ORIGINAL ARTICLE

Habitat availability does not explain the species richness patterns of European lentic and lotic freshwater animals

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ABSTRACT

Aim In Europe, the relationships between species richness and latitude differ for lentic (standing water) and lotic (running water) species. Freshwater animals are highly dependent on suitable habitat, and thus the distribution of available habitat should strongly influence large-scale patterns of species richness. We tested whether habitat availability can account for the differences in species richness patterns between European lentic and lotic freshwater animals.

Location Europe.

Methods We compiled occurrence data of 1959 lentic and 2445 lotic species as well as data on the amount of lentic and lotic habitats across 25 pre-defined biogeographical regions of European freshwaters. We used the range of elevation of each region as a proxy for habitat diversity. We investigated the relationships between species richness, habitat availability and habitat diversity with univariate and multiple regression analyses.

Results Species richness increased with habitat availability for lentic species but not for lotic species. Species richness increased with elevational range for lotic species but decreased for lentic species. For both groups, neither habitat availability nor diversity could account for previously reported latitudinal patterns in species richness. For lotic species, richness declined with latitude, whereas there was no relationship between habitat availability and latitude. For lentic species, richness showed a hump-shaped relationship with latitude, whereas available habitat increased with latitude.

Main conclusions Habitat availability and diversity are poor predictors of species richness of the European freshwater fauna across large scales. Our results indicate that the distributions of European freshwater animals are probably not in equilibrium and may still be influenced by history, namely the recurrent European glaciations and possible differences in post-glacial recolonization. The distributions of lentic species appear to be closer to equilibrium than those of lotic species. This lends further support to the hypothesis that lentic species have a higher propensity for dispersal than lotic species.

Keywords

Aquatic species, biogeography, dispersal, distribution, diversity, Europe, freshwater animals, habitat, history, macroecology.

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INTRODUCTION

Habitat is the template for the evolution of species traits, e.g. the propensity for dispersal (Southwood, 1962, 1977). Lentic (standing water) habitats are generally more ephemeral than lotic (running water) habitats (Dobson & Frid, 1998), and because there is a negative relationship between the persistence of a habitat and the propensity for dispersal of its inhabitants (Southwood, 1962; Wiener & Tuljapurkar, 1994; Dingle & Drake, 2007), lentic species should have evolved a higher

propensity for dispersal than lotic species. Accordingly, several recent studies have suggested that species of lentic freshwater animals are stronger dispersers than lotic species (e.g. Ribera & Vogler, 2000; Ribera *et al.*, 2001, 2003; Hof *et al.*, 2006; Marten *et al.*, 2006; see Ribera, 2008, for an overview).

The distribution data for European freshwater fauna published by Illies (1966a, 1978) were analysed by Hof *et al.* (2008), who showed that the patterns of species richness of lentic and lotic species strongly differ: the species richness of lentic species shows a hump-shaped relationship with latitude, with a peak in central Europe, whereas the species richness of lotic species decreases with increasing latitude. The authors attributed these patterns to differences in post-glacial recolonization of both groups as a result of the different dispersal abilities of lentic and lotic species (Hof *et al.*, 2008). By definition, freshwater animals are confined to aquatic habitats; therefore their distribution is completely dependent on the distribution of suitable habitat. For terrestrial animals, species richness and area (Rosenzweig, 1995) and species richness and suitable habitat (MacArthur, 1964; Storch *et al.*, 2003) each commonly have a positive relationship. The same holds true for freshwater organisms (Hugueny, 1989; Rosenzweig & Sandlin, 1997; Allen *et al.*, 1999). The distribution of freshwater habitats should there-fore be a strong predictor of freshwater species richness in Europe, and the observed differences in the relationship of species richness with latitude between lentic and lotic species may simply reflect differences in the distribution of lentic and lotic habitats across Europe. In their analysis, Hof *et al.* (2008) tested for a relationship between the size of the biogeographical regions and species richness. However, it is doubtful that area per se is a good proxy for suitable habitat. In the present study, we analysed the spatial distribution and number of lentic and lotic water bodies across Europe in relation to the observed patterns of species richness of lentic and lotic freshwater animals.

