

## Does habitat use explain large scale species richness patterns of aquatic beetles in Europe?

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Regularities in species richness are widely observed but controversy continues over its mechanistic explanation. Because richness patterns are usually a compound measure derived from taxonomically diverse species with different ecological requirements, these analyses may confound diverse causes of species numbers. Here we investigate species richness in the aquatic beetle fauna of Europe, separating major taxonomic groups and two major ecological types, species occurring in standing and running water bodies. We collated species distributions for 800+ species of water beetles in 15 regions across western Europe. Species number in any of these regions was related to three variables: total area size, geographic connectedness of the area, and latitude. Pooled species numbers were accurately predicted, but correlations were different for species associated with either running or standing water. The former were mostly correlated with latitude, while the latter were only correlated with the measure of connectedness or with area size. These differences were generally also observed in each of the four phylogenetically independent lineages of aquatic Coleoptera when analysed separately. We propose that effects of habitat, in this case possibly mediated by different long term persistence of running and standing water bodies, impose constraints at the population or local level which, if effective over larger temporal and spatial scales, determine global patterns of species richness.

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Geographic patterns of species richness, such as the species–area relationship or latitudinal gradients, are among the best documented and most robust ecological regularities (Arrhenius 1921, Preston 1962, Williams 1964, MacArthur and Wilson 1967, Lawton 1999). Numerous studies attempted to establish the underlying causal mechanisms from counts of species numbers and their statistical correlates at regional and global scales (see Ricklefs and Schluter 1993, Brown 1995, Rosenzweig 1995, Gotelli and Graves 1996, for reviews). This practice ignores the possible heterogeneity of the data set due to the inclusion of divergent ecological and taxonomic groups, and rarely establishes a link to the local level where many of the processes regulating species richness are likely to operate (Brown 1999,

Huston 1999, Rohde 1999, Gaston and Blackburn 1999), although recently a few examples have been provided where habitat-related variables are included in the interpretation of macroecological patterns (Rohde and Heap 1998, Holt et al. 1999, Roy et al. 2000, Bellwood and Hughes 2001, Crawley and Harral 2001). The role of habitat constraints in shaping the evolution of species traits has received substantial attention (Southwood 1977, 1988, Korfiatis and Stamou 1999), but the possibility that they also determine large scale patterns of species distribution has been much less explored.

To explore the possible role of habitat constraints in determining large scale diversity patterns it would be necessary to select a group of organisms occupying two

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contrasting habitat types, where habitat association differ between closely related species. The inclusion of close sister species, or species groups, in the comparison keeps confounding historic factors to a minimum. If, in addition, both habitat types occur side-by-side along a latitudinal gradient, and in roughly equal spatial distributions, many large-scale geographical and climatic variables are also fixed across groups and can be ruled out for explaining observed differences.

Here we provide some intriguing observations from such a system. We conducted a detailed investigation of species richness for the entire fauna of aquatic Coleoptera across western Europe. Aquatic beetles can be categorised by their main habitat association into those that occur in standing (lentic) and running (lotic) waters, with comparatively few species able to inhabit both habitats (Foster et al. 1992, Larson 1997a, b, Ribera and Vogler 2000). Differences in habitat occur at all phylogenetic levels, often among sister species, or groups of closely related species. Moreover, the Coleoptera have colonised the aquatic medium several times independently and hence disparate groups of beetles provide a number of independent evolutionary replicates.

This provides an opportunity to investigate how various factors determining large scale diversity patterns are affected by habitat. We compare species richness in lotic and lentic habitats across a latitudinal gradient in western Europe, introducing only two predictive variables other than habitat: total area and a rough measure of the ease of dispersion across areas. Both area and dispersal are fundamental variables in any neutral model of large scale diversity patterns (Hubbell 2001).

## Material and methods

### Data

We compiled species numbers of aquatic Coleoptera for 10 countries of western Europe plus the five largest western European islands from recent checklists, which were completed and updated if necessary (see Appendix for the complete dataset and associated references). Only a small fraction of the whole European surface area was not included in the analysis, but faunas in these regions have a very low degree of endemism and hence should not affect general conclusions.

