# Species distribution modelling of stream macroinvertebrates under climate change scenarios

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# Abstract

There is increasing evidence that climate change will have a severe impact on species' distributions by altering the climatic conditions within their present ranges. Especially species inhabiting stream ecosystems are expected to be strongly affected due to warming temperatures and changes in precipitation patterns. The aim of this thesis was to investigate how distributions of aquatic insects, i.e., benthic stream macroinvertebrates would be impacted by warming climates. The methods comprised of an ensemble forecasting technique based on species distribution models (SDMs) and climate change scenarios of the Intergovernmental Panel on Climate Change of the year 2080. Future model projections were generated for a wide variety of species from a number of taxonomic orders for two spatial scales: a stream network within the lower mountain ranges of Germany, and the entire territory across Europe. In addition, the effect of the modelling technique on habitat suitability projections was investigated by modifying the choice of study area (continuous area vs. stream network) and the choice of predictors (standard vs. corrected set).

Projections of future habitat suitability showed that potential climate-change impacts would be dependent on species' thermal preferences, and with a similar pattern for both spatial scales. Future habitat suitability was projected to remain for most or all of the modelled species, and species were projected to track their climatically suitable conditions by shifting uphill along the river continuum within the lower mountain ranges, and into a north-easterly direction across Europe. Cold-adapted headwater and high-latitude species were projected to lose suitable habitats, whereas gains would be expected for warm-adapted river and low-latitude species along the river continuum and across Europe, respectively. Additionally, habitat specialist species in terms of endemics of the Iberian Peninsula were identified as potential climate-change losers, highlighting their restricted habitat availability and therefore vulnerability to warming climates.

The main findings of this thesis underline the high susceptibility of stream macroinvertebrates to ongoing climate change, and give insights into patterns of possible consequences due to changes in species' habitat suitability. Concerning the methodology, a clear recommendation can be given for future modelling approaches of stream macroinvertebrates by building models within a stream network and with a careful choice of environmental predictors, to reduce uncertainties and thus to improve model projections.

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## Abbreviations

| | |
|---|---|
| ANN | artificial neural networks |
| a.s.l. | above sea level |
| AUC | area under curve |
| BEM | bioclimatic envelope model |
| CSA | climatically suitable area |
| CTA | classification tree analysis |
| DEM | digital elevation model |
| FDA | flexible discriminant analysis |
| GAM | generalised additive model |
| GBM | gradient boosting machine |
| GCM | global climate model |
| GLM | generalised linear model |
| IPCC | Intergovernmental Panel on Climate Change |
| SDM | species distribution model |
| SRC | species range change |
| SRE | surface range envelope |
| SRS | species range size |
| TSS | true skill statistic |
| WA | weighted average |

## Definitions

The terms “bioclimatic envelope model” and “species distribution model” refer to the same modelling technique, however I make a distinction between these two terms based on the environmental predictors used for modelling:

- “bioclimatic envelope model”: only bioclimatic predictors are used to build the model
- “species distribution model”: a variety of different types of environmental predictors, e.g., bioclimatic, topographic, and land use predictors, are used to build the model.

# General Introduction

Global climate change is considered to pose – next to habitat destruction, pollution and species invasions – a major threat to biodiversity (Millennium Ecosystem Assessment, 2005). While climate models predict global mean surface air temperatures to increase on average by 1.1 – 6.4°C until the end of the 21st century, accompanied by altered precipitation patterns in terms of the amount and seasonality of precipitation (IPCC, 2007), climatic isotherms are predicted to shift towards a pole ward direction (Loarie *et al.*, 2009; Burrows *et al.*, 2011). Organisms may cope with these climatic alterations in two ways: adapt in terms of phenotypic plasticity (Thackeray *et al.*, 2010), or disperse with the shifting suitable climatic conditions (Chen *et al.*, 2011). While species are expected to face huge challenges by adapting to novel climatic conditions in such a short time frame of ongoing warming climates (Davis, 2001; Hampe & Petit, 2005, but see Hof *et al.*, 2011), they have been observed to track their climatically suitable conditions in a northward direction as well as towards higher altitudes (e.g., Parmesan & Yohe, 2003; Chen *et al.*, 2011). The risk of potential climate-change induced species' extinctions is at hand because of limiting dispersal abilities and a potential 'nowhere to go' situation for e.g., high-altitude species (Sala *et al.*, 2000), while possible consequences of species' range shifts on local community structure and species composition remain unknown. Nevertheless, profound alterations of future biodiversity patterns are expected for terrestrial, marine and freshwater ecosystems (Pereira *et al.*, 2010; Bellard *et al.*, 2012).

Freshwater ecosystems cover approximately only 0.8% of the Earth's surface but contain almost 6% of the described species globally, not to mention their invaluable ecosystem services (Dudgeon *et al.*, 2006). Climate warming is expected to impact freshwater ecosystems severely by an increased frequency of droughts and floods occurring unequally around the globe (Milly *et al.*, 2005; Xenopoulos *et al.*, 2005; IPCC, 2007; Döll & Zhang, 2010), and the decline in freshwater biodiversity is likely to exceed that of terrestrial ecosystems (Ricciardi & Rasmussen, 1999; Sala *et al.*, 2000; Bates *et al.*, 2008). Here, especially streams and rivers are considered highly sensitive to climate change because they respond stronger to altered runoff patterns than lakes (Poff *et al.*, 1997; Sala *et al.*, 2000). Species inhabiting stream ecosystems are thus among the most vulnerable species due to multiple stressors (Ormerod *et al.*, 2010), consisting of warming temperatures accompanied by lowered water oxygen levels, altered flow dynamics, and additional anthropogenic impacts such as land use changes, chemical loads, and water withdrawals. Not only that these factors are likely to have an effect on species' life history characteristics, ultimately resulting in changes in species assemblages (Mulholland *et al.*, 1997), they may result in habitat fragmentation and consequently in limited habitat availability (Sala *et al.*, 2000; Dudgeon *et al.*, 2006; Heino *et al.*, 2009).

The focus of this thesis lies on investigating climate-change impacts on aquatic insects, i.e., on benthic stream macroinvertebrates' distributions, a very diverse organism group which are also used as indicator species for assessing stream condition (Wallace, 1996; Haase *et al.*, 2004; Hof *et al.*, 2008). These organisms play an important role in the ecological function of streams (Wallace, 1996; Covich *et al.*, 1999), and are highly sensitive and vulnerable when exposed to climate change (Hering *et al.*, 2009, and references therein). Based on observations, several studies have assessed the effects of warming temperatures and hydrological changes on these species' distributions. For instance, Hickling *et al.* (2005) observed an overall shift of species ranges in a northward direction as a response to shifting climatic isotherms. Whereas range contractions of cold-adapted species' have been observed as a response to climate change, thermophilic as well as non-indigenous species have been found to take advantage of gradually warming climates (Brown *et al.*, 2007; Daufresne *et al.*, 2007; Chessman, 2009). However, the effects of climate change on stream macroinvertebrates' future potential distributional patterns still need to be further explored and quantified (Heino *et al.*, 2009; Hering *et al.*, 2009).

These examples show that long-term analyses of species' range dynamics are possible and feasible. However, they have the disadvantage to be geographically restricted, obviously tend to focus on past climatic changes, not to mention the costly and time-consuming observation and quantification of species observations in the field to measure potential range shifts. An alternative research approach is provided by species distribution models (SDMs), often referred to as bioclimatic envelope models, ecological niche models or habitat suitability models, depending on the purpose of the modelling approach, and provide an useful first assessment of potential climate-change effects on species' future distributions (Elith & Leathwick, 2009). These models offer a possibility to project species potential distributions in space and / or time, and are increasingly used for conservation and climate-change related vulnerability assessments (Elith & Leathwick, 2009; Araújo & Peterson, 2012). By means of the niche concept (Hutchinson, 1957), these statistical models correlate species' presences and absences with environmental predictors at those locations to describe a species' realized niche using modelling algorithms, based on the given predictors (a description of the general work-flow of the modelling procedure in this thesis is given in Box 1 and Fig. 1). As an output, SDMs provide an extrapolated map of a species' habitat suitability in geographic space. Next to obtaining information about the present potential distribution, SDMs can be used to project future potential distributions based on future environmental predictors to infer potential thermal refugees under warming climates (Elith & Leathwick, 2009). Here, SDMs base on the assumption of niche conservatism, i.e., the realized niche of a species with its biotic interactions remains unchanged over time (Pearman *et al.*, 2008). In addition, species' potential abilities regarding adaptation and plasticity in the course of warming climates are not taken into account (Pearman *et al.*, 2008; Elith & Leathwick, 2009). Despite these rather static assumptions of species' distributions (Hampe, 2004), SDMs offer an useful and cost-effective assessment of the potential distribution of species (Raxworthy *et al.*, 2003), as well as the impact of climate warming on these potential distributions (Araújo & Peterson, 2012).

Thus far, SDM-based climate-change analyses on species' distributional patterns have been applied for a wide variety of organisms, ranging from plants (e.g., Baselga & Araújo, 2009; Engler *et al.*, 2011) and terrestrial vertebrates (e.g., Hof *et al.*, 2011; Garcia *et al.*, 2012), to marine organisms (e.g., Robinson *et al.*, 2011), and freshwater fish (e.g., Buisson *et al.*, 2008; Grenouillet *et al.*, 2010). However, modelling approaches dealing with the climate-change related vulnerability of stream macroinvertebrates have begun only recently, and have focused on either single species (e.g., Cordellier & Pfenninger, 2009; Taubmann *et al.*, 2011) or single taxonomic orders (Hof *et al.*, 2012), or on habitat specialists such as cold-adapted headwater species (Bálint *et al.*, 2011; Sauer *et al.*, 2011). These results give first insights into the potential vulnerability of stream macroinvertebrates in terms of possible changes in habitat suitability under climate change scenarios. However, potential climate-change impacts have not been investigated for a variety of species with, for instance, different thermal adaptations, or specific habitat requirements and ecological traits (*sensu* Kotiaho *et al.*, 2005). Moreover, as the impact of environmental predictors on stream macroinvertebrates is dependent on the spatial scale (Poff, 1997; Vinson & Hawkins, 1998), the question remains if and how climate-change effects may occur at different spatial scales for these organisms, i.e., whether small scale climate-change effects within a mountainous area can be detected on a large scale such as Europe, and vice versa *sensu* Pearson & Dawson (2003) and Engler *et al.* (2011). Furthermore, the effect of the modelling procedure itself on projecting potential distributions of stream macroinvertebrates has not been studied thoroughly. For instance, the effects of the usage of different study areas on model projections, such as a continuous area as used in previous studies, or a stream network, have not been investigated. Similarly, analyses concerning the impact of different predictors on model performance have been neglected, therefore leaving a gap in the methodology for a proper application of SDMs for this species group.

### *Outline of the thesis*

The objective of this thesis was the application of SDMs on stream macroinvertebrates with distinct thermal preferences to investigate potential climate-change effects on their distributions on different spatial scales. For doing so, species' present distributions were modelled using SDMs, and subsequently projected into the future by means of two climate change scenarios of the year 2080 (IPCC, 2007). Further, as SDMs are rather new tools for assessing climate-change impacts for stream macroinvertebrates, the effects of different study areas and predictors on model projections were assessed. The thesis consists of the following three studies:

In **Chapter 1**, the focus lied on a species set consisting of 38 stream macroinvertebrates inhabiting the lower mountain ranges of Germany. Species were selected according to their stream zonation preference along the river continuum (Vannote *et al.*, 1980), ranging from cold-adapted headwater species, to generalist and warm-adapted river species. While cold-adapted species inhabiting mountainous areas are expected to be highly vulnerable to warming climates in terms of the predicted summit trap, i.e. a decrease in available area with increasing altitudes (Thuiller *et al.*, 2005), generalist species may show an indifferent pattern, whereas warm-adapted river species might take advantage of the gradual warming of streams (Heino *et al.*, 2009). In particular, the following hypothesis was tested (H1):

- **Effects of climate change on the future distributions of stream macroinvertebrates along the river continuum are dependent on species' thermal preferences.**

In **Chapter 2**, the modelling extent, i.e., the study area, was expanded to a continental scale to test whether general patterns of climate-change impacts on species distributions would persist independently on the spatial scale on which the effects are assessed on. In this study, the impact of warming climates was simulated for 191 stream macroinvertebrates' distributions across Europe. Next to all-species analyses, species were divided into five ecological and biological trait-based sets to assess the vulnerability of habitat specialists. Here, the hypothesis was (H2):

- **Climatically suitable areas of cold-adapted stream macroinvertebrates and specialists in terms of specific ecological and biological traits are more threatened by climate change than those of thermophilic or non-specialist species across Europe.**

**Chapter 3** focused on the methodology of SDMs for stream macroinvertebrates. Here, the objective was to compare the effects of the usage of different study areas and predictors, and how they affect the model statistics and results in terms of the magnitude of predicted areas classified as suitable for species. Specifically, the study area and the predictors were altered for four different modelling designs, ranging from a continuous area to a stream network, and from a non-corrected to a corrected set of predictors. Models were build for a set of 224 stream macroinvertebrate species across Germany, and the following hypothesis was tested (H3):

- **A stream network as a study area combined with corrected predictors improves the quality of species distributions models for stream macroinvertebrates by means of model statistics and habitat suitability projections.**

**Box 1** *General work flow of the species distribution modelling procedure in this thesis*

Species' geographic records are divided into a training and a testing set, which combined with present environmental predictors serve as the input data for building the model. The modelling technique is based on an ensemble forecasting technique using the BIOMOD package in R , i.e., several algorithms are combined to reduce uncertainties derived from the usage of different algorithms (Thuiller *et al.*, 2009). Using a consensus rule based on weighted averages (Marmion *et al.*, 2009), algorithms providing weak models receive less weight in the final consensus projection than robust ones. As a next step, this consensus projection delineating the probability of a species' present occurrence in geographic space, is converted to a map indicating the presence and absence of a species using a threshold based on the sensitivity (true positive predictions) and specificity (true negative predictions, Liu *et al.*, 2005).

To infer the impact of climate change on species' distributions, the model which was build under present conditions may then be projected into the future using future environmental predictors, such as the future emission scenarios derived from the Intergovernmental Panel on Climate Change (IPCC, 2007). By combining the map describing the future distribution with the present one, changes in species' geographic habitat suitability may be calculated to deduce information about species' potential vulnerability under warming climates, their range dynamics in terms of potential geographic shifts, or potential thermal refugees in the study area.

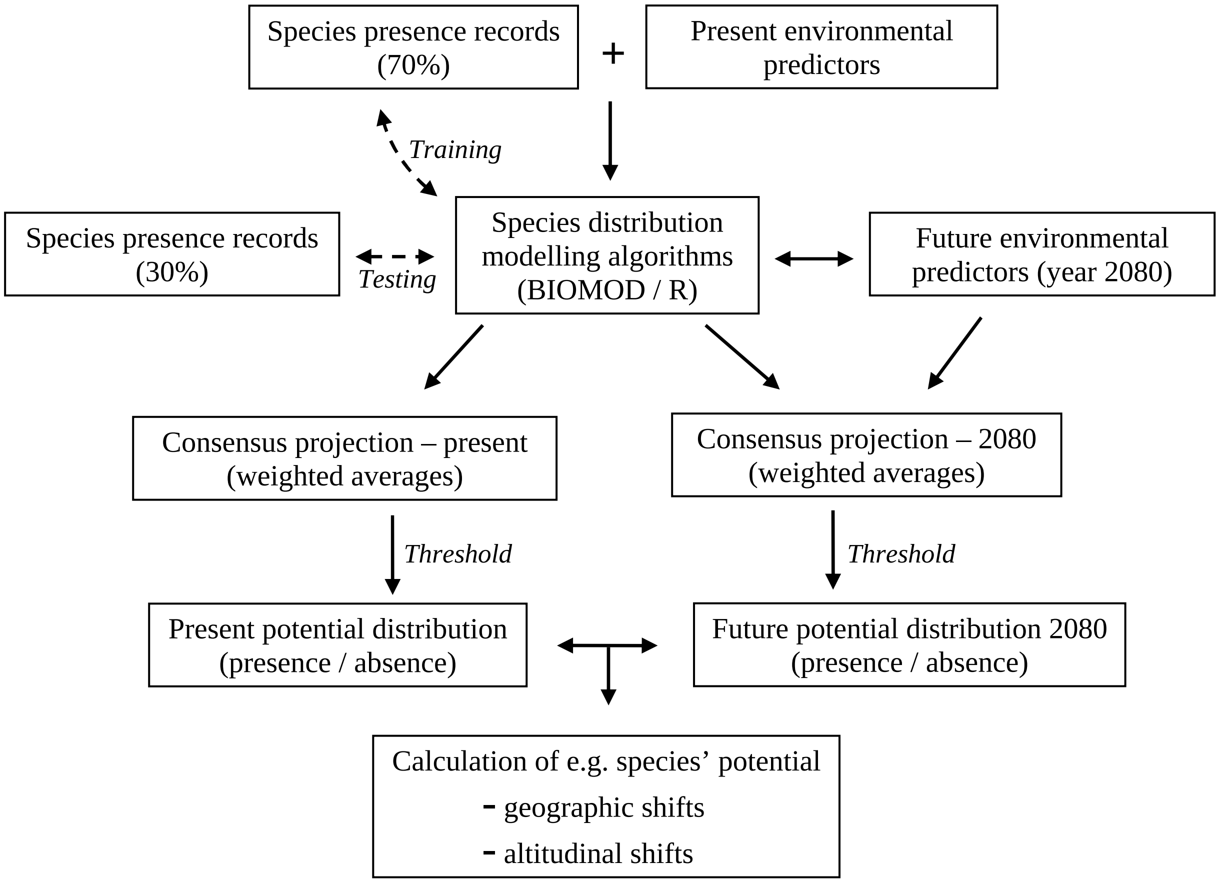

**Figure 1** General work flow of the species distribution modelling procedure in this thesis.

# Chapter 1

## Climate-change winners and losers: stream macroinvertebrates of a submontane region in Central Europe

### Abstract

Freshwater ecosystems will be profoundly affected by global climate change, especially those in mountainous areas, which are known to be particularly vulnerable to warming temperatures. We modelled impacts of climate change on the distribution ranges of 38 species of benthic stream macroinvertebrates from nine macroinvertebrate orders covering all river zones from the headwaters to large river reaches. Species altitudinal shifts as well as range changes up to the year 2080 were simulated using the A2a and B2a Intergovernmental Panel on Climate Change climate-warming scenarios. Presence-only species distribution models were constructed for a stream network in Germany's lower mountain ranges by means of consensus projections of four algorithms, as implemented in the BIOMOD package in R (GLM, GAM, GBM and ANN). Species were predicted to shift an average of 122 and 83 m up in altitude along the river continuum by the year 2080 under the A2a and B2a climate-warming scenarios, respectively. No correlation between altitudinal shifts and mean annual air temperature of species' occurrence could be detected. Depending on the climate-warming scenario, most or all (97% for A2a and 100% for B2a) of the macroinvertebrate species investigated were predicted to survive under climate change in the study area. Ranges were predicted to contract for species that currently occur in streams with low annual mean air temperatures but expand for species that inhabit rivers where air temperatures are higher. Our models predict that novel climate conditions will reorganise species composition and community structure along the river continuum. Possible effects are discussed, including significant reductions in population size of headwater species, eventually leading to a loss of genetic diversity. A shift in river species composition is likely to enhance the establishment of non-native macroinvertebrates in the lower reaches of the river continuum.