Illies (1961) divided watercourses into different segments (e.g. krenal, rhithral, potamal) that usually occur in a similar order downstream, from relatively high elevations (springs, brooks) to relatively low elevations (river mouths). The different segments have different physical (e.g. water current) and chemical (e.g. oxygen, nutrients) properties and species compositions, and there is a high species turnover between different river segments (Illies, 1961; Dobson & Frid, 1998). Lentic water bodies also have different characteristics at different elevations. In Europe, lakes at higher elevations are usually deeper and smaller, have smaller catchment areas and have lower concentrations of organic matter and nutrients than lowland lakes (Nõges, 2009). Consequently, regions with a large elevational range should contain more different types of freshwater habitats. In our analysis, we thus included the elevational range of a region as a simple proxy for habitat diversity.

We specifically addressed the following questions: (1) Do the distributions and quantities of lentic and lotic habitats differ across Europe? (2) Is there a relationship between the availability of habitat and species richness of European freshwater animals? (3) Does species richness increase with the elevational range as a proxy for habitat diversity within a region? (4) Do differences in habitat availability and habitat diversity account for the different species richness patterns of lentic and lotic freshwater animals?

MATERIALS AND METHODS

We compiled data on the distribution and habitat use of all European freshwater species from Illies (1978). Together with leading experts in the field of freshwater zoology, Illies (1966a, 1978) defined 25 zoogeographical regions of European fresh-water and recognized 42 habitat types. Most of these habitat types are very specialized, e.g. those used by Tardigrada and Culicidae (five habitat types) and those used by parasites (more than 20 habitat types). Of the 42 habitat types, seven are lentic (lakes; ephemeral small water bodies; phytotelmata; inland saltic waters; bogs; thermal waters; swamps) and three are lotic (springs; brooks and rivulets; rivers and streams). Illies (1978) provides data on the presence/absence of all European freshwater species in each of the regions and their habitat use. For further information on the compilation of the data set and on habitat categories see Hof *et al.* (2008). For the present analysis, we only used data for species occurring exclusively in these seven (lentic) and three (lotic) habitats. The number of species per region is presented in Table S1 in Supporting Information. The habitat data correspond to the species used in the data set.

Data on standing and running waters were compiled from the Global Lakes and Wetland Database (Lehner & Döll, 2004) and from the Digital Chart of the World Server (ESRI, 1993; http://www.maproom.psu.edu/dcw/, data accessed 18 December 2007). Our data set included all European lentic waters with a surface area ≥ 0.1 km^2 and lotic waters of a Strahler stream order of ≥ 2 (Strahler, 1952). We defined lotic habitat availability as the sum of the length of all parts of a river within a region (henceforth called river length) and lentic habitat availability as the sum of the perimeter of all standing waters (henceforth called lake perimeter). Lake perimeter is a more suitable proxy of lentic habitat availability than lake area (Bohle, 1995; see also discussion in Ribera *et al.*, 2003).

Elevational data were compiled from the GTOPO30 data set (EROS, 1996), which includes a digital elevation model with a grid spacing of 30 arcsec. For our analysis, we determined the elevational range of every region as the difference between maximum and minimum elevation. We used GLOBAL MAPPER 7.04 (Global Mapper Software LLC, Parker, CO, USA, 2006) and ARCGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA, 2006) for all GIS analyses.

Since our habitat data set does not include very small, temporary lentic water bodies, we excluded from the analysis all lentic species that occur exclusively in such habitats (based on Illies' classification). We also excluded those lotic species that occur exclusively in springs. The final data set included

1959 lentic and 2445 lotic species (see taxonomic overview in Table S2). Although this classification of species differs slightly from that of Hof *et al.* (2008), it had no effect on the general outcome of the analyses: lentic ($R^2 = 0.33$, $P = 0.012$) and lotic ($r^2 = 0.33$, $P = 0.003$) species richness of the reduced data set showed virtually the same relationship with latitude as the one including all lentic ($R^2 = 0.32$, $P = 0.015$) and lotic ($r^2 = 0.32$, $P = 0.003$) species. The relationships between lentic and lotic species richness and latitude were consistent among taxonomic groups (Figs S1 & S2).

