

# Modelling distribution in European stream macroinvertebrates under future climates

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## Abstract

Climate change is predicted to have profound effects on freshwater organisms due to rising temperatures and altered precipitation regimes. Using an ensemble of bioclimatic envelope models (BEMs), we modelled the climatic suitability of 191 stream macroinvertebrate species from 12 orders across Europe under two climate change scenarios for 2080 on a spatial resolution of 5 arc minutes. Analyses included assessments of relative changes in species' climatically suitable areas as well as their potential shifts in latitude and longitude with respect to species' thermal preferences. Climate-change effects were also analysed regarding species' ecological and biological groupings, namely (1) endemism and (2) rarity within European ecoregions, (3) life cycle, (4) stream zonation preference and (5) current preference. The BEMs projected that suitable climate conditions would persist in Europe in the year 2080 for nearly 99% of the modelled species regardless of the climate scenario. Nevertheless, a decrease in the amount of climatically suitable areas was projected for 57–59% of the species. Depending on the scenario, losses could be of 38–44% on average. The suitable areas for species were projected to shift, on average, 4.7–6.6° north and 3.9–5.4° east. Cold-adapted species were projected to lose climatically suitable areas, while gains were expected for warm-adapted species. When projections were analysed for different species groupings, only endemics stood out as a particular group. That is, endemics were projected to lose significantly larger amounts of suitable climatic areas than nonendemic species. Despite the uncertainties involved in modelling exercises such as this, the extent of projected distributional changes reveals further the vulnerability of freshwater organisms to climate change and implies a need to understand the consequences for ecological function and biodiversity conservation.

**Keywords:** bioclimatic envelope model, BIOMOD, climatically suitable area, endemic species, invertebrates, range shift, river

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## Introduction

Global climate change is forecasted to impose severe challenges to biodiversity across several ecosystems (Sala *et al.*, 2000; Pereira *et al.*, 2010; Bellard *et al.*, 2012), and studies have proposed that freshwater biodiversity is likely to decline more severely than terrestrial or marine biodiversity (Ricciardi & Rasmussen, 1999; Sala *et al.*, 2000). Streams and rivers, specifically, rank among the most threatened freshwater systems due to the combined effects of warming climates, increased frequency of droughts and floods (Milly *et al.*, 2005; Xenopoulos *et al.*, 2005), habitat fragmentation and

multiple anthropogenic stressors (Ormerod *et al.*, 2010; Vörösmarty *et al.*, 2010; Woodward *et al.*, 2010).

Several experimental and long-term studies have documented the local impacts of climate change and associated stressors on aquatic insects, an important group of benthic stream macroinvertebrates (Hickling *et al.*, 2005; Durance & Ormerod, 2009; Hering *et al.*, 2009; Woodward *et al.*, 2010). Observed changes in community composition and structure were often associated with long-term warming or extreme hydroclimatic events (Daufresne *et al.*, 2003), affecting the species composition in alpine and headwater ecosystems (Brown *et al.*, 2007; Durance & Ormerod, 2009), or across the river continuum (Daufresne *et al.*, 2007; Chessman, 2009, 2012). Moreover, the establishment of nonnative species (Rahel & Olden, 2008) and alterations in species' life history characteristics following

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changing climatic conditions (Mulholland *et al.*, 1997) have the potential to impact species assemblages.

Streams and rivers across Europe are expected to respond strongly to climate change, which is expected to shape the potential fate of stream macroinvertebrates distributions under warming climates (Milly *et al.*, 2005; IPCC, 2007; Vörösmarty *et al.*, 2010). Recent studies indicate that the distribution of stream macroinvertebrates may be impacted by a reduction in habitat for (1) cold-adapted species in high latitudes and altitudes (Bálint *et al.*, 2011), as well as for (2) warm-adapted (endemic) species of the lower latitudes (Ribera & Vogler, 2004; Bonada *et al.*, 2009), for (3) habitat specialists (Kotiaho *et al.*, 2005) and for species with (4) specialized life history traits, such as short emergence periods or (5) narrow ecological niches, e.g., specialized feeding ecologies (Hering *et al.*, 2009).

So far, assessments of possible climate-change effects on stream macroinvertebrates at continental scale have used bioclimatic envelope models (BEM) (Peterson *et al.*, 2011) applied to single species (e.g., Taubmann *et al.*, 2011), specific taxonomic orders (Hof *et al.*, 2012) or cold-adapted headwater species (Bálint *et al.*, 2011). Freshwater ecologists have also used trait-based analyses of single taxonomic orders to gain insights on possible patterns of species vulnerability to warming climates (Hering *et al.*, 2009; Tierno de Figueroa *et al.*, 2010). If carefully designed implementations of BEMs provide useful estimates of the size and location of potential species distributions as well as their changes through time (Araújo & Guisan, 2006; Elith & Leathwick, 2009; Peterson *et al.*, 2011), trait-based analyses can potentially help provide first approximations regarding their potential vulnerability (Hering *et al.*, 2009; Tierno de Figueroa *et al.*, 2010).

Our study is the first to assess the climatic vulnerability of a wide range of stream macroinvertebrates from 12 orders across Europe using a combination of SDMs and trait-based analyses. Specifically, we modelled the distribution of climatically suitable areas (CSA) in the present and future for 191 macroinvertebrate species. Once distributions were modelled, we combined projections of species' potential range changes in the following ecological and biological grouping: (1) endemism; (2) rarity within European ecoregions; (3) life cycle; (4) stream zonation preference; (5) current preference. In general, we hypothesized that CSAs would shift northwards (Parmesan & Yohe, 2003; Chen *et al.*, 2011), and that the extent of climate-change effects would be related to species thermal preferences (Domisch *et al.*, 2011). Furthermore, we expected that endemic and rare species would be more threatened by warming climates than their respective counterparts, as specific habitat requirements may not be present under future

climate conditions (Malcolm *et al.*, 2006; Ohlemüller *et al.*, 2008). Similarly, we expected that species with a fully aquatic life cycle would lose more CSA than species with an aquatic larval and terrestrial adult stage, as changing precipitation patterns with longer periods without precipitation may lead to a restriction of habitat availability in fully aquatic species (Xenopoulos *et al.*, 2005). As species occurring in specific stream zones along the river continuum are expected to respond differentially to climate change due to different thermal regimes (Carpenter *et al.*, 1992; Mulholland *et al.*, 1997; Hering *et al.*, 2009), we expected that cold-adapted headwater species would be more vulnerable to warming climates than warm-adapted species distributed along the mid- and lower-reaches of the river continuum. Last, we hypothesized that CSAs for species adapted to high current velocities would decrease because of expected droughts and alterations in stream flow (Lancaster & Hildrew, 1993; Bonada *et al.*, 2007b).

