudes (Letcher and Harvey, 1994). However, the Southern European Iberian and Italian peninsulas are isolated from the rest of the continent by the Pyrenees and Alps, respectively. These mountain chains may act as effective dispersal barriers for land snails, thereby limiting the ranges of taxa on both sides.

The area of the present-day species range covered by the maximum Pleistocene glaciation explained the largest proportion of the variance in both cross-species and phylogenetically controlled analyses (Tables 3 and 4). It is responsible for much of the observed Rapoport effect. This pattern may be explained by differential expansion into these post-glacially unoccupied areas, either from southern (Pfenninger and Posada, 2002) or local refuges (Haase *et al.*, 2003; Pfenninger *et al.*, 2003b). The lack of correlation between the availability of potential habitat for each species and the influence of Pleistocene glaciation (Table 2) shows that these are different processes. Six of the 16 species whose present-day ranges were affected by Pleistocene glaciations are associated with woods. Assuming that their habitat preference has not changed, their range expansion to the present size must have happened with or after the Holocene reforestation that was ended 9000 years ago (Küster, 1999). The majority of the remaining rather open habitat species appear to have profited from the subsequent human influence on the landscape, namely the partial deforestation in the course of the spread of agriculture. The criterion used to infer the effect of Pleistocene climate changes on present-day range sizes most certainly underestimates this impact, because it is very likely that other species ranges also profited from the post-glacial shift of climate zones, even if the present-day species ranges were not directly affected by the glaciations. Differential colonization abilities after the retreat of the glaciers were also suggested by Price *et al.* (1997) to explain the increase in range size with latitude in leaf warblers.

Another factor determining in part the size of the species ranges was the amplitude of seasonal temperature variation and the minimum monthly precipitation occurring within the species ranges (Tables 3 and 4). This suggests that species with tolerance to seasonal thermal variation and desiccation, due to physiological and/or behavioural adaptations, can attain larger ranges. However, given the potential circularity inherent in the estimation of climatic tolerance, these findings must be interpreted with caution. The range of seasonal variation in climatic conditions increases with latitude. Therefore, species with greater tolerance against climatic variation can extend their ranges to higher latitudes (Addo-Bediako *et al.*, 2000). This may explain in part the observed increase of range size with latitude. Such a pattern was found also for tree and shrub species (Pither, 2003) and dung beetles (Gaston and Chown, 1999). However, in the study area, annual rainfall increases with latitude, too. Consequently, a desiccation resistance will allow larger range sizes in the Mediterranean area. In a study on land snails in Israel, mean annual rainfall was indeed the major factor determining local community composition, thereby limiting the range of individual species (Kadmon and Heller, 1998).

The size of a species also determined its range size (Tables 3 and 4). In most other taxa, this correlation is straightforward: larger species need larger home ranges, and therefore the space required for a viable population is larger. Additionally, larger species are usually more mobile and may therefore reach more suitable places. The first argument is not valid here, because even large land snails can maintain viable populations in very small areas compared with the species range (Pfenninger and Bahl, 1997). The second argument appears to apply at first sight, because range size increased with active dispersal capacity where data were available. However, active dispersal capacity explained no additional variance in multiple regression because of its interrelation to size. So it would appear that size alone matters, most likely because of the attractiveness of snails as a food resource, in particular for humans. This led to documented cases of large-scale dispersal in the past. For example, *Helix aspersa* arrived on the British Isles, where this species was introduced for alimentary reasons, with the Roman conquest in A.D. 44 if not earlier (Godan, 1996). A similar introduction process was suspected for some Mediterranean species whose appearance in the fossil record on the Western Mediterranean coasts coincides with the beginning of the Greek settlement in this area from 500 B.C. on (F. Magnin, personal communication). Birds, another candidate vector for long-range dispersal, favour larger species like *Arianta arbustorum* and *Cepaea* as prey and drop them accidentally from time to time (Tucker, 1991).

Surprisingly, neither the preference of a particular habitat type, nor the ecological amplitude of a species or the area of potential habitat, seem to be good predictors for range size (Tables 3 and 4). Even though there is a correlation between the potential habitat area, habitat range and the actual species range (Table 2), these correlations vanish after correcting for phylogenetic interdependence, indicating a phylogenetic clustering of habitat generalists. On the one hand, the almost ubiquitous presence of small but, for the maintenance of viable populations, sufficiently large patches of almost all types of habitat on the landscape level may be the reason why neither the total area of the potential habitat nor habitat range was important. This is exemplified by the wood-dwelling species, for which human activities must have caused a considerable loss of total habitat area. However, this seems not to have influenced the geographic extent of the species ranges, because even very small remaining wood patches are sufficient to maintain viable populations. In general, the severe restructuring of the landscape has diversified the number of available habitats in the study area rather than eradicated any one of them completely. On the other hand, availability of potentially suitable habitat areas alone seems not to ensure their colonization, most likely due to the limited capacity of land snails to search and colonize suitable habitat on a larger spatial scale.

In contrast to other passively dispersed taxa like freshwater plankton or plants, the shape of the Helicidae *s.l.* did not play a significant role in shaping range size. Obviously, passive adherence to vectors or drifting with wind or water are not as important for passive dispersal in snails as for these other taxa. Active adherence to objects, however, favours the current, rapid spread of *Xeropicta derbentina* in France (Labaune, 2001), where this species was introduced in the 1950s. But this characteristic seems to be independent of shell shape.

CONCLUSIONS

The size of species ranges of Western Palaearctic Helicidae *s.l.* is mainly determined by three processes: (1) the possibility of expansion into the natural or man-created habitats available after the Holocene shift of climate zones; (2) the degree of tolerance against large annual temperature ranges and drought; and (3) size-dependent attractiveness as prey or food, which results in purposeful or unintentional large-scale displacement. Apart from climatic tolerance, other processes are more or less directly associated with the post-glacial climate shift in the Holocene. One can therefore conclude that the present-day distribution of species ranges in the Helicidae *s.l.* was significantly shaped in this relatively short period, despite the proverbial immobility of the taxon. Another conclusion is the relative independence of distributional range size from characters inherent to the species like shape, habitat preference or active dispersal capacity. The relation to rather historic – that is, unpredictable – processes indicates that the current global warming, together with the increasing mobility of persons and goods, may trigger significant yet unpredictable transformations of land snail range sizes in the future.

ACKNOWLEDGEMENTS

I thank Sid Staubach for the literature search on active dispersal capacities of land snails. Constructive comments and suggestions from Tim Blackburn, Robert Cameron and Frédéric Magnin improved the manuscript. The study was performed with financial support of the DFG (grant no Pf390/1).

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