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Published in:
Global Ecology and Biogeography

DOI:
[10.1111/j.1466-8238.2008.00394.x](https://doi.org/10.1111/j.1466-8238.2008.00394.x)

Publication date:
2008

Document version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
Hof, C., Brändle, M., & Brandl, R. (2008). Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. *Global Ecology and Biogeography*, 17(4), 539-546.
<https://doi.org/10.1111/j.1466-8238.2008.00394.x>

RESEARCH
PAPER



Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types

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ABSTRACT

Aim We analysed the variation of species richness in the European freshwater fauna across latitude. In particular, we compared latitudinal patterns in species richness and β -diversity among species adapted to different habitat types.

Location Europe.

Methods We compiled data on occurrence for 14,020 animal species across 25 pre-defined biogeographical regions of European freshwaters from the *Limnofauna Europaea*. Furthermore, we extracted information on the habitat preferences of species. We assigned species to three habitat types: species adapted to groundwater, lotic (running water) and lentic (standing water) habitats. We analysed latitudinal patterns of species richness, the proportion of lentic species and β -diversity.

Results Only lentic species showed a significant species–area relationship. We found a monotonic decline of species richness with latitude for groundwater and lotic habitats, but a hump-shaped relationship for lentic habitats. The proportion of lentic species increased from southern to northern latitudes. β -Diversity declined from groundwater to lentic habitats and from southern to northern latitudes.

Main conclusions The differences in the latitudinal variation of species richness among species adapted to different habitat types are in part due to differences in the propensity for dispersal. Since lentic habitats are less persistent than lotic or groundwater habitats, lentic species evolved more efficient strategies for dispersal. The dispersal propensity of lentic species facilitated the recolonization of central Europe after the last glaciation. Overall, we stress the importance of considering the history of regions and lineages as well as the ecological traits of species for understanding patterns of biodiversity.

Keywords

β -Diversity, dispersal, Europe, freshwater, glaciations, history, latitude, species richness.

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INTRODUCTION

Although it has been known about for more than 200 years, the decrease of species richness with latitude is still poorly understood (Fischer, 1960; for recent reviews see Willig *et al.*, 2003; Hillebrand, 2004; Mittelbach *et al.*, 2007). Besides the mid-domain effect (Colwell & Lees, 2000), three classes of hypotheses have been proposed to explain this pattern: (1) the species–energy hypothesis, which states that species richness is determined by energy availability (Currie, 1991; Hawkins *et al.*, 2003); (2) the species–area hypothesis, which points to the importance of space for species richness (Terborgh, 1973; Rosenzweig, 1995); and (3)

the historical hypothesis which emphasizes the importance of history, in particular climatic fluctuations (Fischer, 1960; Dynesius & Jansson, 2000; Graham *et al.*, 2006). In Europe the climatic fluctuations during the Pleistocene had dramatic impacts on diversity patterns, since the east–west orientation of the major mountain ranges impeded rearrangements of distributional areas in response to climatic fluctuations (see, e.g., Whittaker *et al.*, 2007, and references therein).

Habitat is an important template for the evolution of species traits, in particular for dispersal ability (Southwood, 1962; 1977). For freshwater ecosystems, studies initiated by I. Ribera and co-workers highlighted the importance of interactions between

habitat stability, dispersal ability and patterns of species distributions (Ribera & Vogler, 2000; Ribera *et al.*, 2001, 2003; see also Hof *et al.*, 2006; Marten *et al.*, 2006; Ribera, 2008). Our study is an extension of this work covering a broader range of taxonomic groups and habitat types and analyzing β -diversity among biogeographical regions. It is, like the foregoing investigations, based on the following hypothetical framework: On geological time-scales lentic habitats (standing waters) are less stable than lotic (running waters) or groundwater habitats (Gibert *et al.*, 1994; Dobson & Frid, 1998; Griebler & Mösslacher, 2003; Ribera, 2008). The majority of the larger lakes in Europe, for instance, date back to the Pleistocene (Schwoerbel, 1999). On the contrary, several European river systems originated in the Mesozoic (Hantke, 1993). Depending on size, lentic waters may even disappear within decades as sediments accumulate in the basins (Hutchinson, 1957; Harper, 1992). Overall, lentic habitats are likely to vanish within shorter periods of time than lotic habitats. Hence, one would expect species living in lentic habitats to be characterized by a higher propensity for dispersal than species living in lotic or groundwater habitats (Dobson & Frid, 1998; Ribera & Vogler, 2000; Ribera *et al.*, 2003; Marten *et al.*, 2006; Ribera, 2008).