*Sami Domisch, Sonja C. Jähnig, Peter Haase (2011). Freshwater Biology 56, 2009–2020*

## 1.1 Introduction

Freshwater ecosystems will be profoundly affected by global climate change, especially those in mountainous areas, which are known to be particularly vulnerable to warming temperatures (Burgmer *et al.*, 2007; Durance & Ormerod, 2007; Hering *et al.*, 2009). Here, we focus on streams of the lower mountain ranges of Central Europe, which comprise the largest mountainous area in Europe and range in altitude up to 1500 m a.s.l. Streams within this area provide habitats for a wide variety of benthic macroinvertebrates and are thought to contain the highest level of biodiversity among aquatic macroinvertebrates in Central Europe outside the Alps (Braukmann, 1987).

The mean temperatures of running waters increase with increasing distance from the source and, according to the river continuum concept (Vannote *et al.*, 1980), headwater streams are dominated by cold-adapted species and the lower reaches by thermophilic species, with a number of generalist species distributed over a wide range along the entire river continuum. In terms of climate change, cold-adapted headwater macroinvertebrates are likely to experience a loss of thermal refuges because of warming temperatures (Mulholland *et al.*, 1997). Moreover, these species may be progressively replaced by generalist species taking advantage of the gradual warming of streams, as shown in long-term data sets by (Daufresne *et al.*, 2007). While river species are expected to move up in altitude, river warming might additionally facilitate invasion by non-native macroinvertebrates (Daufresne *et al.*, 2007; Whitehead *et al.*, 2009). A climate change–driven displacement of species towards higher altitudes will consequently change species assemblages at each altitude and therefore result in an altitudinal shift of the river continuum and lead to a major reorganisation of the species composition and community structure of streams (Mouthon & Daufresne, 2006; Burgmer *et al.*, 2007; Daufresne *et al.*, 2007; Durance & Ormerod, 2007; Haidekker & Hering, 2008).

While these predictions are based on experimental studies as well as long-term data sets, projections of the impacts of climate change on the ranges of freshwater macroinvertebrate species are scarce (Heino *et al.*, 2009). Whereas experimental or case studies are often geographically restricted, future model projections can consider a larger geographical region as well as estimate and quantify possible future range shifts under climate change. Species distributions models (SDMs) are valuable tools for predicting and evaluating such species range shifts and for following future distributions under climate change and have been increasingly used in ecology and conservation management (reviewed in Elith & Leathwick, 2009). These statistical models use environmental predictors to correlate a species' geographical distribution with present environmental conditions and produce a probability map of the species' distribution in geographical space and time. However, previous distribution-modelling approaches for stream macroinvertebrates were based on habitat suitability models (reviewed in Goethals *et al.*, 2007) or on SDMs covering the whole landscape (Cordellier & Pfenninger, 2009). These landscape-based SDMs have the disadvantage of confounding terrestrial and aquatic realms by using predictors that are not restricted to the stream network but rather to the entire landscape. Consequently, estimations of species' ranges remain inaccurate and coarse. Distributional predictions for aquatic species should therefore take care to not confound aquatic and terrestrial sites and should include predictors that relate to the stream environment as well as climatic predictors. In our approach, we focused on SDMs within a stream network to limit these erroneous predictions – an approach that, to our knowledge, has been applied so far only to fish (e.g. Buisson *et al.*, 2008).

To assess the responses of stream macroinvertebrates with different thermal tolerances to climate change, we calculated future distribution ranges under two Intergovernmental Panel on Climate Change (IPCC) climate-warming scenarios for the year 2080. Following the river continuum concept, we selected a set of 38 representative species from nine macroinvertebrate orders covering all river zones from the source to the large river reaches. We tested the following hypotheses: (i) as a response to climate change, all species are predicted to shift towards higher altitudes along the river continuum and (ii) the distributions of species adapted to different parts of the river continuum will change in distinct ways. While the suitable habitat area of species from the upper parts of the river continuum will be reduced by a 'summit trap effect' (i.e., a reduction in area with increasing elevation), the suitable habitat area of species adapted to warmer temperatures from lower parts of the river continuum will increase because of warming temperatures.

## 1.2 Methods

### *Study area*

The study area covered Germany's lower mountain range (6°10'–14°90'E, 47°50'–52°30'N, Fig. 1.1), which is a submontane region with an altitudinal range up to 1,493 m a.s.l. We restricted our analysis to a digitised stream and river network within this area (LAWA, 2003) because only running waters were considered potential habitats for the modelled organisms. The running waters ranged from small, coarse, substratumdominated highland streams (catchment size 10–100 km$^2$) to large highland rivers (catchment size 1,000–10,000 km$^2$). In total, the spatial extent of streams and rivers used for modelling comprised 93,049 grid cells with a spatial resolution of 30 arc seconds (grid cells were ca. 1 km$^2$).

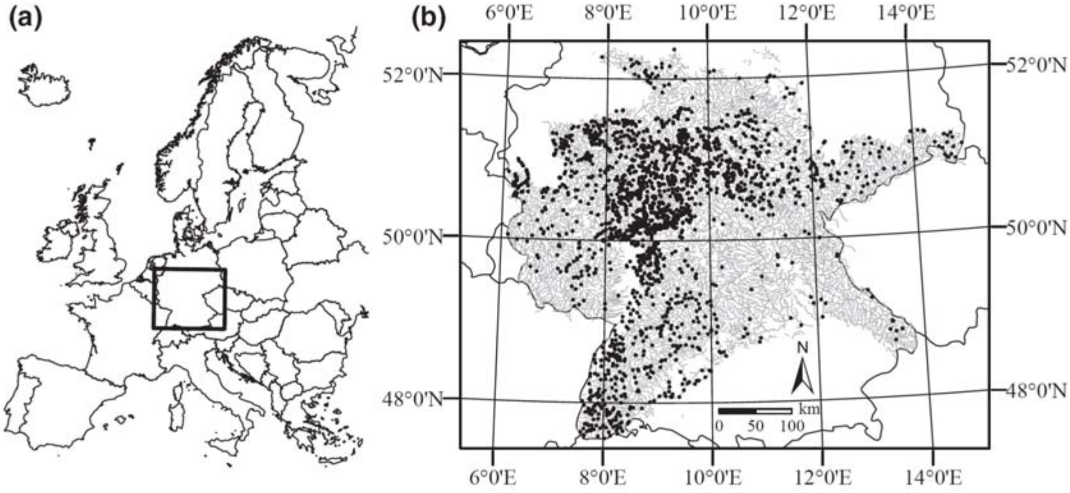

**Figure 1.1** (a) Location of the study area in Central Europe. (b) The stream network of the lower mountain range (grey lines) and all presence records used for modelling (points).

*Species data*

Because climate change may be perceived differently by species with different thermal tolerances (‘winners’ and ‘losers’), we selected for analysis species assumed to represent such different tolerances. However, information on thermal tolerance was not available for all species. Instead, we considered their stream zonation preference, using this as a substitute for their temperature range tolerance along the river continuum (*sensu* Vannote *et al.*, 1980). Species’ stream zonation preferences were extracted from a database that contains information on the autecology of freshwater organisms (http://www.freshwaterecology.info/, accessed on 25.05.2010, Euro-limpacs Consortium, 2011).

The following species were selected: first, species occurring in the upper reaches (i.e., from the eucrenal to the epirhithral, Illies, 1961), with preferences for cooler temperatures (Fig. 1.2, Table 1.1); second, species occurring only in the lower reaches (i.e. from the hyporhithral to the metapotamal), representing a preference for warmer temperatures; and last, species occurring over a wide range of zones (i.e., within the hypocrenal and the epipotamal) and thereby exhibiting a broad temperature range preference.

We then searched for species that fulfilled these criteria in three national databases to retrieve geographical presence records for the SDMs (Umweltbundesamt; Hessisches

Landesamt für Umwelt und Geologie; Landesamt für Umwelt, Messungen und Naturschutz Baden-Württemberg, unpublished data). These databases provide stream macroinvertebrate data from surveys carried out annually in the spring from 2002 to 2008 and hold a total of 42,576 species presence records from 2,484 sites within our study area. As a precondition for selection in our study, species needed to have at least 10 presence records (Stockwell & Peterson, 2002). The databases yielded 38 stream macroinvertebrates from nine taxonomic groups that fulfilled these criteria, 12 species from the upper reaches, 12 species from the lower reaches and 14 species occurring over a wide range of zones. The selected organisms provided a total of 6564 presence records from 2,151 sites within our study area (Fig. 1.1, Table 1.1).

We then analysed the relationships between the presence records of the selected species and mean annual air temperature derived from the WorldClim database for the respective grid cells (http://www.worldclim.org, accessed on 12.03.2010, Hijmans *et al.*, 2005). Detailed stream temperatures were not available for the entire extent of our study area. Therefore, we used air temperatures as a surrogate for average stream temperature, which, except in source zones, tend to be similar to the average air temperature (Caissie, 2006).

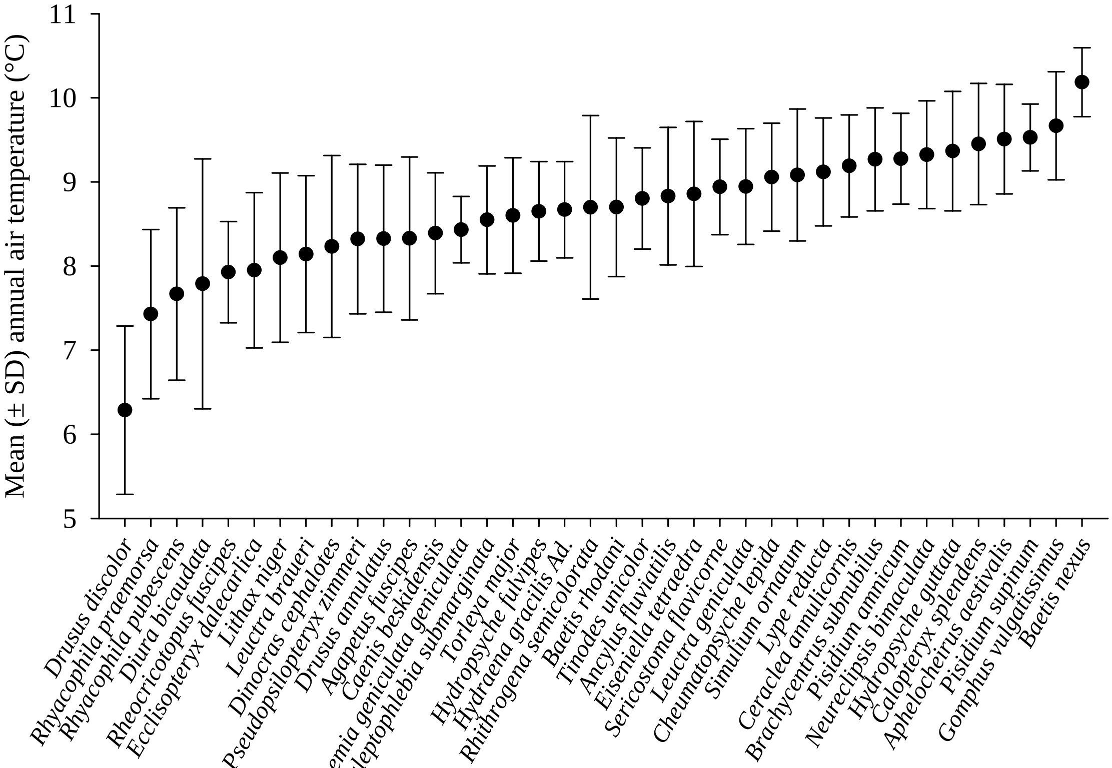

**Figure 1.2** Mean (±SD) annual air temperatures of species' occurrences. Gridded temperature data were derived from the WorldClim dataset.

**Table 1.1** Macroinvertebrates used for species distribution models. Species information is presented with the corresponding taxonomic groups, number of species records, species range changes for the year 2080 under the A2a and B2a climate-warming scenarios and AUC values (AUC, area under curve; SRC, species range change; SD, standard deviation; WA, weighted average). The order is equal to that of Fig. 1.2, i.e. according to increasing mean annual air temperatures of the species' occurrences.

| Species | Taxonomic group | Species records | SRC A2a ± SD (%) | SRC B2a ± SD (%) | AUC (WA) |
|---|---|---:|---|---|---|
| *Drusus discolor* (Rambur, 1842) | Trichoptera | 12 | -97.0 ± 1.0 | -91.8 ± 0.9 | 0.99 |
| *Rhyacophila praemorsa* McLachlan, 1879 | Trichoptera | 24 | -83.1 ± 11.8 | -48.3 ± 8.7 | 0.98 |
| *Rhyacophila pubescens* Pictet, 1834 | Trichoptera | 10 | -77.5 ± 14.5 | -52.9 ± 12.8 | 0.99 |
| *Diura bicaudata* (Linnaeus, 1758) | Plecoptera | 26 | -94.7 ± 3.7 | -73.0 ± 0.9 | 0.90 |
| *Rheocricotopus fuscipes* (Kieffer, 1909) | Diptera | 13 | -100.0 ± 0.0 | -96.6 ± 1.8 | 0.99 |
| *Ecclisopteryx dalecarlica* Kolenati, 1848 | Trichoptera | 47 | -99.7 ± 0.2 | -97.3 ± 0.3 | 0.95 |
| *Lithax niger* (Hagen, 1859) | Trichoptera | 31 | -45.1 ± 4.0 | -10.8 ± 7.9 | 0.93 |
| *Leuctra braueri* Kempny, 1898 | Plecoptera | 17 | -88.4 ± 3.6 | -56.8 ± 0.1 | 0.96 |
| *Dinocras cephalotes* (Curtis, 1827) | Plecoptera | 92 | 34.2 ± 4.9 | 42.7 ± 10.0 | 0.95 |
| *Pseudopsilopteryx zimmeri* (McLachlan, 1876) | Trichoptera | 16 | -98.7 ± 0.9 | -36.8 ± 23.2 | 0.87 |
| *Drusus annulatus* (Stephens, 1837) | Trichoptera | 182 | -31.0 ± 48.7 | 37.7 ± 7.5 | 0.89 |
| *Agapetus fuscipes* Curtis, 1834 | Trichoptera | 60 | -64.2 ± 23.6 | 20.5 ± 31.9 | 0.92 |
| *Caenis beskidensis* Sowa, 1973 | Ephemeroptera | 50 | -81.2 ± 2.2 | -55.3 ± 1.9 | 0.95 |
| *Plectrocnemia geniculata geniculata* McLachlan, 1871 | Trichoptera | 10 | -99.6 ± 0.3 | -85.4 ± 5.0 | 0.97 |
| *Paraleptophlebia submarginata* (Stephens, 1835) | Ephemeroptera | 173 | -95.4 ± 3.3 | -59.7 ± 1.1 | 0.93 |
| *Torleya major* (Klapálek, 1905) | Ephemeroptera | 440 | -97.0 ± 2.1 | -71.9 ± 1.9 | 0.85 |
| *Hydropsyche fulvipes* (Curtis, 1834) | Trichoptera | 18 | 15.3 ± 9.4 | 50.8 ± 7.9 | 0.95 |
| *Hydraena gracilis Ad.* Germar, 1824 | Coleoptera | 66 | -93.6 ± 4.5 | -73.2 ± 2.3 | 0.97 |
| *Rhithrogena semicolorata* (Curtis, 1834) | Ephemeroptera | 89 | 16.6 ± 13.6 | 67.0 ± 20.7 | 0.95 |
| *Baetis rhodani* (Pictet, 1843) | Ephemeroptera | 1766 | -27.6 ± 19.1 | 35.1 ± 18.0 | 0.79 |
| *Tinodes unicolor* (Pictet, 1834) | Trichoptera | 15 | -83.9 ± 10.2 | -70.6 ± 12.3 | 0.96 |
| *Ancylus fluviatilis* O.F. Müller, 1774 | Gastropoda | 1134 | 38.9 ± 32.2 | 106.5 ± 18.6 | 0.80 |
| *Eiseniella tetraedra* (Savigny, 1826) | Oligochaeta | 935 | 28.5 ± 21.5 | 104.7 ± 26.4 | 0.82 |
| *Sericostoma flavicorne* Schneider, 1845 | Trichoptera | 57 | 29.1 ± 71.5 | 223.2 ± 23.9 | 0.98 |
| *Leuctra geniculata* (Stephens, 1836) | Plecoptera | 168 | 123.8 ± 90.9 | 174.3 ± 39.8 | 0.95 |
| *Cheumatopsyche lepida* (Pictet, 1834) | Trichoptera | 133 | -95.2 ± 3.0 | -75.5 ± 5.7 | 0.95 |
| *Simulium ornatum* Meigen, 1818 | Diptera | 212 | 244.5 ± 35.0 | 253.4 ± 3.1 | 0.90 |
| *Lype reducta* (Hagen, 1868) | Trichoptera | 66 | -73.0 ± 17.0 | 64.2 ± 5.9 | 0.96 |
| *Ceraclea annulicornis* (Stephens, 1836) | Trichoptera | 23 | 552.2 ± 15.3 | 400.9 ± 23 | 0.96 |
| *Brachycentrus subnubilus* Curtis, 1834 | Trichoptera | 90 | 94.9 ± 15.8 | 119.5 ± 8.7 | 0.98 |
| *Pisidium amnicum* (O.F. Müller, 1774) | Bivalvia | 64 | -80.8 ± 12.0 | -3.0 ± 0.4 | 0.96 |
| *Neureclipsis bimaculata* (Linnaeus, 1758) | Trichoptera | 11 | 1931.4 ± 109.9 | 1387.8 ± 102.7 | 0.91 |
| *Hydropsyche guttata* Pictet, 1834 | Trichoptera | 11 | 949.7 ± 1.0 | 913.9 ± 30.7 | 0.94 |
| *Calopteryx splendens* (Harris, 1782) | Odonata | 229 | 403.5 ± 12.4 | 347.9 ± 7.9 | 0.93 |
| *Aphelocheirus aestivalis* (Fabricius, 1794) | Plecoptera | 197 | 444.8 ± 13.8 | 374.8 ± 11.8 | 0.94 |
| *Pisidium supinum* Schmidt, 1851 | Bivalvia | 28 | -88.7 ± 6.3 | -41.7 ± 6.3 | 0.99 |
| *Gomphus vulgatissimus* (Linnaeus, 1758) | Odonata | 25 | 720.5 ± 13.9 | 622.7 ± 17.5 | 0.94 |
| *Baetis nexus* Navás, 1918 | Ephemeroptera | 24 | 1403.6 ± 21.6 | 1244.7 ± 21.6 | 0.99 |

*Environmental predictors*

The environmental predictors considered for the SDMs derived from bioclimatic, topographic and stream-specific categories. From a set of more than 25 predictors, we selected those deemed most relevant for describing the distribution of stream macroinvertebrates, with care taken to avoid colinearity among predictors.

