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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.

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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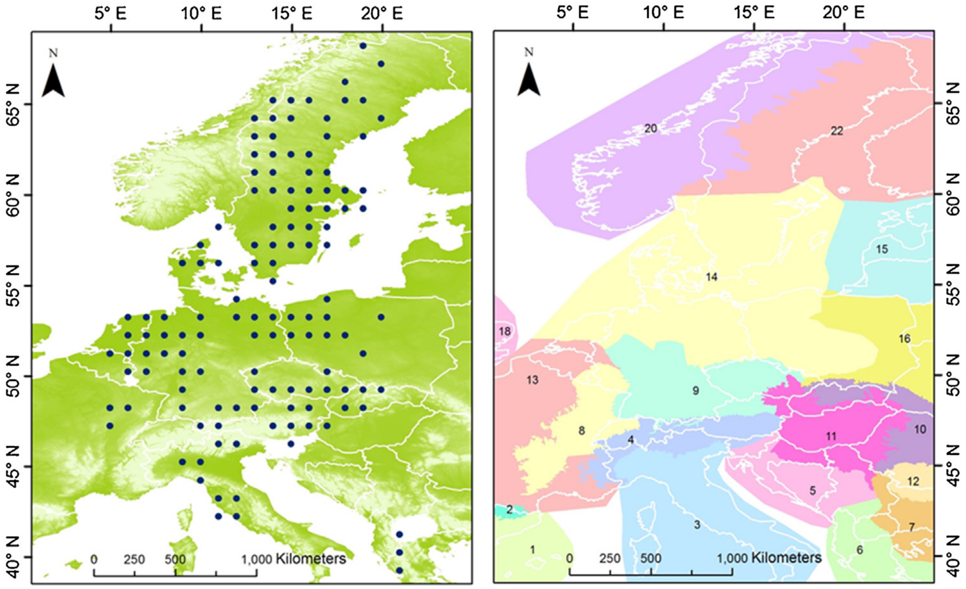

Fig. 1. Map of Europe with countries boundaries (white lines). (A) The black dots (●) represent the center point of grids of size 1° × 1°. Sampling points ranged in latitude from 39° to 68° N and in longitude from 4° to 20° E across Europe. (B) The freshwater ecoregions (Illies, 1978) analysed in this 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 Carpathiens, 11 – Hungarian Lowlands, 12 – Pontic Province, 13 – Western Plains, 14 – Central Plains, 15 – Baltic Province, 16 – Eastern Plains, 18 – England, 20 – Borealic 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° × 1° 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 earlier glaciations, much of Europe was heavily glaciated (Ehlers and Gibbard, 2006).

2.2. Benthic macroinvertebrates

We assessed richness patterns of stream insects using two different datasets at two different spatial scales: latitudinal bands and ecoregions.

2.2.1. Grid data

Stream macroinvertebrate data of 1318 sampling sites (33,543 taxa records of species, subspecies, species groups) for Europe (Fig. 1) was obtained from the STAR project (Furse et al., 2006), Swedish University of Agricultural Sciences (www.slu.se, accessed 15 April 2011), and from personal contacts. Altogether, 463 taxa (E – 154, P – 93 and T – 216) belonging to 148 genera (E – 39, P – 24 and T – 85) from Ephemeroptera, Plecoptera and Trichoptera orders were included in the study. The data were explicitly of benthic nymphs/larvae sampled using a 500-μm mesh net.

To avoid spurious results based on sampling biases, we standardized the data by assessing the completeness of the inventories (Gañán et al., 2008). The number of sample records per grid cell was used as a proxy for the sampling effort carried out, as greater sampling effort produces more records (Gañán et al., 2008). The data of each sample was placed on a map of Europe divided into 1° × 1° grid cells using ArcGIS 10 to assess the presence and number of records for each species in each grid. To quantify the degree of completeness of the data from each grid cell, four non-parametric estimators were calculated: Chao 2, Jackknife 1, Jackknife 2 and Bootstrap (Gañán et al., 2008). These estimators were computed using the Vegan package in R version 2.12.2 (R Development Core Team, 2011). The mean of these four estimators was taken as a good estimate of the potential species richness of each grid cell. An arbitrary cut-off point was established, whereby those grid cells in which the observed species richness was equal to or greater than 70% of the estimated species richness were considered to be well sampled; only data for these grid cells were used in the subsequent analysis. Once grids of 1° × 1° were selected, all grids at the same latitude were merged into a latitudinal band of 1° N.

2.2.2. Ecoregion data

We calculated EPT richness i.e., total number of taxa at the ecoregion scale based on the European zoogeographical regions introduced by Illies (1978). Latitude for ecoregions was taken as the geographic midpoint derived from the mean point between the northern and southern boundary of each region. We extracted EPT species lists for each of these ecoregions from the www.freshwaterecology.info database (Graf et al., 2009a; Schmidt-Kloiber and Hering, 2015). This data set contains species information based on literature review and expert knowledge and thus results in higher species numbers. In addition, we compared species richness based on these list data with observed taxa richness based on the 1318 sampling sites from the grid data for each ecoregion. The data of each sample was placed on a map of Europe divided into ecoregions using ArcGIS 10 and the species richness was calculated for each.