From this, we deduce two predictions concerning latitudinal patterns of species richness and β -diversity in European freshwater

animals. Firstly, if lentic species have a higher propensity for dispersal, they should have more rapidly recolonized central and northern regions. Hence we expect that species richness of lentic habitats should decrease with latitude at a lower rate compared with lotic or groundwater habitats. This implies also that the proportion of lentic species increases with latitude. Furthermore, dispersal influences species turnover (β -diversity) (Soininen *et al.*, 2007a,b). Therefore, we secondly expect lower levels of β -diversity among regions for lentic compared with lotic and groundwater species.

METHODS

The data for the present analyses were extracted from the *Limnofauna Europaea* (Illies, 1978). The biogeographical regions of Europe outlined in this book were used for all analyses (Table 1). For each region, data on latitude (northern and southern boundary), longitude (western and eastern boundary) and maximum altitude were compiled from <http://earth.google.com/>. From this information we calculated the mean latitude and longitude of each region. Areas of regions were estimated by weighing pieces of paper cut from a copied map. Note that four of the 25 regions are open at their eastern border, which may

Table 1 Geographical data and species richness of all habitats, and of the different habitat types of the 25 biogeographical regions of Europe as defined in the *Limnofauna Europaea* (Illies, 1978).

Region code	Region	Latitudinal centre (°N)	Longitudinal centre (°E)	Maximum altitude (m)	Area (km ²)	Species richness			
						All habitats	Groundwater habitats	Lotic habitats	Lentic habitats
IBE	Ibero-Macaronesian region	38.23	-12.24	3717	560,736	2543	99	633	741
PYR	Pyrenees	42.53	0.54	3404	49,548	1684	82	510	395
ITA	Italy, Corsica and Malta	40.98	12.97	3380	264,311	3284	135	709	1018
ALP	Alps	45.81	10.82	4808	210,580	4479	96	989	1426
DIN	Dinaric western Balkans	44.37	17.71	2656	161,032	2543	170	683	682
HEL	Hellenic western Balkans	39.13	23.76	2917	173,419	2258	100	566	729
EAB	Eastern Balkans	41.73	25.07	2925	177,548	2161	74	564	623
WEH	Western highlands	47.36	5.53	1886	156,903	2776	101	706	888
CEH	Central highlands	49.74	12.50	1602	260,129	4922	133	927	1717
CAR	Carpathians	47.15	22.07	2655	185,806	3842	130	884	1112
HUN	Hungarian lowlands	46.48	19.72	500	169,290	3187	67	421	1098
PON	Pontic province	45.83	30.18	1545	264,258	2819	50	345	939
WEP	Western plains	46.90	0.61	1000	404,644	3690	106	609	1280
CEP	Central plains	55.17	9.27	500	540,902	5465	77	627	2213
BAP	Baltic province	56.93	24.23	318	210,580	3163	13	347	1263
EAP	Eastern plains	53.48	38.66	1000	2,320,511	3792	27	445	1442
IRE	Ireland and Northern Ireland	53.39	-8.01	1041	82,580	1669	9	249	691
GBR	Great Britain	56.16	-3.44	1344	235,354	3490	33	492	1350
ICE	Iceland	64.91	-19.02	2110	103,226	475	2	28	204
BOR	Borealic uplands	64.13	13.06	2469	309,677	2153	4	276	1004
TUN	Tundra	71.53	44.68	1590	330,219	1365	6	193	540
NSW	Northern Sweden	64.60	17.44	1200	231,225	1954	12	254	849
TAI	Taiga	63.03	39.71	1000	1,606,190	2896	9	312	1221
CAU	Caucasus	42.12	44.07	5642	363,354	2089	65	391	606
CAS	Caspic depression	48.08	47.03	500	627,612	1591	5	144	532

introduce some bias due to the distribution of singletons or the calculation of areas. All these areas are located in the European part of Russia. Therefore, we used the Ural Mountain chain as the eastern boundary of these regions. It is well known that the Ural Mountains act as a biogeographical boundary, which is not crossed by most of the species occurring in central Asia or Siberia.