## Materials and methods

### Study area

BEMs were constructed for a larger window of Europe (24°W–52°E longitude and 33°–72°N latitude), including Iceland and parts of Northern Africa, Middle East and Russia, with a spatial resolution of 5 arc minutes (ca. 10 × 10 km). The large extent was chosen to overcome the limitation of using truncated environmental gradients for calibrating models within species' known ranges (Thuiller *et al.*, 2004). Moreover, this procedure minimizes the constraints of nonanalogous climates, i.e., future novel climatic conditions on the predictive model performance for projecting climatic suitability under future climate scenarios (Fitzpatrick & Hargrove, 2009).

### Species data

Rigorous criteria were used to select the species included in the study, as several studies have shown the limitation of poor quality species' records (i.e., incomplete distributional data) on the predictive performance of BEMs (Araújo *et al.*, 2009; Barbet-Massin *et al.*, 2010; Sánchez-Fernández *et al.*, 2011).

We compiled a set of geographic records across Europe for 1733 stream macroinvertebrate species from data collected by taxonomists. These records were sourced from the EU-funded STAR project (Furse *et al.*, 2006), the GUADALMED projects and an International Cooperation project with Morocco (Bonada *et al.*, 2004, 2008), collection material from S.U. Pauls and data digitized for Portugal by M. B. Araújo (Terra, 1994).

Furthermore, we considered data compiled by the Swedish University of Agricultural Sciences ([www.slu.se](http://www.slu.se), accessed 26 September 2011), three national databases (Umweltbundesamt; Hessisches Landesamt für Umwelt und Geologie; and Landesamt für Umwelt, Messungen und Naturschutz Baden-Württemberg, unpublished data), the SeSam database of the

Senckenberg Museum (<http://sesam.senckenberg.de>), the ZOBODAT database ([www.zobodat.at](http://www.zobodat.at)) and the Global Biodiversity Information Facility database ([www.gbif.org](http://www.gbif.org)) as additional data sources to retrieve presence records for species listed in our set. For public databases, only records were retrieved which were published by natural history museums or research facilities, where the resolution of records was not coarser than that of our models, and where terms of use allowed the usage of data. Historic occurrences recorded earlier than 1950 were discarded, as the climatic baseline for modelling ranged from 1950 to 2000. After scanning these databases for species listed in our initial data, records were resampled to a 5 arc minute grid resolution, and species needed to occupy at least 15 grid cells while duplicate records of a single species falling into one grid cell were omitted. This criterion was fulfilled for 986 species.

We then checked for geographic biases in the records and investigated, how well species records represented the known species ranges by using the classification of European ecoregions as a reference (Illies, 1978) by means of a digitized map (<http://www.eea.europa.eu/data-and-maps/figures/ecoregions-for-rivers-and-lakes>, EEA 2011). Here, records for each species needed to be present in at least two of the three ecoregions where the species is known to occur (described in *Limnofauna Europaea* (Illies, 1978) and the freshwater ecology.info database (Euro-limpacs Consortium, 2011; Schmidt-Kloiber & Hering, 2012). This procedure resulted in discarding the vast majority of species with highly incomplete records. In total, our final species list used for BEMs comprised 191 species from 12 macroinvertebrate orders. Species records ranged from Morocco to arctic Norway, covered 23 of 25 European ecoregions (all but Iceland and the Caspian depression), and in some species also included North Africa and the Middle East. The ranges of individual species covered one (i.e., endemic) to 24 ecoregions (widespread species, see Supporting Information, Table S1). The match between the distributional data (i.e., species records) and their known ranges (i.e., ecoregions) was on average  $81 \pm 13\%$  (mean  $\pm$  standard deviation).

#### Climate data

To build the BEMs, we chose climatic predictors that affect energy and water regimes (Whittaker *et al.*, 2007): mean annual air temperature ( $^{\circ}\text{C}$ ), sum of annual precipitation (mm) and precipitation seasonality (coefficient of variation). Although these predictors correspond to a small subset of available variables, they have been used for modelling stream macroinvertebrates on a continental scale (e.g., Taubmann *et al.*, 2011; Hof *et al.*, 2012) as well as plants (e.g., Baselga & Araújo, 2009; Engler *et al.*, 2011) and many vertebrate taxa (e.g., Hof *et al.*, 2011; Triviño *et al.*, 2011; Garcia *et al.*, 2012). Climatic predictors for the present were averaged across 1950–2000 (hereafter referred to as 'baseline') and retrieved from the WorldClim dataset in a 5 arc minute grid resolution ([www.worldclim.org](http://www.worldclim.org), accessed 1 August 2011, Hijmans *et al.*, 2005). Bioclimatic predictors for the future, averaged across 2070–2099 (hereafter referred to as '2080'), were obtained from the CIAT database ([www.ccafs-climate.org](http://www.ccafs-climate.org), Ramirez & Jarvis, 2008) and from four global climate models (GCMs): HCCPR HADCM3 (Gordon

*et al.*, 2000), CCCMA-CGCM2 (Flato *et al.*, 2000), CSIRO-MK2 (Gordon *et al.*, 2002) and NIES99 (Emori *et al.*, 1999). For each model, we used the A2a and B2a scenarios from the 4th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2007) respectively. The A2a scenario is referred to as the 'extreme' scenario with a projected warming of the mean annual temperature of  $5.8 \pm 1.3$   $^{\circ}\text{C}$ , whereas the B2a scenario reflects a 'moderate' scenario with a projected mean annual temperature increase of  $4.4 \pm 1.0$   $^{\circ}\text{C}$  in our study area ( $\pm$  standard deviation). Uncertainties associated with the emergence of novel future climatic conditions in our study area were assessed by calculating nonanalogous climates for each GCM (see also Araújo *et al.*, 2011; Garcia *et al.*, 2012).