Habitat data were obtained from published sources and validated by water-beetle specialists (see Acknowledgements). "Running water" was considered to include all water bodies associated with rivers or streams, even if the actual flow is weak or occasionally nil, such as in residual pools in dry periods. Species were assigned to one category (running or standing) according to their main habitat association, ignoring occasional findings in a different habitat, particularly for wide-

spread common species (see Ribera and Vogler 2000 for more details on habitat choice criteria).

Three geographical parameters were used to predict species numbers: total area size (Area), southernmost latitude of a geographic area (sLat) and the extent of the land connection to adjacent areas ("Connectivity", Con). Area refers to the total size of a country or island; using politically defined areas as a sampling unit means that areas of arbitrary dimension and shape are the basic units of this analysis. While a coarse measure, it ensures the inclusion of diverse regions reducing possible biases due to differences in the prevalence of some habitat types, or other possible unknown factors (see Discussion). Statistical correlations with latitude were based on the southern-most point of each region, as this will be the highest value of a variable that decreases with latitude. Other measures (e.g. latitudinal range, average latitude) were used in preliminary analyses, but proved to have significantly less explanatory power. The coarseness of the measure will bias the results only if the variables for which latitude is a surrogate vary differently for running and standing water habitats along the explored gradient.

"Connectivity" is a measure of the maximum interception profile that a region would offer to the species flow across Europe known to have taken place during the Pleistocene (Coope 1994) (i.e. the width of the "gate" for faunal interchange). The connectivity of regions within mainland Europe (France, Germany, Holland and Finland) was the maximum linear length within the country (and not the actual length of the border, as its shape is irrelevant for the magnitude of the species flow across the region). In peninsulas, connectivity is the width of the land connection with the mainland: for Iberia the length of the Pyrenean chain, for Sweden and Norway the lowest distance between the Gulf of Bothnia and the Barents Sea, and for Italy the length of an arc defining its northern border. Britain was considered a peninsula with a connectivity value of 250 km, the distance between Norfolk and East Sussex, corresponding approximately to the connection with the mainland after the last glaciation (Lambeck 1991). If Britain was considered an island, its number of species was consistently underestimated but this did not affect the overall conclusions of the detected patterns. For Denmark the measure of connectivity was the cross-section of the mainland plus the islands of Fyn and Sjaelland which were connected to the mainland after the last glaciation (250 km), and the value for Area was that of the entire surface of the country.

### Statistical analysis

Area, connectivity and number of species were log-transformed in all analyses. In the analyses including all

regions, islands were considered to have a logCon of zero, which, at the scale used, implies an arbitrary corridor width of 1 km. The log-transformed variables were not significantly different from a normal distribution, with the exception of logCon which had a bimodal distribution when islands were included, as measured with a Chi-squared test (Sokal and Rohlf 1995). sLat was not correlated with logArea or logCon; logArea and logCon were correlated for all regions and for mainland ( $r^2 = 0.67$  and  $r^2 = 0.41$  respectively,  $p < 0.05$ ). Multiple stepwise regression models were constructed by forward selection (Sokal and Rohlf 1995). The variable with the highest correlation was introduced first, and the residuals were regressed with the variable with the next highest correlation until the new regression was no longer significant. Multiple regression was used to check if the inclusion of all variables significantly improved the explained variance even if some of them did not have a significant correlation when tested individually. Asymptotic non-linear regression models (e.g. negative exponential, Colwell and Coddington 1994, He and Legendre 1996), or the Weibull model (a modified negative exponential with two additional parameters, Brown and Mayer 1998) did not significantly improve the correlation with the independent variables, as computed with the Levenberg-Marquardt method implemented in CurveExpert 1.3.

## Results

The western European fauna of water beetles included a total of 813 species, and numbers in the fifteen areas used in our analysis were between 141 in Mallorca and

478 in Italy (Table 1). The overall numbers of species in running and standing water across Europe were similar, although in all regions the number of lentic species exceeded that of the lotic, the only exception being the Iberian peninsula (Table 1). Total species number in the fifteen regions was predicted with extreme accuracy based on the three geographical parameters (Table 2). All three variables added significant independent information, as measured by a stepwise least-square regression model, with area contributing the strongest information. Thus, species numbers in any given region are to a very large degree explained by only three variables, the size of the area under consideration, the ease of access for dispersing species, and the latitude.

