# Low mountain ranges: summit traps for montane freshwater species under climate change

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**Abstract** Global climate change (GCC) is expected to lead to massive loss of global biodiversity in the alpine regions of mountain ranges. Studies on the potential effects of GCC on low mountain areas remain sparse, however, despite the high conservation value of these areas as biodiversity refugia. We chose a species distribution modeling approach to assess potential GCC impacts on the future distributions of montane freshwater invertebrates under two different greenhouse gas scenarios and three averaged general circulation models. For this, ensemble models consisting of six algorithms [generalized linear model (GLM), generalized boosted model (GBM), generalized additive model (GAM), classification tree analysis (CTA), artificial neural networks (ANN), and multivariate adaptive regression splines (MARS)] were applied to project areas of 23 cold-stenothermic aquatic insects from montane regions of Central Europe. We found an average loss of 70–80% of the potential distribution for the study species until 2080, depending on the underlying Intergovernmental Panel on Climate Change scenario. Species distribution ranges below 1000 m above sea level were found to decrease by up to ∼96% according to the severest greenhouse gas emission scenario. While the Alps remain the single main refugium under the A2a greenhouse gas emission scenario, the more moderate climate scenario B2a shows fragmented potential persistence of montane insects in some low mountain ranges. The results show that montane freshwater assemblages in low mountain ranges are particularly threatened by ongoing GCC. As vertical dispersal is limited by elevational restriction, low mountain ranges may act as summit traps under GCC. We thus propose that GCC will lead to the extinction of several species and unique genetic lineages of postglacial relict species, resulting in a significant decline in Central European fauna.

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**Abbreviations**

GCC    Global climate change
GCM    General circulation model
IPCC   Intergovernmental Panel on Climate Change
SDM    Species distribution model
a.s.l.   Above sea level

## Introduction

Global climate change (GCC) impacts biological patterns, such as species distribution, phenology, and community composition (Walther et al. 2002; Parmesan 2006), and severe negative effects on biodiversity have been predicted to occur until the end of this century (e.g., Root et al. 2003; Thomas et al. 2004; IPCC 2007a). However, the severity of GCC impacts on biological communities is expected to vary among geographical regions and ecosytem types (Thuiller 2007), depending, among other factors, on temperature sensitivities and the potential for latitudinal or longitudinal tracking of climatic niches (Parmesan and Yohe 2003; Hickling et al. 2006). The predicted temperature rise of 1.8–4.0°C by the end of this century (IPCC 2007b) will thus particularly influence cold-adapted and dispersal-limited species, which are frequently found in montane and alpine ecosystems (Pauli et al. 2007; Winterbourn et al. 2007; Hering et al. 2009; Bässler et al. 2010).

Mountain ecosystems are disproportionably sensitive to alterations in climatic conditions (e.g., Thuiller et al. 2005; Schröter et al. 2005; Beniston 2006). Thus, these regions might face large-scale losses of biodiversity under GCC due to (i) adaptation of species to cold climates, (ii) strong dispersal limitation, combined with high degrees of spatial isolation, (iii) decreasing area size at higher elevations, and (iv) often restricted population sizes.

These factors are of particular relevance for the montane biota of Europe, where mountain regions harbor a significant proportion of the continent's biodiversity and comprise its last patches of wilderness (Lomolino 2001; Diaz et al. 2003). In addition, high and low mountain ranges are important post-glacial refugia for cold-adapted species in Central and Southern Europe (Hering et al. 2009; Habel et al. 2010). This fact, combined with frequently restricted dispersal potential and long-term spatial isolation, leads to high levels of endemism in European mountain regions (e.g., Hewitt 2000, Essl et al. 2009; Kubow et al. 2010). Due to the presence of unique biological communities and high species diversity, mountain regions are considered biological hotspots in Europe and deserve particular conservation efforts.

The focus of studies on GCC effects in mountain regions has typically been on alpine regions (e.g., Grabher et al. 1994; Beniston 2006; Randin et al. 2009; Dirnböck et al. 2011), and there is a surprising lack of studies on the potential effects of GCC on biodiversity in low mountain ranges (but see Bässler et al. 2010; Domisch et al. 2011). Headwater systems of Central European low mountain ranges, for instance, contain the highest level of diversity of aquatic invertebrates in this region (Braukmann 1987). These montane streams harbor assemblages of cold-stenothermic insects, which frequently coexist in aquatic