To account for uncertainties derived from meteorological data to describe in-stream conditions, error margins of model results were calculated under different parameterizations of the relationship between air and water temperature, and between precipitation and discharge. Here, varying slopes of the relationship between stream and air temperature were taken from Clews *et al.* (2010), while possible rates of reduction in stream flow due to evapotranspiration were taken from Calder & Newson (1979) and Hudson *et al.* (1997).

#### Bioclimatic envelope modelling

We fitted BEMs using an ensemble forecasting framework (Araújo & New, 2007) based on seven algorithms as implemented in the BIOMOD package version 1.1.7 in R (generalized linear models, GLM; generalized additive models, GAM; gradient boosting machine, GBM; flexible discriminant analysis, FDA; classification tree analysis, CTA; artificial neural networks, ANN; surface range envelopes, SRE; Thuiller *et al.*, 2009; R Development Core Team, 2011). Models were calibrated using climate predictors for the baseline period after species presence records were randomly split into a training set (70%) and a testing set (30%, Fielding & Bell, 1997). Each algorithm used 10 000 pseudoabsences and a tenfold cross validation which yielded an average model for each species and algorithm. Model evaluation based on the true skill statistic (TSS), which has been shown to be superior in measuring the performance of BEMs when the predictions are expressed in presence-absence maps (Allouche *et al.*, 2006). TSS scores incorporate sensitivity (true positive predictions) and specificity (true negative predictions) and range from 0 to 1, where 0 describes a model no better than random while 1 describes a perfect agreement with the model and species' records. To reduce uncertainties derived from different modelling algorithms, consensus was obtained by weighted averaging of species projections where the weights were obtained from the TSS evaluation scores. Here, a weight decay of 1.6 was used, while only models performing better than TSS >0.4 were used in the consensus, discarding weak models for the consensus model (e.g., Araújo *et al.*, 2011; Engler *et al.*, 2011). At least two algorithms yielding a TSS score higher than 0.4 were required, otherwise no consensus model was created, and the respective species was removed from further analyses.

The consensus models were then projected on the entire study area for the baseline and future times. Variability

accrued from different greenhouse gas emission assumptions was examined by averaging consensus projections of each GCM within the A2a and B2a scenarios. Maps indicating the probability of climatic suitability under present and future projections were transformed into binary presence-absence maps by applying a cut-off value which minimizes the difference between sensitivity and specificity (Liu *et al.*, 2005; Nenzén & Araújo, 2011).

### Climate change effects on species

*All-species analyses.* First, we measured proportional changes in CSAs between baseline and future projections, by first examining the numbers of grid cells kept stable, lost and gained. Species were identified as either climate-change losers or winners depending on a species' overall loss or gain of CSA.

Furthermore, we tested for an overall geographic shift of species' CSAs, and analysed whether the arithmetic mean of the modelled latitude and longitude of the present CSAs differed from those of the future by means of paired *t*-tests.

To test whether climate-change effects on species climate suitability across their ranges were related with their thermal preferences, we correlated percent changes of CSAs, and the latitudinal and longitudinal shifts against the mean temperature of occurrence. A shift was defined as the difference between present and future projections in terms of grid cells classified as climatically suitable, with shifts in a northward and eastward direction as positive, and shifts in a southward and westward direction as negative respectively (*sensu* Parmesan & Yohe, 2003).

*Analyses by trait-based sets.* We were further interested in climate-change effects of species pertaining to specific biological and ecological groupings (*sensu* Kotiaho *et al.*, 2005). We created five subsets, based on the classification in the freshwater-ecology.info database (Euro-limpacs Consortium, 2011; Schmidt-Kloiber & Hering, 2012), and tested for the differences in shifts between species matching the given criterion vs. those which explicitly did not. Species not classified under specific criteria were omitted from the analyses.

First, we divided species into endemic (species present only in one ecoregion,  $n = 24$ ) and nonendemic species ( $n = 167$ ). Eighty-eight percent of the endemics occurred in the Iberian-Macaronesian region, while the remaining 12% occurred in the Alps.

Second, we divided a total of 187 species according to their classification for being either rare ( $n = 26$ ) or common ( $n = 161$ ). Rare species may be located in several ecoregions, having a wide continental distribution, but tolerate narrow habitat requirements and are therefore restricted to specific habitats within the ecoregions similar to endemic species (*sensu* Mills & Schwartz, 2005).

Third, we divided our species set into merolimnic (i.e., species with aquatic larval and aerial adult stages,  $n = 176$ ) and hololimnic (i.e., species with a fully aquatic life cycle,  $n = 15$ ), because species with contrasting life cycles are likely to respond differentially to climate change due to restricted habitat availability under changing precipitation patterns (*sensu* Xenopoulos *et al.*, 2005).

A fourth subdivision was based on species' stream zonation preferences ( $n = 73$ ). Species were classified as headwater species (coded with five or more points for 'eucrenal' and 'hypocrenal' in the database,  $n = 32$ , Hering *et al.*, 2009), or as lowland river species (species occurring between the 'epipotamal' and 'hypopotamal',  $n = 17$ ). Generalist species were those occurring over a wide range of the river continuum (present in each zone within the 'hypocrenal' to 'epipotamal',  $n = 21$ ).

Species' current preference was considered as a fifth criterion for a subdivision ( $n = 77$ ). Species were coded for their preference for low (limnophilic) to high current river velocities (rheobiontic), and classified as limnophilic ( $n = 8$ ), limno- to rheophilic ( $n = 18$ ), rheo- to limnophilic ( $n = 39$ ), rheophilic ( $n = 77$ ), rheobionts ( $n = 20$ ) or as indifferent species ( $n = 6$ ).