Lake perimeter, river length and elevational range were $\log_{10}$-transformed to approximate normality. We fitted multiple general linear models (type I sum of squares) to evaluate the effect of habitat availability and habitat diversity on species richness. After inclusion of habitat availability and diversity, we subsequently added latitude and its squared term into the model to test whether the spatial structure remained in the data (cf. Legendre & Legendre, 1998) after accounting for habitat availability. A significant and negative regression coefficient of the squared latitude after accounting for habitat availability would indicate that a hump-shaped relationship remained between lentic species richness and latitude. None of the final models showed spatial autocorrelation of residuals; it

was therefore not necessary to include space in our tests. We used R v. 2.7 (R Development Core Team, 2008) for all statistical analyses.

RESULTS

The distributions and quantities of lentic and lotic habitats differed across Europe. Lentic habitat availability increased with increasing latitude ($r^2 = 0.44$, $P < 0.001$) whereas there was no relationship between lotic habitat availability and latitude ($r^2 = 0.06$, $P = 0.25$; Figs 1 & 2a,b). Habitat availability was significantly and positively correlated with the size of the bioregion. The relationship was stronger for lotic habitats ($r^2 = 0.98$, $P < 0.001$) than for lentic habitats ($r^2 = 0.56$, $P < 0.001$).

The species richness of lentic freshwater animals tended to increase with habitat availability ($r^2 = 0.14$, $P = 0.06$; Fig. 2c); that of lotic species did not ($r^2 = 0.01$, $P = 0.65$; Fig. 2d). The total species richness of freshwater animals was not correlated with the size of the bioregion ($r^2 = 0.09$, $P = 0.14$). Tested separately, lentic species richness increased with the size of the bioregion ($r^2 = 0.19$, $P = 0.03$), whereas there was no correlation for lotic species richness ($r^2 = 0.01$, $P = 0.60$).