2.3. Topoclimatic data

To understand stream insect diversity at large spatial scales, macro-variables such as bioclimatic data are considered reliable parameters (e.g., Domisch et al., 2013). Topoclimatic variables (factors related to altitude, temperature, and precipitation) were obtained from WorldClim 1.4 (Hijmans et al., 2005), and mean values were calculated for each grid cell (again with a resolution of 1° × 1°) using ArcGIS 10 (Table 1). The predictor variables were transformed as necessary to meet assumptions of normality (Shapiro–Wilk test, $\alpha < 0.05$) and constant variance in the analysis. Only the independent and significant variables were used in the analysis to estimate variance partitioning (see statistical analyses below). We also included altitudinal bands in the analysis by coding altitude into three range categories (1 = <200 m, 2 = 200–800 m, 3 = >800 m asl) (Schmidt-Kloiber and Hering, 2015). For spatial (geographic location) variables, we used the nine terms of a third degree polynomial of the X (longitude) and Y (latitude) coordinates usually used in spatial analysis (i.e., terms included were: x, y, x^2, xy, y^2, x^3, x^2y, xy^2 and y^3 as introduced by Legendre and Legendre, 1998).

We also determined the elevational range of every band (based on sample points) and ecoregion (based on 1 km × 1 km grid) (Dehling et al., 2010) as the difference between the maximum and minimum elevation.

Slope and aspect were extracted from the altitude layer with the "3D Analyst Tools" Toolbox in ArcGIS.

2.4. Statistical analyses

We first evaluated the taxon richness pattern of each order and as combined EPT taxon richness for both latitudinal bands and ecoregion data in relation to latitude with simple linear regression using the 'lm' method in R (R Development Core Team, 2011). We also compared patterns at the ecoregion-scale between list-based data from www.freshwaterecology.info and grid-based observed data compiled for each region. To better display any non-linear trends in the relationship and determine if trends were different from random patterns, we also fitted a smoothing curve to the data using the locally weighted sums of squares (LOWESS) regression technique (Cleveland, 1979). This regression technique is designed to identify the underlying trend in a data set without a priori specification of a model (Cleveland, 1979). The tension parameter was set to 0.5, the mid-point value, in the LOWESS model. Moreover, we assessed whether significant thresholds were present in richness along these latitudinal gradients using change-point analysis in the change-point package (AMOC [At Most One Change] method) in R. The heterogeneity of habitats and variability of thermal conditions depends on the elevational variation (Heino, 2009). Therefore, as a simple proxy for habitat diversity, we analysed whether species richness increased with the increasing elevational range. To estimate whether this factor changed with latitude we regressed elevational range with latitude.

We used function (varpart) in R package to determine the relative importance of the pure and combined effects of spatial, topographic and climatic variables on taxonomic richness. Prior to the analysis, simple linear regression was conducted between taxonomic richness of E, P, T, and combined EPT and individual environmental variables. Only significant environmental variables (Table 1) were then employed in final variance partitioning for taxonomic richness.

Later, we partitioned the variance among sets of matrices (see below) to quantify the relative importance of the pure effects of spatial, topographic and climatic variables and their respective shared influences (Borcard et al., 1992; Heikkinen et al., 2004) using Canonical Correspondence Analysis (CCA) in the program CANOCO (version 4.5, ter Braak and Šmilauer, 2002).

Four fundamental matrices were used in the analysis: species, spatial, topographic and climatic variables. Species matrices were also constructed for spatial + topographic variables, climate + spatial variables and climate + topographic variables. Canonical Correspondence Analysis (CCA) was applied (Lepš and Šmilauer, 2003), following an initial Detrended Correspondence Analysis (DCA, gradient lengths > 4.0 SD for the longest axes).

Table 1

Relationships of E, P, T, and combined EPT richness with climatic, spatial and topographic variables. Increasing number of strike (*) shows higher significance level. Only significant variables in respective insect orders were used in variation partitioning analysis. The values presented are adjusted R^2.

Environmental predictors	Code	Transformation	E	P	T	EPT
Climate:						
Annual mean temperature	Bio 1		0.21***	0.06**	0.18***	0.18***
Mean diurnal range (mean of monthly (maximum temperature – minimum temperature))	Bio 2		0.19***	0.33***	0.28***	0.3***
Isothermality (BIO2/BIO7) (×100)	Bio 3		0.22***	0.17***	0.31***	0.29***
Temperature Seasonality (SD ×100)	Bio 4		0.04*	−0.007	0.03	0.02
Maximum temperature of warmest month	Bio 5		0.26***	0.16***	0.25***	0.26***
Minimum temperature of coldest month	Bio 6		0.13***	0.008	0.10***	0.09**
Temperature annual range (BIO5–BIO6)	Bio 7		−0.009	0.02	−0.01	−0.06
Mean temperature of wettest quarter	Bio 8	x^4	−0.004	0.004	−0.002	−0.01
Mean temperature of driest quarter	Bio 9	logx	0.04*	0.01	−0.002	0.02
Mean temperature of warmest quarter	Bio 10		0.21***	0.08**	0.17***	0.19***
Mean temperature of coldest quarter	Bio 11		0.18***	0.03*	0.14***	0.14***
Annual precipitation	Bio 12	logx	0.13***	0.13***	0.07**	0.13***
Precipitation of wettest month	Bio 13	logx	0.19***	0.32***	0.01**	0.2***
Precipitation of driest month	Bio 14		0.02	−0.005	0.04*	0.02
Precipitation seasonality (coefficient of variation)	Bio 15		0.22*	0.12***	−0.01	0.02
Precipitation of wettest quarter	Bio 16	logx	0.17***	0.28***	0.08**	0.18***
Precipitation of driest quarter	Bio 17		0.06*	0.01	0.06**	0.05*
Precipitation of warmest quarter	Bio 18	logx	−0.005	0.03*	0.004	0.005
Precipitation of coldest quarter	Bio 19	logx	0.1***	0.02	0.04*	0.07*
Spatial:						
Latitude	Y		0.42***	0.3***	0.41***	0.44***
Longitude	X		0.006	−0.004	0.02	−0.003
Topographic						
Altitude		sqrt	0.1***	0.27***	0.12***	0.14***
Altitude.range			0.13***	0.27***	0.18***	0.18***
Slope		logx	0.19***	0.29***	0.15***	0.22***
Aspect			−0.01	−0.006	−0.01	−0.01