Present and future bioclimatic predictors included mean annual air temperature, isothermality (mean diurnal temperature range divided by the annual temperature range), annual temperature range, annual precipitation and precipitation seasonality (standard deviation of the weekly precipitation estimates expressed as a percentage of the annual mean estimates) and were downloaded from the WorldClim database (Hijmans *et al.*, 2005). The future projections of bioclimatic predictors of the year 2080 were derived from the global climate models of the Hadley Centre for Climate Prediction and Research (UKMO-HadCM3, Gordon *et al.*, 2000) and the Canadian Centre for Climate Modelling (CCCMA-CGCM2, Flato *et al.*, 2000). For each, we used the A2a ('business as usual') and B2a ('moderate') climate-warming scenarios published by the IPCC (2007).

We chose slope and aspect as input topographic predictors in the SDMs. Slope is considered to be an important proxy for flow velocity and oxygen content, whereas aspect accounts for exposure to sun-induced heating of streams.

Concerning stream-specific predictors, we chose stream type, flow direction and flow accumulation. Stream type is considered a proxy for stream size, catchment area, ecoregion and geology (for a detailed description of German stream types, see http://www.fliessgewaesser-bewertung.de/en/, Pottgiesser & Sommerhäuser, 2004). Flow direction is defined as the direction of flow from each cell to its steepest down-slope neighbour. Flow accumulation is based on the flow direction and defines the number of cells that flow into each down-slope cell and can thus be seen as a proxy for the drainage area (USGS). Both represent flow dynamics in the stream network. The stream-type layer was derived from (LAWA, 2003), whereas the layers representing slope, aspect, flow direction and flow accumulation were obtained from a hydrologically corrected digital elevation model (Hydro1k dataset, http://eros.usgs.gov/, accessed on 07.04.2010, USGS). All 10 environmental predictors were analysed for colinearity by means of Pearson correlation coefficients. The predictors were not strongly correlated ($-0.7 < r < 0.7$, Green, 1979).

### *Species distribution models*

We simulated the distribution of stream macroinvertebrates by means of presence-only SDMs. Four algorithms consisting of two regression methods (generalised linear models, GLM and generalised additive models, GAM) and two machine-learning methods (gradient boosting machine, GBM and artificial neural networks, ANN) were used according to the BIOMOD package version 1.1.5 in R (Thuiller *et al.*, 2009; R Development Core Team, 2011). Species occurrence data were split into a training set (70%) and a testing set (30%) by applying a random partition (Araújo *et al.*, 2005). Each algorithm used 5,000 pseudo-absences and a tenfold cross-validation to yield an average model for each species and algorithm, and prevalence was internally kept constant at 0.5 within the BIOMOD package for all species. These average models, which were calibrated under the present conditions, were then projected to the year 2080 using future bioclimatic predictors from the two global climate models. Non-bioclimatic environmental predictors (i.e., topographic and stream-specific predictors) were kept constant, as they are considered independent of climate.

Model evaluation was conducted by means of area under curve (AUC) statistics from a receiver-operating characteristic analysis, which is a threshold-independent evaluation of model discrimination (Fielding & Bell, 1997). AUC values range from 0.5 to 1, where 0.5 represents no discrimination and 1 represents perfect discrimination (Hosmer & Lemeshow, 2000). Araújo *et al.* (2005) showed that a consensus projection significantly improves the predictive accuracy of SDMs. We therefore used a consensus projection for each species and scenario, with weighted averages (WA) based on the predictive performance of single-model outputs for each species and algorithm. The relative importance of each algorithm for the final consensus models was obtained by multiplying the averaged AUC value by a weight decay of 1.6 (default settings). Finally, the distribution probability maps of present and future projections were transformed into binary presence–absence maps by applying a cut-off value that minimises the difference between sensitivity (true-positive predictions) and specificity (true-negative predictions, Fielding & Bell, 1997).

### *Species' responses to climate change*

Binary consensus model outputs were first calculated for each species individually, and the results of the two global climate models were averaged to yield an A2a and a B2a 2080 climate-warming projection. We then analysed the results for each species by correlating with their mean annual air temperature of occurrence using Spearman rank correlations. One species that was predicted to go extinct and thus lacked future projections was omitted from these analyses.

Altitudinal shifts in species' ranges were analysed using the mean altitude of the species' suitable habitat area in their present distribution and the mean altitude of future suitable habitat area under the A2a and B2a scenarios.

Species' range changes (SRC) were calculated as the difference between the number of grid cells gained and lost as a percentage of the number of grid cells presently classified as suitable habitat. We set no dispersal limitations but rather considered the entire stream and river network as available area for dispersal. Further, in contrast to relative range changes, we calculated the differences in species' range sizes (SRS, i.e., the difference between the number of present and future grid cells classified as suitable habitat area).

The relative contributions of environmental predictors demonstrated which predictors contributed most significantly to the predictions of species' present distributions. As for the consensus models, the results of all algorithms were averaged using an identical weighting factor, thus making the relative contributions of environmental predictors match the final consensus model for each species.

## 1.3 Results

### *Model performance*

The overall model performance was good for all species (AUC = 0.94 ± 0.05, weighted average ± SD, Table 1). For all modelled species, a combination of three bioclimatic predictors (mean annual temperature, annual precipitation and precipitation seasonality) made the most substantial contribution (50%) to the present distribution of the species (Fig. 1.3).

### *Altitudinal shifts in species' ranges*

The models showed that species were predicted to shift on average 122 and 83 m towards higher altitudes by the year 2080 under the A2a and B2a climate-warming scenarios, respectively, generally supporting the stated hypothesis of an altitudinal shift (Paired *t*-tests: A2a: $t_{36} = -5.33$, $P < 0.001$; B2a: $t_{37} = -5.82$, $P < 0.001$; Fig. 1.4). Species occurring at higher altitudes displayed larger altitudinal shifts (left part of Fig. 1.4) compared with species occurring at lower altitudes (right part). However, no correlation could be detected between the mean annual air temperature of occurrence and the altitudinal shifts between the present and future suitable habitat areas (Spearman rank correlation tests: A2a: r = -0.19, *P* = 0.261; B2a: r = -0.03, *P* = 0.880, Fig. 1.5a–b).

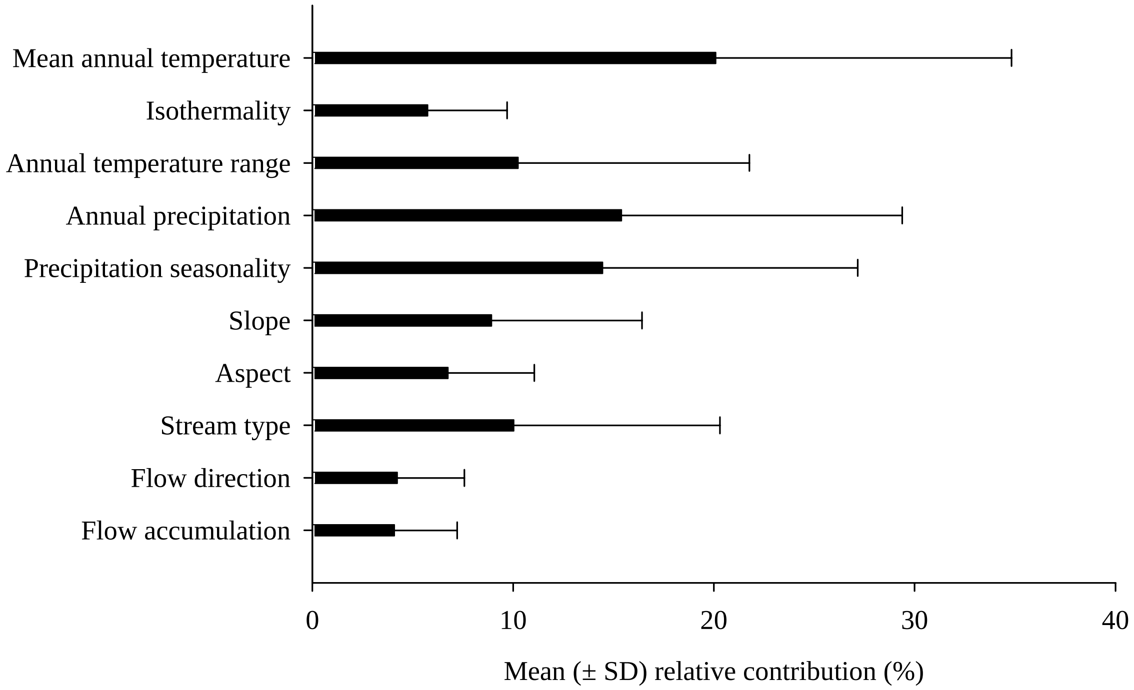

**Figure 1.3** Mean (± SD) relative contributions of environmental predictors for determining the present distributions of macroinvertebrate species. The relative contributions of environmental predictors of all algorithms were averaged using identical weights as for the consensus models and were then averaged for all species.

### *Species' range changes and sizes (SRC and SRS)*

The models showed that SRC and SRS correlated positively with the mean annual air temperatures of occurrence from the headwaters to large river reaches under both climate-warming scenarios (Spearman rank correlation tests: SRC A2a: r = 0.67, *P* < 0.001; B2a: r = 0.72, *P* < 0.001, Fig. 1.5c–d; SRS A2a: r = 0.53, *P* < 0.001; B2a: r = 0.66, *P* < 0.001, data not shown). Generally, species occurring at lower mean annual air temperatures experienced losses in range size, whereas species occurring at higher mean annual air temperatures mostly showed pronounced increases in range size.

In general, the overall effects on species range and size changes were stronger under the A2a scenario ('business as usual') than under the B2a ('moderate') scenario (Fig. 1.5c–d, Table 1.1). Of the 38 investigated species, one species (3%) was predicted to go extinct under the A2a climate-warming scenario (*Rheocricotopus fuscipes*, Diptera, Table 1.1), while all species were predicted to survive under the B2a scenario.

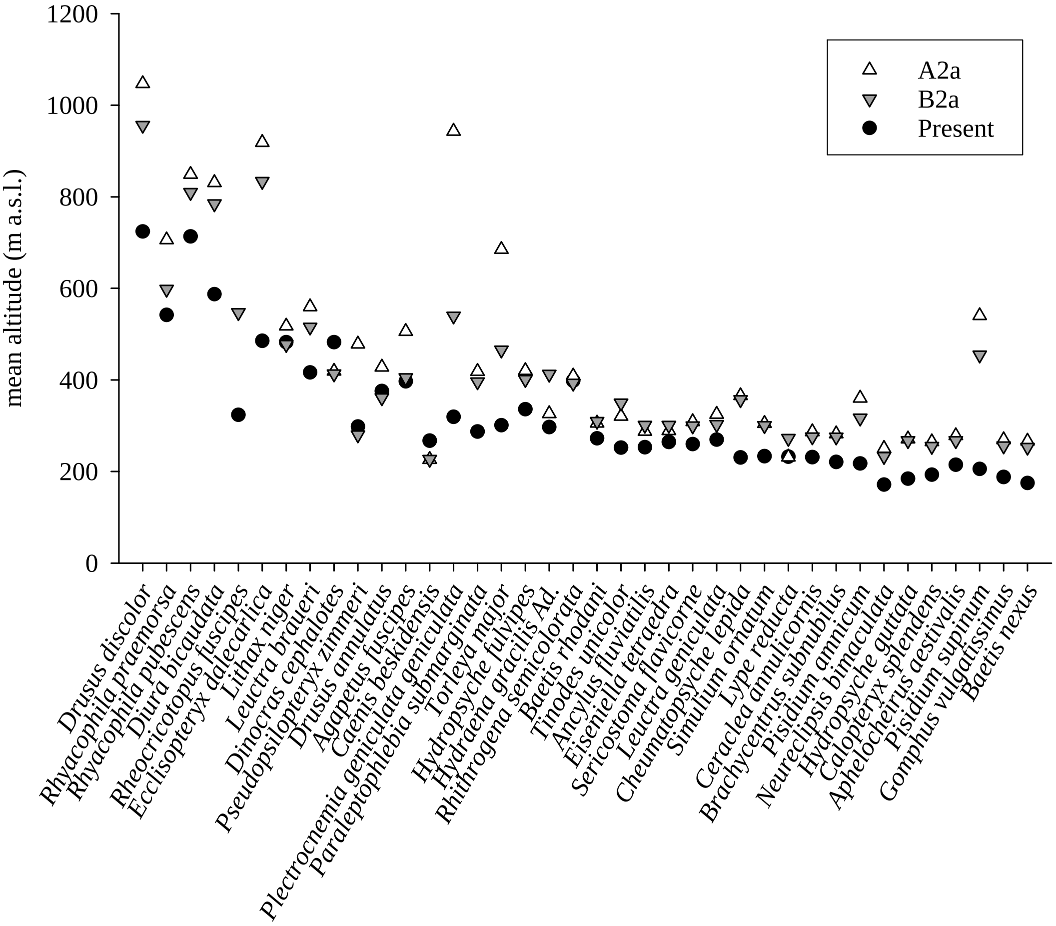

**Figure 1.4** Mean altitudes of present and future suitable habitat areas for the investigated species under the A2a and B2a climate-warming scenarios.

## 1.4 Discussion

*Model performance and environmental predictors*

We obtained good consensus models for each species, giving confidence that the models will be useful for future attempts to understand possible changes in species' ranges driven by climate change. However, two general issues are crucial to bear in mind when predicting the distributions of stream macroinvertebrates. First, there is a scarcity of data for the most appropriate predictors, and second, there is a major lack of information concerning the ecological preferences of macroinvertebrates (Heino *et al.*, 2009).

One of the most appropriate environmental predictors for which there is a deficiency of data is stream temperature, which strongly influences the distribution of stream macroinvertebrates (Haidekker & Hering, 2008) and affects their life history characteristics and productivity (Mulholland *et al.*, 1997; and references therein). This deficiency particularly affects species considered as headwater species in the SDMs, a fact that is likely to derive from the use of air temperatures as a surrogate. Temperatures in head-

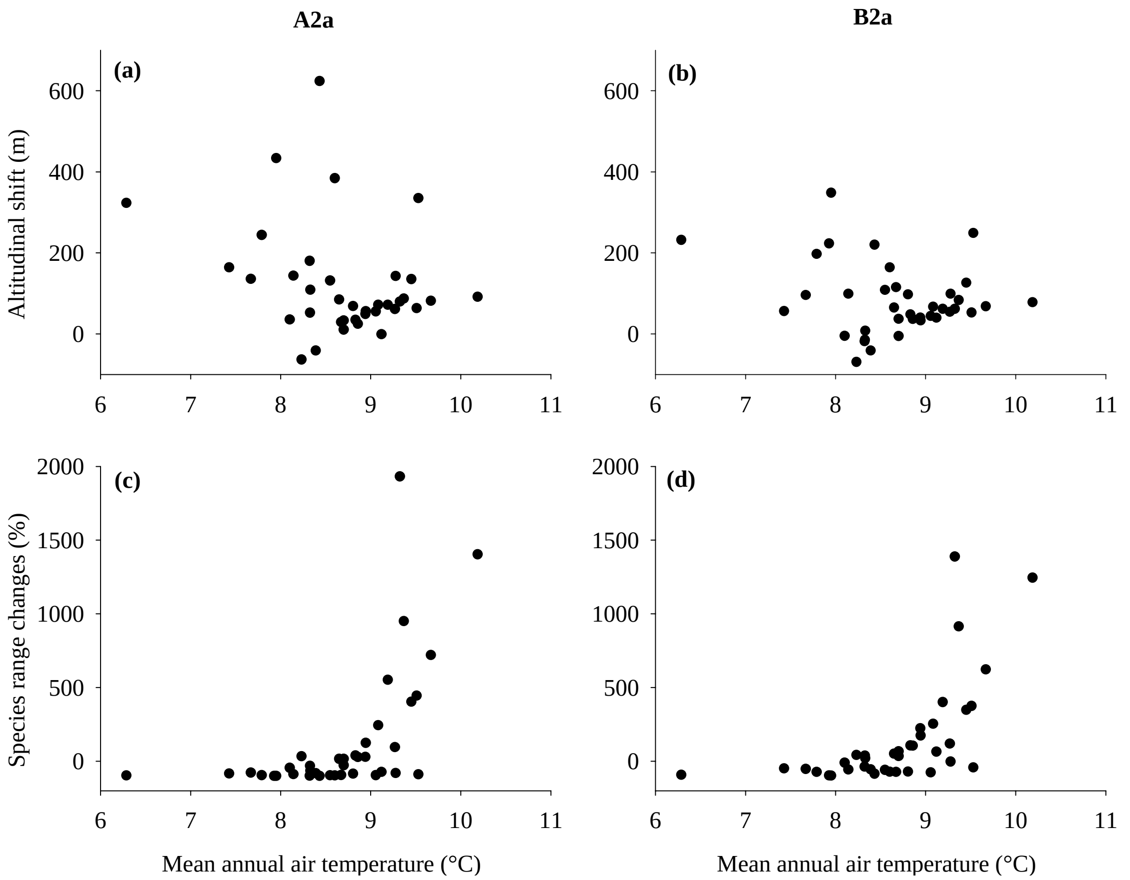

**Figure 1.5** The mean annual air temperature of species' occurrences (compare with Fig. 1.2) correlated with altitudinal shifts (a–b) and species range changes (c–d) under the A2a and B2a climate-warming scenarios.

water streams are strongly influenced by groundwater temperatures, which can be substantially lower than ambient air temperatures. Consequently, air temperature may be a poor surrogate for water temperature in these streams, leading to high variability in our SDMs, which in turn may have resulted in prediction errors for these species. This is corroborated by the fact that the standard deviations of the mean annual air temperatures of the species' occurrences decreased as the temperature increased, (i.e., from the headwaters to large river reaches, Spearman rank correlation test: r = -0.60, *P* < 0.001). Although several methods for estimating stream temperatures from air temperatures were reviewed by Caissie (2006), such estimations are only feasible for single streams or subcatchments. In contrast, stream temperatures in the mid and lower reaches are strongly influenced by air temperatures (Vannote & Sweeney, 1980), and the corresponding estimates are thus more likely to be correct.