For each region we compiled species presences or absences. The taxonomy as well as recent changes in species names were updated using the Fauna Europaea Web Service (2004). Our initial compilation listed 14,457 species, and after considering taxonomic changes and uncertain species the final list comprised 14,020 species of fish, annelids, water mites, crustaceans, insects, molluscs, nematodes, rotifers, flatworms and several taxa of fewer than 150 species (for an overview on species numbers of these major taxonomic groups, see Table S1 in Supplementary Material). The *Limnofauna Europaea* provides information of the habitat requirements for most of the species listed. From the more than 40 habitat categories given in the *Limnofauna* we grouped species into three major habitat types: groundwater, lotic (running waters from springs to large streams) and lentic habitats (standing waters from phytotelmata to large lakes). For a number of reasons we had to exclude 46% of the total species pool: (1) we had to exclude the 2663 species for which no habitat preferences were available; (2) we excluded 1958 generalists for which a habitat assignment was impossible; (3) we excluded 1025 parasitic species, as they rather rely on a specific host than on a certain type of habitat; (4) we excluded the 476 species occurring in brackish waters or with very special habitat requirements (e.g. leaf miners of aquatic plants, species living in mosses like tardigrades etc.).

Geographical variables and species richness of the different habitat types were tested for normality using the Kolmogorov–Smirnov test (StatSoft Inc., 2002). All variables except area approximated a normal distribution. Area was \log_{10} -transformed in all analyses, after which it also attained normality. We calculated simple linear regressions to test for the effect of area on species richness across the 25 regions. To analyse the relationship between species richness and latitude, we used multiple linear regressions. We always tested for the effect of latitude on species richness after correcting for all other geographical variables (for a visual inspection of the relationships between species richness and latitude, longitude, altitude and area see Fig. S1). The plot of species richness vs. latitude suggested a hump-shaped

Table 2 Slope and correlation coefficients for the relationship between species richness and area (\log_{10} -transformed) for the three different habitat types (simple linear regressions, $n = 25$).

Habitat type	Slope	R	P
Groundwater habitats	−29.16	0.044	0.32
Lotic habitats	−48.58	0.0050	0.74
Lentic habitats	+537.4	0.19	0.031

relationship. Therefore, we also included squared latitude as an independent variable in some analyses. To investigate the relationship between the proportion of lentic species and latitude, we used a multiple generalized linear model (binomial error term, logit link function, forward selection; Crawley, 2002). Patterns of β -diversity among regions were investigated by means of additive partitioning of species diversity (Crist *et al.*, 2003) for each of the three habitats. For this analysis, regions were grouped into four latitudinal bands according to their latitudinal centres (< 45° N, between 45° N and 50° N, between 50° N and 60° N, > 60° N; see Fig. 2). Areas of regions were used as weights.

RESULTS

We found a significant species–area relationship only for lentic habitats (Table 2). The relationship of species richness and latitude differed between lentic habitats compared with lotic and groundwater habitats. In the latter species groups, species richness declined monotonically with latitude, whereas lentic species exhibited a hump-shaped relationship (Table 3, Fig. 1, Fig. S2). Species richness of lentic species peaked in central Europe, within a region covering the Netherlands, the northern part of Germany, the southern part of Scandinavia and parts of Poland (region CEP, see Table 1 and Fig. 2). The proportion of lentic species increased significantly from southern to northern latitudes (deviance = 647.2, $P < 0.0001$; Fig. 3). Even after considering the other geographical variables this pattern remained significant (Table 4). Additive partitioning of species diversity revealed a decline of β -diversity from groundwater to lotic to lentic species (Fig. 2). Furthermore, for each of the three habitat types, β -diversity decreased from southern to northern latitudes (Fig. 2).