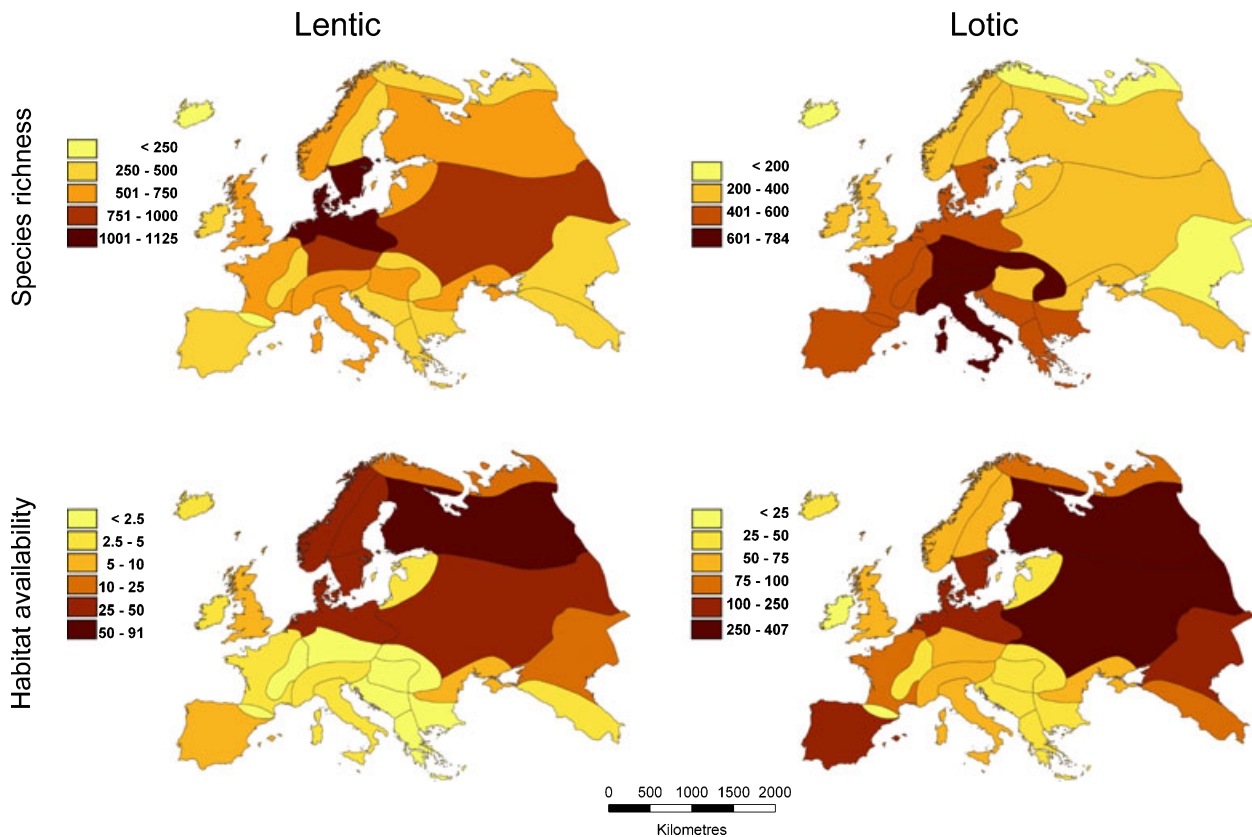
Figure 1 Species richness and habitat availability of lentic and lotic animals in Europe. Lentic habitat availability is defined as the perimeter of all standing water bodies (km $\times 10^3$), and lotic habitat availability as the sum of the length of all parts of a river (km $\times 10^3$) within a bioregion. The 25 biogeographical regions of the European freshwater fauna were defined by Illies (1966a, 1978). Map projected in Aitoff's equal-area projection.
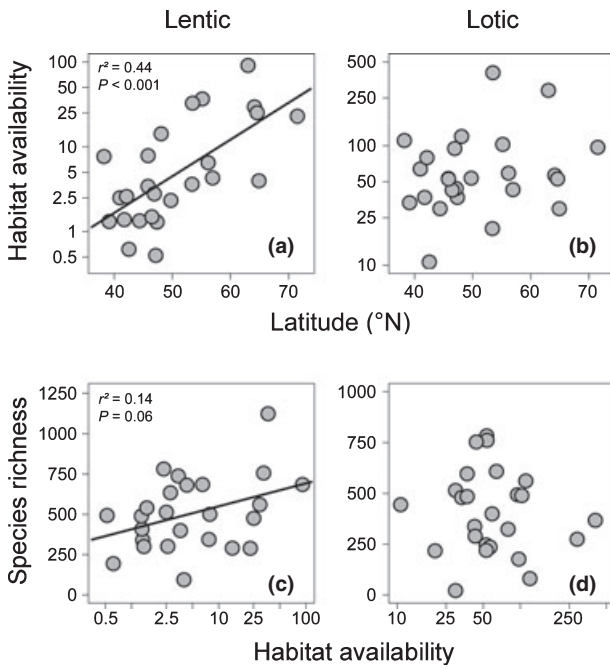
Figure 2 Relationship of (a, b) habitat availability and latitude and (c, d) species richness and habitat availability of lentic (a, c) and lotic (b, d) species ($n = 25$ in both cases). Each point represents 1 of the 25 biogeographical regions of European freshwater species defined by Illies (1966a, 1978). Habitat availability is $\log_{10}$-transformed. Lentic habitat availability is defined as the perimeter of all standing water bodies ($km \times 10^3$) and lotic habitat availability as the sum of the length of all parts of a river ($km \times 10^3$) within a bioregion.

Table 1 Dependency of species richness of lotic and lentic species on habitat availability and latitude (general linear models, type I sum of squares). River length and lake perimeter were $\log_{10}$-transformed. Note the significant and negative regression coefficient for latitude^2 for lentic species.

	Mean sum of squares ($n = 25$)	F	Regression coefficient	P-value
Lotic species				
River length	9353	0.32	44.70	0.579
Elevational range	181,389	6.17	269.57	**0.022**
Latitude	175,575	5.97	62.27	**0.024**
Latitude^2	51,247	1.74	−0.66	0.202
Residuals	29,409			
Lentic species				
Lake perimeter	174,180	5.69	202.12	**0.027**
Elevational range	27,090	0.88	93.79	0.358
Latitude	64,429	2.10	178.15	0.162
Latitude^2	332,661	10.87	−1.70	**0.004**
Residuals	30,614			