Little to no information is available on the ecological preferences of the vast majority of stream macroinvertebrates, such as those regarding temperature and its impact on the life cycle (Heino *et al.*, 2009; Hering *et al.*, 2009). Furthermore, our limited understanding of dispersal capabilities hinders attempts to make reliable predictions of range changes. As a consequence, range shifts and expansions of the investigated species are best viewed as approximations. The true dispersal capabilities of these species are likely to be lower than the predicted levels. Moreover, the species predicted to experience increases in their suitable habitat areas will encounter new environmental conditions at their new locations. For example, there are likely to be different patterns of hydrodynamics and different substrata in the stream bed owing to altered flow patterns, making reliable predictions of future ranges challenging.

### *Ecological consequences of species range changes*

Our models show that the projected changes in species' ranges generally depend on the mean annual air temperature of each species' current range, although this does not apply to the altitudinal shifts. The suitable habitat areas of species occurring at higher temperatures were predicted to expand under both climate-warming scenarios and vice versa.

Our models indicate that the suitable habitat areas of species occurring at lower temperatures (i.e., cold-adapted headwater species) will decrease. Contractions in the suitable habitat areas of these species induced by climate warming were recently predicted by Haidekker & Hering (2008) and Chessman (2009). Likewise, the ability of these species to survive climate warming at higher altitudes of the lower mountain ranges under the assumption of unrestricted migration seems probable and has been also predicted by Wilson *et al.* (2005) and Burgmer *et al.* (2007). Thus, the models are corroborated by findings from previous experimental studies as well as long-term data sets. However, cold-adapted hololimnic species (with a fully aquatic life cycle) often have small geographical ranges, poor active dispersal abilities and narrow habitat requirements and are considered particularly threatened by climate change (Wilson *et al.*, 2007). They might, therefore, encounter a 'nowhere to go' situation as a result of the summit trap effect (Thuiller *et al.*, 2005; Bässler *et al.*, 2010). Taking into account that headwaters can constitute three-quarters or more of the total stream channel length in a drainage basin (Clarke *et al.*, 2008), the predicted loss of suitable habitat area in such a large part of the continuum might result in a significant reduction in population size or even population extinctions. This would inevitably lead to a loss of genetic diversity, as these species form highly isolated populations in mountainous ecosystems (Clarke *et al.*, 2008; Lehrian *et al.*, 2009; Taubmann *et al.*, 2011). In small catchment areas, the genetic diversity might fall below that required to sustain a minimum population size and thus eventually lead to species extinctions in these areas.

An overall trend towards enlargement of the suitable habitat areas of species occurring at higher temperatures (i.e., warm-adapted river species) under both climate-warming scenarios is evident despite the great variability among the investigated species, most likely reflecting their ecological characteristics (McPherson & Jetz, 2007). Besides the expansion of these species' suitable habitat areas into gaps within their present suitable habitat areas, the models showed that the suitable habitat areas of these species might extend towards higher elevations along the stream network. However, our modelling approach did not take evaporative cooling of streams into account, which might constrain the rise in stream temperatures. Although the altitude of the stream network used for modelling ranged from 29 to 1351 m a.s.l., and a wide range of temperatures were included at each elevation to calibrate the models, the altitudinal shifts of these species may have been overestimated if temperature-dependent predictors of future climate scenarios ranged beyond the present calibration data.

Nonetheless, the warming of the lower reaches of the continuum may in general provide accessible habitat for non-native species, which may already be adapted to higher temperatures and ⁄ or lower oxygen contents (Daufresne *et al.*, 2007; Rahel & Olden, 2008). This could lead to major changes in species composition and community structure in the lower reaches, especially if potential newcomers show characteristics of keystone or ecosystem engineering species.

Under both climate-warming scenarios, our models suggest that most species will shift up in altitude along the river continuum. Species in headwater regions were predicted to lose large amounts of suitable habitat area, while species of the mid and lower reaches might progressively replace cold-adapted species by taking advantage of the gradual warming of streams, in agreement with current opinion (Daufresne *et al.*, 2007). Although the models showed that species occurring in river reaches are favoured by warming temperatures, the question remains open as to whether this will result in less specialised communities, as previously suggested by Haidekker & Hering (2008).

However, the variable species range changes under the two global climate models indicate that clearly defined predictions are difficult to render. The heavier losses of suitable habitat areas under the A2a scenario compared with the B2a scenario can probably be attributed to temperatures increasing beyond the species' tolerances. For instance, our study predicted the extinction of the chironomid species *Rheocricotopus fuscipes* (Diptera) under the A2a scenario (Table 1.1). The annual temperature range (the difference between the minimum temperature of the coldest period and the maximum temperature of the warmest period) accounted for 67% of the present distribution of *R. fuscipes* (results not shown). In contrast, the same predictor contributed on average only 10% to all other species (Fig. 1.3). On average, the annual temperature range in our study area will increase by 3°C under the A2a scenario and by 1.7°C under the B2a scenario. Increases in the annual temperature range under the A2a scenario could therefore delimit the future distributions of certain species.

### *Implications for mitigation*

In general, our models indicate that climate warming will alter the ranges of macroinvertebrate species across the river continuum, from the headwaters to the lower reaches. This raises the question of how climate change-driven effects on the diversity of stream macroinvertebrates in the lower mountain ranges might be mitigated. Vulnerable macroinvertebrates might possibly be conserved by reducing interacting stressors, either directly (e.g., reduction in chemical loads and contamination) or indirectly (e.g., land use changes). Furthermore, the establishment and maintenance of dispersal corridors and dispersal networks in protected areas should be enacted to especially if potential newcomers show characteristics of keystone or ecosystem engineering species.

Under both climate-warming scenarios, our models suggest that most species will shift up in altitude conserve minimum viable populations (Heino *et al.*, 2009). For this purpose, there is, however, a clear need for information on the dispersal abilities of different species (Kappes & Haase, 2011) and for SDMs that account for this factor. For merolimnic invertebrates (species with an aquatic larval and a terrestrial adult stage) in particular, we propose a two-model solution that does not confound aerial and aquatic predictors. The aquatic stage of these species is modelled with predictors that are important for describing the larval phase (aquatic stage model), whereas the adult stage is modelled with predictors that are important for describing the aerial stage (aerial stage model). The results of these two models are then combined to further improve estimations of dispersal. Moreover, predictions for especially cold-adapted hololimnic species (fully aquatic life cycle) could be improved by using more relevant predictors for these species, such as water temperatures at a fine scale ($<1\ km^2$).

This study sheds light onto possible impacts of climate change on the ranges of selected species along the river continuum in streams of a mountainous ecosystem. Our stated predictions that climate change will have differential impacts on stream macroinvertebrates with different thermal tolerances were corroborated by the SDM runs. In addition, the results showed that the SDMs of macroinvertebrates within stream networks are useful for predicting possible shifts in species' ranges. Further investigations are required to understand the direct and indirect impacts of climate change and its interactions with other stressors on stream macroinvertebrates.

# Chapter 2

## How would climate change affect European stream macro-invertebrates' distributions?

### Abstract

Climate change is predicted to have profound effects on freshwater organisms due to warming temperatures and altered precipitation patterns, that will affect the distribution of species climatically suitable areas. We modelled the future climatic suitability for 191 stream macroinvertebrate species from 12 orders across Europe under two climate change scenarios for 2080 using an ensemble of bioclimatic envelope models (BEMs). 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. Additionally, the effects of climate change on species were analysed by subdividing them into the following ecological and biological trait-based sets: 1) endemic / non-endemic and 2) rare / common species within European ecoregions; 3) species with an aquatic larval and a terrestrial adult stage / species with a fully aquatic life cycle; and species based on their 4) stream zonation preference and 5) current preference. Suitable climates in the future were projected to remain in Europe for nearly 99% of the modelled species under both scenarios. Nevertheless, BEMs projected a decrease of climatically suitable areas for 57-59% of the species depending on the scenario. Climatically suitable areas were projected to shift on average 4.7-6.6° northward and 3.9-5.4° eastwards. Cold-adapted and high-latitude species were projected to lose climatically suitable areas, while gains were expected for warm-adapted and low-latitude species. Endemic species of the Iberian-Macaronesian region were an exception. Even under the assumption of unlimited dispersal these thermophilic species were projected to lose significantly higher amounts of climatically suitable areas than non-endemic species, whereas no significant differences in changes of climatically suitable areas could be observed for other trait-based sets. Modelled shifts of climatically suitable areas thus underpin the high vulnerability of freshwater organisms to ongoing climate change.

*Sami Domisch, Miguel B. Araújo, Núria Bonada, Steffen U. Pauls, Sonja C. Jähnig, Peter Haase. Submitted to Global Change Biology*

## 2.1 Introduction

Europe harbours a great diversity of stream macroinvertebrates (see e.g., Hof *et al.*, 2008), which are highly sensitive and vulnerable when exposed to climate change (Hering *et al.*, 2009 and references therein). Climate change will impose severe challenges for stream biota across Europe due to warming temperatures in northern Europe, increasing risks for flood events in temperate regions, and an increasing frequency of droughts in southern Europe (IPCC, 2007). Specifically, predicted climate-change impacts on the distribution of stream macroinvertebrates include a reduction of habitat for cold-adapted species in high latitudes and altitudes (Bálint *et al.*, 2011), as well as for Southern European (endemic) species (Ribera & Vogler, 2004; Bonada *et al.*, 2009), habitat specialists (Kotiaho *et al.*, 2005), and species with specialized life history traits (Hering *et al.*, 2009).

Thus far, assessments on possible climate-change effects, describing the potential fate of stream macroinvertebrates under warming climates on a continental scale, have focused either on single species (e.g., Taubmann *et al.*, 2011) or taxonomic orders (Hof *et al.*, 2012), on cold-adapted headwater species (Bálint *et al.*, 2011), or using expert knowledge and the categorisation of single taxonomic orders according to their potential vulnerability (Hering *et al.*, 2009; de Figueroa *et al.*, 2010). To our knowledge no study has yet assessed possible alterations in terms of species potential distributions for a wide variety of stream macroinvertebrates using bioclimatic envelope models (BEMs). These statistical models have proven to be valuable tools in conservation and climate-change analyses by projecting species habitat suitability in space and/or time, based on climatic predictors (Elith & Leathwick, 2009; Araújo & Peterson, 2012, and references therein). While small scale modelling analyses within mountainous regions (Domisch *et al.* 2011) corroborate observed responses to warming climates for species along the river continuum (Daufresne *et al.*, 2004; Chessman, 2009), the use of different spatial extents and resolutions for modelling studies is likely to result in different patterns of species responses (see e.g., Engler *et al.*, 2011), based on methodological biases rather than differences in species sensitivities and responses to changing climate conditions. On a continental scale, a particular challenge for modelling stream macroinvertebrates is to compile a reliable and comprehensive set of range-wide species records for building BEMs (Sánchez-Fernández *et al.*, 2008), since models are highly sensitive to the quality of species distributional data (Barbet-Massin *et al.*, 2010).

We carried out an extensive search for species records to limit the impacts of using incomplete distributional data. Following a thorough data quality program, we modelled the present and future climatically suitable areas for 191 species across Europe. We analysed relative changes in species' climatically suitable areas as well as their potential shifts in latitude and longitude with respect to species' thermal preferences. Additionally, the effects of climate change on species were analysed by subdividing them into the following ecological and biological trait-based sets: 1) endemic / non-endemic species and 2) rare / common species within European ecoregions; 3) species with an aquatic larval and a terrestrial adult stage / species with a fully aquatic life cycle; and species groups based on their 4) stream zonation preference and 5) current preference.

We hypothesized that climatically suitable areas would shift northwards due to warming temperatures (Chen *et al.*, 2011), and that the extent of climate-change effects would be dependent on species thermal preferences (Domisch *et al.*, 2011). Further, we expected that endemic and rare species would be more threatened by warming climates than the respective counterparts, as specific habitat requirements may not be present under future climate conditions (Malcolm *et al.*, 2006; IPCC, 2007). Similarly we expected that species with a fully aquatic life cycle would lose more climatically suitable area than species with an aquatic larval and terrestrial adult stage, as changing precipitation patterns may force the restriction of habitat availability (Xenopoulos *et al.*, 2005). Since species occurring at specific stream zones along the river continuum are expected to respond differentially to climate change due to different thermal regimes (Hering *et al.*, 2009; Domisch *et al.*, 2011), we expected that cold-adapted headwater species would be more vulnerable to warming climates than thermophilic species distributed along the mid- and lower-reaches of the river continuum. Last, climate warming is expected to result in changes in water availability as well as in stream discharge changes (Milly *et al.*, 2005; Xenopoulos *et al.*, 2005), and we hypothesized that climatically suitable areas for species adapted to fast running waters would decrease because of expected droughts and alterations in stream flow (Bonada *et al.*, 2007b).

## 2.2 Methods

### *Study area*

BEMs were set up for the extent of Europe including Iceland (24°W–52°E longitude and 33°–72°N latitude) with a spatial resolution of 5´ (approximately 10 km$^2$). The large extent (including parts of Northern Africa and Middle East) 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 minimises the constraints of non-analogue climates on the predictive model performance for projecting climatic suitability under future climate scenarios (Fitzpatrick & Hargrove, 2009).

*Species data*

Thorough 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 & Guisan, 2006; 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; Bonada *et al.*, 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, accessed on 26.09.2011), 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, accessed on 30.09.2011), the ZOBODAT database (www.zobodat.at, accessed on 28.09.2011), and the Global Biodiversity Information Facility database (www.gbif.org, accessed on 22.09.2011) 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 species set, records were resampled to a 5´ 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 a geographic bias of these 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 digitised map (http://www.eea.europa.eu/data-and-maps/figures/ecoregions-for-rivers-and-lakes, accessed on 28.09.2011, EEA, 2011). Here, records for each species needed to be present in at least two out of three ecoregions where the species is known to occur (described in Limnofauna Europaea, Andrássy *et al.*, 1967) and the freshwaterecology.info database (http://www.freshwaterecology.info/, accessed on 28.09.2011, 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 out of 25 European ecoregions (all but Iceland and the Caspic 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 Appendix 1). The match between the distributional data (i.e., species records) and their known ranges (i.e., ecoregions) was on average 81 ± 13% (mean ± standard deviation).

### *Climate data*

To build the BEMs, we chose climatic predictors that characterize energy and water regimes (Whittaker *et al.* 2007): mean annual air temperature (°C), sum of annual precipitation (mm), and precipitation seasonality (coefficient of variation). Though these predictors correspond to a small subset of available variables they have been successfully 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., Garcia *et al.*, 2012; Hof *et al.*, 2011). Climatic predictors for the present, from here on referred to as the 'baseline' from 1950-2000, were retrieved from the WorldClim dataset in a 5´ grid resolution (www.worldclim.org, accessed on 01.08.2011, 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, accessed on 01.08.2011, 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, we used the A2a and B2a climate warming scenario of 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 ± 1.3°C, whereas the B2a scenario reflects a ‘moderate’ scenario with a projected mean annual temperature increase of 4.4 ± 1.0°C in our study area (± standard deviation). Uncertainties deriving from novel future climatic conditions in our study area were assessed by calculating non-analogue climates for each GCM.

### *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 (generalised linear models, GLM; generalised 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; Araújo *et al.*, 2009). Each algorithm used 10,000 pseudo-absences 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, single algorithm results for each species were averaged to a consensus model based on model performance (TSS, see also Araújo *et al.*, 2011). Here, a weight decay of 1.6 was used, while only models performing better that TSS > 0.4 were used in the consensus, discarding weak models from the consensus model (e.g., Araújo *et al.*, 2011; Engler *et al.*, 2011). At least two algorithms were required to yield a TSS score higher than 0.4, 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 scenarios. Inter-model variability was handled by averaging consensus projections of each GCM within a single A2a and B2a scenario. 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 minimises the difference between sensitivity and specificity (Liu *et al.*, 2005).

### *Climate change effects on species*

#### *All-species analyses*

First, we tested for percent changes in climatically suitable areas between present and future projections, incorporating the relative number of grid cells lost, kept stable and gained. Species were identified as either climate-change losers or winners, depending on a species' overall loss or gain of climatically suitable area, respectively.

Further, we tested for an overall geographic shift of species' climatically suitable areas, and analysed whether the arithmetic mean of the modelled latitude and longitude of the present climatically suitable areas 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 climatically suitable areas, 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.

#### *Analyses by trait-based sets*

We were further interested in climate-change effects of species based on specific biological and ecological trait-based sets (*sensu* Kotiaho *et al.*, 2005). We created five subsets, based on the classification in the freshwaterecology.info database (Euro-limpacs Consortium, 2011; Schmidt-Kloiber & Hering, 2012), and tested for the differences in shifts between species matching the given criterion versus 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 non-endemic species (n = 167). Eighty-eight percent of the endemics occurred in the Iberian-Macaronesion region, while the remaining 12% occurred in the Alps.

Second, we divided a total of 187 species upon 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), since 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 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 = 34, Hering *et al.*, 2009), or as downstream 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 = 22).

Species' current preference was considered as a fifth criterion for a subdivision (n = 77). Species were coded for their preference for calm (limnophilic) to fast running waters (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), 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 case of highly unbalanced sample sizes, Man-Whitney-U tests were computed additionally. Since results did not differ between the two tests, we show only results from Student's *t*-tests to keep analyses fixed. Climate change effects for subsets 4-5 were analysed using nonparametric Kruskal-Wallis tests because of unbalanced sample sizes. Future climatically suitable areas 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.

## 2.3 Results

*Model performance*

Model performance was high, with average TSS scores of 0.96 ± 0.03 (mean ± standard deviation, Appendix 1), and consensus projections were created for all of our 191 species. Analyses of climate projections revealed that non-analogue 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 (Appendix 2).