The climatic, spatial, and topographic variables were included in a procedure of 'forward selection' (see Økland and Eilertsen, 1994). This procedure allows the selection of variables by sequential testing and helps to reduce inflation of explained variation due to pure chance by the retention of redundant parameters in the model (Borcard et al., 1992). The variable with the highest variance inflation factor (VIF) was eliminated and the model was run repeatedly until the remaining variables had VIF < 20 (ter Braak and Šmilauer, 2002). In forward selection of the explanatory variables the Monte Carlo permutation test was run with 999 unrestricted permutations. Only the significant variables were used in the analysis to estimate variance partitioning (Table 2).

A series of steps, involving constrained and/or partial CCA, were done using CANOCO (see Anderson and Gribble, 1998). For each step, unrestricted permutation tests (with 999 permutations) were done for the overall trace statistic (for details of this statistic and the permutation method used in CANOCO see ter Braak, 1992). The permutation test for this statistic indicates the significance of the effects of constraining variables on the species variables (removing the effects of covariables, when present) (Anderson and Gribble, 1998).

3. Results

3.1. Latitudinal richness gradients

Species richness of all groups and combined EPT decreased with increasing latitude (Fig. 2, Table 3) for latitudinal bands in European streams. However, while there was a significant linear trend for all relationships, the pattern was not monotonic. In general, a sharp decrease in richness was observed, with a significant threshold (change-point) at 48° N. The species richness pattern of Ephemeroptera and Trichoptera was similar to that of combined EPT, but Plecoptera richness was low in the middle portion of the latitudinal range and increased slightly in the north (Fig. 2). Richness of Ephemeroptera, Plecoptera and combined EPT, was highest at 42° N, and Trichoptera at 46° N.

The species richness per ecoregion decreased monotonically with latitude (Fig. 3, Table 3). The pattern was similar between list-based (www.freshwaterecology.info) and grid-based data, but richness at the ecoregion level (list-based), which included the maximum theoretically known number of species in each ecoregion, was generally higher.

The elevational range showed quadratic response ($R^2 = 0.30$, $F_{2,24} = 4.23$, $p = 0.02$) with increasing latitude for band level while the relationship at ecoregion level was not significant. Species richness response to elevational range was variable (Fig. 4, Table 4). Where a significant relationship was present, richness increased with increasing elevational range for band and ecoregion data as predicted. However, Ephemeroptera and Plecoptera species richness of the band data and Ephemeroptera species richness at the ecoregion level were not related to elevational range.

3.2. Regional control of richness patterns

Using variation partitioning, climatic variables had a higher explanatory power than the spatial and topographic variables on taxonomic richness for all groups. Combination of climatic and spatial variables explained about half of the total explained variation in taxonomic richness of all groups (Fig. 5). The employed regional environmental variables explained more than 50% in variability of taxonomic richness.

Table 2
The explanatory variable groups (climatic, spatial and topographic) considered in our study determining latitudinal patterns across Europe between latitudes 39° and 68° N. The significant variables used in the analysis to estimate variance partitioning are marked with black dots.

Environmental predictors	Transformation	E	P	T	EPT
Climatic					
Bio 1				●*	
Bio 2		●*	●*	●*	●*
Bio 3					
Bio 4		●*	●*	●*	●*
Bio 5		●*	●*		●*
Bio 6					
Bio 7					
Bio 8	x^4	●*			●*
Bio 9	logx	●*	●**		●*
Bio 10					
Bio 11					
Bio 12	logx				
Bio 13	logx			●*	
Bio 14		●*			●*
Bio 15		●*	●**		●*
Bio 16	logx				
Bio 17					
Bio 18	logx	●*	●*	●*	●*
Bio 19	logx	●*	●*	●*	●*
Spatial					
Y		●*	●*		
X		●*	●*	●*	●*
XY					
X^2					
Y^2					
X^2Y					
XY^2					
X^3		●*	●*	●*	●*
Y^3				●*	●*
Topography					
Altitude	sqrt	●*	●**	●*	●*
Alt band		●**	●**	●**	●**
Slope	logx	●*	●*	●*	●*
Aspect				●**	

The levels of significance are shown with the stars:
[*] $p < 0.01$.
[**] $p < 0.05$.