For further details on these subdivisions and classifications, see Hering *et al.* (2009), Tierno de Figueroa *et al.* (2010), Euro-limpacs Consortium (2011) and Schmidt-Kloiber & Hering (2012). Species subsets 1–3 were analysed using Student's *t*-tests, and homogeneity of variances was confirmed with Levene's tests. In the case of highly unbalanced sample sizes, Mann-Whitney *U*-tests were computed additionally. As results did not differ between the two tests, we show only results from Student's *t*-tests to keep analyses consistent. Climate change effects for subsets 4–5 were analysed using non-parametric Kruskal-Wallis tests because of unbalanced sample sizes. Future CSAs were expected to vanish for two and one species under the A2a and B2a warming scenario, respectively, and these were thus removed from analyses concerning geographic shifts.

## Results

### Model performance

Model performance was generally high with average true skill statistic (TSS) scores of  $0.96 \pm 0.03$  (mean  $\pm$  standard deviation, see Supporting Information, Table 1). So, consensus projections were created for all the 191 species considered. Analyses of climate projections revealed that nonanalogous climates were restricted to parts of North Africa and the Middle East for all four GCMs, and to a minor part of the Iberian Peninsula for the HADCM and the NIES climate projections (see Supporting Information, Fig. S1).

### All-species analyses

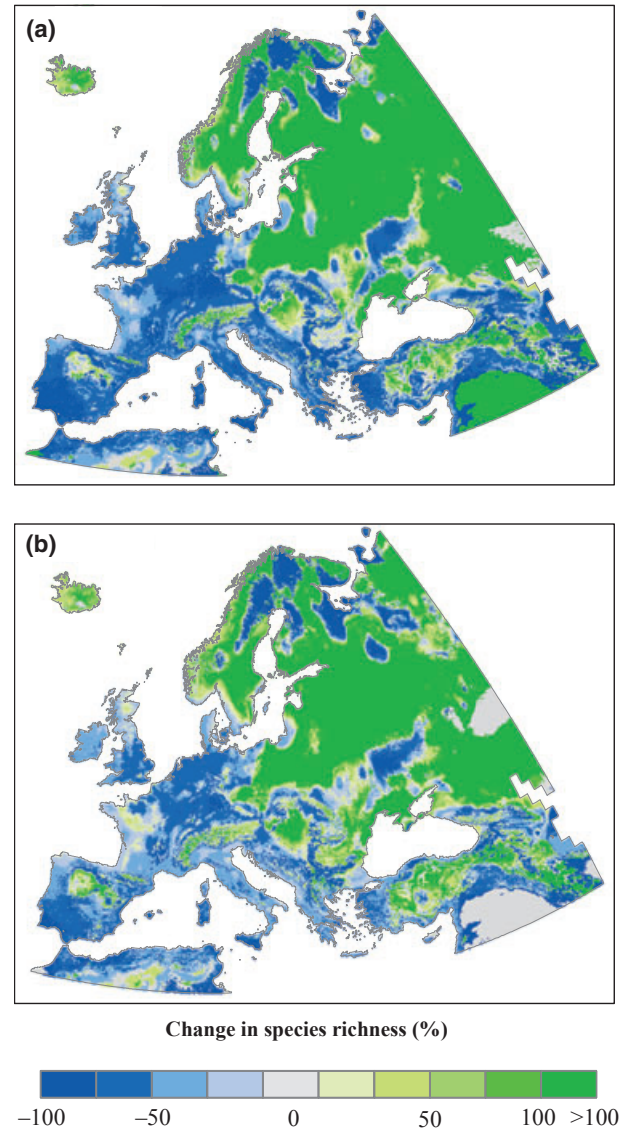
A total of 112 (59%) and 109 (57%) species were projected to lose CSA under the A2a and B2a scenarios respectively. Climate-change loser species were projected to lose on average  $44.0 \pm 29.8\%$  under the A2a and  $38.1 \pm 27.0\%$  under the B2a scenario, whereas winner species were projected to gain on average  $55.4 \pm 59.1\%$  and  $47.7 \pm 42.0\%$  of CSA under the two scenarios. Two species were projected to lose their entire CSA under the A2a (*Oxycera morrisii* and *Orthocladius holsatus*, Diptera) and the B2a scenario (only



**Table 1** Comparisons of percent changes, and latitudinal and longitudinal shifts of climatically suitable areas (CSA) under the A2a and B2a scenario 2080 of species grouped as endemic/nonendemic, rare/common and holo-/merolimnic species (mean  $\pm$  standard deviations, Paired *t*-tests). Losses and gains of CSA as negative and positive values respectively. Significant results in bold.