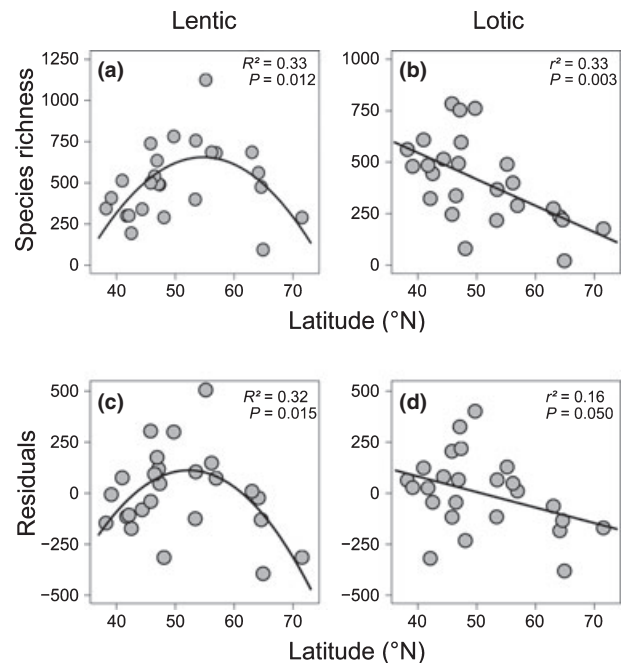Significant correlations ($P < 0.05$) are in bold.

We also analysed whether species richness increased with the elevational range to determine whether elevation could be used as a proxy for habitat diversity within a region. For lentic freshwater animals, the species richness tended to decrease with the elevational range of a region ($r^2 = 0.15$, $P = 0.06$), whereas for lotic species it increased ($r^2 = 0.19$, $P = 0.03$). Habitat availability and diversity together accounted for 20.3 and 19.5% of the variance in lentic and lotic species richness, respectively.

We then determined whether the differences in habitat availability and habitat diversity accounted for the different species richness patterns of lentic and lotic freshwater animals. After accounting for habitat availability, elevational range was not positively correlated with the species richness of lentic freshwater animals, but it was positively correlated for lotic species (Table 1). Adding latitude and its squared term into the model showed that after controlling for habitat and elevational range, the relationship between species richness and latitude for lentic freshwater animals was still hump-shaped (regression coefficient of squared latitude negative; $R^2 = 0.32$, $P = 0.015$; Fig. 3c, Table 1); for lotic freshwater animals, species richness still monotonically decreased with latitude ($r^2 = 0.16$, $P = 0.050$; Fig. 3d). The patterns of habitat availability did not correspond to the patterns of species richness

Figure 3 Relationship of (a, b) species richness and (c, d) residuals of species richness after controlling for differences in habitat availability and habitat diversity (i.e. elevational range) compared to latitude for lentic (a, c) and lotic (b, d) species ($n = 25$).

(Fig. 1). The available habitat of lentic species increased with increasing latitude (Fig. 2a), in contrast to the hump-shaped relationship of species richness and latitude (Fig. 3a); the habitat availability of lotic species was not related to latitude (Fig. 2b), in contrast to the decline in species richness with increasing latitude (Fig. 3b).

DISCUSSION

Differences in species diversity are most commonly attributed to area (MacArthur & Wilson, 1967; Connor & McCoy, 1979; Rosenzweig, 1995), contemporary climatic conditions (Wright, 1983; Currie, 1991; Hawkins et al., 2003) or historical factors (Haffer, 1969; Latham & Ricklefs, 1993; Dynesius & Jansson, 2000). With respect to habitat area, we found a positive, albeit weak, relationship between species richness and habitat availability for lentic freshwater animals ($r^2 = 0.14$), but not for lotic species ($r^2 = 0.01$). These values are much lower than values reported for species–area relationships of terrestrial as well as aquatic species (Barbour & Brown, 1974; Connor & McCoy, 1979; Hugueny, 1989; Watters, 1992; Oberdorff et al., 1995, 1997; Rosenzweig & Sandlin, 1997). Furthermore, the latitudinal species richness patterns of both lentic and lotic animals remained virtually the same after controlling for habitat (Table 1, Fig. 3). Hence, the patterns of species richness of lentic and lotic freshwater animals across Europe do not reflect the distribution of the respective freshwater habitats. We conclude that the availability of habitat is a poor predictor of the broad-scale patterns of species richness of freshwater animals across Europe.