*All-species analyses*

On average, the 191 modelled species were projected to lose climatically suitable area by 2.9 ± 66.0% and 1.2 ± 54.7% under the A2a and B2a scenario, respectively. From these, a total of 112 (59%) and 109 (57%) species were projected to lose climatically suitable area under the A2a and B2a scenarios, respectively. Climate-change loser species were projected to lose on average 44.0 ± 29.8% and 38.1 ± 27.0%, whereas winner species were projected to gain on average 55.4 ± 59.1% and 47.7 ± 42.0% of climatically suitable area under the two scenarios, respectively. Two species were projected to lose their entire climatically suitable area under the A2a (*Oxycera morrisii* and *Orthocladius holsatus*, Diptera) and the B2a scenario (only *O. holsatus*). Species' climatically suitable areas were projected to shift significantly northwards (6.6 ± 2.5° and 4.7 ± 2.2° under the A2a and B2a scenarios, respectively; paired *t*-tests: A2a: $t_{188} = -36.58$, $P < 0.001$; B2a: $t_{189} = -29.80$, $P < 0.001$, Fig. 2.1a,b). Similarly, climatically suitable areas were projected to shift significantly eastwards by 5.4 ± 8.8° and 3.9 ± 6.5° under the two scenarios, respectively (Paired *t*-test: A2a: $t_{188} = -8.40$, $p < 0.001$; B2a: $t_{189} = -8.27$, $P < 0.001$, Fig 2.1a,b).

Percent changes in climatically suitable areas 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. 2.2a,b).

Species' mean temperature of occurrence correlated negatively with projected latitudinal shifts of climatically suitable areas 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: $r= -0.01$, $P = 0.831$).

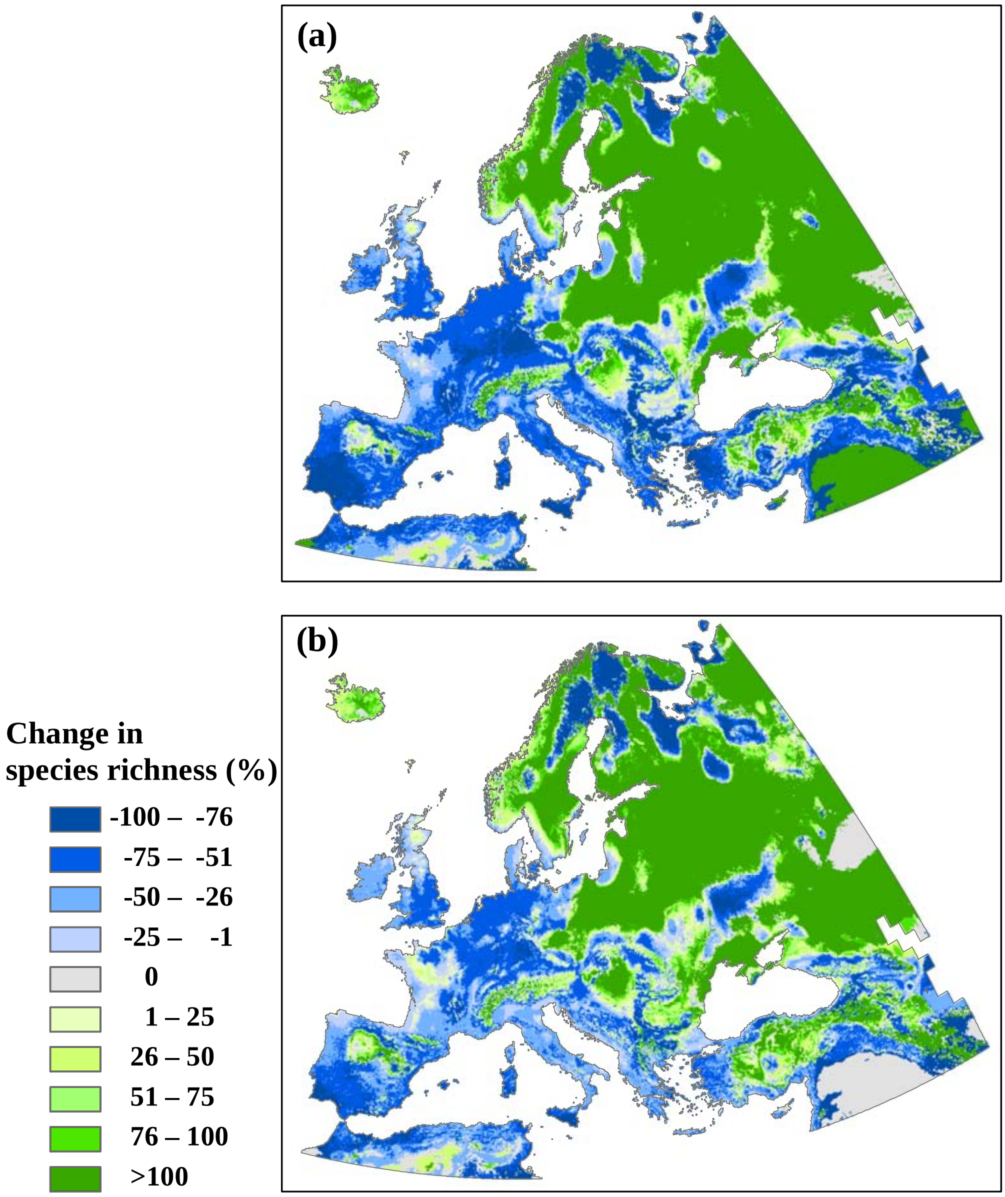

**Figure 2.1** Relative changes in the number of species for each grid cell for which climatically suitable areas were projected under the A2a (a) and the B2a (b) climate warming scenarios compared to the baseline.

*Analyses by trait-based sets*

In total, 83% and 79% of the endemic species and 55% and 56% of the non-endemic species were identified as climate-change losers under the A2a and B2a scenario, respectively. On average, endemic species lost significantly more climatically suitable areas than non-endemic species (Table 2.1). Similarly, climatically suitable areas of non-endemic species were projected to shift significantly stronger into a north-easterly direction, while only a minor northward but a westward shift was observed for endemic species' climatically suitable areas under the A2a and B2a scenario, respectively (Table 2.1).

Fifty-five percent and 58% of the rare species were projected to lose climatically suitable areas under the two scenarios, while 59% and 57% of the common species were projected to lose climatically suitable areas under the two scenarios, respectively. Climatically suitable areas 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 climatically suitable areas were found (Table 2.1).

The ratio of hololimnic climate-change loser species was 53% and 60%, while 59% and 57% of the merolimnic species were projected to lose climatically suitable areas under the two scenarios. Climatically suitable areas of hololimnic species were projected to shift on average 5.3° more eastwards than merolimnic species under the A2a scenario (Table 2.1). No significant shifts in longitude were projected under the B2a scenario, nor were shifts in latitude or percent changes in climatically suitable areas significantly different between holo- and merolimnic species.

Species mean temperature of occurrence was significantly lower for headwater than for river species, but not significantly different from the mean temperature of occurrence for generalist species (Kruskal-Wallis test: $H_2 = 6.48$, $P = 0.039$). On average, 75%, 52% and 53% of the headwater, generalist and river species lost climatically suitable areas under the A2a scenario, respectively, while 72%, 71%, and 41% of the respective groups were predicted to lose climatically suitable areas under the B2a scenario. Considering the average distance, climatically suitable areas of generalist species were projected to shift significantly more northwards than those of headwater and river species under both climate warming scenarios (Table 2.2, Kruskal-Wallis test: A2a: $H_2 = 11.49$, $P = 0.003$, B2a: Kruskal-Wallis test: $H_2 = 13.11$, $P = 0.014$). Eastwards shifts of climatically suitable areas were on average almost 8 times higher for generalist species than for headwater species under the two scenarios, respectively (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 climatically suitable areas could be observed (Kruskal-Wallis test: A2a: $H_2 = 3.47$, $p = 0.177$, B2a: $H_2 = 2.89$, $P = 0.235$).

BEMs showed a non-significant tendency in decreasing losses of climatically suitable areas from calm to fast running waters (Table 2.2). Further, no significant differences in latitudinal or longitudinal shifts of projected climatically suitable areas could be detected among species divided by their current preference (Table 2.2, Kruskal-Wallis tests: $P > 0.05$).

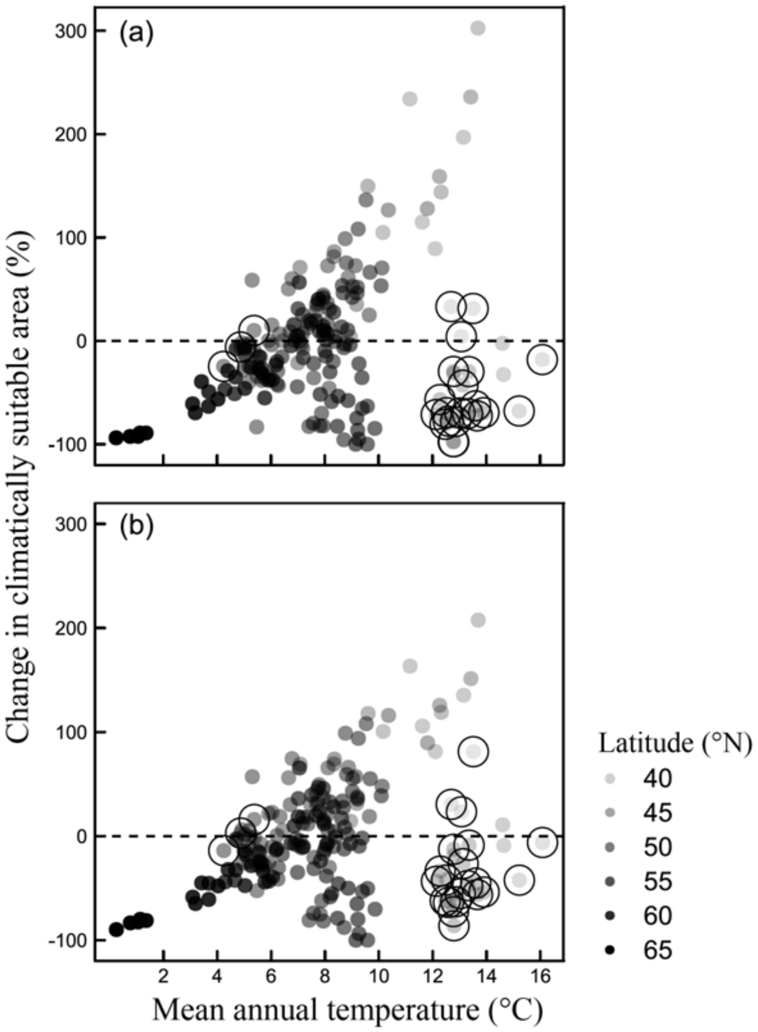

**Figure 2.2** Mean annual air temperature of species occurrence plotted against the changes of climatically suitable areas under the A2a (a) and B2a (b) climate warming scenarios of the year 2080. Increasing intensity of greyscale represents increasing mean latitude of species presence records. Circles mark endemic species.

**Table 2.1** 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/non-endemic, rare/common and holo-/merolimnic species (mean ± 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 *t*-statistics | Merolimnic species | Hololimnic species | Mero- vs. hololimnic *t*-statistics | Rare species | Common species | Rare vs. common *t*-statistics |
|---|---|---|---|---|---|---|---|---|---|---|
| A2a | CSA (%) | -46.4 ± 38.6 | 3.4 ± 66.9 | **$t_{189} = 3.56, P < 0.001$** | -3.3 ± 64.1 | 1.7 ± 88.1 | $t_{189} = -0.27, P = 0.783$ | 9.8 ± 57.7 | -4.2 ± 67.4 | $t_{185} = -0.99, P = 0.321$ |
| A2a | Latitude | 2.7 ± 1.9°N | 7.1 ± 2.0°N | **$t_{187} = 10.12, P < 0.001$** | 6.5 ± 2.5°N | 7.23 ± 1.5°N | $t_{187} = -1.06, P = 0.287$ | 7.6 ± 1.6°N | 6.4 ± 2.5°N | **$t_{183} = -2.41, P = 0.017$** |
| A2a | Longitude | 6.5 ± 7.5° W | 7.1° ± 7.5°E | **$t_{188} = 8.24, P < 0.001$** | 4.9 ± 8.9°E | 10.2 ± 5.8°E | **$t_{187} = 2.25, P = 0.026$** | 10.1 ± 6.0°E | 4.6 ± 8.7°E | **$t_{183} = -3.08, P = 0.003$** |
| B2a | CSA (%) | -28.4 ± 38.9 | 2.7 ± 55.6 | **$t_{189} = 2.65, P = 0.009$** | -1.2 ± 53.7 | -0.8 ± 67.2 | $t_{189} = -0.02, P = 0.979$ | 7.6 ± 50.23 | -1.9 ± 55.4 | $t_{185} = -0.82, P = 0.411$ |
| B2a | Latitude | 1.9 ± 1.9°N | 5.1 ± 2.0°N | **$t_{188} = 7.93, P < 0.001$** | 4.7 ± 2.2°N | 4.7 ± 1.5°N | $t_{188} = 0.04, P = 0.966$ | 5.75 ± 1.15°N | 4.5 ± 2.3°N | **$t_{184} = -2.70, P = 0.008$** |
| B2a | Longitude | 4.0 ± 6.9° W | 5.1 ± 5.6° E | **$t_{188} = 7.17, P < 0.001$** | 3.7 ± 6.6°E | 6.2 ± 4.7°E | $t_{188} = -1.42, P = 0.156$ | 6.86 ± 4.72°E | 3.5 ± 6.6°E | **$t_{184} = -3.08, P = 0.002$** |

**Table 2.2** 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 ± standard deviations, paired *t*-tests). Losses and gains of CSA as negative and positive values, respectively. The asterisk (*) marks significant differences among species groups (Kruskal-Wallis test, see main text for results).

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

## 2.4 Discussion

*Climate-change effects – general pattern*

Climatically suitable areas were projected to remain in the future for the vast majority of the modelled stream macroinvertebrates. The BEMs, however, projected a decrease of climatically suitable areas for 57-59% of the species depending on the scenario. Trait-based analyses revealed that not only cold-adapted species inhabiting the European high latitudes, but thermophilic endemic species of the Mediterranean would be nearly equally vulnerable to climate change (Figs. 2.1a,b and 2.2a,b). Thus, there would be no linear relationship between a temperature or latitude gradient of species preferred climates and predicted losses of climatically suitable areas, making the two extremes highly vulnerable to ongoing climate change.

This pattern therefore resulted only in a weak tendency of species' sensitivity to climate change along the gradient: species adapted to cooler temperatures and occurring at higher latitudes (Fig. 2.2a,b) were projected to lose climatically suitable areas which were projected to shift more strongly northward until 2080, compared to thermophilic species for which climatically suitable areas were projected to increase and shift northwards less strongly. These results suggest that a reorganisation of species assemblages in terms of a structural and functional composition due to climate change is not only apparent along the river continuum on smaller scales (Daufresne *et al.*, 2004; Bonada *et al.*, 2007a; Burgmer *et al.*, 2007; Chessman, 2009; Domisch *et al.*, 2011). Potential large scale shifts of species' climatically suitable areas resulting from warming climates might lead to an overall northward shift of stream macroinvertebrates, as it has been observed for freshwater organisms in general (Hickling *et al.*, 2005), as well as terrestrial organisms (Hickling *et al.*, 2006; Chen *et al.*, 2011). Thus, thermophilic and especially generalist species, which 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 climatically suitable areas (Fig. 2.2a,b, and see Sauer *et al.*, 2011; Jacobsen *et al.*, 2012), and ultimately from a non-trivial loss of regional genetic diversity (Bálint *et al.*, 2011). The heterogeneous effects concerning the linearity of climate-change effects along a temperature gradient were further enhanced by a number of temperate lowland species and species of the low mountain ranges, for which climatically suitable conditions are not projected under future climate scenarios (Appendix 3). On the one hand, the Alps may remain as a thermal refuge for species inhabiting currently the Central European low mountain ranges (Fig. 2.1a,b and 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 in a gain of suitable habitats (Mulholland *et al.*, 1997; Daufresne *et al.*, 2004; Domisch *et al.*, 2011), however species-specific ecological characteristics may play an important role when predicting potential climate-change effects for these species (McPherson & Jetz, 2007).

Complete losses of climatically suitable areas, as reported in our study for two species, need to be approached carefully. As species records covered on average 81% of species' known ranges, thus leaving space for a small amount of incomplete distributional data, complete losses of climatically suitable areas are therefore likely to be overestimated (Barbet-Massin *et al.*, 2010; Sánchez-Fernández *et al.*, 2011), nevertheless underlining their high vulnerability to warming climates. Moreover, recent studies suggest that distributions of stream biota of running waters are not in climatic equilibrium and are still likely to be influenced by post-glacial recolonization (Dehling *et al.* 2010; Hof *et al.*, 2012). Thus species, except Mediterranean / endemic ones, may not have reached all potential habitats holding climatic suitability, influencing model calibration and thus future projections.

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

Models confirmed our initial hypothesis regarding the higher losses of climatically suitable areas for endemic species than for non-endemics, while only differences in the magnitude of latitudinal or longitudinal shifts of climatically suitable areas were projected for other trait-based sets. A majority of 85% of the endemic species occurring in the Iberian-Macaronesian region were identified as climate-change losers under both climate warming scenarios (Fig. 2.2a,b). The high endemicity in Southern Europe is a result of the speciation during the Pleistocene (see e.g., Ribera & Vogler, 2004, and references therein). Although dispersal was not limited in the BEMs, future climatically suitable areas were found to remain only by a fraction within this region, indicating the high vulnerability of these species to climate change (Bonada *et al.*, 2009; Hering *et al.*, 2009; de Figueroa *et al.*, 2010). Though stream macroinvertebrates of the Mediterranean provide traits with a high resistance against droughts as well as a high resilience after droughts (Bonada *et al.*, 2007a), the question remains whether the magnitude of warming temperatures and the declining amount of (summer) precipitation exceed beyond the adaptation ability of these species.

Stronger northward shifts of both rare and generalist species’ climatically suitable areas than for the respective counterparts, seem to be contradicting at the first glance. For rare species, this implies that they would need to track temperature changes faster than common species. Though species are capable of rapid range changes (Chen *et al.*, 2011) as well as plasticity in terms of adaptation to some degree (Hampe & Petit, 2005), potential range changes depend strongly on species’ dispersal abilities and life history characteristics. Limited habitat availability under warming climates (Heino *et al.*, 2009) will impose an additional major threat for stream macroinvertebrates. Predicted changes in discharge patterns and droughts, combined with land use changes and large scale irrigation measures are predicted to contribute to increased habitat fragmentation, limiting habitat availability beyond losses of climatically suitable areas in the future.