When the species pool was separated according to the two main ecological types (lotic and lentic), species numbers were still predicted with high accuracy, although the contribution of the three parameters changed dramatically. For lotic species the only significant variable was latitude (Table 2 and Fig. 1). However, when all three variables were used in a combined model the correlation was significantly better than with latitude alone, indicating that area and connectivity provided useful information. For lentic species, the main explanatory variable, and the only one included in the stepwise model, was connectivity (Table 2 and Fig. 1). The regression of the number of species in the category occurring in running plus standing water was very similar to that of the total species pool (Table 2).

To avoid the possible bias introduced by the joint analysis of mainland and island faunas, in particular with regard to connectivity, the ten mainland areas were analysed separately. For the pooled species, latitude and connectivity alone explained 98% of the vari-

Table 1. Number of species and geographical variables used in the analysis. Area (km<sup>2</sup>); sLat: southernmost latitude (degrees); Con: length of the connection with mainland ("connectivity") (km); S: total number of species; run: number of running water species; sta: number of standing water species; run and sta: species in both type of habitats; unkn: species of unknown habitat.

Region	Predictive variables			number of species										
	Area	sLat	Con	total S	by habitat				by phyletic lineage					
					run	sta	run and sta	unkn	Hydra-dephaga	Hydro-philoidae	Dryo-poidea	Hydrae-nidae	Myxo-phaga	
Britain	227 937	50.0	250	248	43	142	63	0	145	61	13	29	0	
Denmark	42 532	54.5	250	245	33	162	50	0	150	56	20	19	0	
Finland	356 145	60.0	1025	243	29	167	47	0	168	48	10	17	0	
France	543 255	42.5	925	460	145	207	105	3	212	101	49	95	3	
Germany	352 261	47.5	750	358	89	190	79	0	180	84	39	54	1	
Holland	34 174	51.3	300	272	47	155	70	0	142	68	30	32	0	
Iberia	589 806	36.0	390	469	220	144	105	0	184	105	44	134	2	
Italy	297 702	38.0	750	478	174	193	106	5	208	93	40	134	3	
Norway	320 463	58.0	518	219	25	150	44	0	153	44	9	13	0	
Sweden	444 582	55.0	518	273	32	185	56	0	181	57	16	19	0	
Corsica	8622	41.3	1	192	55	81	54	2	92	46	20	32	2	
Ireland	83 451	51.5	1	180	31	104	45	0	108	44	4	24	0	
Mallorca	3640	39.3	1	141	32	67	42	0	70	43	6	22	0	
Sardinia	23 811	39.0	1	237	65	110	59	3	120	55	17	43	2	
Sicily	25 403	36.5	1	235	85	95	55	0	115	47	18	54	1	
All	3881 781			813	346	307	151	9	352	150	57	250	4	

Table 2. Values of  $r^2$  for the regression models on the number of species separated by habitat. Entries are the  $r^2$  of the regression of the logarithm of the number of species in a forward stepwise analysis (see Methods). The order of inclusion of variables coincide with the magnitude of  $r^2$ , with the exception of running and standing species in the analysis including all areas, in which the order is indicated in brackets. The "combined" column shows the  $r^2$  of the model with all significant variables in a single multiple regression, indicated as "-" when only one variable was significant. Correlations with sLat are negative, all other correlations are positive. F and sig. F value and significance of the F-associated distribution for the combined analysis or, when only one variable was significant, for this single regression. logArea (km<sup>2</sup>). sLat: southernmost latitude (degrees). logCon: log of the connectivity value (km). DF: degrees of freedom (regression and residual). n.s.: not significant at a  $p < 0.05$  level.