Scenario	Changes in	Endemic species		Non-endemic species		Endemic vs. non-endemic <i>t</i> -statistics		Merolimnic species		Hololimnic species		Mero- vs. hololimnic <i>t</i> -statistics		Rare vs. common <i>t</i> -statistics	
		Endemic species	Endemic species	Non-endemic species	Non-endemic species	Endemic vs. non-endemic <i>t</i> -statistics	Merolimnic species	Hololimnic species	Mero- vs. hololimnic <i>t</i> -statistics	Rare species	Common species	Rare vs. common <i>t</i> -statistics			
A2a	CSA (%)	-46.4 $\pm$ 38.6	3.4 $\pm$ 66.9	<b><i>t</i><sub>189</sub> = 3.56 <i>P</i> &lt; 0.001</b>	3.4 $\pm$ 66.9	<b><i>t</i><sub>189</sub> = 3.56 <i>P</i> &lt; 0.001</b>	-3.3 $\pm$ 64.1	1.7 $\pm$ 88.1	<b><i>t</i><sub>189</sub> = -0.27 <i>P</i> = 0.783</b>	9.8 $\pm$ 57.7	-4.2 $\pm$ 67.4	<b><i>t</i><sub>185</sub> = -0.99 <i>P</i> = 0.321</b>			
A2a	Latitude	2.7 $\pm$ 1.9°N	7.1 $\pm$ 2.0°N	<b><i>t</i><sub>187</sub> = 10.12 <i>P</i> &lt; 0.001</b>	7.1 $\pm$ 2.0°N	<b><i>t</i><sub>187</sub> = 10.12 <i>P</i> &lt; 0.001</b>	6.5 $\pm$ 2.5°N	7.23 $\pm$ 1.5°N	<b><i>t</i><sub>187</sub> = -1.06 <i>P</i> = 0.287</b>	7.6 $\pm$ 1.6°N	6.4 $\pm$ 2.5°N	<b><i>t</i><sub>183</sub> = -2.41 <i>P</i> = 0.017</b>			
A2a	Longitude	6.5 $\pm$ 7.5° W	7.1 $\pm$ 7.5° E	<b><i>t</i><sub>188</sub> = 8.24 <i>P</i> &lt; 0.001</b>	7.1 $\pm$ 7.5° E	<b><i>t</i><sub>188</sub> = 8.24 <i>P</i> &lt; 0.001</b>	4.9 $\pm$ 8.9° E	10.2 $\pm$ 5.8° E	<b><i>t</i><sub>187</sub> = 2.25 <i>P</i> = 0.026</b>	10.1 $\pm$ 6.0° E	4.6 $\pm$ 8.7° E	<b><i>t</i><sub>183</sub> = -3.08 <i>P</i> = 0.003</b>			
B2a	CSA (%)	-28.4 $\pm$ 38.9	2.7 $\pm$ 55.6	<b><i>t</i><sub>189</sub> = 2.65 <i>P</i> &lt; 0.009</b>	2.7 $\pm$ 55.6	<b><i>t</i><sub>189</sub> = 2.65 <i>P</i> &lt; 0.009</b>	-1.2 $\pm$ 53.7	-0.8 $\pm$ 67.2	<b><i>t</i><sub>189</sub> = -0.02 <i>P</i> = 0.979</b>	7.6 $\pm$ 50.23	-1.9 $\pm$ 55.4	<b><i>t</i><sub>185</sub> = -0.82 <i>P</i> = 0.411</b>			
B2a	Latitude	1.9 $\pm$ 1.4°N	5.1 $\pm$ 2.0°N	<b><i>t</i><sub>188</sub> = 7.93 <i>P</i> &lt; 0.001</b>	5.1 $\pm$ 2.0°N	<b><i>t</i><sub>188</sub> = 7.93 <i>P</i> &lt; 0.001</b>	4.7 $\pm$ 2.2°N	4.7 $\pm$ 1.5°N	<b><i>t</i><sub>188</sub> = 0.04 <i>P</i> = 0.966</b>	5.8 $\pm$ 1.2°N	4.5 $\pm$ 2.3°N	<b><i>t</i><sub>184</sub> = -2.70 <i>P</i> = 0.008</b>			
B2a	Longitude	4.0 $\pm$ 6.9° W	5.1 $\pm$ 5.6° E	<b><i>t</i><sub>188</sub> = 7.17 <i>P</i> &lt; 0.001</b>	5.1 $\pm$ 5.6° E	<b><i>t</i><sub>188</sub> = 7.17 <i>P</i> &lt; 0.001</b>	3.7 $\pm$ 6.6° E	6.2 $\pm$ 4.7° E	<b><i>t</i><sub>188</sub> = -1.42 <i>P</i> = 0.156</b>	6.9 $\pm$ 4.7° E	3.5 $\pm$ 6.6° E	<b><i>t</i><sub>184</sub> = -3.08 <i>P</i> = 0.002</b>			

*O. holsatus*). Species' CSAs were projected to shift significantly northwards ( $6.6 \pm 2.5^\circ$  under the A2a scenario, and  $4.7 \pm 2.2^\circ$  under the B2a scenario; paired *t*-tests: A2a:  $t_{188} = -36.58$ ,  $P < 0.001$ ; B2a:  $t_{189} = -29.80$ ,  $P < 0.001$ , Fig. 1a and b). Similarly, CSAs were projected to shift significantly eastwards by  $5.4 \pm 8.8^\circ$  under the A2a scenario, and  $3.9 \pm 6.5^\circ$  under the B2a scenario (Paired *t*-test: A2a:  $t_{188} = -8.40$ ,  $P < 0.001$ ; B2a:  $t_{189} = -8.27$ ,  $P < 0.001$ , Fig. 1a and b).



**Fig. 1** Relative changes in the number of species for each grid cell for which climatically suitable areas (CSA) were projected under the A2a (a) and the B2a (b) climate warming scenarios compared with the baseline on a spatial resolution of 5 arc minutes.

Percent changes in CSAs were positively correlated with species' mean temperature of occurrence under both climate warming scenarios (Pearson correlation coefficients, A2a:  $r = 0.27$ ,  $P < 0.001$ ; B2a:  $r = 0.29$ ,  $P < 0.001$ , Fig. 2a and b).

Species' mean temperature of occurrence correlated negatively with projected latitudinal shifts of CSAs under the two scenarios, while no significant correlation could be found for longitudinal shifts (Pearson correlation coefficients, latitude: A2a:  $r = -0.29$ ,  $P < 0.001$ ; B2a:  $r = -0.33$ ,  $P < 0.001$ , longitude: A2a:  $r = -0.01$ ,  $P = 0.895$ , B2a:  $r = -0.01$ ,  $P = 0.831$ ).