Amongst headwater, generalist and downstream river species, generalists are best buffered against climate change impacts as shown by their ability to colonise 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 climatically suitable areas were not projected northwards as was the case for generalists, meaning that they will lose climatically suitable areas within their ranges until 2080 because of a the predicted summit trap, i.e., a decrease in available area with increasing altitudes. However, as air temperatures may be a poor surrogate for depicting stream temperatures in headwater reaches located in lower altitudes (*sensu* Caissie, 2006), potential changes of climatically suitable areas were presumably underestimated, probably resulting in even stronger losses of climatically suitable areas (Bálint *et al.*, 2011; Sauer *et al.*, 2011). In turn, no strong geographic shifts were projected for downstream river species, as they are predicted to gain climatically suitable areas due to climate warming (i.e., range filling, Table 2.2, Domisch *et al.*, 2011), potentially influencing the downstream community structure and composition (Daufresne *et al.*, 2004).

The coarse resolution seemed to blur consistent patterns for specialists based on current preference and life cycle. Streams and rivers across Europe are expected to respond strongly to climate change due to increased temperatures and changes in annual as well as seasonal precipitation patterns (Milly *et al.*, 2005), resulting in discharge changes and ultimately in current velocity. BEMs revealed a non-significant tendency of a high ratio of climate-change loser species among species inhabiting standing running waters (i.e. limnophilic species) and a high ratio of winner species inhabiting fast running waters (rheobionts). However, assuming that species inhabiting calm running waters have high dispersal abilities, our models may have overestimated the loss of climatically suitable areas for these species, since they have proven to be good dispersers (*sensu* Hof *et al.*, 2012, and references therein). Moreover, during the process of aggregating species records for BEMs, stream and river sites from which species' records were sampled and which fall within one grid cell, were aggregated. Consequently, site-specific hydrological conditions were aggregated as well, and model calibration did not take all available information into account. Similarly, models might have not been able to separate the required habitat characteristics of holo- and merolimnic species. Although hololimnic species were predicted to track their climatically suitable areas eastwards, this pattern might be additionally forced by the coarse resolution as well as the fact that these species' distributions are likely not yet in equilibrium (Dehling *et al.*, 2010).

### *Conclusions*

In contrast to expert knowledge and the categorisation of single taxonomic orders according to their potential vulnerability (Hering *et al.*, 2009; de Figueroa *et al.*, 2010), BEMs allowed us to quantify the magnitude of potential losses and gains, as well as geographic shifts of stream macroinvertebrates' climatically suitable areas under climate change on a continental scale.

BEMs base on the assumption of niche conservatism, and species' potential abilities regarding adaptation and plasticity in the course of warming climates are not taken into account (Pearman *et al.*, 2008; Elith & Leathwick, 2009). Nevertheless, a lack of information concerning the ecological preferences for the majority of stream macroinvertebrates still hinders reliable estimations of possible consequences of climate change (Heino *et al.*, 2009). On the species level, changes in life history characteristics are expected for a number of species, which consequently have a profound impact on species assemblages (Mulholland *et al.*, 1997). Moreover, an additional driver for alterations of community composition is expected by non-native species adapted to higher temperatures (Daufresne *et al.*, 2007). While species' dispersal abilities and traits, combined with habitat availability play a crucial role in coping with warming temperatures, climate change has, and is expected to have profound impacts on stream macroinvertebrates distributions.

# Chapter 3

## Choice of study area and predictors affect species distribution models of stream macroinvertebrates

### Abstract

Species distribution models (SDMs) are valuable and increasingly used tools for analyses, such as conservation- or climate-change-related vulnerability analyses. However, SDMs must be optimised for study area, predictors, and presence-absence data to avoid false positive predictions. In stream ecosystems, for which such models were only recently adopted, this optimisation is particularly challenging, as false positive predictions may be projected in terrestrial areas and not in the stream network, with unknown effects on habitat suitability simulations. To test for effects derived from the use of different study areas and predictors, we used consensus projections of a fixed set of 224 stream macroinvertebrate species, using five algorithms implemented in BIOMOD/R (GLM, GAM, BRT, ANN, CTA). Four modelling designs were applied: (1) a continuous study area without any discrimination between terrestrial and aquatic realms, (2) results from this design masked *a posteriori* with a stream network, (3) the stream network only considered as the study area during the model-building stage, and (4) same as (3) but with a corrected set of predictors. The true skill statistic (TSS) and accuracy of the consensus projections were not influenced by the different designs, as they were consistently high (TSS: 0.80 to 1.00, accuracy: 0.70 to 0.96). The models built on a stream network yielded a strong reduction in false positive predictions compared with those built on a continuous area, whereas the differences derived from non-corrected vs. corrected predictors were small. The models created in the stream network with corrected predictors were able to diminish the false positive predictions by an average of 56%, yielding the highest rate among the four designs. SDMs of stream macroinvertebrates should thus be built on a stream network rather than on a continuous area, and the predictors should be chosen carefully. We discuss several methods for developing predictor accuracy to improve forecasts of potential climate-change effects on species' ranges.

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## 3.1 Introduction

Estimations of the potential effects of climate change on species' ranges are important for understanding species' habitat suitability patterns under changing climatic conditions and for mitigation and possible conservation efforts (Elith & Leathwick, 2009; Araújo *et al.*, 2011). Species distribution models (SDMs) are promising and increasingly used tools for this task. One great challenge when using SDMs is their optimisation regarding study area, predictors, and presence-absence data to avoid false positive predictions. In stream ecosystems, for which such models were only recently adopted, this optimisation is particularly challenging, as false positive predictions may be projected in terrestrial areas and not in the stream network. The effects of building a model on a continuous landscape as a study area, without taking into consideration the stream network in which species were recorded (Cordellier & Pfenninger, 2008; Bálint *et al.*, 2011; Sauer *et al.*, 2011), are unknown, which constitutes a major disadvantage for the further development of models, e.g., in terms of sensitivity analyses. Landscape-based models clearly provide a useful first approximation, e.g., in terms of climate-change-related vulnerability analyses, such as the means by which warming and changes in precipitation patterns might affect species' distributions (*sensu* Pearson & Dawson, 2003). However, the distribution and abundance of freshwater biodiversity also depend on other factors too, considered in catchment-related variables (Poff, 1997). In the case of certain stream organisms, such as benthic macroinvertebrates or fish, stream flow conditions are known to influence the composition of the community (Clausen & Biggs, 1997). Such variables are inevitably ignored in landscape-based models.

The choice of whether the continuous landscape or stream network is used as the study area for predicting the distributions of stream macroinvertebrates has several relevant aspects, but the issues of species' presence-absence data and the choice of predictors used for delineating species ranges are considered to be the most important. In general, SDMs require both species' presence and species' absence data, which are combined with environmental predictors that yield species' habitat suitability after being extrapolated in space or time. SDMs can be roughly divided into two groups depending on the origin of the species records: presence-absence and presence-only SDMs (Elith & Leathwick, 2009, and references therein). SDMs of the former type use species' recorded absences and are thus based on species' true environmental envelopes, whereas those of the latter require background data or pseudo-absences for generating probabilities of species' habitat suitability. Because recorded absences of species are scarce, pseudo-absences are widely used (Lobo & Tognelli, 2011; Stokland *et al.*, 2011). Obviously, the properties of pseudo-absences are highly dependent on the study area and can be allocated either distant (i.e., on the continuous landscape) or near (within the stream network) to species' environmental envelopes, likely affecting model performance (Lobo *et al.*, 2010; Barbet-Massin *et al.*, 2012). In general, Lobo *et al.* (2010) define three types of species absences, which may be applied to stream ecosystems: contingent absences (i.e., the habitat is potentially suitable but the species is absent due to, e.g., peaks in stream discharge changes or species' lifecycles); environmental absences (e.g., lack of favourable long-term temperature or physico-chemical conditions, Poff, 1997), and methodological absences (e.g., sampling season and methodology, Haase *et al.*, 2004; Haase *et al.*, 2006). The examples of contingent and methodological absences show that true absence data of stream organisms are particularly difficult to record. Though the use of pseudo-absences is partially seen as a violation of true ecological assumptions and species' niche occupancy, resulting ultimately in a reduction in the model accuracy, this practise presents a suitable work-around solution for calibrating and fitting SDMs in stream ecosystems (*sensu* Lobo *et al.*, 2010). In the case of stream ecosystem modelling, the choice of study area is likely to affect the environmental absences, which can be allocated either on the entire landscape or exclusively within the stream network. Thus, the model accuracy and the quantity of species' false positive predictions are likely being affected because these absences differ in their distances to species' recorded presence records.

Second, the choice of the study area inevitably influences the choice of predictors used in SDMs through the medium itself but also through scale, resolution, and availability of the data. On a continuous landscape, coarse-scale predictors, such as air temperature and precipitation, take priority over predictors describing stream-specific conditions (e.g., stream type, flow accumulation), which play a larger role at fine scales (hierarchical modelling framework *sensu* Pearson & Dawson, 2003). In contrast, when moving into finer scales, SDMs based on a stream network may include more specific predictors that allow simple hydrological predictors, such as stream type, flow accumulation or stream order, to be included, which are of relevance for characterising the habitat suitability of stream assemblages and communities (Poff 1997). However, working at such scales also means dealing with extra uncertainties. For instance, small-scale variations of the stream topography are important to take into account, and predictors may need to be corrected because of spatial differences between the underlying digital elevation model (DEM) and the digitised stream network layer. The correction of relevant predictors based on the DEM can therefore have a significant effect on model performance and thus on the projections of species' habitat suitability (Adriaenssens *et al.*, 2004).

In this study, we analyse the effects of the extent of the modelled area and the choice of predictors on species' predictions using stream macroinvertebrates, a very important organism group in streams used as indicator species for assessing stream condition. Based on a fixed set of species, we vary the choice of study area from the continuous landscape to a stream network during and after the model-building stage using a fixed set of predictors. Moreover, we vary the choice of predictors from a non-corrected to a corrected set within a fixed study area. We hypothesise that (1) the usage of a continuous landscape as the study area yields a high degree of species' false positive predictions because the terrestrial and aquatic realms are confounded at the model-building stage, (2) using a stream network as the study area at the model-building stage will increase the model accuracy and strongly reduce the number of false positive predictions because pseudo-absences will not include those ranging beyond species environmental absences, i.e., the terrestrial areas, and (3) a corrected set of predictors during the model-building stage will further enhance the model accuracy and reduce the number of false positive predictions, as it may delineate species' environmental envelopes, and thus the environmental absences, more accurately than a non-corrected set.

## 3.2 Methods

### *Modelling designs*

Four different modelling designs were applied (see Fig. 3.1a-d). In the most basic approach, we modelled species' distributions on a continuous landscape area (hereafter referred to as a 'landscape' design, Fig. 3.1b), without any discrimination between streams and the terrestrial area.

In the second design, a stream network mask was applied to the 'landscape' projections, as the species are supposed to inhabit the streams and rivers (hereafter 'landscape masked', Fig. 3.1c). This design is thus identical to the previous 'landscape' design except that it is restricted to the grid cells of the river network.

In the third design, the stream network area was masked prior to fitting the models; thus, only the stream network was considered at the model-building stage (Fig. 3.1d). For this design, we used an identical set of predictors as in the 'landscape' and 'landscape masked' designs (hereafter referred to as the 'stream network' design).

The last design also modelled species' distributions on the stream network, but used a partially different set of predictors to test for effects derived from using corrected predictors (hereafter referred to as the 'stream network corrected' design, Fig. 3.1d).

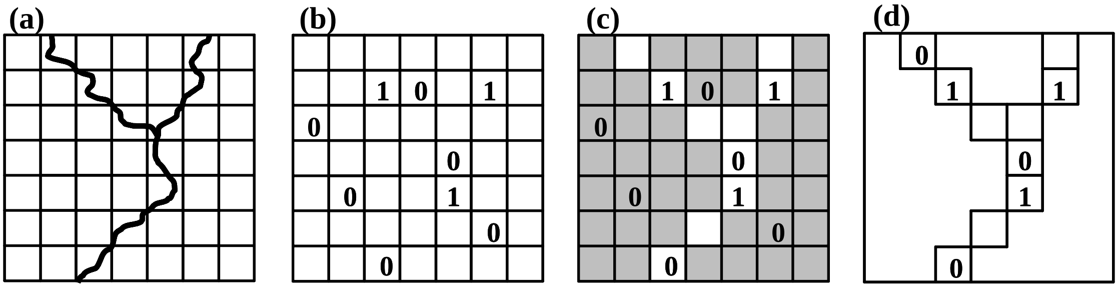

**Figure 3.1** (a) Scheme of a stream section (black lines); the grid cells represent the division of the area for modelling. (b-d) Four modelling designs based on the stream section: (b) 'landscape', (c) 'landscape masked', (d) 'stream network', and 'stream network corrected' design, the latter of which used a different set of predictors. The numbers represent presence records (1) and pseudo-absences (0), respectively. The grey cells in the 'landscape masked' design represent the terrestrial realm and was masked after the model-building stage.

### *Area for model calibration*

Our models were calibrated either on the continuous area of Germany (5°86´–15°04´E, 47°27´–55°06´N, Fig. 3.2a,b) or on the stream network within this area (LAWA, 2003). The area ranged from the foothills of the Alps to the coast of the North and Baltic Seas. The running waters of the stream network included all river sizes from small alpine streams (catchment size 10–100 km$^2$) to large lowland rivers (catchment size > 10,000 km$^2$). The resolution for both areas was 0.01 degree (ca. 1 km$^2$), and the spatial extents were 321,735 and 136,207 grid cells for the continuous area and stream network, respectively.

All of the models were fitted using these extents to overcome the limitation of using truncated environmental gradients for calibrating models within species' known ranges (Thuiller *et al.*, 2004). For the final assessment of model results, we considered an area limited to four federal states (Westphalia, Hesse, Thuringia, Baden-Wuerttemberg), as this area provides the highest density of species records, i.e., a high accuracy of species presence data (Fig. 3.2b, shaded area, hereafter referred to as the 'study area').

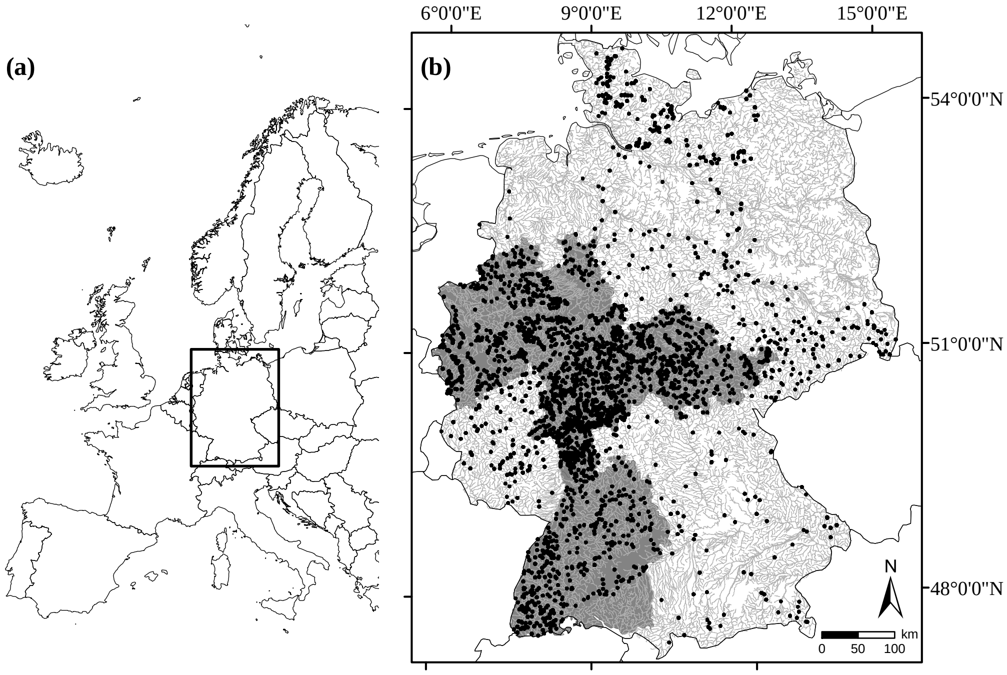

**Figure 3.2** (a) The location of the study area in Central Europe. (b) The stream network of Germany (grey lines) and all presence records (points) used for calibrating the models. The shaded area represents the study area used for the final assessment.

### *Species data*

Species records were obtained from three national databases (Umweltbundesamt; Hessisches Landesamt für Umwelt und Geologie; and Landesamt für Umwelt, Messungen und Naturschutz Baden-Württemberg, unpublished data). These databases provide stream macroinvertebrate data from surveys conducted in spring from 2002 to 2008 and hold a total of 55,513 species presence records from 2,849 sites within the entire area used for calibrating the models. As a precondition for selection in our study, species needed to have at least 10 presence records listed within the study area (Stockwell & Peterson, 2002). Individual models were fitted for the 269 species that fulfilled this criterion.

### *Environmental predictors*

For each modelling design, we used 10 environmental predictors consisting of climatic, land cover and stream-specific predictors (Table 3.1). Only the predictors relevant for describing the distributions of stream macroinvertebrates were selected, and pairwise correlations were used to reduce the initial candidate set of 35 predictors ($-0.7 < r < 0.7$, Green, 1979).

The present climate data were generated by averaging interpolated mean monthly climate data from a 30-year time period (1980-2010) at a resolution of 0.01 degree, obtained from the German Weather Service (Müller-Westermeier, 1995). The monthly data included minimum and maximum temperatures (°C), sum of precipitation (mm) and water budget (mm, incorporating precipitation, evapotranspiration and runoff), which were in turn averaged to obtain annual means. From these variables, four predictors were used in the models: mean annual temperature (°C), annual temperature range (°C), mean annual water budget (mm $a^{-1}$) and water budget seasonality (coefficient of variation).

Land cover data were derived from the CORINE land cover 2006 dataset (http://www.eea.europa.eu/, accessed on 18.10.2011; EEA, 2011). The 44 predefined land cover categories were merged to five major categories (urban settlement, agricultural area, vegetation, wetlands and lakes) and were subsequently resampled from an initial resolution of 250 m to 0.01 degree to match the cell size of our SDMs.

These five climatic and land use predictors were used in all four modelling designs “as is”, i.e., without further changes.

We included further stream-specific predictors, such as stream slope, flow direction, and flow accumulation. Stream slope is used as an important proxy for flow velocity and oxygen content. Flow direction is defined as the direction in which each cell flows to its steepest down-slope neighbour. Flow accumulation is based on the flow direction and defines the number of up-slope cells that flow into a cell and can be seen as a proxy for drainage area (USGS). Stream slope, flow direction and flow accumulation were obtained from the Hydro1k dataset (http://eros.usgs.gov/, accessed on 07.04.2010, USGS). Furthermore, we included the compound topographic index (CTI, Beven & Kirkby, 1979) and European hydro-ecoregions (Wasson *et al.*, 2007). The CTI, which is often referred to as the wetness index, is a function of the upstream contributing area and the slope of the landscape (USGS) and can be used to quantify the runoff potential of different landscape elements. For the ‘landscape’ and ‘landscape masked’ designs, the models were calibrated on the entire continuous area.