Table 3
Linear relationships between latitude and E, P, T, and combined EPT species richness at latitudinal band and ecoregion levels[a] in European streams (latitude 39° to 68° N). Significant relationships with $p < 0.05$ are marked with bold R^2 values.

Taxa	Latitudinal band (obs. data)			Ecoregions (obs. data)			Ecoregions (database)		
	R^2	F	p	R^2	F	p	R^2	F	p
E	**0.71**	62.70	<0.001	0.35	4.79	0.056	**0.52**	8.64	0.019
P	**0.55**	31.55	<0.001	0.30	3.81	0.083	**0.74**	22.63	0.001
T	**0.74**	61.67	<0.001	**0.44**	6.98	0.027	**0.72**	20.13	0.002
EPT	**0.77**	82.94	<0.001	**0.40**	5.96	0.037	**0.80**	32.60	<0.001

[a] The species richness at ecoregion levels is based on the data from www.freshwaterecology.info online database. This is the theoretical maximum number of species that can occur in each ecoregion and is derived from both juvenile and adult stage specimen.

Table 4
Relationships between species richness and elevational range for latitudinal band data and ecoregion data. The study area is across Europe between latitudes 39° and 68° N. Significant relationships with $p < 0.05$ are marked with bold R^2 values.

Taxa	Latitudinal band				Ecoregion			
	R^2	F	df	p	R^2	F	df	p
E	0.10	2.80	1,26	0.106	0.07	0.79	1,10	0.395
P	0.14	4.09	1,26	0.054	**0.62**	16.06	1,10	0.002
T	**0.29**	9.02	1,22	0.007	**0.69**	22.05	1,10	0.001
EPT	**0.18**	5.67	1,25	0.025	**0.59**	14.54	1,10	0.003

Similarly, the largest pure effect of these three variable groups on taxonomic composition was explained by current climate, while the pure effect of spatial and topographic variance was small but significant (Fig. 6). The climatic variables explained approximately double the variance of spatial and topography predictors for Trichoptera composition. Topography was a relatively poor contributor to the prediction of EPT composition. The joint effect of climate, spatial and topography were negligible for all groups. Current climate, spatial, and topographic predictors explained between 28% and 38% of the variation in taxonomic composition

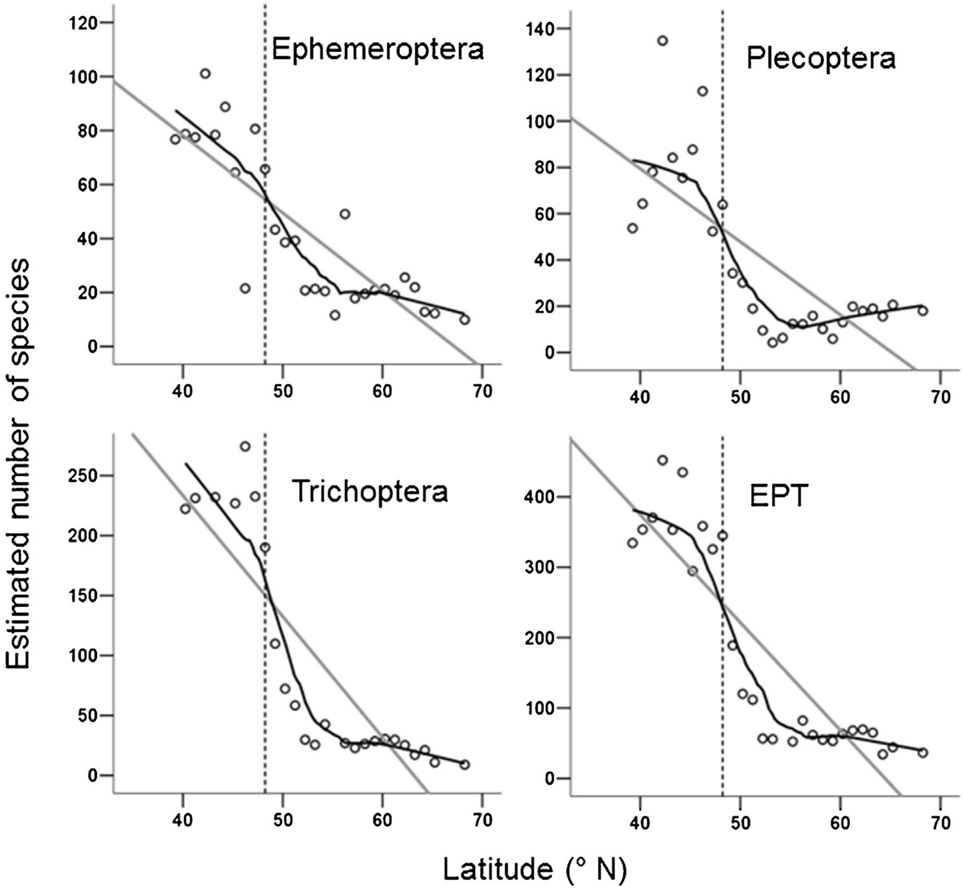

Fig. 2. Latitudinal gradients in species richness of stream insects across Europe (39°–68° N). The empty circles represent the number of species at each latitudinal band. The pattern is shown with the regression line (gray color) and by fitting a smooth curve (black line) using the LOWESS technique. The vertical dotted line marks the change-point of species richness at 48°. Regression results are shown in Table 2.