Ribera et al. (2003) found that total area is a good predictor of total species richness of aquatic Coleoptera, but not of the species richness of lentic and lotic species, when tested separately. In our analysis, total species richness of European freshwater animals was not correlated with the total area of a bioregion. When tested separately, lentic, but not lotic, species richness increased with the total area of a bioregion. The relationship between lentic species richness and total area was a bit stronger ($r^2 = 0.19$, $P = 0.03$) than that between lentic species richness and available lentic habitat ($r^2 = 0.14$, $P = 0.06$). Both relationships, however, are rather weak and differ only slightly. We thus conclude that neither total area nor habitat area is a good predictor of the species richness of European lentic freshwater animals.

Illies (1966b) argued that montane regions such as the Pyrenees or the Alps have relatively fewer species than other regions, probably because they largely lack typical lowland habitats such as eutrophic lakes or potamal river segments, and consequently lack species that occur in these kinds of habitats. The diversity of both lentic and lotic habitats should thus be highest in regions that span a wide elevational range (Illies, 1961, 1966b; Dobson & Frid, 1998; Nõges, 2009; see also the Introduction). In our analysis, the elevational range of a region accounted for 15.0 and 19.5% of the variation in lentic and lotic species richness, respectively. Lotic species richness increased with the elevational range of a region as expected, but lentic species richness tended to decrease. The relationship, however, was rather weak for both groups, and for lentic species it disappeared in the multivariate analysis. This might indicate either that elevational range is not a suitable proxy for the diversity of lentic habitats or that its effects are superimposed by other relationships. The eleva-

tional ranges of the regions are highest in southern and northern Europe and show a minimum in central Europe; lentic species richness shows the opposite trend, peaking in central Europe and then gradually declining both northwards and southwards. Given the rather weak correlation and the complex history of the European continent, with its recurrent glaciations during the ice ages, it is likely that the peak of lentic species richness in central Europe is predominantly caused by factors other than habitat diversity (see Hewitt, 1999, 2000; Hof et al., 2008). The observed negative trend between species richness and elevational range could merely present a random pattern caused by their opposing relationships with latitude.

Our habitat data set does not and cannot include all European water bodies but only those with a surface area ≥ 0.1 km^2 (lentic) and rivers of a Strahler stream order of ≥ 2 (lotic). Any river, however, is fed from its tributaries, therefore its presence will be due to the presence of smaller ones (Bohle, 1995; Dobson & Frid, 1998). As a consequence, each river in our data set stands for a similar number of smaller rivers that are not included in the data. Kristensen et al. (1995) estimated that Europe has about 500,000–700,000 water bodies with a surface area of 0.01–0.1 km^2, 65–90% of which are estimated to be located in northern Europe (Scandinavia and northern Russia). These water bodies are thus not likely to explain the peak of species richness in central Europe. Furthermore, in our analysis, we removed all lentic species from the original data set that occur exclusively in small temporary pools, i.e. in habitats that are too small to be included in our habitat data set. We also excluded all lotic species that occur exclusively in springs. Hence, our data set includes only species typical for the water bodies that were included in our data sets of habitat availability. Nevertheless, species richness of these removed species showed similar relationships with latitude as the species included in the analyses (Figs S3 & S4). Hence, small water bodies that are not included in our habitat data set are not responsible for the observed patterns of lentic and lotic species richness.

Available energy, measured, e.g. as mean annual temperature or primary productivity, has been suggested to be a strong predictor of species richness and shown to decrease with increasing latitude (Wright, 1983; Currie, 1991; Hawkins et al., 2003). With respect to our data, it appears as if the decrease in lotic species richness with latitude followed a decrease of available energy. We tested species richness against climatic data taken from WorldClim (Hijmans et al., 2005). However, because of the rather coarse resolution of our species distribution data, climatic data have to be averaged over relatively large bioregions, which makes it very difficult to disentangle the effect of energy from a possible influence of space (i.e. history). We therefore decided not to follow up these tests. More highly resolved species distribution data are required to test how energy is related to lentic and lotic species richness in Europe. Nevertheless, because European lentic and lotic species show strikingly different patterns of species richness, energy alone has to be ruled out as a *universal*

determinant of species richness of European freshwater animals (Hof *et al.*, 2008). Moreover, it certainly cannot account for the differences in the distribution of lentic and lotic species richness.