systems of mountain ranges extending beyond 800 m above sea level (a.s.l.). This unique montane freshwater assemblage of insularly distributed insect species forms a characteristic element of montane freshwater biota and thus can be used as indicator of the montane character of streams (Haase 1999). However, most European low mountain ranges do not reach far beyond 1000 m in elevation. Thus, suitable habitats of these species in low mountain ranges are usually restricted to small and isolated higher mountain reaches. Along with the strong restriction of dispersal capacities of many freshwater insects (e.g., Collier and Smith 1997; Petersen et al. 2004; MacNeale et al. 2005), this leads to insular population patterns of these organisms. Low mountain ranges may thus act as summit traps under GCC. This is in contrast to the Alps and other European high mountain ranges, where the species occupy wider areas. Because freshwater ecosystems are considered at least as vulnerable to GCC as terrestrial ecosystems (Sala et al. 2000), we expect that future GCC scenarios will strongly affect these montane freshwater species in the Central European low mountain ranges.

In this study, we analyze potential GCC effects on montane freshwater invertebrates in Central European mountain ranges. Our main assumption was that GCC will lead to a dramatic reduction in suitable habitats of this cold-stenothermic freshwater species especially in low mountain ranges. We consequently expect multiple extinction events. To test this, we applied a species distribution modeling (SDM) approach for 23 cold-stenothermic insect species (Ephemeroptera, Plecoptera, Trichoptera) which are typically restricted and frequently coexist in montane stream systems (Haase 1999). We projected future range alterations of this montane freshwater assemblage using commonly applied Intergovernmental Panel on Climate Change (IPCC) scenarios of GCC. Our approach provides a first estimate of the potential GCC effects to montane freshwater species in Central Europe and allows the identification of potential future conservation hotspots for these species.

## Methods

### Locality data and investigated species

To investigate GCC effects on the montane freshwater assemblage, we applied a SDM approach, using presence data for 23 cold-stenothermic aquatic insects in Central Europe. This taxa list was taken from Haase (1999), who identified a set of 28 Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies), that frequently coexist in montane streams, under cold climatic conditions, above 800 m a.s.l. As we only included species with at least 20 presence sites/species to assure a sufficient data set for SDMs (Stockwell and Peterson 2002), our data set comprises 11 species of the order Trichoptera 10 species of Plecoptera, and 2 species of Ephemeroptera (Table 1). In order to prevent a biased sampling design towards montane regions, we included all presence data for the 23 species irrespective of region and habitat type. The presence data for all species were compiled from several sources (own data, published records, databases of renowned taxonomical experts, and databases available to the public, such as Global Biodiversity Information Facility "GBIF" 2007 and Centre Suisse de Cartographie de la Faune "CSCF" 2010). A total of 4475 presence data points from France, The Netherlands, Belgium, Germany, the northern parts of Switzerland, Austria, northern Italy, and the Czech Republic were collected and used in this study (Fig. 1).