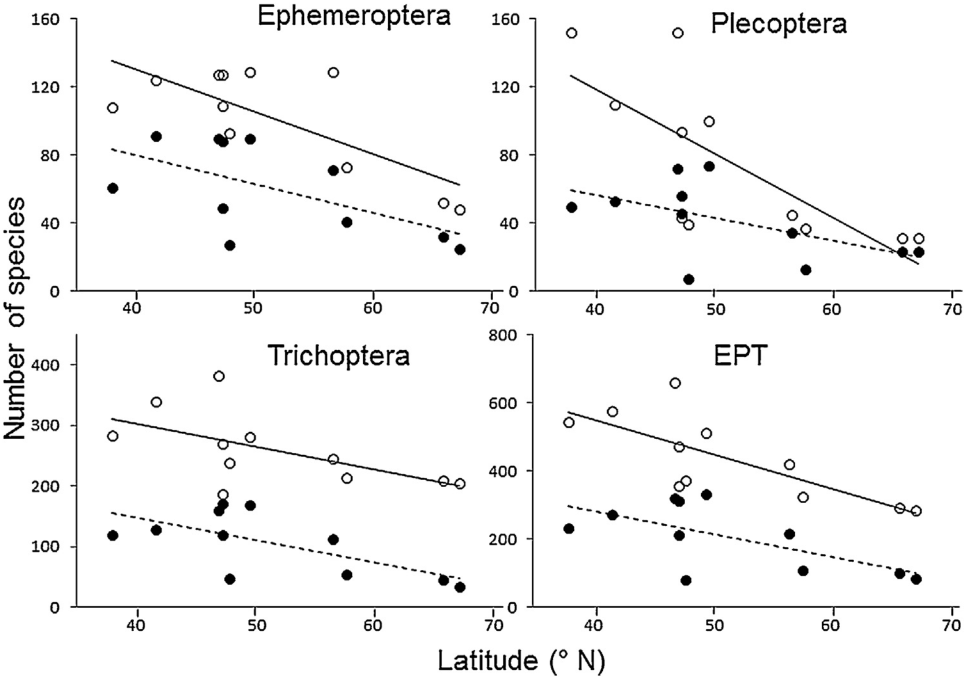

Fig. 3. Latitudinal gradients in species richness of stream insects across Europe (39°–68° N). The empty circles represent the theoretical maximum number of species in each ecoregion (based on www.freshwaterecology.info) while black filled circles represent the observed species richness in each ecoregion (based on grid data, using estimated number of species per grid, see Section 2). The linear relationships are shown with solid and dotted lines using regression analysis for theoretical maximum richness and observed data respectively. Regression results are shown in Table 2.

