



Are latitudinal richness gradients in European freshwater species only structured according to dispersal and time?

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The latitudinal gradient in species richness of the European freshwater fauna is usually depicted as a contrasting pattern between lentic (standing waters) and lotic (running waters) habitats. Species richness decreases from south to north in lotic habitats, while lentic habitats show an intermediate richness peak in central Europe (Hof et al. 2008). In this Brevia we question the strict dichotomic split in latitudinal richness patterns between lentic and lotic habitats in Europe. We do this by demonstrating that the differences in richness patterns between headwater streams and rivers are as great as the differences between lentic and lotic habitats. We also show that species richness can be explained solely by the hypervolume defined by the variety of lotic habitats preferences in a region.

It has been proposed that the interaction between colonization ability and time elapsed since the last major glaciation has been responsible for the differences in latitudinal richness gradients of animal species between lentic and lotic habitats in Europe. Long-term stability of lotic habitats and a higher turnover rate of lentic habitats are thought to be the main evolutionary mechanism promoting high dispersive species in lentic habitats and low dispersive species in lotic habitats (Arribas et al. 2012). Sánchez-Fernández et al. (2012) stated that the current ranges of lentic species are in equilibrium with their climatic niches, while lotic species are constrained to their pleistocene refugia due to dispersal limitations, creating the contrasting latitudinal species richness pattern in Europe. This spatio-temporal hypothesis of European freshwater species assumes that environmental habitat conditions do not influence the large-scale species richness patterns. However, it is well known that environmental conditions do in fact structure freshwater species communities in lotic habitats from headwaters to lower reaches (Vannote et al. 1980). Also, Azevedo et al. (2013) has shown that environmental factors structure freshwater species richness across large spatial scales.

If geological stability, together with colonization rates since the last glacial maximum, is the only driver of species

richness patterns in European freshwater habitats, the latitudinal decrease in species richness should be independent of the sheer volume of different species' habitat preferences for a given region (referred to as the habitat hypervolume). Moreover, the decreasing latitudinal richness patterns in lotic habitats from south to north should be constant across zonation classes from headwater streams to lower rivers reaches.

We tested these two assumptions across 22 biogeographic regions in Europe, using the distribution and habitat preference of the European fauna of the three insect orders: Ephemeroptera, Plecoptera, and Trichoptera (EPT) (methods in Supplementary materials Appendix 1). The diversity of the EPT fauna strongly correlates with total regional freshwater species richness ($\beta = 0.45$, p -value < 0.001 and Supplementary materials Appendix 1, Fig. A1) and shows the same decreasing latitudinal richness pattern from south to north ($\beta = -5.72$, p -value < 0.001 and Supplementary materials Appendix 1, Fig. A2).

In an initial regression model including habitat hypervolume, latitudinal midpoint, and two cofounding variables (altitude and $\log(\text{region area})$), only habitat hypervolume and altitude structured EPT species richness in an average model (Supplementary materials Appendix 1, Table A4). This result indicates that higher species richness is related to regions with a broad spectrum of habitats and not to the spatial location of a given region. Furthermore, EPT-species richness within lotic zonation classes showed a change in the relationship to latitude from headwaters to lower reaches (Fig. 1). Richness and latitude had a linear relationship for headwater classes, resembling the classic decreasing richness patterns to the latitudinal gradient (Hof et al. 2008). However, in larger streams and rivers between the Hyporhithral (grayling region) and Epipotamal (barbel region) zone this relationship shifted from being linear to becoming unimodal. When sub-setting the data by removing habitat generalist species and using habitat specialist species only, the same shift in latitude–richness relationship was also evident (Supplementary materials Appendix 1, Fig. A3).