#### Analyses by trait-based sets

In total, 83% and 79% of the endemic species and 55% and 56% of the nonendemic species were identified as climate-change losers under the A2a and B2a scenario respectively. On average, endemic species lost

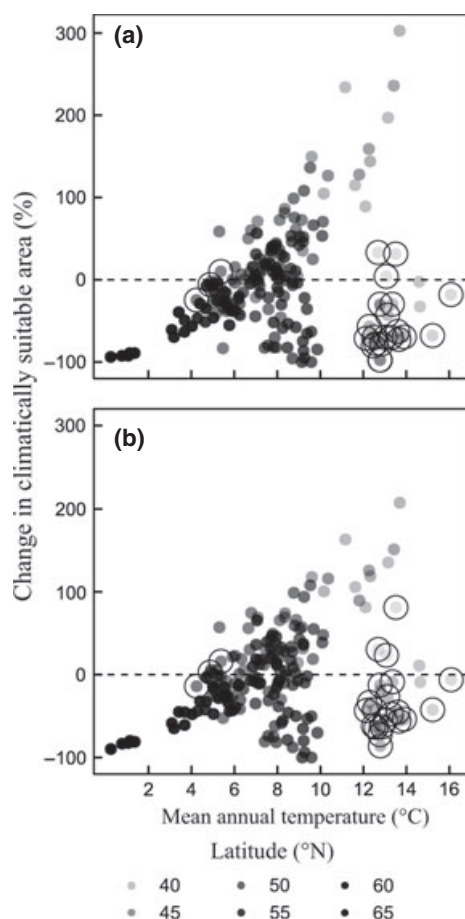
significantly more CSAs than nonendemic species (Table 1). Similarly, CSAs of nonendemic species were projected to shift significantly more strongly into a north-easterly direction, while only a minor northward, but a westward shift was observed for endemic species' CSAs under the A2a and B2a scenarios (Table 1).

Fifty-five percent and 58% of the rare species were projected to lose CSAs under the two scenarios, while 59% and 57% of the common species were projected to lose CSAs under the two scenarios respectively. CSAs of rare species were projected to shift on average one degree more northwards, and on average more than two times further eastwards than those of common species under both climate warming scenarios, while no significant differences in shifts regarding percent changes in CSAs were found (Table 1).

The ratio of hololimnic climate-change loser species was 53% and 60%, while 59% and 57% of the merolimnic species were projected to lose CSAs under the two scenarios. CSAs of hololimnic species were projected to shift on average  $5.3^\circ$  more eastwards than merolimnic species under the A2a scenario (Table 1). No significant shifts in longitude were projected under the B2a scenario, nor were shifts in latitude or percent changes in CSAs significantly different between holo- and merolimnic species.

Species mean temperature of occurrence was significantly lower for headwater than for lowland river species, but not significantly different from the mean temperature of occurrence for generalist species (Kruskal–Wallis test:  $H_2 = 6.477$ ,  $P = 0.039$ ). On average, 75%, 52% and 53% of the headwater, generalist and lowland river species lost CSAs under the A2a scenario, respectively, while 72%, 71% and 41% of the respective groups were predicted to lose CSAs under the B2a scenario. Considering the average distance, CSAs of generalist species were projected to shift significantly more northwards than those of headwater and lowland river species under both climate warming scenarios (Table 2, Kruskal–Wallis test: A2a:  $H_2 = 11.49$ ,  $P = 0.003$ , B2a: Kruskal–Wallis test:  $H_2 = 13.11$ ,  $P = 0.014$ ). Eastward shifts of CSAs were on average almost eight times higher for generalist species than for headwater species under the two scenarios (Kruskal–Wallis test: A2a:  $H_2 = 16.49$ ,  $P = 0.003$ , B2a: Kruskal–Wallis test:  $H_2 = 19.93$ ,  $P < 0.001$ ). No significant differences in percent changes of CSAs could be observed (Kruskal–Wallis test: A2a:  $H_2 = 3.47$ ,  $P = 0.177$ , B2a:  $H_2 = 2.89$ ,  $P = 0.235$ ).

BEMs showed no significant differences in projected CSAs for species grouped for their current preference (Table 2). Furthermore, no significant differences in latitudinal or longitudinal shifts of projected CSAs could be detected among species divided by their current preference (Table 2, Kruskal–Wallis tests:  $P > 0.05$ ).



**Fig. 2** Mean annual air temperature of species occurrence plotted against the changes of climatically suitable areas (CSA) under the A2a (a) and B2a (b) climate warming scenarios of the year 2080. Increasing intensity of greyscale represents increasing mean latitude of species presence records. Circles mark endemic species.

**Table 2** Comparisons of percent changes, and latitudinal and longitudinal shifts of climatically suitable areas (CSA) under the A2a and B2a scenario 2080 of species grouped for their stream zonation preference and current preference along the river continuum. (mean  $\pm$  standard deviations, paired *t*-tests). Losses and gains of CSA as negative and positive values respectively.

Scenario	Changes in	Headwater species	Generalist species	Lowland river species	Limnophilic species	Limno- to rheophilic species	Rheo- to limnophilic species	Rheophilic species	Rheobiontic species	Indifferent species
A2a	CSA (%)	-19.2 $\pm$ 49.4	-9.7 $\pm$ 35.1	15.2 $\pm$ 73.0	53.2 $\pm$ 85.6	-23.3 $\pm$ 83.7	6.5 $\pm$ 99.7	-3.6 $\pm$ 119.7	-50.7 $\pm$ 97.6	9 $\pm$ 62.4
A2a	Latitude	6.3 $\pm$ 2.1°N	8.1 $\pm$ 1.6°N*	6.4 $\pm$ 1.9°N	5.9 $\pm$ 54.5°N	-20 $\pm$ 45.4°N	2.9 $\pm$ 45.7°N	21.3 $\pm$ 49.2°N	7.2 $\pm$ 61.7°N	6.5 $\pm$ 2.1°N
A2a	Longitude	1.4 $\pm$ 9.3°E	10.8 $\pm$ 6.1°E*	7.5 $\pm$ 6.2°E	5 $\pm$ 1.4°E	5.1 $\pm$ 1.4°E	5.1 $\pm$ 2°E	4.9 $\pm$ 1.8°E	4.1 $\pm$ 2.1°E	5.7 $\pm$ 11.7°E
B2a	CSA (%)	-13.1 $\pm$ 45.1	-8.7 $\pm$ 32.1	15.1 $\pm$ 61.7	-22 $\pm$ 45.6	8.9 $\pm$ 76.6	-17 $\pm$ 59.1	1.5 $\pm$ 54.5	16.9 $\pm$ 58.4	5.9 $\pm$ 54.5
B2a	Latitude	4.5 $\pm$ 1.7°N	6.1 $\pm$ 1.3°N*	4.5 $\pm$ 1.6°N	5.6 $\pm$ 2.2°N	5.9 $\pm$ 5°N	4 $\pm$ 7.7°N	3.4 $\pm$ 5.2°N	2.6 $\pm$ 6.1°N	4.6 $\pm$ 1.8°N
B2a	Longitude	0.6 $\pm$ 6.2°E	8.0 $\pm$ 4.5°E*	5.3 $\pm$ 4.3°E	7 $\pm$ 1.5°E	7 $\pm$ 1.8°E	7 $\pm$ 2.5°E	6.8 $\pm$ 2.1°E	5.8 $\pm$ 2.6°E	5.3 $\pm$ 6.4°E

\*Significant differences among species groups (Kruskal–Wallis test, see main text for results).