**Table 1** Percentage range change for the montane insect assemblage until 2080

| Species | Taxonomic Group | Species (N) | SRC A2a | SRC B2a | SRL A2a | SRL B2a | AUC weighted | Kappa mean |
|---|---|---|---|---|---|---|---|---|
| *Ameletus inopinatus* | Ephemeroptera | 87 | −40.7 (±20.5) | −39.5 (±14.3) | 89.9 (±5.5) | 84.2 (±5.3) | 0.98 | 0.91 |
| *Allogamus uncatus* | Trichoptera | 384 | −57.1 (±9.7) | −32.3 (±19.3) | 76.2 (±8) | 20.8 (±6.9) | 0.96 | 0.91 |
| *Chaetopterygopsis maclachlani* | Trichoptera | 315 | −88.7 (±4.5) | −78.1 (±12.5) | 98.2 (±8.7) | 62.0 (±14.9) | 0.97 | 0.92 |
| *Capnia vidua* | Plecoptera | 134 | −61.6 (±2.) | −45.1 (±2.1) | 71.7 (±2.9) | 90.5 (±12.2) | 0.95 | 0.90 |
| *Drusus discolor* | Trichoptera | 564 | −67.7 (±4.4) | −49.8 (±9.2) | 76.4 (±3.9) | 55.6 (±3.6) | 0.95 | 0.91 |
| *Ecclisopteryx guttulata* | Trichoptera | 257 | −58.2 (±14.7) | −42.5 (±17.6) | 85.2 (±7.1) | 61.8 (±11.1) | 0.94 | 0.88 |
| *Glossosoma intermedium* | Trichoptera | 51 | −91.0 (±5.2) | −84.3 (±5) | 98.5 (±16.6) | 70.4 (±22.1) | 0.98 | 0.94 |
| *Hydropsyche silfvenii* | Trichoptera | 85 | −99.9 (±0) | −99.6 (±0.2) | 100.0 (±1.3) | 92.7 (±3.1) | 0.99 | 0.97 |
| *Hydropsyche tenuis* | Trichoptera | 343 | −27.7 (±37) | −3.5 (±24.7) | 65.8 (±0) | 100.0 (±0) | 0.95 | 0.93 |
| *Isoperla rivulorum* | Plecoptera | 509 | −60.6 (±12.2) | −37.6 (±10.7) | 65.3 (±26.3) | 45.1 (±15.7) | 0.96 | 0.92 |
| *Leuctra autumnalis* | Plecoptera | 89 | −97.4 (2.5) | −94.4 (±2.1) | 99.0 (±9.7) | 45.1 (±7.9) | 0.97 | 0.91 |
| *Leuctra pseudocingulata* | Plecoptera | 79 | −99.7 (±0.6) | −98.1 (±1.5) | 99.7 (±0.7) | 95.9 (±2.1) | 0.99 | 0.97 |
| *Leuctra rauscheri* | Plecoptera | 241 | −61.7 (±0.4) | −43.1 (±2.7) | 67.6 (±0.3) | 98.3 (±1.4) | 0.96 | 0.93 |
| *Nemoura mortoni* | Plecoptera | 486 | −47.5 (±17.9) | −25.4 (±10.6) | 54.7 (±1.4) | 50.4 (±3.9) | 0.95 | 0.89 |
| *Protonemura hrabei* | Plecoptera | 53 | −98.4 (±1.2) | −94.5 (±3.8) | 99.7 (±14.8) | 37.0 (±7.8) | 0.98 | 0.94 |
| *Protonemura nimborum* | Plecoptera | 266 | −55.6 (±3.6) | −35.4 (±1.6) | 61.3 (±0.6) | 97.5 (±1.9) | 0.96 | 0.94 |
| *Pseudopsilopteryx zimmeri* | Trichoptera | 109 | −62.7 (±3.6) | −47.4 (±3.7) | 76.0 (±2.1) | 42.9 (±3.2) | 0.96 | 0.89 |
| *Rhyacophila evoluta* | Trichoptera | 149 | −99.1 (±0.5) | −95.7 (±1.5) | 99.9 (±2.6) | 62.5 (±1.4) | 0.98 | 0.92 |
| *Rhithrogena hercynia* | Ephemeroptera | 30 | −99.1 (±1.1) | −97.4 (±3) | 100.0 (±0.2) | 98.7 (±1.1) | 0.99 | 0.99 |
| *Siphonoperla neglecta* | Plecoptera | 34 | −84.3 (±22.1) | −80.1 (±21.4) | 97.2 (±0) | 100.0 (±0) | 0.98 | 0.98 |
| *Taeniopteryx auberti* | Plecoptera | 78 | −84.6 (±19.1) | −69.9 (±29.1) | 91.6 (±4.7) | 96.4 (±5.4) | 0.99 | 0.96 |
| *Wormaldia copiosa* | Trichoptera | 111 | −9.6 (±28.2) | 18.0 (±21.3) | 35.3 (±14) | 85.5 (±15.2) | 0.97 | 0.94 |
| *Wormaldia pulla* | Trichoptera | 21 | −25.7 (±37.9) | −5.8 (±47.4) | 88.3 (±19.3) | 17.2 (±11.4) | 0.95 | 0.90 |

Species, taxonomic groups, and the number of presence data are shown in the first columns. The percentages of species range change (SRC) and species range loss (SRL) are given for the averaged weighted scenarios (A2a and B2a; ±standard derivation SD), as well as weighted AUC and Kappa values
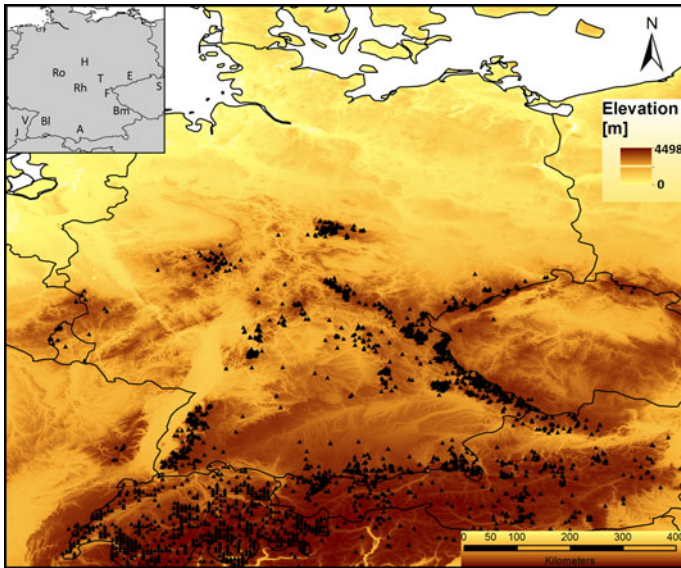
**Fig. 1** Map of study area and mountain ranges with data points (*triangles*) of 23 montane insect species. *A* Alps, *Bm* Bohemian Massif, *Bl* Black forest, *E* Erzgebirge, *F* Fichtelgebirge, *H* Harz, *J* Jura mountains, *Rh* Rhoen, *Ro* Rothaargebirge, *S* Sudety mountains, *T* Thuringian Forest, and *V* Vosges mountains