	R <sup>2</sup>				F	p
	logArea	sLat	logCon	Combined		
<b>All areas (n = 15)</b>						
All species	0.52	0.50	0.40	0.91	37.86	<0.00001
Running	n.s.	0.56	n.s.	*0.93	48.87	<0.000001
Standing	n.s.	n.s.	0.84	-	69.32	<0.000001
Running and standing	(1) 0.27	(2) 0.58	(3) 0.42	0.88	26.26	<0.0001
DF	1 and 13	1 and 13	1 and 13	3 and 11		
<b>Mainland (n = 10)</b>						
All species	n.s.	0.88	0.79	0.98	138.71	<0.00001
Running	n.s.	0.95	0.71	0.99	256.59	<0.000001
Standing	n.s.	n.s.	0.51	-	8.21	<0.05
Running and standing	n.s.	0.93	n.s.	-	101.74	<0.00001
DF	1 and 8	1 and 8	1 and 8	2 and 7		

\*Combined model including sLat, logArea and logCon.

ance in species numbers, after which the effect of area was not significant (Table 2). Forcing latitude and area as predictive variables resulted in a decreased explanatory power of 8%. When species were separated according to main ecological types the two groups showed, again, different correlations: lotic species were highly correlated first with latitude and then connectivity, but lentic species only with connectivity. The effect of area, after taking into account the other variables, was not significant for any of them (Table 2), and its enforcement instead of connectivity always resulted in a loss of explanatory power.

Due to their low number, results for the five islands have to be interpreted with caution, although they clearly suggest differences of correlates of species richness in running and standing water in line with those observed in mainland faunas. The number of lotic

species was highly significantly correlated with total area ( $r^2 = 0.78$ ,  $p < 0.05$ ). Numbers of lotic species were not significantly correlated with any of the variables due to the disproportionately low species richness of Mallorca, with the smallest area. If Mallorca is excluded, the correlation of the number of lotic species with latitude became highly significant ( $r^2 = 0.98$ ,  $p < 0.01$ ), in accordance with the observations for mainland species. When the number of lotic species was regressed with latitude after removal of the effect of area and connectivity, the slopes of the regression lines for mainland and islands were not significantly different (within 95% confidence intervals), with a lower intercept for islands (residuals of the regression of mainland running water species with area and connectivity =  $-0.04sL + 1.9$ ,  $r^2 = 0.93$ ; residuals of the regression of island running water species with Area =  $-0.03sL + 1.4$ ,  $r^2 = 0.85$ ). This suggests that the number of lotic species on islands is generally determined by the same factors as on the mainland, but the consistently lower level may be due to an additional insularity effect not accounted for by the zero value of the variable measuring connectivity. When a dummy insularity factor was introduced with value "1" for islands and "0" for mainland, the regression of latitude with the residuals of the regression of the number of lotic species with logArea and logCon increased from  $r^2 = 0.73$  (Fig. 1) and residuals of the islands significantly lower than those of mainland (one-tailed t-test,  $p < 0.05$ ), to  $r^2 = 0.91$  and residuals of islands and mainland not significantly different.

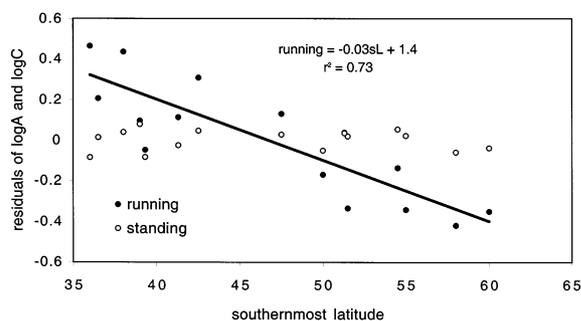


Fig. 1. Relationship between number of species and latitude. In the Y axis, the residuals of the regression of log(number of species) with logArea and logCon. The regression of the standing water species with southernmost latitude was not significant.

The total species pool was also divided according to the phylogenetically independent lineages of aquatic beetles. There have been at least five independent invasions of the Coleoptera into the aquatic medium, in-

Table 3. Results of the combined regression models on the total number of species separated by monophyletic groups.  $r^2$ : value of the regression of the combined model, including logArea, sLat and logCon for all 15 regions (the low number of species in Myxophaga did not allow a separate analysis); F and sig. F: value and significance of the F-associated distribution of the combined model (DF: 3 and 11); +: significant values ( $p < 0.05$ ) of the coefficients of the individual variables in the multiple regression model, as measured with a t-function. In brackets, marginally significant values ( $p < 0.1$ ); other variables as in Table 2.