## Discussion

### *Climate-change effects – general patterns*

Climatically suitable conditions were projected to remain in Europe under future scenarios for the vast majority of the modelled stream macroinvertebrates. The BEMs, however, projected a decrease in CSAs for 57–59% of the species depending on the scenario. Trait-based analyses revealed that cold-adapted species inhabiting the European high latitudes, and warm-adapted endemic species of the Mediterranean would be nearly equally vulnerable to climate change (Figs 1a, b and 2a, b). The lack of a linear relationship between a temperature or latitude gradient of species preferred climates and predicted losses of CSAs suggests that the two extremes are highly vulnerable to ongoing climate change.

Although species' sensitivity to climate change along the latitudinal gradient was weak indicating only a small effect size, the BEMs suggest that a reorganization of species assemblages in terms of a structural and functional composition is not only apparent along the river continuum on smaller scales as shown in previous studies (Daufresne *et al.*, 2003; Bonada *et al.*, 2007a; Burgmer *et al.*, 2007; Chessman, 2009; Domisch *et al.*, 2011). Potential large-scale shifts of species' CSAs resulting from warming climates might lead to an overall northward shift of stream macroinvertebrates, as observed for freshwater organisms in general (Hickling *et al.*, 2005), as well as terrestrial organisms (Hickling *et al.*, 2006; Chen *et al.*, 2011). Thus, warm-adapted and generalist species, which also tend to have a high dispersal ability (Hering *et al.*, 2009), are predicted to progressively replace cold-adapted species, which in turn are at risk to suffer from a strong loss of CSAs (Fig. 2a and b; see Sauer *et al.*, 2011; Jacobsen *et al.*, 2012), and ultimately from a nontrivial loss of regional genetic diversity (Bálint *et al.*, 2011; Pauls *et al.*, 2013). The non-linear effects along a temperature gradient were further enhanced by a number of temperate lowland species and species of the low mountain ranges, for which large changes in the relative species richness were projected under future climate scenarios (Fig. 1a and b; Supporting Information Fig. S2a and b). On the one hand, the Alps may remain as a thermal refuge for species inhabiting currently the Central European low mountain ranges (Fig. 1a and b; Bálint *et al.*, 2011; Sauer *et al.*, 2011; Taubmann *et al.*, 2011). On the other hand, lowland and downstream species of the temperate region are expected to respond to warming temperatures by range expansion due to an increased availability of suitable habitats (Carpenter *et al.*, 1992; Mulholland *et al.*, 1997; Daufresne *et al.*, 2003; Domisch *et al.*, 2011). However, species-specific ecological characteristics may play

an important role when predicting potential climate-change effects for these species (Sweeney *et al.*, 1992; McPherson & Jetz, 2007).

Complete losses of CSAs in Europe, as reported in our study for two species, need to be interpreted carefully. On Average, species records covered 81% of the species' known ranges. Thus, complete losses of CSAs are likely to be overestimated (e.g., Barbet-Massin *et al.*, 2010; Sánchez-Fernández *et al.*, 2011). Nevertheless, such losses do potentially underscore high species vulnerability as those climates that species currently inhabit in Europe are projected to disappear. Moreover, recent studies suggest that parts of the stream biota are still likely to be influenced by postglacial recolonization processes, and that their current distributions do not reflect their spatial climatic equilibrium (Dehling *et al.*, 2010; Hof *et al.*, 2012). Next to climate, local topography and variations of individual river systems that affect stream size, channel character, water chemistry, along with anthropogenic impacts, such as land use and pollution, may also contribute to nonequilibrium in species distributions (Vaughan & Ormerod, 2012). Therefore, a number of species may not have reached all potential suitable habitats, influencing model calibration and thus future projections in our study (Araújo & Pearson, 2005).

#### *Climate-change effects of trait-based species sets*

Models supported our initial hypothesis that higher losses of CSAs would be expected for endemic species rather than nonendemics, while only differences in latitudinal or longitudinal shifts of CSAs were projected for other species groups. In our study, 85% of the endemic species in the Iberian-Macaronesian region were identified as climate-change losers under both climate warming scenarios (Fig. 2a and b). The high level of endemism in Southern Europe is in part a result of the speciation during the Pleistocene (see e.g., Ribera & Vogler, 2004; and references therein, but see Klicka & Zink, 1997). Although dispersal was not limited in our implementation of the BEMs, only small parts within this region were identified as future CSAs, indicating potentially high vulnerability of these species to climate change (Bonada *et al.*, 2009; Hering *et al.*, 2009; Tierno de Figueroa *et al.*, 2010). Although stream macroinvertebrates of the Mediterranean provide traits with a high resistance against droughts as well as a high resilience after droughts (Ward & Stanford, 1982; Sweeney *et al.*, 1992; Bonada *et al.*, 2007a), the question remains whether the magnitude of warming temperatures and the declining amount of (summer) precipitation exceeds the ecological plasticity or adaptation potential of these species.

At first glance, stronger northward shifts of CSAs in both rare and generalist species' than in common and headwater or lowland specialists seem counterintuitive. For rare species, this implies that they would need to track temperature changes faster than common species. Although some species are capable of rapid range changes (Chen *et al.*, 2011), and others maintain sufficient plasticity or have rapid adaptation potential (Hampe & Petit, 2005), potential range changes strongly depend on species' dispersal abilities and life history characteristics. In our models, missing effects of percent changes in habitat suitability imply that rarity reflects factors other than climate space, which were not taken into account in our study (see Vaughan & Ormerod, 2012).