Environmental variables

We used bioclimatic variables with a spatial resolution of 2.5 arc-minutes ($\sim 5$ km$^2$) for current and future climate conditions. The current climatic data (monthly mean, minimum, and maximum temperature and mean monthly precipitation), as interpolated observed data from the year 1950 to 2000, were downloaded from the public database WorldClim (Hijmans et al. 2005a) and transformed with DIVA-GIS 7.1.7 (Hijmans et al. 2005b) into 19 bioclimatic variables. We also considered non-climatic variables which are strongly associated with montane aquatic species, such as topographic variables (Earth Resources Observation and Science Center 1996), geology (Asch 2005), and European hydro-eco-regions (Wasson et al. 2007). We constructed a Spearman correlation matrix of all 24 variables, and we omitted variables by expert knowledge that were highly correlated ($r > |0.8|$). As a result, the following 12 variables were used for the further modeling procedure: annual mean temperature, mean diurnal range, isothermality, annual tempera-ture range, maximum temperature of the warmest period, minimum temperature of warmest period, annual precipitation, precipitation seasonality, slope, aspect, geology, and European hydro-ecoregions. For future climate projections we used climatic data from the 3rd IPCC Assessment Report, which are also available from the public database "WorldClim". These climatic future projections are provided by three different global circulation models: (i) HadCM3 (Gordon et al. 2000; Pope et al. 2000), (ii) CCCma (Flato et al. 2000), and (iii) CSIRO (Gordon and O'Farrell 1997). For each General circulation model (GCM) we investigated two different greenhouse gas emission scenarios. The emission scenario A2a reflects an unrestricted increase of $CO_2$ emission due to a highly heterogeneous future world with regionally oriented economies. The main driving forces are a high rate of population growth, increased energy use, land-use changes and slow

Fig. 2 Current (a) and future
potential distribution ranges of
the montane insect assemblages
according to the averaged
weighted scenarios HadCM3
A2a, CCCma A2a, and CSIRO
A2a (b) and HadCM3 B2a,
CCCma B2a, and CSIRO B2a (c)
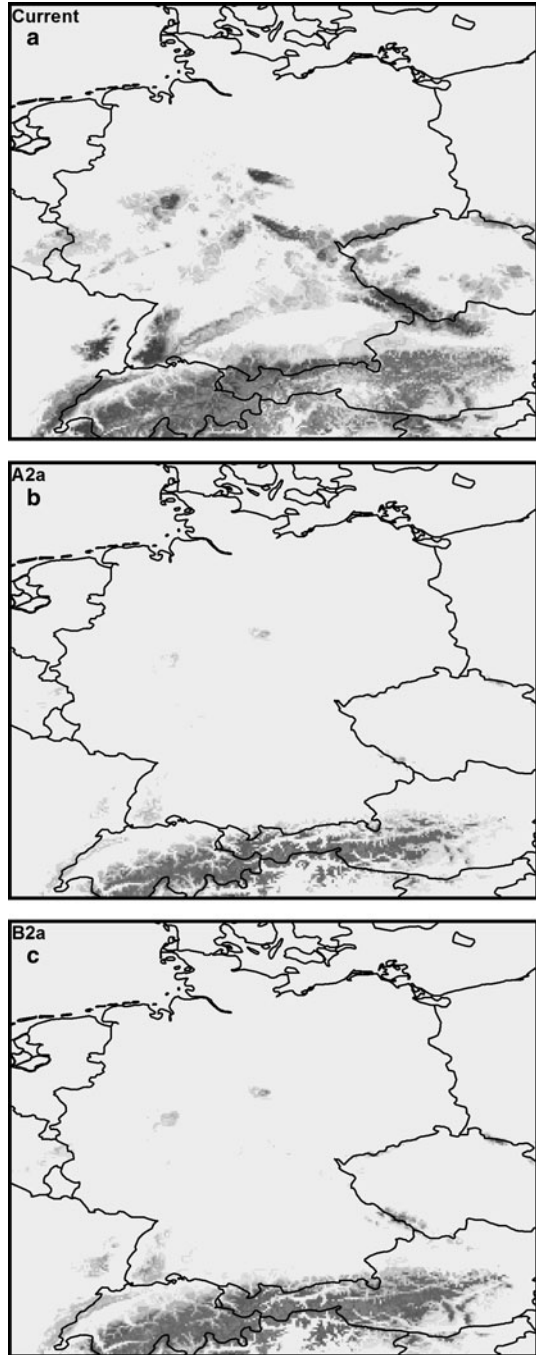