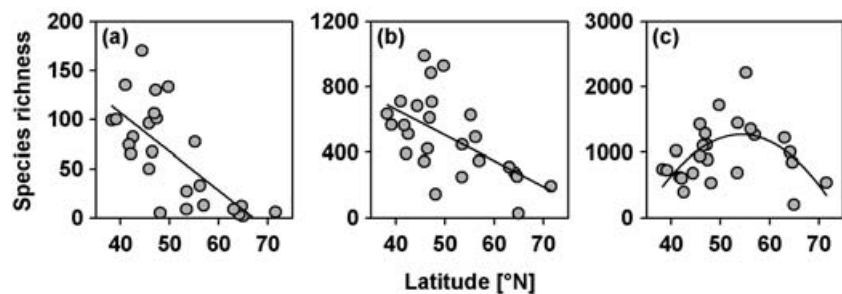


Figure 1 Relationship between latitude and species richness for freshwater species occurring within three different habitat types: (a) groundwater habitats, (b) lotic habitats, (c) lentic habitats. Each point represents the number of species occurring in the respective habitat within one of the 25 regions shown in Fig. 2.

Table 3 Multiple linear regressions of species richness for freshwater animals within 25 European biogeographical regions vs. geographical variables (type I sum of squares; StatSoft Inc., 2002) according to different habitat types. Significant relationships are indicated in bold.

	β	MSS	F	P		β	MSS	F	P
Groundwater habitats					Lentic habitats				
Area	0.001	2589	1.7	0.206	Area	0.48	894,966	6.8	0.017
Longitude	-0.13	557	0.37	0.551	Longitude	-0.18	289,230	2.2	0.154
Altitude	0.14	9485	6.3	0.021	Altitude	-0.037	225,321	1.7	0.206
Latitude	0.37	19,174	12.7	0.002	Latitude	5.4	73,866	0.56	0.462
Latitude ²	-1.0	349	0.23	0.636	Latitude ²	-5.4	820,983	6.3	0.022
Residuals		1510			Residuals		131,343		
Lotic habitats									
Area	0.15	7008	0.16	0.690					
Longitude	-0.17	39,051	0.91	0.352					
Altitude	0.31	222,965	5.2	0.034					
Latitude	2.8	289,894	6.8	0.018					
Latitude ²	-3.3	90,277	2.1	0.163					
Residuals		42,815							

MSS, mean sum of squares; β , standardized regression coefficient.