Among headwater, generalist and lowland river species, generalists are best buffered against climate change impacts as shown by their ability to colonize northern Europe after the Pleistocene (see e.g., Hering *et al.*, 2009 and references therein). They tolerate a broad range of climatic conditions, enabling them to potentially take advantage of suitable climates along a wider range of latitudes. In turn, the highest ratio of climate-change loser species among the three groups was identified for headwater species, which are restricted to cooler temperatures. For these species, shifts in CSAs were not projected northwards as was the case for generalists, meaning that they will lose CSAs within their ranges until 2080 because of a predicted summit trap, i.e., a decrease in available area with increasing altitudes. In turn, no strong geographic shifts were projected for lowland river species, as they are predicted to gain CSAs due to climate warming (i.e., range filling, Table 2, Domisch *et al.*, 2011), potentially influencing the community structure and composition of downstream river reaches (Daufresne *et al.*, 2003).

#### *Limitations of modelling distribution in stream macroinvertebrates*

The BEMs allowed us to quantify the magnitude of potential losses and gains, as well as geographic shifts of stream macroinvertebrates' CSAs under climate change on a continental scale. Nevertheless, several limitations remain.

First, we projected species' habitat suitability based on climatic predictors only. However, stream macroinvertebrates distributions and abundances are influenced by local factors, such as habitat structure or water quality, the interaction of multiple global-change stressors (Ormerod *et al.*, 2010), and complex abiotic and biotic processes through which climate affects freshwater organisms (e.g., Brown *et al.*, 2007; Durance & Ormerod, 2009; Woodward *et al.*, 2010).



Second, the use of meteorological data may have influenced the accuracy of model projections by simplifying in-stream hydroclimatic conditions. Air temperature and precipitation are useful proxies for describing the energy and water regimes (Whittaker *et al.*, 2007) and may be used to describe range changes of stream macroinvertebrates (Chessman, 2012). However, they might not relate linearly with in-stream conditions. Although stream and air temperatures are highly correlated, the relationship between stream and air temperature is  $<1$  (Durance & Ormerod, 2009), and slopes may vary between 0.48 and 0.97 (Clews *et al.*, 2010). As our study covered a wide range of stream types as well as different river sections from headwaters to large rivers, it was not feasible to model and take into account the evapotranspirative cooling of streams. In addition, air temperatures may be a poor surrogate for stream temperatures in headwater reaches located in lower altitudes (Caissie, 2006). Therefore, the projected warming rates for streams and rivers may have been overestimated. Similarly, discharge may be influenced by evapotranspiration and catchment-specific land-use and vegetation, therefore precipitation is not related linearly to discharge in the same way in all locations (Carpenter *et al.*, 1992). For instance, long-term studies of Calder & Newson (1979) and Hudson *et al.* (1997) showed how evapotranspiration may account for losses of precipitation by 15% in moorland areas up, and to 40% in forested areas, ultimately reducing the stream flow.

Calculating error margins of model results (CSA, and species' latitudinal and longitudinal shifts) with varying parameterizations of relationships between stream and air temperature, and between discharge and precipitation, showed that uncertainties can locally be as high as 50% (Supporting Information Table S2), with unknown synergistic and antagonistic effects.

Third, the coarse spatial and temporal resolution may have failed to capture the effects of local relief on climate and distribution, and stochastic elements in climate respectively. For example, drought severity, drought duration or extreme hydroclimatic events can have varying effects on species distributions at local scales (Daufresne *et al.*, 2007), but are neglected in our coarse scale models. Models were therefore calibrated where existing conditions may be in long-term non-equilibrium due to background climatic variation (e.g., Bradley & Ormerod, 2001), or due to confounding, but widespread changes in river ecological conditions (e.g., Durance & Ormerod, 2009; Vaughan & Ormerod, 2012). It is thus particularly challenging to obtain projections for habitat specialists based on current preference and life cycle. Assuming that species inhabiting slow flowing waters have high dispersal abilities, our models

may have overestimated the loss of CSAs for these species, because they have proven to be good dispersers (*sensu* Hof *et al.*, 2012; and references therein). Moreover, site-specific hydrological conditions were aggregated within the grid cells, and models might not have been able to separate the required habitat characteristics of e.g., holo- and merolimnic species. In this regard, it is also important to consider that BEMs rely on presence-absence data rather than abundances. However, changes in density and abundance appear to be a marked consequence of warming climates (Brown *et al.*, 2007; Durance & Ormerod, 2009).

In summary, several sources of uncertainty exist when making projections of altered stream macroinvertebrate species potential distributions under future climate scenarios. In this regard, a possible validation of BEMs could be accomplished by hindcasting species distributions using historic climate data, and by comparing the projections with independent historic species occurrences (see e.g., Nogués-Bravo, 2009). However, limited data availability on comprehensive past distributions of stream macroinvertebrates would pose a major challenge for this procedure. Furthermore, lack of information concerning the ecological preferences for the majority of stream macroinvertebrate species still hinders reliable estimations of the possible consequences of climate change (Heino *et al.*, 2009). Limited and fragmented habitat availability under warming climates – beyond losses of CSAs – will impose an additional major threat for stream macroinvertebrates (Heino *et al.*, 2009; Woodward *et al.*, 2010). While species' dispersal abilities and traits, combined with habitat availability, play a crucial role in coping with warming temperatures, climate change is likely to have profound impacts on stream macroinvertebrates distributions.

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## Supporting Information

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

**Table S1.** List of all 191 species used for BEMs, their classification into trait-based sets, projected changes of climatically suitable areas under climate change scenarios and TSS scores.

**Table S2.** Assessment of uncertainties of modelled results derived from meteorological data vs. in-stream response under varying parameterisations between stream and air temperature, and between discharge and precipitation.

**Figure S1.** Non-analogue climates of the four future climate projections used for the A2a and B2a emission scenarios.

**Figure S2.** Mean annual air temperature of species occurrence plotted against the percent changes of climatically suitable areas under the A2a and B2a scenarios of the year 2080, representing mean altitudes of species' presence records.