technological change. A moderate increase of $CO_2$ emission is reflected by the B2a sce-
nario, which reflects regionally oriented economies but with a general trend toward
environmental protection and social equity (Hijmans et al. 2005a; IPCC 2007b).

Species distribution modeling

Species distribution models for the investigated montane freshwater assemblage were computed using six different algorithms according to the BIOMOD package in R (Thuiller et al. 2009; R Development Core team 2010). We ran the generalized linear model (GLM), generalized boosted model (GBM), generalized additive model (GAM), classification tree analysis (CTA), artificial neural networks (ANN), and multivariate adaptive regression splines (MARS). We further used the following settings for the algorithms: GLM, polynomial terms by stepwise ranked Akaike Information Criterion (Akaike 1973); GBM, a fivefold cross-validation approach and a maximum of 3,000 trees; GAM, a spline function with a degree of smoothing of four; CTA, a 50-fold cross-validation, and ANN, a 5 N-fold cross-validation. Each algorithm was applied with 5000 pseudo-absences and a tenfold cross-validation which gives a more robust estimate of the predictive performance of each selected model. Model evaluation was conducted by a data splitting procedure into a training set (70%) and a testing set (30%) with a random partition (Araujo et al. 2005) and by means of area under the curve (AUC) from a receiver operating characteristic analysis (ROC), which is a threshold-independent evaluation of model discrimination (Fielding and Bell 1997), as well as Cohen's Kappa statistic. AUC scores range from 0.5 to 1, values of 0.5 indicate a performance no better than random, whereas 1 reflects a perfect model prediction accuracy (Swets 1988). Like AUC scores, Kappa of 1 indicate a perfect agreement, whereas values of zero indicate a very poor performance. To reduce model uncertainties in predictive accuracy we used a consensus projection with weighted averages based on AUC scores for all algorithms. Recent studies demonstrated that this technique is superior to a single model approach and consequently improves SDM results (Araujo et al. 2005). The relative importance of the weights for the final consensus models were calculated by the default weighting factor of 1.6. To reduce uncertainties in future projections we finally averaged the results of the three used GCMs to yield one single output for each species and emission scenario (A2a and B2a respectively) and applied a threshold that maximizes the percentages of absence and presence that are correctly predicted to get binary presence-absence maps (Thuiller 2003). Based on this binary system, we used ArcGIS 9.3 (Environmental Systems Research Institute 2006) to infer future effects of climate change by calculating current and future potential distribution ranges. Assemblage results were assessed by stacked 95% transparent layers of each investigated species, leading to darker areas in regions, where more species are projected. Species range changes (SRC) were calculated by means of the percentage lost, gained or stable suitable distribution areas from current to future projections. We inferred future range shifts in elevation by counting the number of suitable pixels for current and future projections in 200 m elevational steps and by calculating the cumulative percentage of predicted occurrence area. Finally, we calculated the importance of each variable of species current distribution. The measure of relative importance of each variable was internally calculated by BIOMOD. We used the relative importance of the weights for the averaged model results (see above) to achieve the percentage relative contributions of each variable for the consensus projection.