If neither habitat availability nor energy is likely to be responsible for the observed differences in the distribution of species richness of lentic and lotic animals, this suggests that the distribution of certain taxa of freshwater species in Europe is not in equilibrium with current environmental conditions and to some extent is still influenced by historical factors (Svenning & Skov, 2004; Araújo *et al.*, 2008). It is well known that the European biota were strongly influenced by the glacial cycles during the Pleistocene (Hewitt, 1999, 2000), and signals of these impacts remain detectable in present-day patterns of species richness and composition as well as in the distribution of genotypes (Svenning & Skov, 2004; Araújo *et al.*, 2008). Many European species spent the Last Glacial Maximum in refugia on the Mediterranean peninsulas (Holdhaus, 1954; Taberlet *et al.*, 1998; Hewitt, 1999). When the ice masses retreated, species recolonized central and northern Europe from these refugia (Hewitt, 1999). Lentic species are expected to have a higher propensity for dispersal than lotic species, as expressed by larger geographical ranges (Ribera & Vogler, 2000; Hof *et al.*, 2006; Reyjol *et al.*, 2007), faster colonization (Ribera *et al.*, 2003), lower beta diversity (Hof *et al.*, 2008) and a lower population differentiation (Bohonak *et al.*, 2004; Marten *et al.*, 2006) but higher intra-population and overall genetic diversity (Zickovich & Bohonak, 2007). Since recolonization is strongly dependent on the dispersal ability of a species (Diamond, 1972; Svenning & Skov, 2007; Araújo *et al.*, 2008), the higher dispersal ability of lentic species may have allowed them to recolonize central and northern European regions faster than lotic species.

This theory is supported by the fact that the proportion of lentic to lotic species increases from southern towards northern Europe, whereas beta diversity decreases (Hof *et al.*, 2008). Furthermore, the positive species–area (or species–habitat) relationship of lentic species may indicate that the distributions of lentic species are closer to equilibrium with the current distribution of their habitats than those of lotic species. Both the hump-shaped relationship between lentic species richness and latitude and the decrease of lotic species richness with increasing latitude were consistent when individual taxa were tested separately (Figs S1 & S2). Recolonization routes of lentic species from different refugia may have met in central Europe (see Hewitt, 2000, for terrestrial animals), which may have led to a mixing of species and the observed peak of richness there. Lotic species, on the other hand, probably recolonized central and northern Europe much more slowly, leading to less-pronounced mixing or a lack of mixing.

Our study corroborates earlier results that suggested non-equilibrium situations for European biota (Svenning & Skov, 2004; Araújo *et al.*, 2008). We emphasize that a consideration of both the ecological traits of a species (Ribera *et al.*, 2003; Vogler & Ribera, 2003; Marten *et al.*, 2006; McPherson & Jetz,

2007) and the history of the region studied (Graham *et al.*, 2006; Svenning & Skov, 2007) is indispensable for understanding large-scale species richness patterns and differences among taxa in this regard.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Relationship between species richness and latitude for different lentic taxa.

Figure S2 Relationship between species richness and latitude for different lotic taxa.

Figure S3 Relationship between species richness and latitude for lentic species that occur exclusively in small and ephemeral water bodies.

Figure S4 Relationship between species richness and latitude for lotic species that occur exclusively in springs.

Table S1 Number of lentic and lotic species per bioregion.

Table S2 Number of species per taxon in the data sets for European lentic and lotic freshwater animals.

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BIOSKETCH

Matthias Dehling has broad interests in biology, especially in macroecology, biogeography, herpetology and ornithology. He is particularly interested in large-scale patterns of species diversity and in species interactions. This study formed a part of his diploma (MSc) thesis at the Department of Ecology, Philipps-Universität Marburg. He is now a doctoral student at the Biodiversity and Climate Research Centre Frankfurt (BiK-F).

Author contributions: All four authors conceived the ideas; C.H. and D.M.D. collected the data; D.M.D. and M.B. analysed the data; all authors discussed the findings; D.M.D. wrote the manuscript; all authors commented on the manuscript.

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