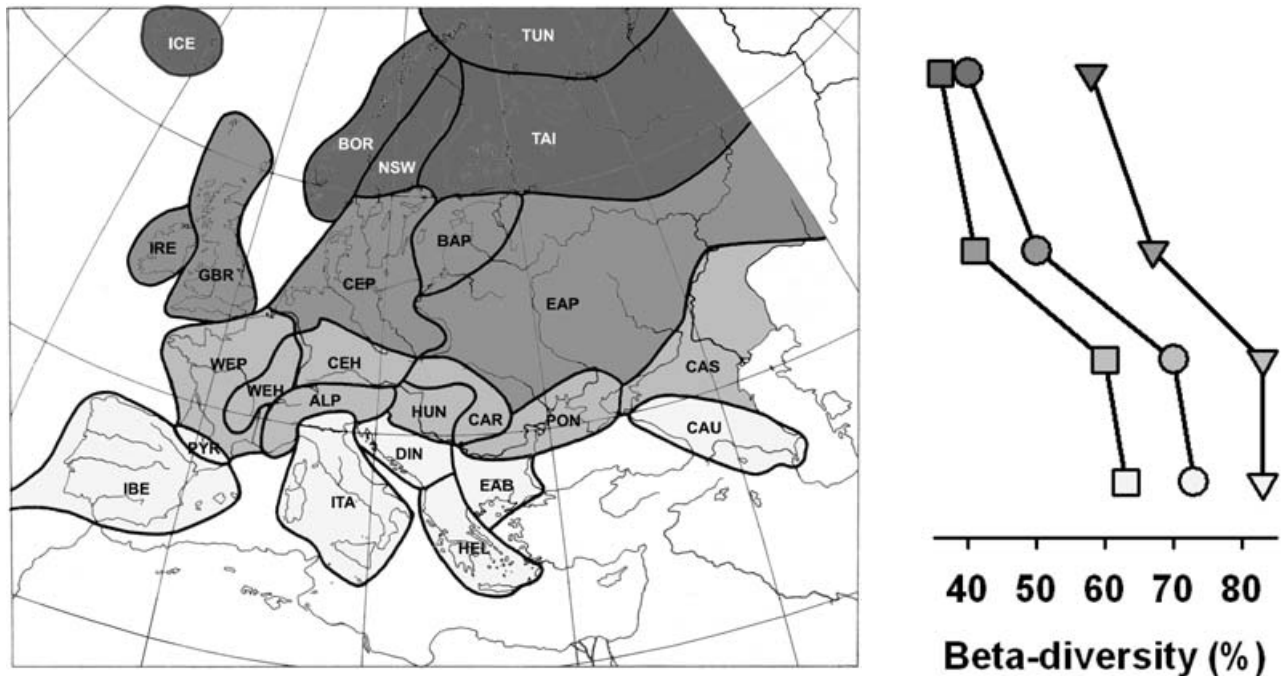


Figure 2 β -Diversity of freshwater animals within four bands of regions across Europe. We calculated β -diversity for each band and habitat using additive partitioning of species richness (Crist *et al.*, 2003). A value of 100% would indicate that all species occur in only one region of a band and a value of 0% that all species occur in all regions of a band. Regions of a band are marked by the same colour. β -Diversity decreased from groundwater species to lotic species for all four bands and β -diversity decreased with latitude for all habitat types (square, lentic habitats; circle, lotic habitats; triangle, groundwater). Region codes are listed in Table 1.

DISCUSSION

Our analyses showed (1) a monotonic decline of species richness with latitude for groundwater and lotic habitats, but a hump-shaped relationship for lentic habitats; (2) an increase in the proportion of lentic species with increasing latitude; and (3) a decline in β -diversity from groundwater to lotic to lentic habitats and from southern to northern latitudes.

The observed patterns in species richness might be caused by a variation in the sampling effort among regions (Bardgett *et al.*, 2005; Moerman & Estabrook, 2006). As many, if not most, ecologists and taxonomists reside in central Europe, the fauna of this region is very well known (Illies, 1966; Bardgett *et al.*, 2005). We argue that this bias does not sufficiently explain the observed variation of richness. First, since the fauna of groundwater habitats is not very well known (Gibert *et al.*, 1994; Griebler &

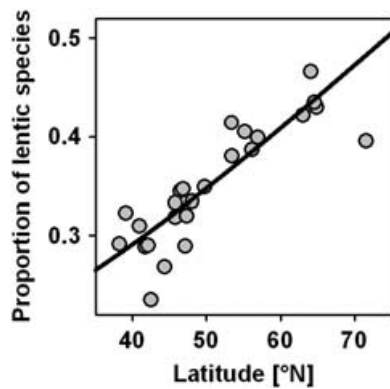


Figure 3 Proportion of lentic species in relation to latitude. Each point represents the proportion of species occurring in lentic habitats of the 25 regions shown in Fig. 2. The curve visualizes a generalized linear model (deviance = 647.2; $P < 0.0001$; $y = e^{-1.93 + 0.026 \times \text{latitude}} (1 + e^{-1.93 + 0.026 \times \text{latitude}})^{-1}$).

Table 4 Relationships between the proportion of lentic species within 25 biogeographical regions of Europe vs. geographical variables (multiple generalized linear model, binomial error term, logit link function, forward selection, Crawley, 2002, $n = 25$).

	Estimate	Deviance	<i>P</i>
Area	0.13	134	< 0.001
Longitude	-0.0029	16.9	< 0.001
Altitude	-0.000028	238	< 0.001
Latitude	0.037	324	< 0.01
Latitude ²	-0.00013	1.03	0.31

Mösslacher, 2003), sampling should particularly influence the species numbers within this group. However, species richness of the groundwater fauna declined with latitude (Fig. 1a). Second, the number of species recorded in only one sample (singletons) is a good indicator of the sampling effort (Novotný & Basset, 2000). In our case the number of singletons in a region has two components: species with a restricted geographical range (endemics) and species accidentally recorded in only one region. The latter is an indication of the sampling effort. If the hump-shaped pattern is a consequence of the extensive sampling in central Europe, then we would expect: (1) that species groups with a hump-shaped relationship have a high proportion of singletons; and (2) that there is also a hump-shaped relationship between the number of singletons and latitude. However, the hump-shaped relationship occurs in species adapted to lentic habitats (Table 3, Fig. 1c), which have a rather low proportion of singletons compared with lotic and groundwater species (Table S2). Furthermore, for all three species groups the number of singletons declines with increasing latitude (Fig. S3).

