



Latitudinal patterns and large-scale environmental determinants of stream insect richness across Europe



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ABSTRACT

Latitudinal patterns have been widely studied in many organism groups, such as terrestrial vertebrates or plants, along with a suite of other large-scale biodiversity–environment gradients. Much less is known about these patterns for freshwater organisms, particularly stream insects. We evaluated European stream insect richness along a latitudinal gradient (39°–68° N) and estimated how much of the variation in taxon richness patterns could be explained by natural drivers: current climate, geographic location and topography. We assessed richness patterns using two datasets. First, based on 1318 sampling sites, we calculated taxon richness of juveniles stages of aquatic insects in 1° × 1° grid cells and converted these into latitudinal bands. Second, we calculated taxonomic richness using species lists from www.freshwaterecology.info for the ecoregions of European freshwaters. We evaluated Ephemeroptera, Plecoptera and Trichoptera (EPT) richness patterns for both latitudinal band and ecoregion data using linear regression, comparing list-based with grid-based data compiled for each region. We then estimated both pure and combined effects of each group of environmental variables using variance partitioning. Both individually and combined, EPT taxon richness declined with increasing latitude. Taxon richness was high between 42° and 46° N, geographically representing the Alps, and a threshold was detected at 48° N for all three groups and combined EPT using the grid data. Current climate, geographic location, and topographic predictors explained over 50% of the variation in taxonomic richness (E – 52%; P – 59%; T – 57%; overall EPT – 57%). A greater pure effect was observed for current climate than geographic locations and topographic predictors. We discuss other potential factors such as past glaciation, dispersal and anthropogenic stressors such as land use, river engineering, or pollution that might have shaped the present distribution of species.

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1. Introduction

Considerable progress has been made in documenting biodiversity patterns of organisms at different scales worldwide (e.g., [Mutke and Barthlott, 2005](#); [Kreft and Jetz, 2007](#); [Qian, 2008](#)). The decline in species richness from the equator to the poles is among the most consistent biogeographical patterns and has been observed in many disparate taxonomic groups and habitat types ([Lomolino et al., 2006](#); [Scott et al., 2011](#)). Recurring explanations employed

include area-effects, energy availability and climate, with varying importance depending on the study region or organism groups ([Gaston, 2000](#); [Hof et al., 2008](#)) and continuing debate about the scale at which some of these factors operate ([Caley and Schluter, 1997](#); [Scott et al., 2011](#)). Identifying causal influences is particularly difficult as factors that may vary over the latitudinal range of the study area, such as climate history (mainly from glaciations), landscape types, elevation, and geology also determine population size and composition at regional scales ([Ricklefs, 2004](#); [Mittelbach et al., 2007](#); [Heino, 2009](#)).

While there are notable exceptions, geographical studies on patterns of stream insect distributions are less common than for other taxonomic groups, and have shown contrasting results ([Vinson and Hawkins, 2003](#); [Heino, 2009](#); [Mori et al., 2010](#); [Scott et al., 2011](#)), with some indicating higher richness in the tropics ([Boyero, 2002](#)) and others in temperate regions ([Vinson and Hawkins, 2003](#)). These

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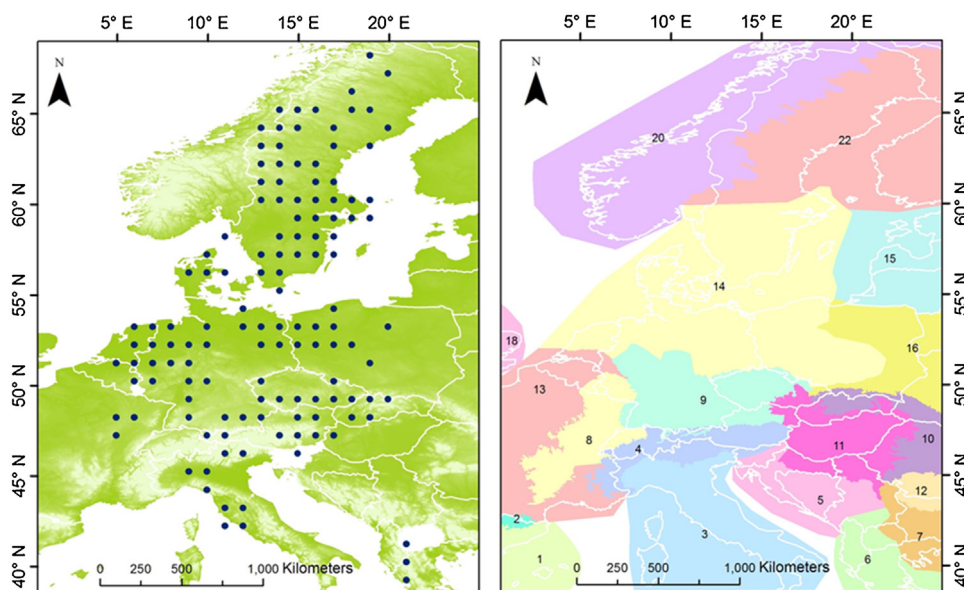