	Number of species					Regression values					
	S	run	sta	run and sta	unkn	$r^2$	F	p	logArea	sLat	logCon
Hydradephaga	352	95	185	70	2	0.91	36.52	<0.0001	+	(+)	+
Hydrophiloidea	150	27	83	40	0	0.87	24.07	<0.0001	-	+	+
Dryopoidea	57	45	4	8	0	0.75	10.80	<0.01	-	+	+
Hydraenidae	250	176	35	32	7	0.91	39.19	<0.0001	+	+	(+)
Myxophaga	4	3	0	1	0						

cluding the Hydradephaga (families Gyrinidae, Haliplidae, Noteridae, Hygrobiidae and Dytiscidae), Hydrophiloidea (families Helophoridae, Spercheidae, Hydrochidae, Georissidae and Hydrophilidae), Dryopoidea (families Elmidae and Dryopidae) and Myxophaga (families Microsporidae and Hydroscaaphidae). Each of these lineages (Myxophaga was not analysed separately because of their low species numbers) showed a significant correlation with the combined predictive variables (ranging from  $r^2 = 0.75$  to  $r^2 = 0.91$ , Table 3), indicating that the correlation of species richness patterns can be detected in evolutionarily independent subsets of the species pool. If further divided according to main habitat type, lotic species of the four taxonomic groups were significantly and negatively correlated with latitude (Table 4). Lentic species were significantly and positively correlated with connectivity and area, with the exception of Hydraenidae, for which species numbers were correlated with latitude only (although with a lower value than lotic species in this group). It is interesting to note that for species occurring in both habitats types, those of Hydradephaga and Dryopoidea had correlations very similar to the ones occurring in standing water only, while those of Hydraenidae and Hydrophiloidea had correlations similar to the ones occurring in running water only (Tables 3 and 4). This suggests that these species do not form an ecologically uniform group, and species richness may follow a pattern predominant in either one or the other two main habitat types.

The nested species–area accumulation curve for all species across all areas had a z value of 0.26 ( $r^2 = 0.67$ ), almost precisely the canonical value of Preston (Preston 1962, May 1975, Leitner and Rosenzweig 1997) (Fig. 2). Again, the heterogeneity of the data set is manifest when species are split according to their habitat: for lotic species  $z = 0.38 \pm 0.08$ , and for lentic species  $z = 0.21 \pm 0.01$  ( $\pm 95\%$  confidence intervals). The curve also has a much higher variance for lotic species, as measured by total variance of the data points, variance of the residuals, or 95% confidence intervals of the parameters of the regressions. Differences in the species

accumulation curves indicate a higher spatial turnover of lotic species, i.e. species have smaller distributional ranges on average, with large differences in the accumulated number of species depending on the initial area in the analysis. Lentic species, on the contrary, have much lower spatial turnover rates, with accumulated areas quickly reaching a large proportion of the total species pool, owing to their generally larger ranges (Fig. 2).

## Discussion

### Parameters determining species richness

Our results show strongly significant differences in the patterns of species richness across Europe depending on the species' main habitat type. The number of species in standing waters, with larger ranges, was mostly correlated with connectivity (or area size on islands), after which the correlation with area and latitude was not significant. On the contrary, the number of species in running water, with on average smaller ranges, was

Table 4. Correlation of the predictive variables with the number of species separated by habitat type and monophyletic group. Values are correlation coefficients ( $r^2$ , sign of the negative correlations included for convenience) using all 15 regions. n.s.: not significant at a  $p < 0.05$  level; other variables as in Table 2.

	logArea	sLat	logCon
running			
Hydradephaga	n.s.	0.58 (-)	n.s.
Hydrophiloidea	n.s.	0.64 (-)	n.s.
Dryopoidea	n.s.	0.28 (-)	n.s.
Hydraenidae	n.s.	0.87 (-)	n.s.
standing			
Hydradephaga	0.71	0.33	0.77
Hydrophiloidea	0.50	n.s.	0.66
Dryopoidea	0.25	n.s.	0.52
Hydraenidae	n.s.	0.45 (-)	n.s.
running and standing			
Hydradephaga	0.48	n.s.	0.37
Hydrophiloidea	n.s.	0.30 (-)	n.s.
Dryopoidea	0.25	n.s.	0.48
Hydraenidae	n.s.	0.56 (-)	n.s.