Although the areas of the biogeographical regions differed by a factor of more than 40 (Table 1), area was a poor predictor of species richness for species adapted to lotic and groundwater

habitats. One may argue that terrestrial surface area is not a good surrogate for area covered by freshwaters. For groundwater habitats, though, the terrestrial surface area roughly approximates habitat area, as groundwater is a type of freshwater habitat that should be available almost everywhere below the surface (Gibert *et al.*, 1994; Griebler & Mösslacher, 2003). However, for groundwater species, the relationship between species richness and area was negative (Table 2). If one accepts that our failure to find a species–area relationship for groundwater or lotic habitats is not due to a bias, the difference in the significance between lotic and lentic habitats becomes interesting. A non-significant relationship between area and species richness may be due to non-equilibrium conditions (MacArthur & Wilson, 1963; Ricklefs & Bermingham, 2004), which points to differences in the equilibrium conditions between groundwater and lotic vs. lentic biota. We will return to this point below.

Many papers have documented that species richness increases with several surrogates of energy available to the communities of plants or animals (Wright, 1983; Currie, 1991; Badgley & Fox, 2000; Hawkins *et al.*, 2003). Even if the geographical resolution of our data is not sufficient for a meaningful evaluation of the energy-availability hypothesis, the monotonic decline of species richness with latitude that was observed for lotic and groundwater habitats is consistent with a latitudinal decline of energy availability. Nevertheless, the surprising difference in the latitudinal variation of species richness among species adapted to different habitats rejects the energy-availability hypothesis as a *general* explanation.

We are aware of four possible explanations for the observed differences in diversity patterns among habitats: (1) evolutionary idiosyncrasies; (2) differences in habitat availability; (3) differences in the location of refugia; and (4) differences in the dispersal propensity of species among habitats. These are discussed in turn below.

(1) We pooled a wide variety of taxa with very different phylogenetic backgrounds. This could lead to differences in diversity patterns between habitats if certain taxa of species adapted to a particular habitat dominate certain regions. To investigate if such evolutionary idiosyncrasies are responsible for the decrease of species richness with latitude in lotic and groundwater habitats, we tested whether the observed correlations are expected by chance, i.e. whether the phylogenetic assignment drives the pattern. For this, we randomized habitat preference across species and calculated the correlation coefficient for the relationship between species richness and latitude (for a detailed explanation see Fig. S4). For both lotic and groundwater habitats, the correlation coefficient expected by chance was negative, but all simulated coefficients were larger than the observed coefficients. Consequently, evolutionary idiosyncrasies are not sufficient to explain the decrease of species richness with latitude.

(2) The availability of the habitat types across the 25 biogeographical regions might also explain the observed differences in the latitudinal variation of species richness. This argument is partly related to our discussion of the species–area relationship. For groundwater habitats, terrestrial area approximates the available

habitat area. Our failure to find a species–area relationship for this habitat type suggests that the availability of habitats is not sufficient to explain the diversity patterns of freshwater species. Ribera *et al.* (2003) also argued consistently against this habitat-availability hypothesis. Nevertheless, further investigations are needed for a convincing test of this hypothesis.

(3) After the last glaciation many species recolonized central Europe from Mediterranean refugia (de Lattin, 1957; Hewitt, 1999). However, recent studies have demonstrated the existence of glacial refugia north of the Alps (Stewart & Lister, 2001; Pauls *et al.*, 2006; Kristjánsson & Svavarsson, 2007). Furthermore, a considerable number of species may have colonized central Europe from eastern regions (e.g. Banarescu, 1990; Kotlík *et al.*, 2004). Irrespective of the location of the refugia, the recolonization of Europe should be biased towards species with a high dispersal propensity. The decrease of β -diversity from southern to northern regions may also be a legacy of the recolonization of the higher latitudes after the Pleistocene (Hewitt, 1999; 2000).