In the ‘stream network’ design, the same predictors were used as for the ‘landscape’ and ‘landscape masked’ models, but the predictors were clipped to the stream network extent before the models were fitted. Thus, only the stream network served as the study area at the model-building stage.

For the ‘stream network corrected’ design, the stream-specific predictors were corrected by reconditioning the underlying digital elevation model (DEM) after ‘burning’ the stream network into it (LAWA, 2003; USGS). This approach has the advantage of attaching the information concerning the sources and mouths of streams to the DEM. We then used ArcHydro tools (Maidment, 2005) to fill sinks (i.e., artificial valleys in the DEM derived from inaccurate remote sensing data, disconnecting continuous streams) and recalculated the stream slope, flow direction and flow accumulation more accurately. Stream order (Strahler, 1957) was included in the models as a proxy for stream size and distance to source. Furthermore, stream type was included as a proxy for catchment area, ecoregion and geology (for a detailed description of German stream types, see http://www.fliessgewaesser-bewertung.de/en/, Pottgiesser & Sommerhäuser, 2004). The stream order and stream type were derived from LAWA (2003).

**Table 3.1** The predictors used for calibrating SDMs for the four modelling designs.

| **Predictors** | **Landscape** | **Landscape masked** | **Stream network** | **Stream network corrected** |
|---|---|---|---|---|
| Mean annual temperature | x | x | x | x |
| Annual temperature range | x | x | x | x |
| Mean annual water budget | x | x | x | x |
| Water budget seasonality | x | x | x | x |
| Land cover | x | x | x | x |
| Stream slope | x | x | x | |
| Stream slope corrected | | | | x |
| Flow direction | x | x | x | |
| Flow direction corrected | | | | x |
| Flow accumulation | x | x | x | |
| Flow accumulation corrected | | | | x |
| Compound Topographic Index | x | x | x | |
| Stream order | | | | x |
| Hydro-Ecoregions | x | x | x | |
| Stream type | | | | x |

### *Species distribution modelling*

SDMs were generated using five algorithms as implemented in the R package BIOMOD (generalised linear models, GLM; generalised additive models, GAM; boosted regression trees, BRT; artificial neural networks, ANN; and classification tree analysis, CTA; Thuiller *et al.*, 2009; R Development Core Team, 2011). Single models were calibrated by splitting species occurrence data randomly into a training set (70%) and a testing set (30%, Araújo *et al.*, 2005). Absence records were not available, so we used pseudo-absences, which were allocated throughout the entire landscape or along the stream network, depending on the modelling design. Each design used 10,000 randomly drawn pseudo-absences, referring to Stokland *et al.*, (2011) and Barbet-Massin *et al.*, (2012), who showed that excluding pseudo-absence data involves arbitrary assumptions about unsuitable environments for the species being modelled, and Lobo & Tognelli (2011), who recommend the incorporation of many pseudo-absences to obtain more accurate predictive models.

Each algorithm used a tenfold cross validation that yielded an average model for each species and algorithm, and the prevalence was kept constant at 0.5 for all species (weighted prevalence, Barbet-Massin *et al.*, 2012). The average models, comprised of the single models, were calibrated on 100% of the species data, as the exclusion of presence records significantly increases the amount of uncertainty (Araújo *et al.*, 2009). These average models were then projected to the whole study area (i.e., the entire territory or stream network, Fig. 3.2b). Model evaluation was conducted by means of the true skill statistic (TSS), which has been shown to be superior in measuring the performance of SDMs when the predictions are expressed in presence-absence maps that enable effective model comparisons (Allouche *et al.*, 2006). TSS scores incorporate sensitivity (true positive predictions) and specificity (true negative predictions) and range from 0 to 1, of which 0 describes a model no better than random, and 1 describes a perfect agreement with the observed data. The uncertainty derived from different algorithms was reduced using a consensus projection for each species with weighted averages (WA) based on the TSS scores of single model outputs for each species and algorithm (Marmion *et al.*, 2009). The relative importance of each algorithm for the final consensus models was obtained by multiplying the averaged TSS score with a weight decay of 1.6 (default settings). To overcome the limitation of mixing weak models with robust ones, we set a threshold of TSS > 0.4 for models to be included in the consensus, adopting methods from (Engler *et al.*, 2011). At least two models were required to receive a TSS score higher than 0.4; otherwise, no consensus projection was created, and the species was removed from further analyses. Occurrence probability maps of present projections were finally transformed into binary presence-absence maps by applying a cut-off value that minimises the difference between sensitivity and specificity, based on the TSS scores (Jimenez-Valverde & Lobo, 2007). This modelling procedure was performed for each species and design, resulting in a total of 45,192 models.

*Comparison of modelling designs*

To keep the study design balanced, results were only analysed for those species for which consensus projections were created for all designs. The relative predictor contributions show how each predictor contributes to each species' distributions. The results of the algorithms were averaged using the same weighting factor that was used for building the consensus projections and were finally averaged over all of the species for each modelling design. The TSS scores of species' consensus projections were evaluated among all modelling designs. In this comparison, the relative predictor contributions and the TSS scores rely on the entire area for calibrating the SDMs.

For all further analyses, the consensus projections were masked to the extent of the study area (94,661 and 41,590 grid cells available for landscape and stream network, respectively).

Because we were interested in the model performance in our study area, we assessed the model validity, i.e., the accuracy and significance of the consensus projections within this area. Adopting methods from Anderson *et al.* (2003), the accuracy was calculated by means of exact one-tailed binomial probabilities of presence records falling into grid cells classified as suitable. The model accuracy ranged from 0, for a consensus projection no better than random, to 1, for the maximum success rate. For a more detailed description of this method, see Anderson *et al.* (2003). To measure the significance of the models, we tested whether the probability of making $n$ successful predictions is higher than by chance alone (where $n$ is the number of presence records).

To evaluate the size of the area predicted to be suitable habitat for each species and modelling design, we compared the sum of the grid cells classified as suitable among the different designs derived from binary consensus projections relative to the available study area (relative occurrence area ROA, Lobo *et al.*, 2008). Furthermore, we calculated pairwise differences in the number of grid cells classified as suitable between the different modelling designs by means of paired *t*-tests.

To explore the effect of how and where the suitable habitat area differed among the modelling designs, the proportion of overlapping grid cells classified as suitable was compared. These proportions were evaluated by overlaying single species' projections from the different designs and identifying the number of overlapping grid cells classified as suitable.

The results of the TSS scores, model accuracy and ROA were analysed using a one-way ANOVA to evaluate the differences between the different designs. Percent data were arcsin-transformed prior to the analyses, and where appropriate, data were log-transformed to meet the assumptions of normality and homogeneity of variances. Additionally, a Kruskal-Wallis-ANOVA was computed for data with heterogeneous variances after transformation. Post-hoc tests (Tukey HSD) were performed to detect significant differences between model results.

## 3.3 Results

For the ‘landscape’, ‘landscape masked’, ‘stream network’ and ‘stream network corrected’ designs, consensus projections were created for 251 (93%), 251 (93%), 232 (86%) and 237 (88%) species out of the initial set of 269 species, respectively. From these, 224 species from 17 macroinvertebrate orders were successfully modelled in all of the designs and were thus considered for further analyses (Appendix 4). For all of the modelling designs, the predictors that contributed most to the consensus projections were hydro-ecoregions and stream type, as well as the mean annual temperature and annual temperature range (Fig. 3.3). The consensus TSS scores for all of the designs and species were consistently high, ranging from 0.80 to 1.00, and did not differ significantly between modelling designs (Kruskal-Wallis ANOVA: $H_3 = 7.48$, $P = 0.058$).

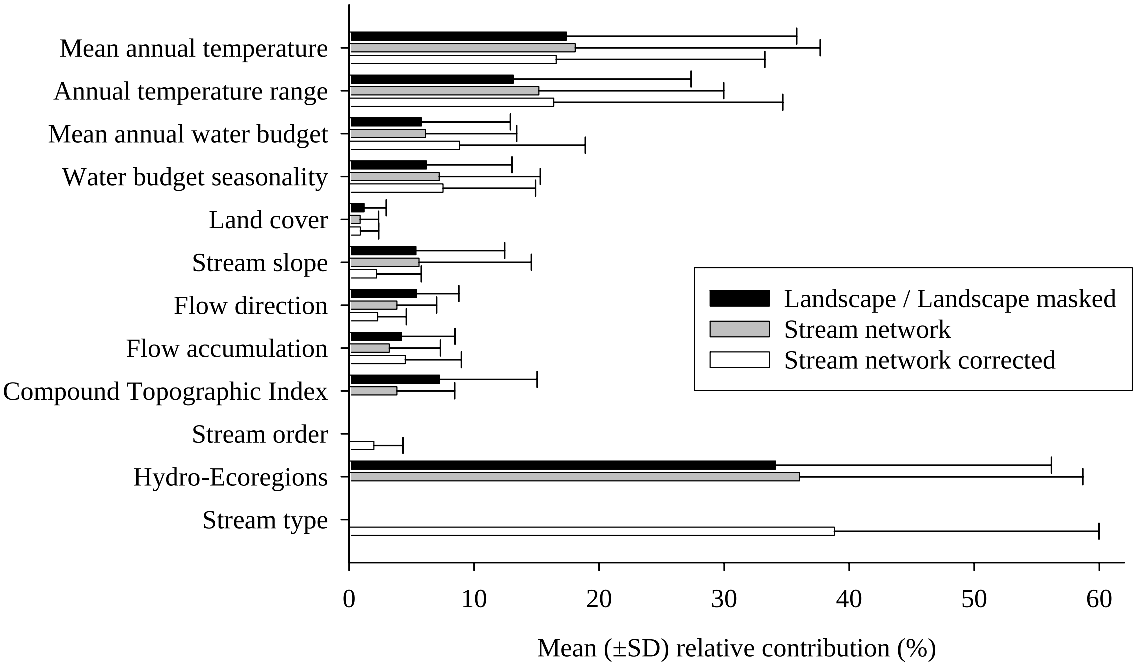

**Figure 3.3** The relative predictor contributions of the final consensus models for the four modelling designs, averaged over all species.

The results of model accuracy, i.e., the rate of successful predictions of known occurrence locations, revealed no significant differences between the modelling designs

(ANOVA: $F_{3,892} = 0.30$, $P = 0.809$). The model accuracy was on average 0.96 ± 0.04 (mean ± standard deviation), 0.96 ± 0.04, 0.95 ± 0.05 and 0.96 ± 0.04 for the 'landscape', 'landscape masked', 'stream network', and 'stream network corrected' designs, respectively. In addition, analyses of model validity showed all of the models to be significantly more accurate than random at $P < 0.001$ (results not shown).

The mean number of grid cells classified as suitable was significantly higher in the 'landscape' design than in all other designs. Moreover, the 'landscape masked' design yielded a significantly higher number of grid cells classified as suitable than the consensus projections of the 'stream network corrected' design (ANOVA: $F_{3,892} = 167.40$, $P < 0.001$, Fig. 3.4, and see exemplary maps of modelled suitable habitats of *Aphelocheirus aestivalis* (Fabricius, 1794), Heteroptera, Fig. 3.5). No significant difference between the 'stream network' and 'stream network corrected' designs could be detected. Expressed as a percentage of the continuous study area, the 'landscape' projections yielded an average relative occurrence area (ROA) of 30 ± 11%, whereas the 'landscape masked', 'stream network' and 'stream network corrected' projections yielded ROAs of 15 ± 5%, 14 ± 6% and 13 ± 5%, respectively.

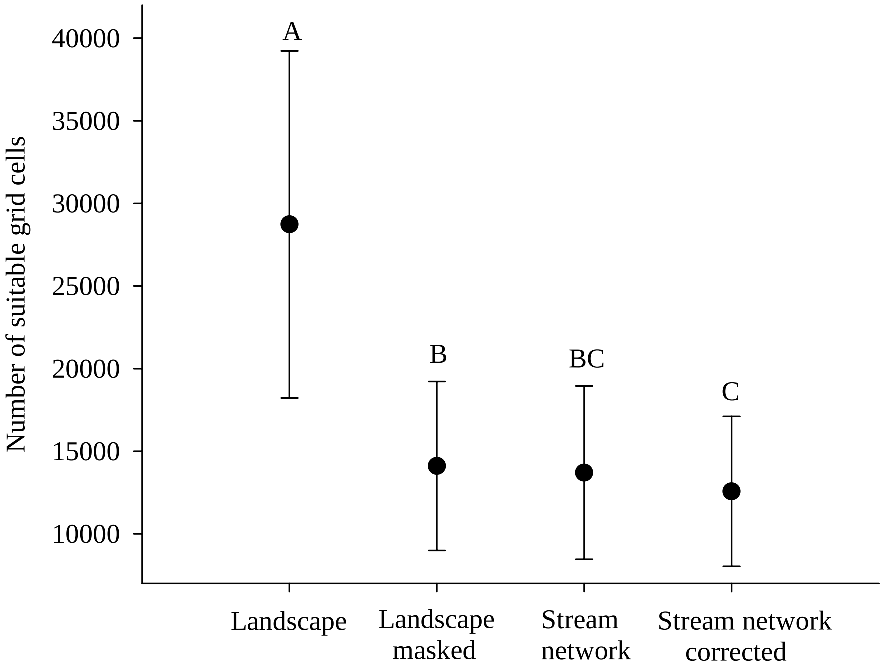

**Figure 3.4** The number of grid cells classified as suitable from the four modelling designs, averaged over all species. Different letters indicate statistically significant differences between the modelling designs at $P < 0.05$.

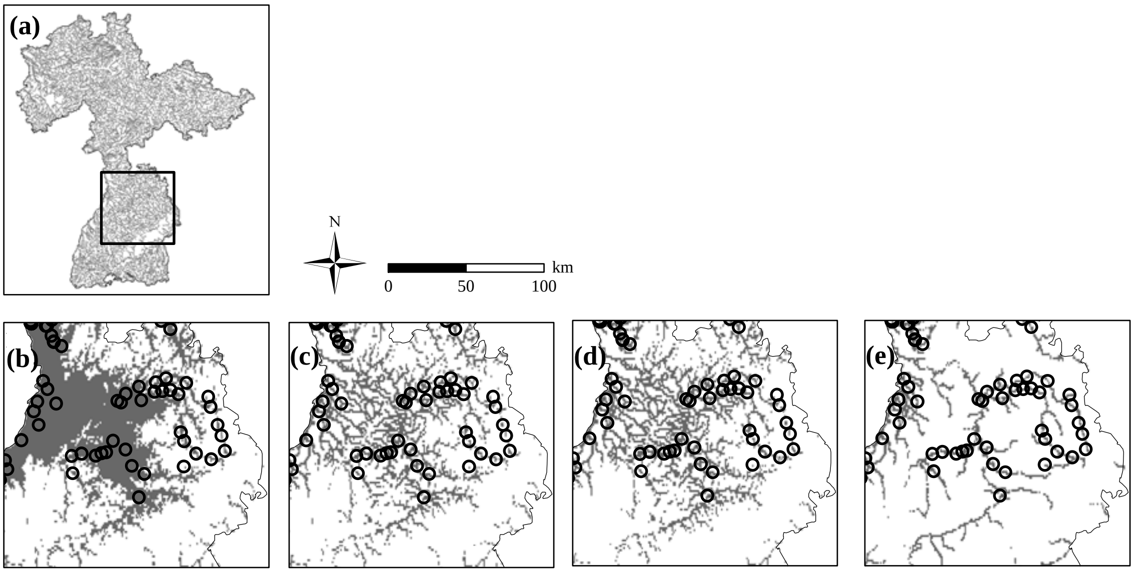

**Figure 3.5** (a) Stream network in the study area with a frame delineating the cut-out for figures b-e. (b-e) Modelled suitable habitats for *Aphelocheirus aestivalis* (Fabricius, 1794), Heteroptera, derived from the different modelling designs: (b) 'landscape', (c) 'landscape masked', (d) 'stream network', and (e) 'stream network corrected' design. The shaded area represents modelled suitable habitat, and the circles mark presence records.

The evaluations of pairwise differences based on the number of grid cells classified as suitable differed significantly between all combinations of the different designs (Paired *t*-tests, Table 3.2).

The percentage of overlapping grid cells classified as suitable between the modelling designs was highest between the 'landscape masked' and 'stream network' designs (93 ± 7%) and lowest between the 'landscape' and 'stream network corrected' designs (36 ± 6%, Appendix 5).

**Table 3.2** Pairwise differences of grid cells classified as suitable between modelling designs, expressed as the mean number and percentage (± standard deviations) with *t*-statistics.

| | **Landscape** | **Landscape masked** | **Stream network** |
|---|---|---|---|
| **Landscape masked** | 14623 ± 5758<br>(51 ± 20%)<br>$t_{223}$=38.01, *P* <0.001 | | |
| **Stream network** | 15024 ± 6097<br>(52 ± 21%)<br>$t_{223}$=36.88, *P* <0.001 | 401 ± 1778<br>(3 ± 13%)<br>$t_{223}$=3.38, *P* <0.001 | |
| **Stream network corrected** | 16158 ± 6931<br>(56 ± 24%)<br>$t_{223}$=34.89, *P* <0.001 | 1535 ± 2782<br>(11 ± 19%)<br>$t_{223}$=8.73, *P* <0.001 | 1134 ± 2782<br>(8 ± 20%)<br>$t_{223}$=6.10, *P* <0.001 |

## 3.4 Discussion

*Model performance*

For all 224 stream macroinvertebrate species analysed, the final consensus projections consistently yielded high TSS scores and high model accuracy, making the results reliable for further analyses. Although the TSS and accuracy scores were similar for all four designs, the results of the relative occurrence area (ROA) revealed apparent differences among designs.

The low variability of the measures of model performance (TSS and accuracy) arises from several instances. As consensus models were used, weak models have less weight than robust ones, obviously resulting in lower variability (Thuiller *et al.*, 2009). Furthermore, we enhanced this effect by omitting models with TSS < 0.4 from the consensus projections (Engler *et al.*, 2011). Last, the consensus projections were transformed into presence-absence maps to enable the direct comparisons of the model outputs; thus, the variability derived from the raw model output was further reduced (Liu *et al.*, 2005).