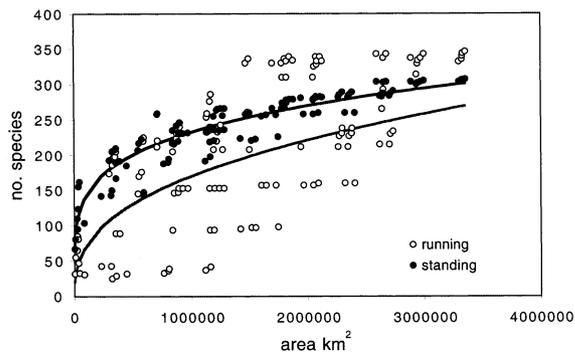


Fig. 2. Nested species–area accumulation curves for standing and running water species (see text for values of the regression lines). Curves were constructed by successively adding the nearest region to each of the 15 initial regions, thus maintaining geographical integrity and minimising species turnover (Palmer 1990, Condit et al. 1996, Crawley and Harral 2001). A simple power model ( $S = cA^z$ ) (Arrhenius 1921) was fitted to the data points obtained from combining the 15 accumulation curves, excluding those that were repeated (121 for running or standing water species, 130 for all pooled species; results using all 225 points were very similar). Asymptotic models did not significantly increase the correlation or reduce the standard error. The standing water species curve (black) has a lower dispersion than the running water species curve (grey), and a higher proportion of the total number of species is reached with smaller areas.

mostly correlated with latitude (and connectivity when only mainland was considered).

The strength of the statistical correlations is surprising, given the small number of data points and the rather crude measures of geographic distributions in the analysis. However, whereas the limited number of data points in our analyses possibly results in the loss of statistical power, any significant correlation is also more robust (Sokal and Rohlf 1995) and hence strengthens the validity of the findings.

In interpreting the results the high correlation between area and our measure of connectedness has also to be taken into account. All significant correlations with connectivity were also significant with area, albeit at a different (usually lower) value. The choice of one or another was determined by the highest initial correlation in the step regression analysis, although it is always possible that underlying unknown factors are biasing these results (Sokal and Rohlf 1995).

The measures of total geographic distribution used here are a simplification, as they do not take into account the actual surface of running or standing waters, which may be quite different from the total land surface. However, the relation of freshwater area with suitable habitat is not a simple one, as both lotic and lentic water beetles tend to occur in small water bodies or only near the shores of larger ones. The main channel of large rivers and the area of large lakes, which could easily be derived from surface maps, are entirely unsuitable for water beetle species.

The use of total geographic area as a proxy of suitable area is fully consistent with standard practice in macroecology studies which generally derive regularities of species richness from total area (Brown 1995, Rosenzweig 1995, Hubbell 2001). Only if the amount of suitable running and standing water bodies varied markedly and consistently along the latitudinal gradient studied would the measure of total area introduce a bias in the comparison. This is difficult to assess given the problems with measuring the area of available habitat in either category. However, a test could be derived from the analysis of lotic vs lentic species richness patterns in other geographic areas. If independent regions, which are likely to have a different distribution of lotic and lentic habitats, would show similar richness patterns this would strongly argue against the possible bias in the amount of suitable habitat in either category as the reason of our observations. Although without a detailed quantitative analysis, both in Roughley and Larson (1991) and Larson (1997b) it is noted that in North America the number of lotic species decreases with latitude. The scarcity of lotic habitats in the north is explicitly discounted as a possible reason (Larson 1997b).

In addition, it is unlikely that differences in the species accumulation curves, and in the size of the geographical range, can be explained based solely on the existence of underlying gradients in the amount of suitable habitat. The combined effect of general smaller geographic ranges (Rappoport's rule, Rappoport 1982) and decreased abundance of standing water habitats in the south could produce this pattern, but differences in range size are also highly significant when only southern species are considered (Ribera and Vogler 2000, with water beetles of the Iberian peninsula).