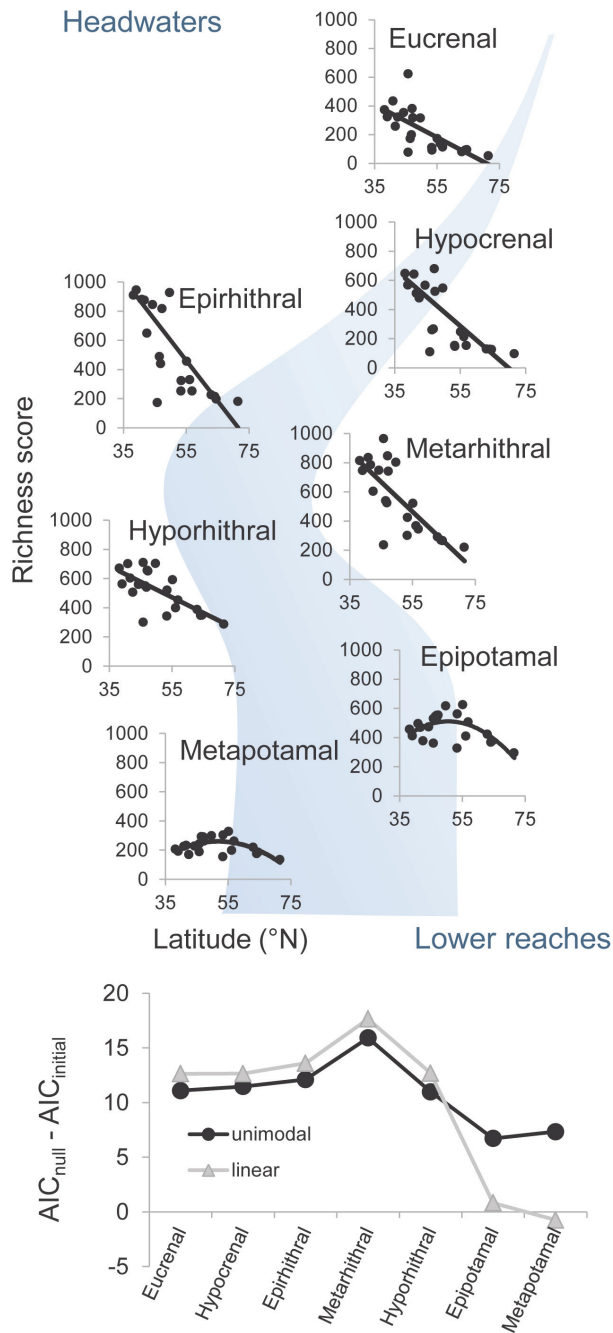


Figure 1. Relationship between latitude and species richness scores for Ephemeroptera, Plecoptera and Trichoptera species in European ecoregions. Each graph represents a specific river zonation class spanning from headwaters to lower reaches. The lower graph shows ΔAIC values from linear regression models within the eight river zonation categories. The values represent differences between a constant model and a unimodal (black circles) and a linear (grey triangles) relationship between EPT-species richness and latitude. High ΔAIC represents a better fit for a given model.

Altogether, we find very little support in a strict dispersal-driven split between lentic (Hof et al. 2008) and lotic habitats when studying species ranges and richness gradients. Species richness in the lower reaches of lotic habitats has the same relationship to latitude as lentic habitats. Moreover, lotic species richness patterns can solely be explained by the

regional spectrum of habitats, even when adjusting for the latitudinal placement of these regions.

These results are in concordance with studies of freshwater species richness in North America, documenting that environmental factors were always more important than spatial factors (latitude or longitude) in structuring species richness (Bêche and Statzner 2009). However, species ability to disperse undoubtedly plays a significant role when recolonizing potential ranges from pleistocene refugia (Baselga et al. 2012). Our findings suggest that processes affecting macroecological richness gradients of European freshwater species are more complex than just differences in geological stability between habitat types. It has already been highlighted that interactions between dispersal and environmental filters organize metacommunities in aquatic systems (Henriques-Silva et al. 2013, Heino et al. 2015).

If our results are a consequence of such interactions, they suggest that the sorting effect of environmental conditions together with dispersal influence not only metacommunities, but also continental species richness patterns in freshwaters (Heino 2011). The increasing availability of local community data from headwaters to lower reaches across the latitudinal range as well as fine-scale environmental data (elevation range, ruggedness, and freshwater habitat availability, see Domisch et al. (2015)) could bridge the current gap between processes sorting local and continental richness gradients. Integrating other factors than dispersal ability when attempting to predict freshwater species ranges is likely to expand our understanding of the mechanisms structuring the current diversity patterns within these habitats.

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Supplementary material (Appendix ECOG-02183 at <www.ecography.org/appendix/ecog-02183>). Appendix 1.