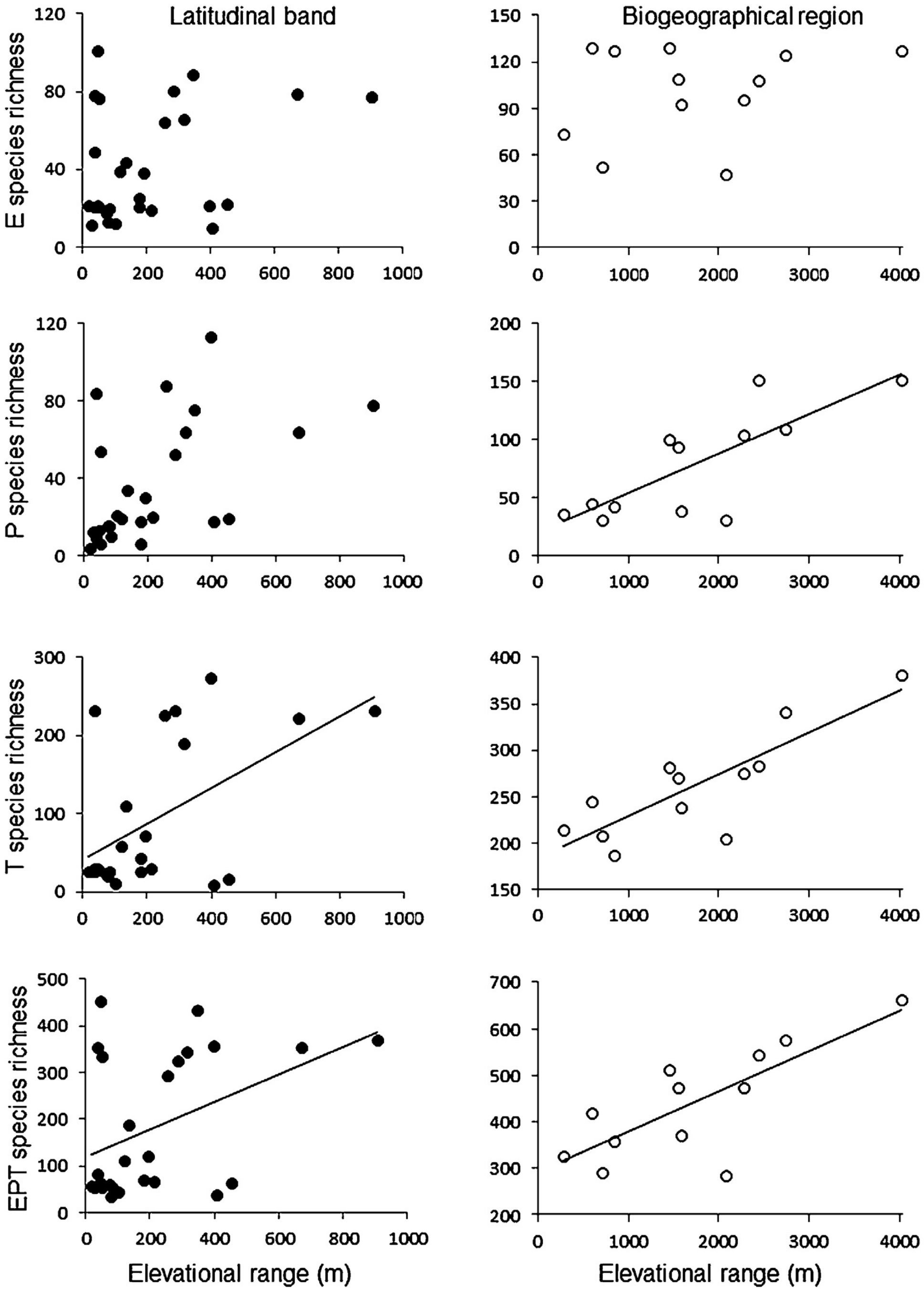

Fig. 4. Species richness as a function of elevational range for both latitudinal band data and ecoregion data for Europe. Black filled circles represent the species richness at each latitudinal band while open circles represent the species richness of the ecoregion. Elevational range in the band is the difference of the average lowest and highest elevation value of each grids in the band while the elevational range in the ecoregions is the difference between highest and lowest elevation of the particular ecoregion. The linear relationships are shown when significant; details of the regression results can be seen in Table 3.

(E – 37.6%, P – 28.2%, T – 28.6% and overall EPT – 31.3%). The shared fractions among the sets of predictors also significantly explained the proportion (E – 10.3%, P – 11.2%, T – 7.3% and EPT – 8.1%) of variance (Fig. 6). However, the amount of unexplained variation was high for all groups (E – 62.4%, P – 71.8%, T – 71.4% and EPT – 68.7%).

4. Discussion

4.1. Latitudinal richness gradients

Overall, EPT taxonomic richness decreased with increasing latitude across Europe. Splitting the macroinvertebrate assemblages into taxonomic groups yielded additional insights into the biodiversity patterns, with individual groups responding slightly different to latitude. The species richness gradients in E, P, T, and combined EPT generally concurred with those found for various plant and animal groups globally (Currie, 1991; Brown and Lomolino, 1998), including freshwater species (Hof et al., 2008; Heino, 2009; Dehling et al., 2010). The highest richness between 40 and 46° N is similar with the findings at global scale (Vinson and Hawkins, 2003; Palma and Figueroa, 2008), but without data south of 40° N, we cannot ascertain whether this is part of a larger monotonic or unimodal trend. Vinson and Hawkins (2003) observed a peak with the highest generic richness near 40° N, but did not find clear

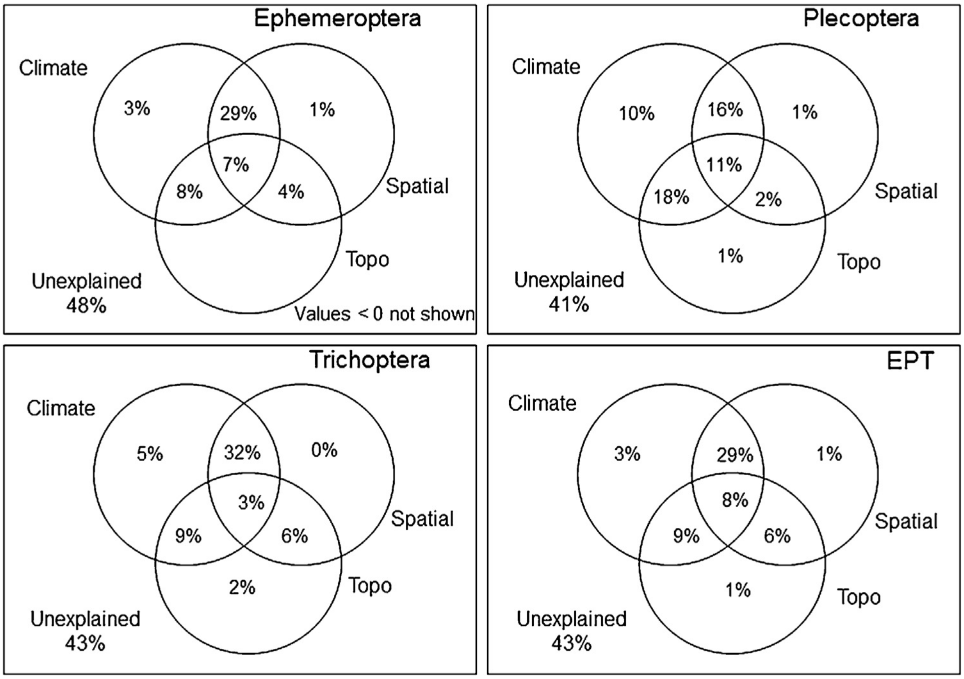

Fig. 5. Venn diagrams, showing the partition of the total variation in stream insects (Ephemeroptera, Plecoptera, Trichoptera and combined EPT) taxonomic richness across Europe (39°–68° N) explained by the sets of climate, spatial and topo (topography) explanatory variables. Negative values are not shown.