## Results

The consensus model accuracy was consistently high, with AUC and Kappa scores exceeding 0.94 and 0.88, respectively, for all investigated species of the montane

freshwater assemblage (Table 1).Three climatic variables (annual mean temperature, minimum temperature of coldest period, and annual precipitation) contributed almost 60% to the consensus model prediction (Fig. 3). Under commonly used IPCC scenarios of GCC a significant loss of potential distribution ranges was detected for the montane freshwater assemblage in Central Europe until 2080 (Fig. 2b, c). Projections show a particularly severe range loss in low mountain regions. According to the A2a greenhouse gas emission scenario, on average 80% (±19.9) of the current potential distribution ranges of the montane freshwater assemblage will be lost by the end of this century (Table 1). Following the more moderate B2a greenhouse gas emission scenario, the potential loss is 70% (±25.8). Both greenhouse gas emission scenarios showed considerable differences regarding the extent of potential distribution ranges (Fig. 2b, c) and the number of species with projected distribution ranges within low mountain ranges (Table 2), the latter comparison being significant (Paired $t$-test: $t_{11} = 5.1$, $P < 0.001$). However, predictions based on both greenhouse gas emission scenarios show considerable similarities: only the Alps emerge as a large-scale potential distribution range for the montane freshwater assemblage in 2080. Distribution ranges within several low mountain ranges, such as Thuringian Forest, Rhoen, and Fichtelgebirge, will be almost unsuitable for cold-stenothermic aquatic invertebrates. Assessments of elevational range shifts under GCC revealed a clear trend toward higher elevations until 2080, depending on the scenario applied (Fig. 4). While approximately 53% of potential current distribution ranges lie below 1000 m a.s.l. within the study area, this value drops to 13% under the "optimistic" B2a scenario and to 4% under the "pessimistic" A2a scenario in the 2080 projections. In turn, the elevational threshold for the presence of 50% of total potential ranges is projected to lie between ∼1800 to ∼2000 m a.s.l., according to the underlying scenario.

The general findings of large-scale range loss and restriction to higher elevations are largely congruent with the future range projections for each of the 23 species considered in this study. The percentage loss of potential distribution ranges derived from the average for the A2a scenario ranges from 32 to 100% across species, while the loss of potential distribution is predicted to range from 17 to 100% for the B2a scenario. The overall range change of a species, as calculated from regional losses and gains, is always predicted to be negative; that is, distribution ranges will shrink in the next decades (Table 1). The only exception is *Wormaldia copiosa*, which likely will expand its potential distribution range
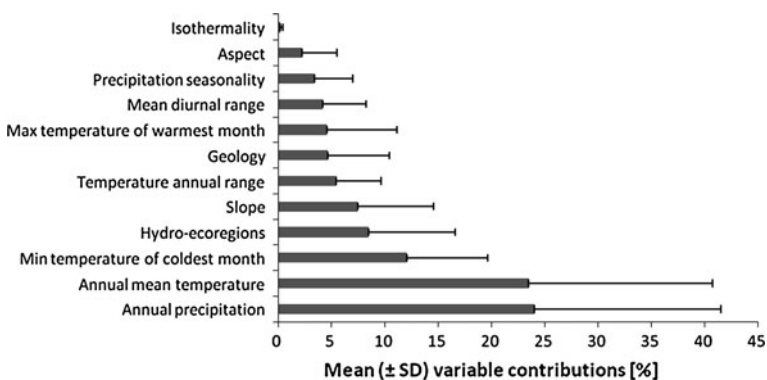


Fig. 3 Mean (±SD) relative contributions of environmental variables for the current species distributions under weighted consensus models. All relative contributions were averaged over all associated species of the montane freshwater assemblage

| Table 2 Current and projected number of species within Central European low mountain ranges for both weighted scenarios (A2a, B2a) | Low mountain range | Species (N) | Species (N) 2080 | |
|---|---|---|---|---|
| | | Current | A2a (%) | B2a (%) |
| | Rhoen | 17 | 0 (0) | 1 (6) |
| | Voges mountains | 21 | 5 (24) | 9 (43) |
| | Thuringian forest | 21 | 1 (5) | 2 (10) |
| | Rothaargebirge | 20 | 4 (20) | 6 (30) |
| | Black forest | 21 | 6 (29) | 11 (52) |
| | Jura mountains | 16 | 3 (19) | 10 (63) |
| | Harz | 23 | 5 (22) | 10 (43) |
| | Fichtelgebirge | 17 | 0 (0) | 1 (6) |
| | Erzgebirge | 19 | 5 (26) | 12 (63) |
| | Bohemian Massif | 22 | 10 (45) | 18 (82) |
| Percentages of remaining species within low mountain ranges are shown in parentheses | Sudety Mountains | 15 | 16 (107) | 19 (127) |
| | Alps | 22 | 19 (86) | 21 (95) |
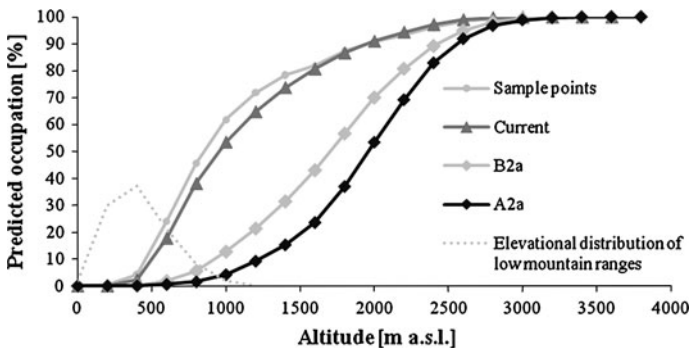