The correlation with latitude in lotic species conforms to a well established pattern, and in this sense it is the lack of correlation of the standing water species that demands explanation. Our comparisons of lotic and lentic species which occur in habitats of the same latitudinal distributions, are of great value for testing existing explanations of species richness based on latitudinal geographic gradients. Parameters proposed to produce latitudinal differences in species richness such as differences in productivity or potential evapotranspiration (Brown 1995, Rosenzweig 1995), are difficult to reconcile with our findings, as it will be necessary that standing waters are not affected by these variables, or if they are, that lentic species do not respond to these latitudinal differences. Similarly, a supposed increase in habitat heterogeneity at lower latitudes (Brown 1995, Rosenzweig 1995) could only explain the smaller average ranges and higher spatial turnover of lotic species if this heterogeneity affects only running, but not standing, water bodies.

Finally, explanations for the differences in overall area sizes and latitudinal gradients based on ecological

or physiological differences between phylogenetically defined groups are not plausible because the split between running and standing water habitats is not along higher taxonomic groups, and in fact habitat switches occur many more times among closely related species even within the same genus (only 6 of the 33 genera with more than 5 species had no variation in habitat type).

### **An alternative explanatory framework for the regularities of species richness**

An alternative explanation can be advanced if we consider possible differences in the long term mobility of the populations in both types of habitat. The higher  $z$  (indicating low geographical turnover) and larger range size of the species in standing compared to running water point to dispersal as being fundamental in explaining their respective species richness. Connectivity, a parameter that reflects the geographical constraints to dispersal, predominantly affects the number of lentic species, which appears to be determined mostly by their propensity to reach a given location. On the contrary, lotic species richness is predominantly correlated with latitude. This can be interpreted in the context of the palaeoclimatic history of Europe: species with comparatively low dispersal power will tend to be slow colonisers, and consequently can be predicted to be poorly represented in recently deglaciated regions (such as northern Europe) compared to areas that may have provided refugia (e.g. the Mediterranean, Hewitt 1999). For poorly dispersing species latitudinal gradients can be interpreted as a function of the distance to glacial refugia (Hewitt 1999, Dynesius and Jansson 2000) and of geological time during which a landscape has existed under largely stable conditions ("effective evolutionary time", Rohde 1999).

This leaves the question as to why dispersal power differs between species inhabiting running or standing waters. Small to medium standing water bodies, such as those typically inhabited by aquatic beetles, are generally short-lived and discontinuous in time and space. In contrast, rivers and streams persist over geological periods, exhibiting spatial and temporal continuity despite changes in the exact location of the channel. We have suggested that the high rates of habitat turnover make the continuity of lentic populations strongly dependent on migration and dispersal, whereas lotic populations can persist without long-distance dispersal (Ribera and Vogler 2000, see also Dynesius and Jansson 2000). As a macroecological consequence, lentic species should exhibit high spatial mobility, larger ranges and low evolutionary turnover rate, while lotic species should tend to have smaller ranges, be genetically isolated, and show higher species turnover (i.e., higher probability of speciation and extinction) (Dynesius and Jansson 2000, Hubbell 2001).

This explanation of observed species richness patterns is still lacking strong factual support, but it has wide implications (see above and Ribera and Vogler 2000) and it is straightforward to test. A first obvious step would be to search for similar patterns among other freshwater organisms. Preliminary results show that for the western European Hydracarina, Rotifera and Mollusca standing water species have larger distributional ranges than running water species, with only Odonata not showing significant differences. Similarly, in all cases but Rotifera running water species were mostly related with latitude, and standing water species more correlated with either area or connectivity (T. Meyer unpubl., and Ribera et al. unpubl.). Species richness patterns in a range of entirely unrelated organisms thus seem affected in the same way, with the lotic-lentic divide as the only variable affecting all of them.

Our data show the complex relationships between large scale diversity patterns and the ecological characteristics of the species, and point to the necessity of considering possible ecological differences when documenting and interpreting these patterns.

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