Fig. 1. Map of Europe with countries boundaries (white lines). (A) The black dots (●) represent the center point of grids of size $1^\circ \times 1^\circ$. Sampling points ranged in latitude from 39° to 68° N and in longitude from 4° to 20° E across Europe. (B) The freshwater ecoregions (Illies, 1978) analysed in this study characterized by different color and code (1 – Ibero-Macaronesian Region, 2 – Pyrenees, 3 – Italy and Corsica, 4 – Alps, 5 – Dinaric Western Balkan, 6 – Hellenic Western Balkan, 7 – Eastern Balkan, 8 – Western Highlands, 9 – Central Highlands, 10 – The Carpathians, 11 – Hungarian Lowlands, 12 – Pontic Province, 13 – Western Plains, 14 – Central Plains, 15 – Baltic Province, 16 – Eastern Plains, 18 – England, 20 – Boreal Uplands, 22 – Fenno-scandian Shield).

inconsistencies have been attributed to the effects of geographic area (Boyero, 2002), sampling design (Vinson and Hawkins, 1996), and diverse evolutionary histories and ecological characteristics (Pearson and Boyero, 2009; Sheldon and Warren, 2009).

In the European context, richness of a wide group of lotic organisms has been found to decline monotonically with increasing latitude (Hof et al., 2008). Heino (2009) found that on a country by country basis species richness of Ephemeroptera, Plecoptera and Odonata exhibited a negative relationship with latitude. In the case of glacial-fed streams, the number of macroinvertebrate taxa also declined from lower (Pyrenees) to higher latitudes (Svalbard, Norway) (Castella et al., 2001). This North South gradient in Europe is special and could be the result of the age of the habitats as the ice age refugia had high speciation in the south and in the Alps, and only a few 1000 generations populated areas in the north.

Information on factors affecting the natural variability of stream insect richness is not only vital for biodiversity conservation, but also as a reference for monitoring, restoring, and maintaining the quality of stream ecosystems (Rosenberg and Resh, 1993; Palmer et al., 1997), as well as evaluating the effects of expected changes on freshwater ecosystems such as climate change (IPCC, 2013). In our study, we focus on taxonomic richness (defined as the number of taxa (species, subspecies, species groups)) of three orders of stream insects (EPT: Ephemeroptera, Plecoptera and Trichoptera), as they comprise an important and large component of freshwater animal biodiversity (Barber-James et al., 2008; Fochetti and Tierno de Figueroa, 2008). These stream benthic organisms are well suited to investigate such patterns, because they have widespread distributions, their ecological requirements are fairly well known, and trends in stream Ephemeroptera, Plecoptera, and Trichoptera richness are often strongly correlated with trends in overall richness (Vinson and Hawkins, 2003), and strongly linked with environmental variation (e.g. Tonkin et al., 2015). Unfortunately, data from other important and highly diverse groups that account for a considerably high relative contribution of stream insects, such as Diptera, are not commonly available at the target taxonomic resolution (species level).

Our goals were twofold: (1) to evaluate the taxonomic richness patterns of Ephemeroptera, Plecoptera, Trichoptera and overall EPT along a latitudinal gradient; and (2) to estimate how much of the variation in taxa richness and taxa assemblages could be explained by current climate, geographic location, topography or interactive influences of these variables. We examined patterns at two levels: $1^\circ \times 1^\circ$ grid cells of observed data and entire ecoregions across Europe. For the latter we were also interested in a comparison of theoretical maximum species richness with observed data as these taxa have already experienced great species losses due to anthropogenic disturbances. We expected species richness of Ephemeroptera, Plecoptera, Trichoptera, and overall EPT should consistently follow the most prominent biodiversity gradient, a decline with increasing latitude. We expected that the area in and around the Alps will have high richness due to varied topography and its role as a refuge area during several glacial cycles (Hewitt, 1999) but that Plecoptera should show a sharp decline north of the European Alps compared to Ephemeroptera and Trichoptera due to their narrow temperature tolerance and sensitivity to anthropogenic disturbances, which are higher north of the Alps. However, it was beyond the scope of this study to analyse the role of colonization history and degradation.

2. Materials and methods

2.1. Study area

The study area lies across Europe (Fig. 1) between latitudes 39° and 68° N, and longitudes 4° and 20° E. From a biogeographic point of view, Europe has some distinctive features and can be seen as a peninsula connected to Asia, with an east–west orientation. There are prominent montane systems including the European Alps, the Pyrenees in the south and the Fennoscandian mountains in northern Europe, with large western, central and eastern plains in the center of Europe. The Mediterranean Sea in the south has isolated the region from Africa. During the Last Glacial Maximum (LGM) and

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