latitudinal patterns. The result of Vinson and Hawkins (2003) could be explained by their study being based on site-level data at higher taxonomic level, with limited data and also by differences in potential pre- and post-glacial dispersal patterns (see below). Results of declining species pattern with increased latitude between freshwater studies like those from Hof et al. (2008) and Heino (2009) can be resolved when considering the different approaches. While Hof et al. conducted an ecoregion-level analysis, Heino (2009) compared countries and e.g. found highest richness values for France – which has substantial shares on the species rich ecoregions of the Pyrenees and the Alps.

The slightly lower species richness shown by Plecoptera than Ephemeroptera and Trichoptera in the middle of the latitudinal gradient could be explained by several factors associated with the large modified plains comprising denser population areas and altered land uses that have occurred at these latitudes affecting river conditions. Most Plecoptera species show other ecological requirements than many other taxa, such as preference for cool

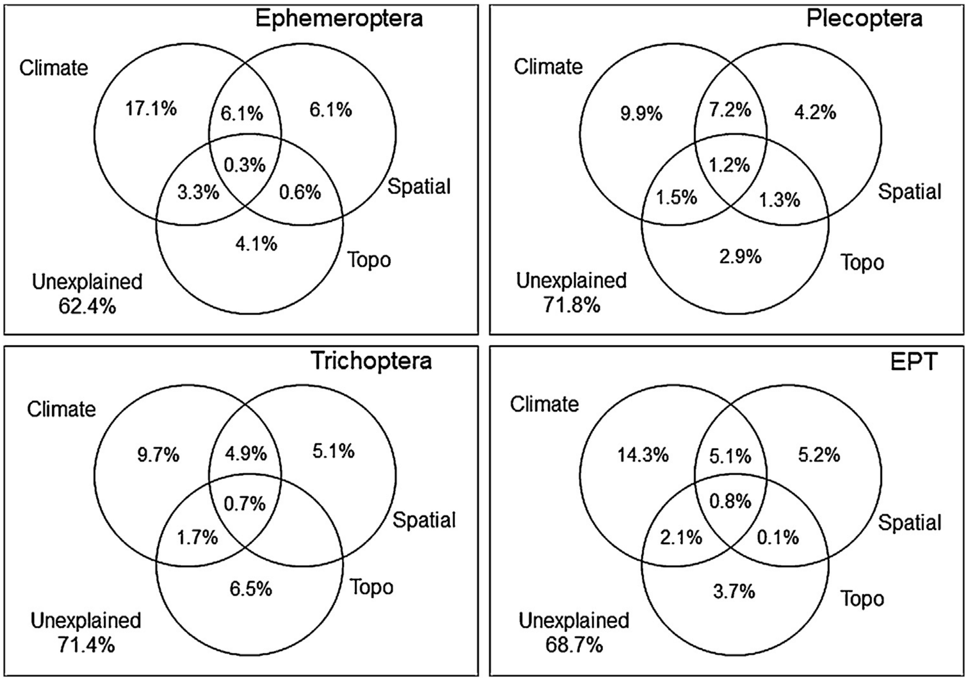

Fig. 6. Venn diagrams, showing the partition of the total variation in stream insects (Ephemeroptera, Plecoptera, Trichoptera and combined EPT) assemblages across Europe (39°–68° N) explained by the sets of climate, spatial and topo (topography) explanatory variables. Negative values are not shown.

water temperature, well oxygenated water and good water quality for nymph development (Palma and Figueroa, 2008; Tierno de Figueroa et al., 2010). While Ephemeroptera occur relatively evenly throughout river basins, Plecoptera show a gradient of richness from headwaters to potamal regions (Haidekker and Hering, 2008; Graf et al., 2009b). The effect of water quality and habitat degradation (Fochetti and Tierno de Figueroa, 2008) is already clearly evident. For example, *Taeniopteryx araneoides* (Klapálek) and *Oemopteryx loewi* (Albarda), once occurring in large central European rivers, are now extinct (Zwick, 2004). The slight increase in Plecoptera richness north of 60° N latitude is potentially due to the presence of mountains in this area, as Plecoptera richness has a positive association with increasing altitude (Pearson and Boyero, 2009). In Finland, Heino et al. (2003) have also observed increasing species richness of Plecoptera with latitude and decreasing species richness of Trichoptera.

Similarly to latitudinal band data, ecoregion richness declined linearly with latitude, which corroborates with the previously found patterns of entire freshwater assemblages (Hof et al., 2008). The combination of single sampling occasions represent ecoregion scale observations adequately, even though confounding issues must be at play like local-regional richness patterns, adequacy of sampling, or temporal variability. Ecoregional richness was much higher than that of latitudinal bands, which is likely as the species lists derived from the freshwaterecology.info comprise the maximum theoretically known number of species, including historical records from the region, while the latitudinal bands dataset is more restricted because of (1) taxonomic shortcomings dealing with larvae and nymphs (many species are not described in their juvenile stages), (2) seasonal occurrence of species, (3) the habitats sampled most probably do not reflect all freshwater types present, and (4) the degradation of aquatic systems which is likely apparent in this dataset.