(4) Lentic species are assumed to show a higher propensity for dispersal than lotic species. The differences in β -diversity among species adapted to groundwater, lotic and lentic habitats are perfectly consistent with the proposed differences in the dispersal propensity of species associated with these habitats, because with an increasing propensity for dispersal one expects a decrease in β -diversity (Soininen *et al.*, 2007a,b). From this, in turn, one may deduce the hypothesis that the decrease of species richness with latitude in lotic as well as groundwater habitats is due to a low recolonization rate. The increase in the proportion of lentic species with latitude supports this argument. Consequently one might argue that the communities of lotic and groundwater habitats have not yet reached equilibrium in central and northern Europe. In contrast, lentic species may have reached equilibrium, which is also suggested by a significant species–area relationship (see above). Furthermore, low dispersal rates facilitate speciation (Bohonak, 1999; Marten *et al.*, 2006), which should lead to a higher speciation rate in lotic as well as groundwater species compared to lentic species (Ribera & Vogler, 2004). The rugged topographic relief of the Mediterranean regions may have further contributed to a higher speciation rate (Mayr, 1942; Hewitt, 1999). The high levels of β -diversity in southern Europe are concordant with a higher speciation rate in the Mediterranean. However, we found this difference in lotic and lentic species. Therefore, differences in the speciation rate of lentic and lotic species do not sufficiently explain the observed difference in the relationship between species richness and latitude among lentic and lotic species.

None of these four factors that may have influenced the difference in the relationship between species richness and latitude among the different habitat types can account for the hump in species richness of lentic freshwater animals in central Europe. We propose three possible processes that might have generated this pattern. First, a considerable number of lentic species could have gone extinct in the southern refugia after the last glaciation, when the Mediterranean climate shifted to semi-arid conditions (Salinas *et al.*, 2000; Oliva-Paterna *et al.*, 2003). Note that this

argument is not consistent with the foregoing, that habitat availability is not supposed to drive the observed patterns. Second, if lentic species are stronger dispersers, more species from eastern refugia may have reached central Europe. At the end of the last Ice Age, huge proglacial lakes provided pathways of recolonization for lentic species (e.g. Schäfer, 1997). However, our data indicate a decrease in the proportion of lentic species from west to east (Table 4). Consequently, this explanation also seems to be rather unlikely. Third, the mid-domain effect predicts a hump in species richness in the centre of a geographical domain (Colwell & Lees, 2000). This model places geographical ranges of species randomly across the available space. Furthermore, it assumes that biota are close to equilibrium. Indeed, due to their higher dispersal ability, lentic species should be near equilibrium conditions (see also above), so the mid-domain effect might be useful to approach an explanation of the species richness peak in lentic species in central Europe.

With our study, we underline that to understand differences in the spatial variation of biological diversity among taxa one has to consider the history of regions and lineages (Graham *et al.*, 2006; Rahbek *et al.*, 2007; Reyjol *et al.*, 2007; Svenning & Skov, 2007) as well as the ecological traits of species (Ribera *et al.*, 2003; Vogler & Ribera, 2003; Hof *et al.*, 2006; Marten *et al.*, 2006; McPherson & Jetz, 2007; Ribera, 2008). Furthermore, our analyses support previous studies which document that various European groups of plants and animals are not in equilibrium with current climate (Svenning & Skov, 2004; Araújo & Pearson, 2005; Araújo *et al.*, 2008).

ACKNOWLEDGEMENTS

We thank, in particular, David G. Jenkins for comments on an earlier draft of this manuscript. Thanks to Miguel B. Araújo, Carsten Rahbek and Andreas Marten for inspiring discussions. Yorick Reyjol, Katrin Böhning-Gaese and two anonymous referees provided helpful remarks on the submitted manuscript. The Cusanuswerk – the German Catholic Scholarship Foundation – provided financial support for C.H. Finally, we are particularly grateful to the freshwater biologists who compiled the data for the *Limnofauna Europaea*.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Taxonomic groups included in the analyses.

Table S2 Habitat types used in the *Limnofauna Europaea*.

Figure S1 Relationships between species richness and geographical variables.

Figure S2 Relationships between latitude and residuals of the regression of species richness and area.

Figure S3 Relationships between number of singletons and latitude.

Figure S4 Distribution of simulated correlation coefficients of the relationship between species richness and latitude for randomized habitat preference.

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BIOSKETCHES

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Editor: Katrin Böhning-Gaese