**Fig. 4** Elevation-related changes in the cumulative percentage of predicted occurrence area under current climatic conditions and averaged weighted GCMs. The occurrences of species of the montane assemblage are summarized in 200 m steps across all mountain ranges, including the Alps. The *dotted line* indicates the percentage elevational distribution of grid cells in low mountain areas

under the B2a scenario (Table 1). Patterns of current and future potential distribution ranges were generally similar across species. In contrast to most other species considered in this study, the potential distribution ranges of *Hydropsyche tenuis* and *Wormaldia copiosa* are predicted to cover several mountain ranges by the end of this century.

Considerable differences were found concerning the average loss of species among mountain ranges (Table 2). While the Alps and the Sudety Mountains retain most or all of the investigated species until 2080, a high level of potential species loss is projected for all other low mountain ranges for both greenhouse gas emission scenarios. The most severe losses within the study area were predicted for several German low mountain ranges (e.g., Rhoen, Thuringian Forest, and Fichtelgebirge) with >90% species loss under the B2a scenario.

## Discussion

Methodological evaluation

Large-scale climatic variables are widely accepted as strong predictors for species and community distributions (e.g., Riordan and Rundel 2009). To improve our SDM results, we selected variables (European hydro-ecoregions, geology, slope, and aspect) that are strongly associated with montane aquatic species. These variables characterize habitat structure such as stream velocity, oxygen concentration, or watersheds. Due to the fact, that model results are sensitive to sampling bias (Araújo and Guisan 2006), we used several data sources to retrieve species' presence records which covered all regions of the study area. Moreover, as a precondition for modeling, only species with a minimum of 20 presence records listed were used (Stockwell and Peterson 2002). However, SDM approaches have several limitations. Migration and the individual dispersal capacity of species, environmental and biological stochastic variability, and genetic adaptations to local environmental conditions are usually not taken into account. Despite the above-mentioned criticism of the general use of SDMs, we obtained good weighted consensus projections for the current potential distribution ranges of all associated species of the montane freshwater assemblage which are largely congruent with known distribution areas from literature and expert knowledge.

GCC effects on species distributions

Projections show a particularly severe range loss in low mountain regions. According to the A2a greenhouse gas emission scenario, on average, 80% ($\pm$20) of the current potential distribution ranges of the montane assemblage will be lost by the end of this century. Following the more moderate B2a greenhouse gas emission scenario, the potential loss is 70% ($\pm$26). Our results support the initial assumption that the investigated species might face severe range losses in low mountain ranges. The consensus of GCMs and greenhouse gas emission scenarios indicate a significant loss of current distribution areas for the montane freshwater assemblage in Central European low mountain ranges by the end of this century. Despite considerable variations among GCMs and both greenhouse gas scenarios, our results indicate two interrelated general patterns: (i) an elevational shift of potential distribution ranges to higher elevations and, as a consequence, (ii) large-scale loss of potential distribution ranges of the entire cold-stenothermic aquatic insect assemblages.

Our results show a substantial elevational shift of montane freshwater insects under climate change (Fig. 4), which is congruent with the results of other studies suggesting a loss of suitable area at lower elevations and range shifts to higher elevated suitable habitats within this century (Walther et al. 2002; Wilson et al. 2005; Domisch et al. 2011). This vertical shift of the species' potential habitat is due to changing climatic factors. We found that annual mean temperature and precipitation, as well as the minimum temperature of coldest period are the dominant factors for species range projections in this study. These factors are highly correlated with altitude (annual mean temperature: $r = -0.90$, annual precipitation: $r = 0.77$, minimum temperature of coldest period: $r = -0.81$; data not shown). This altitudinal gradient of climatic conditions which shape the distribution of the model species explains the upwards shift of suitable areas under GCC scenarios. Montane cold-stenothermic species are thus expected to track the climatic envelopes upward in elevation. Upward-directed vertical migration, however, is restricted because none of the Central European low mountain ranges exceeds 1600 (m a.s.l.) in elevation, and the