Generally, grid-based richness was highest in the vicinity of the Alps, which, along with the Pyrenees and the Mediterranean areas harbor the highest biodiversity in Europe, e.g. found for birds and butterflies (Hawkins and Porter, 2003; Hawkins et al., 2003) and suggested by the freshwaterecology.info data (Fig. 3). Indeed, the great variations in topography, climate and habitat in these regions provide diverse habitats (Hewitt, 1999), having strong potential to explain species richness (Heino, 2009). The Alps acted as a refuge for the biodiversity during the Last Glacial Maximum (Malicky, 2006; Muster, 2000) and species survived several ice ages by ascending and descending the mountains (Hewitt, 1999). Most organisms presently distributed across Europe inhabited refuges in the southern regions during glacial periods; many in the peninsulas of Iberia, Italy, Greece and the Balkans, and some possibly near the Caucasus and Caspian Sea (Hewitt, 1999; Michl et al., 2010; Engelhardt et al., 2011; Previšić et al., 2014). After glaciation, species expanded their ranges from the refuge northwards, but northward expansions are likely influenced by species' dispersal ability (Araújo et al., 2008).

It is clear that species responded individually to this warming with each tracking their particular set of environmental conditions. Species richness of individual orders and combined EPT decreased sharply at 48° N in the present study, reflecting the northern foothills of western parts of the Alps; altogether the Alps can be thought of posing a barrier to the expansion of species further north (Hewitt, 1999). Probably even more important, the large plains north of the Alps (western, central and eastern plains) contain large rivers and are characterized by intensive human land use which may have restricted many of these EPT taxa.

4.2. Regional control of taxonomic richness and composition

Taxonomic richness and composition were more strongly influenced by climatic variables than spatial and topographical factors, but both pure and combined effects of spatial factors contributed significantly to the explanation of richness and composition patterns. The contributions of climatic variables suggest that the selected groups (more on Plecoptera community) of stream insects are sensitive to climate change, as indicated in previous studies (Hering et al., 2009; Conti et al., 2014). Despite this, most of the variation in species composition remained unexplained, similar to other studies that failed to find strong correlations between diversity and environmental variables (e.g., Heino et al., 2008; Gañán et al., 2008). The reason might be that pollution (Vaughan and Ormerod, 2014), river engineering leading to reduced floodplain connectivity (Buijse et al., 2002), and habitat fragmentation (Zwick, 1992; Dudgeon et al., 2006) influence community composition at local scale further shaping the modern biodiversity patterns in central Europe. Inclusion of variables such as land use, population density, and river engineering would likely have increased the explained variation (Ormerod et al., 2010; Mantyka-Pringle et al., 2014), but this was beyond the scope of our study. Furthermore, past changes in the earth's climate, dispersal capacities, extinctions, re-colonization of previously glaciated area after deglaciation and the availability of suitable habitats may play a major role in influencing the patterns today (Barber-James et al., 2008; Tisseuil et al., 2013). To include such variables would be worthwhile, however, the methodological approach that we used here did not allow us to consider these variables in the analysis, and were beyond the scope of the natural drivers of our research.

The significant bioclimatic variables varied across the groups, but mean diurnal temperature range, temperature seasonality and precipitation of warmest or coldest quarter were found important for all groups. These results indicate the major influence of temperature and moisture availability on taxonomic richness patterns, but also reflect the large scale variation of these variables across Europe. Tonkin et al. (2015) found similar explanatory variables at work in a Chinese large scale study, e.g. mean annual temperature being most important for Trichoptera, mean temperature of wettest quarter for Ephemeroptera, or temperature seasonality for all three groups, further indicating that species richness patterns of terrestrial and aquatic organisms are related to productivity and energy availability (Guégan et al., 1998; Kreft and Jetz, 2007).

5. Conclusion

Gaining insight into broad-scale biodiversity patterns is essential for understanding the origins and maintenance of biological diversity and for carrying out appropriate scales of ecosystem protection and preservation (Markovic et al., 2014). Our study provides insight on latitudinal gradients of European stream insect richness, with all orders declining with increasing latitude. The Alps harbor the highest richness with a clear threshold decline at their northern border. However, given we did not incorporate land use variables, it is unclear whether this threshold decline is a function of anthropogenic modification north of the Alps, or a relict of refuge inhabitation and dispersal limitation, such as that documented for plecopteran species (Fochetti and Tierno de Figueroa, 2006). As we also found some influence of climate on richness patterns in our study, it is likely that future climate change will affect the present-day patterns in stream insect biodiversity in Europe and elsewhere (Domisch et al., 2013; IPCC, 2013). Future studies could analyse both of these aspects: a historic perspective of biogeographical developments and how it may explain the pattern of species richness (Tisseuil et al., 2013; Previšić et al., 2014 and references therein) and the potentially strong role that anthropogenic stress has played in certain regions such as the central plains.

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