majority remain well below 1000 m in elevation. Only a minor proportion of suitable areas, however, will persist below 1000 m according to all future projections in this study. As a result, the Alps remain the only Central European mountain range that will ensure the long-term persistence of montane stream insects, because of the availability of large areas at sufficiently high elevations to allow for effective vertical migration. We hypothesize here that, although glacial melting and increasing temperatures in alpine regions will have dramatic effects on alpine communities, these alpine areas will represent new habitats for montane species that presently dominate European low mountain ranges. Considering the projected range shifts of montane insects, future survival under climate change might critically depend on the capacity of these species to move upstream and on species' abilities to disperse long distances across catchments and mountain ranges. However, little is known concerning the dispersal propensities of merolimnic freshwater insects (i.e. semi-aquatic species: larvae occur in water systems whereas imagines have a terrestrial life-style). Flight dispersal occurs mostly along the shoreline within a range of no more than a few hundred meters (Collier and Smith 1997; Petersen et al. 2004; MacNeale et al. 2005). Long-distance dispersal, however, which would be the prerequisite for colonization of new habitats across mountain regions, is less documented. Wilcock et al. (2003) estimated that distances of up to 20 km could be accomplishable for imagines of the Trichoptera species *Plectrocnemia conspersa* over a number of generations. Similar results were also found for the mayfly *Ameletus inopinatus* (Taubmann et al. 2011). While merolomnic insects vary in their dispersal capabilities, it seems highly unlikely, that any of the species considered in this study will be capable of active or passive dispersal among montane regions within a few decades. Thus it is appropriate to consider all montane regions within this study area to be effectively isolated from each other, with no dispersal among them even on longer time scales. This assumption is well supported by phylogeographic surveys of montane stream insects, which often display unique mitochondrial haplotypes for single mountain ranges, suggesting postglacial long-term isolation (Pauls et al. 2006; Engelhardt et al. 2008; Lehrian et al. 2010; Ujvárosi et al. 2010). This isolation of mountain ranges, combined with the elevational restriction that prevents effective vertical migration, makes low mountain ranges summit traps for cold-adapted species under GCC. Based on the lack of stepping stones between mountain ranges and the generally low dispersal capacity of merolimnic insects, montane insect species of low mountain areas may face extinction in Central Europe by 2080.

## Conclusions and conservation remarks

Our study clearly indicates severe negative impacts of GCC on freshwater assemblages within low mountain ranges. Interestingly, these areas have widely been neglected in GCC-related studies to date, despite the considerable conservation relevance of these areas. In Central Europe, for instance, low mountain regions comprise important reservoirs of beech forests and their associated communities (Ellenberg 1996). In addition, these mountain ranges contain multiple populations of glacial relict species and thus make an important contribution to regional biodiversity. These isolated relict populations are often effectively isolated from their main distribution areas in the Alps or Scandinavia, and hence, these populations frequently contain unique genetic lineages. This genetic uniqueness has also been shown for several of the aquatic insects considered in this study (Pauls et al. 2006; Lehrian et al. 2010; Taubmann et al. 2011; Kubow et al. 2010), which allows treating populations of different low mountain ranges as separate conservation units.

While GCC will likely lead to the extinction of local populations in several low mountain ranges, some areas within the study regions were shown to maintain potentially suitable areas and are thus potential future refugia for the long-term persistence of montane freshwater species under GCC. In addition to the Alps, which form the largest potential refugium of montane freshwater insects, freshwater systems at high elevations of low mountain ranges in colder regions, such as the Sudety Mountains and parts of the Bohemian Massif, Black Forest, Harz, Jura Mountains and Erzgebirge, deserve to be the focus of particular conservation efforts to preserve the genetic variation of several glacial relict species in Central Europe.

Besides their relevance for the conservation of cold-adapted species, low mountain streams are of particular conservation relevance for lowland stream species as well. Montane freshwaters are less affected by anthropogenic stressors, such as morphological river degradation, land use within catchment areas, and invasive species, than lowland freshwaters. Thus, montane freshwaters form natural reservoirs for a wide range of freshwater invertebrates and harbor potential source populations for the recolonization of lowland stream systems (Küttner et al. 2008). Because GCC-associated factors such as interactions involving increased water temperatures and pollution, as well as higher rates of species invasions (Heino et al. 2009), might also contribute to the reduction of suitable habitats for freshwater invertebrates in low mountain streams, strict protection of mountain stream refugia is of considerable relevance not only for montane species, but also for the entire biota of running freshwater systems in Central Europe.

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