*Variability of modelling designs*

In summary, the results showed a significant reduction of the relative occurrence area (ROA) using a stream network as the study area, supporting our first hypothesis. However, the ROA was not dependent on whether the study area was restricted to the stream network before or after the model-building stage; thus, our second hypothesis was not supported. The pairwise difference of the ROA derived from the use of different predictors with a fixed study was significant, again supporting our hypothesis (No. 3, Table 3.2, Fig. 3.4).

Consensus projections of the ‘landscape’ design showed that when the continuous area was used for building SDMs, the number of grid cells classified as suitable was on average >50% higher than in the other designs. Although the presence records were located exclusively in streams, the models were, on average, not able to distinguish between the potential suitable habitats (i.e., running waters) and the non-suitable terrestrial area (see Fig. 3.5). Here, the pseudo-absences were scattered randomly over the entire landscape, both inside and outside the stream network. Considering the presence records, this observation implies that more distant absences were used (i.e., terrestrial absences that fall outside the stream network). However, these terrestrial pseudo-absences can be extremely distant from species environmental envelopes and thus uninformative, providing little or no essential information at the model-building stage (VanDerWal *et* *al.*, 2009; Lobo *et al.*, 2010). Ultimately, pseudo-absences within and outside the stream network were treated equally, classifying grid cells of both the aquatic and terrestrial realms as non-suitable for the species. Consequently, there was no differentiation of the truly non-suitable (terrestrial) and environmental (aquatic) absences in the models, leading to higher false positive predictions than were observed in the other three designs.

An exception in the exclusion of terrestrial absences would be merolimnic species (aquatic larval stage and terrestrial adult stage), where the transition between absences falling inside and outside the stream network is smooth. Because the terrestrial area belongs to the range of the species, the omission of this area would lead to a truncation of these species' environmental envelopes. However, presence records need to be available for both life stages, as the different life stages clearly have contrasting habitat preferences, and they need to be treated as two different modelling subjects (Domisch *et al.*, 2011).

The 'landscape masked' design, i.e., applying a stream network mask on the 'landscape' projections afterwards, was effective in eliminating an average of 51% of the false positive predictions that fell outside the stream network (Table 3.2). Although it is possible to further reduce these errors, as shown by the designs relying on the stream network in the model-building stage, this design is, nevertheless, useful in reducing the *a priori* truly non-suitable (i.e., terrestrial) habitats.

In contrast, the 'stream network' design used only absences within the stream network, i.e., their potentially suitable habitat. Surprisingly, no clear advantage was yielded from this design concerning the reduction of false positive predictions. The differences relative to the 'landscape masked' design appear to be negligible, as shown by the small difference between the grid cells classified as suitable (on average, 3%, Table 3.2) together with the high degree of overlapping grid cells classified as suitable (on average, 93%, Appendix 5); hence, the choice of masking the study area to the stream network before or after calibrating the models appears to be negligible when using random pseudo-absences. These results suggest that the information contained in the predictors used in this study for the 'landscape masked' and 'stream network' designs is as accurate as possible, regardless of the modelling extent. Thus, the fact that a model is fitted with the spatial extent of a stream network does not improve the predictions *per se*. It is the fact that the extent of the model projection (i.e., the result) is restricted to the 'stream network' that improves the model outcome by limiting the false positive predictions.

The question remains of how types of species' (pseudo-) absence records perform in a stream network. Though, e.g., Stokland *et al.* (2011) and Barbet-Massin *et al.* (2012) recommend using random pseudo-absences, non-random distributions, e.g., convex or alpha hulls (Burgman & Fox, 2003) and species' range envelope models (SRE, Thuiller *et al.*, 2009) could also provide suitable methods for creating species' pseudo-absences. As species' true absence records are difficult to obtain, the interconnectedness of streams may allow the assumption that species occupy the stream reaches between the most upper and most lower presence records in the stream network via convex or alpha hulls, classifying the reaches beyond as potential areas for drawing pseudo-absences via SREs.

The lowest rate of false positive predictions was derived from the 'stream network corrected' design. In this design, the number of grid cells classified as suitable was lowest compared with the other designs (on average, a difference of 56%, Table 3.2, Figs 3.4 and 3.5); however, the model accuracy was not affected, being consistently high (Appendix 4). The choice of corrected variables thus has the potential to further diminish the degree of false positive predictions, as the number of grid cells classified as suitable differed on average by 8% compared with the 'stream network' design. The results from this design rely very strongly on the additional predictors that, in our case, are intended to incorporate the hydrologic qualities of the catchment. The predictor stream type adds to the model information about the catchment characteristics, such as the catchment size, ecoregion and geology. This variable turned out to be highly relevant at this resolution (0.01 degree), and it displaced other variables from the importance ranking and even reduced the importance of further corrected hydrologic variables employed in this modelling procedure.

### *Whither from here?*

Species distribution models for stream macroinvertebrates are still in the early stages of development. We recommend that, as first steps, a stream network should have preference over a continuous area as study area to reduce false positive predictions, as model accuracy appears not to be diminished by this option. Furthermore, a non-corrected set of predictors should not be used "as is", but predictors should be carefully selected or corrected to delineate species' specific environmental envelopes for predicting their distributions.

Although the first proposal can easily be applied on the appropriate scale and resolution, the latter proposal is a major obstacle because of the scarcity of data ready for modelling. Thus, the development of suitable interpolation techniques should be envisaged, as data in streams are mostly unavailable in a (stream-) continuous but in a point-wise pattern. Thus, these point data, e.g., the sampling points of physico-chemical measurements, must be transformed into continuous predictors along stream sections. Simple interpolations are not sufficient for this task, as confluences of streams of different orders interfere with direct interpolations. Thus, there is an urgent need to develop the underlying methodology for taking into account single-point data that hold relevant information describing the environmental conditions of streams.

Moreover, SDMs on a stream network currently rely on the information for single grid cells without taking into account the impact of adjacent cells. Though this approach is a gross simplification of the stream environments, it is a useful first approximation for predicting species' vulnerabilities to climate warming (e.g., Domisch *et al.* 2011; Sauer *et al.*, 2011). However, future modelling studies should rely instead on the upstream contributing areas influencing the grid cells located below by joining the information of, e.g., precipitation or land use within single subcatchments and evaluating their effects on the grid cells located below. Similarly, a buffer of riparian land use should be included via the adjacent grid cells located along the stream network, having an effect on the streams in the immediate vicinity. Combined, these approaches should clearly enhance the accuracy of predictors used in SDMs.

Ultimately, these improved methods for SDMs for stream macroinvertebrates could be used to evaluate the climate change-related vulnerability of species more accurately than is now possible, not only to understand the possible effects of single predictors at the species level but also to gain knowledge about potential climate-change impacts on species assemblages and to put forward suitable mitigation strategies at the catchment scale. In this way, more accurate predictions of possible species ranges and their changes in different future climate scenarios can help to delineate detailed and more cost-effective conservation efforts to be undertaken.

# Summary and general conclusions

Climate change is predicted to have severe impacts on species' distributions, especially for those inhabiting stream ecosystems due to warming temperatures and changes in precipitation patterns, resulting in a increased frequency of floods and droughts (Sala *et al.*, 2000; Xenopoulos *et al.*, 2005; Döll & Zhang, 2010). To understand to which extent benthic stream macroinvertebrates are impacted by climate change, there is a need to gain further insights into species' potential susceptibility to climate warming. In this context, species distribution models (SDMs) offer a useful tool to forecast the potential impact of climate warming on species habitat suitability by relating species presences and absences with environmental predictors at the locations of those (Elith & Leathwick, 2009).

The main objective of this thesis was to investigate potential patterns of stream macroinvertebrates' distributions under future climate change scenarios of the Intergovernmental Panel on Climate Change (IPCC, 2007) by means of SDMs. Specifically, the purpose was to explore if and how species' habitat suitability would be affected under warming climates on different spatial scales, i.e. in the lower mountain ranges of Germany (Chapter 1), and across Europe (Chapter 2). Further, the emphasis lied on investigating how model projections depend on the study area and the predictors used by applying four modelling designs for a fixed set of species within Germany (Chapter 3).

In summary, projections of future potential suitable habitats for species along the river continuum within the lower mountain ranges of Germany allowed to identify possible climate-change winner and loser species depending on their overall gain or loss of suitable habitat until the year 2080 (Fig. 1.5c,d). Next to an uphill shift of species' suitable habitats along the river continuum, modelled changes of species' habitat suitability showed a clear relationship between the mean temperature of occurrence, i.e. the thermal preference, and future habitat suitability, therefore supporting the first hypothesis (H1, see General Introduction). Specifically, cold-adapted headwater species occurring at higher altitudes were projected to lose suitable habitat, while gains were projected for warm-adapted river species occurring in downstream reaches. This dependency of species' thermal preferences on potential climate-change effects could also be observed on a continental scale for a large number of species (Fig. 2.2a,b): here, cold-adapted and high-latitude species were projected to lose climatically suitable areas, whereas those of warm-adapted and low-latitude species were projected to expand. This pattern was however weakened due to a large number of endemic species of the Iberian-Macaronesian region that were projected as potential climate-change losers by the year 2080. The second hypothesis (H2) was therefore supported by model projections.

Whereas modelling results on a smaller scale revealed that species would track their climatically suitable areas uphill (Fig. 1.4), model projections on a large scale indicated that an overall shift into a north-easterly direction of habitat suitability would occur in Europe (Fig. 2.1a,b). These results corroborate long-term studies, in which these overall patterns have been observed over the last decades for freshwater as well as terrestrial organisms (e.g., Hickling *et al.*, 2005; Chen *et al.*, 2011). Model projections underpin especially the high susceptibility of cold-adapted stream macroinvertebrates to warming climates (Daufresne *et al.*, 2007; Chessman, 2009). These species would likely encounter a summit trap and therefore a ‘nowhere to go situation’ as a consequence of the loss of climatically suitable areas (Sala *et al.*, 2000; Bálint *et al.*, 2011; Sauer *et al.*, 2011). Here, it is important to consider that possible impacts of warming climates may reach far beyond projected changes in habitat suitability. Since these cold-adapted species occur as highly isolated populations in mountainous ecosystems, contractions of habitat suitability could result in a reduction of population size or even population extinctions, possibly leading to a loss in genetic diversity (Bálint *et al.*, 2011; Taubmann *et al.*, 2011). Likewise, for downstream reaches of the river continuum, projected range expansions for warm-adapted river species would likely result in changes in community structure and species composition (Mulholland *et al.*, 1997). In addition, warming temperatures have shown to facilitate the establishment of non-indigenous species (Daufresne *et al.*, 2008), further enhancing changes in species assemblages depending on their potential characteristics as, for instance, keystone or ecosystem engineering species (Dudgeon *et al.*, 2006; Strayer, 2010).

Projected overall losses and gains of generalist species’ habitat suitability (i.e., species occurring over a wide range along the river continuum) did not reach the magnitude of those projected for cold-adapted or warm-adapted species, neither on a small (Fig. 1.5a,b) nor on a larger spatial scale (Fig. 2.2a,b). Models thus propose these species to be best buffered against impacts of climate-change scenarios among the three species groups. These species tolerate wide thermal ranges, a fact that is also shown by their large geographical ranges due to their ability to colonise northern Europe after the Pleistocene during cyclic glaciations and ice retreats (Bonada *et al.*, 2009; Hering *et al.*, 2009). In contrast, these geological events resulted in a high endemicity in the Mediterranean region due to speciation (e,g., Bonada *et al.*, 2009, and references therein). These endemic species have unique habitat requirements, and model projections revealed that endemics of the Iberian Peninsula would be at high risk to warming climates due to a loss of climatically suitable areas (Figs 2.1a,b and 2.2a,b), corroborating their high vulnerability to warming climates. Ultimately, climate change is likely to pose a major threat to this biodiversity hotspot (Malcolm *et al.*, 2006).

In addition to the similar patterns regarding the thermal sensitivity to climate warming for the two studies, suitable habitats were projected to remain for most of the modelled species in the lower mountain ranges and Europe, respectively (Chapter 1 and 2). These results underline the consistency of climate-change effects derived from SDM projections on different spatial scales. However, model projections regarding the exact magnitude of geographical shifts, losses and gains of habitat suitability may not be compared directly between these two approaches to infer possible species-specific alterations in habitat suitability. Instead, these comparisons are useful to detect the overall pattern and the direction of possible changes in species distributions (Araújo *et al.*, 2005). For instance, only coarse-scale bioclimatic predictors *sensu* Whittaker *et al.* (2007) were used on the continental scale (Chapter 2), which did not account for specific hydrologic regimes in streams and rivers. Similarly, the methodological study (Chapter 3) showed that model projections for stream macroinvertebrates depend greatly on the study area and on the predictors used. The SDMs built in a stream network and with corrected predictors were able to reduce commission errors, i.e., false positive predictions on average by 56% compared to projections generated on a continuous area and non-corrected predictors, therefore reducing a considerable amount of uncertainties in model projections. Though the third hypothesis was therefore supported (H3), model statistics were however not affected by different modelling designs by means of the true skill statistic (TSS, incorporating true positive and negative predictions, Allouche *et al.*, 2006) or model validity, i.e., the accuracy and significance of the projections (Anderson *et al.*, 2003). This has important implications for modelling stream macroinvertebrates' distributions, as solely relying on model statistics would not be sufficient. Instead, the design using a stream network during model calibration together with corrected predictors should be preferred over an area-based approach and non-corrected predictors. The advantage of a stream network is, however, dependent on the spatial scale, and is of minor relevance for a large-scale study such as for Europe (Chapter 2, grid cells were approximately 10 km$^2$). Nevertheless, the direction of projected climate-change induced shifts in habitat suitability of the two modelling approaches (Chapter 1 and 2) remain similar, and support the observed vulnerability of stream macroinvertebrates to warming climates.

The studies in this thesis focus essentially on possible changes of future habitat suitability under climate change scenarios, assuming species' thermal preferences to remain constant over time, and without taking biotic interactions or species-specific migration and dispersal abilities into account. The assumption of niche conservatism, and whether it could or should be avoided in habitat suitability models in general, is a key question since the early use of these correlative models (e.g., Pearman *et al.*, 2008). Nevertheless, forecasts of species distributions derived from SDMs should thus be seen as a first assessment of climate-change related vulnerability analyses of species, giving insights into possible patterns derived from warming climates. For instance, SDMs have been successfully applied on various fields related to climate change, ranging from conservation planning and identification of suitable habitat for rare species, to study possible migration routes of invasive species (reviewed in Elith & Leathwick, 2009 and Araújo & Peterson, 2012).

Next to the direction of climate-change effects (i.e., losses or gains of suitable habitats), SDMs provide the information where these changes would likely occur. Concerning the modelled altitudinal and / or latitudinal shifts of future habitat suitability, it remains highly speculative whether species would be able to track the expected shift of climatic isotherms in the future. Though recent studies have shown that species of the terrestrial realm are able to carry out rapid range changes as a response to warming climates (e.g., Chen *et al.*, 2011), the question remains whether this would also be true for stream macroinvertebrates. This task is particularly challenging since the ecological preferences and the dispersal abilities remain still unknown for the vast majority of this species group (Heino *et al.*, 2009; Kappes & Haase, 2011). In addition, it is important to bear in mind that future suitable climatic conditions do not go hand in hand with future habitat availability, the latter being most probably detrimentally impacted by multiple stressors including climate-change induced warming and discharge changes, i.e., droughts and floods, land use changes, structural degradation, chemical loads, or water withdrawals and large scale irrigation measures (Ormerod *et al.*, 2010). Potential mitigation strategies should thus focus on the reduction of multiple stressors in stream ecosystems (Heino *et al.*, 2009; Ormerod *et al.*, 2010), in order to minimise these simultaneously acting drivers potentially altering the diversity of stream macroinvertebrates in the course of warming climates.

*Outlook*

Species distribution models have proven to be promising tools for assessing possible climate change effects on stream macroinvertebrates to detect potential patterns of their future distributions. Several challenges remain, however, to further improve the understanding of stream macroinvertebrates' responses to warming climates.

Most importantly, it is the ecology of stream macroinvertebrates that needs to be better understood, essentially to identify potential tipping points for climate-change induced responses on single species' ecological preferences (e.g., Mulholland *et al.*, 1997). Therefore, further research regarding species' life history characteristics and adaptation potential to novel climatic conditions (Mulholland *et al.*, 1997; Bonada *et al.*, 2007a), dispersal abilities (Kappes & Haase, 2011), and responses to multiple stressors (Ormerod *et al.*, 2010) should be envisaged to gain further insights into possible consequences of climate change on these organisms.

As the application of SDMs on stream macroinvertebrates is rather new, it needs to be further developed to capture the species-specific habitat requirements. In this context, the accuracy of environmental predictors is crucial to delineate projections of species' habitat suitability. Here, integrative modelling approaches for stream macroinvertebrates have shown to be promising tools in improving the hydrology-related predictors for characterising distributions of stream macroinvertebrates (Kuemmerlen *et al.*, 2012), and have therefore the high potential to yield more accurate projections.

In conclusion, the studies provided in this thesis underline the feasibility of the application of species distribution models for stream macroinvertebrates to detect distributional patterns under climate change scenarios, additionally highlighting the importance of the underlying modelling technique in terms of the study area and environmental predictors used to reduce uncertainties and thus to improve model projections.

# Modellierung klimabedingter Arealverschiebungen von Makrozoobenthosarten in Fließgewässern – deutschsprachige Zusammenfassung

*Hintergrund*

Im Zuge des prognostizierten Klimawandels wird ein Anstieg der globalen Lufttemperatur um 1.1 – 6.4°C bis zum Jahr 2100 mit damit verbundenen Niederschlagsveränderungen vorhergesagt (IPCC, 2007). Vor allem Fließgewässer reagieren auf diese klimabedingten Änderungen besonders empfindlich, da neben der direkten Erwärmung auch mit Abflussänderungen zu rechnen ist, die zu Dürren und / oder Hochwassern führen können (Milly *et al.*, 2005; Xenopoulos *et al.*, 2005). Organismen können auf diese klimabedingten Änderungen in ihrem gegenwärtigen Verbreitungsgebiet in zweierlei Hinsicht reagieren: sie können sich mittels phänotypischer Plastizität an die neuen klimatischen Bedingungen anpassen (Thackeray *et al.*, 2010), oder sie können in Richtung geeigneter klimatischer Gegebenheiten wandern (Chen *et al.*, 2011). Da sich Arten in diesem kurzen Zeitrahmen überwiegend nicht an neue klimatische Bedingungen anpassen können (Davis, 2001; Hampe & Petit, 2005), kommt für viele Arten nur eine Verschiebung ihres gegenwärtigen Verbreitungsgebietes in Frage. Letzteres wurde bereits in den vergangenen Jahrzehnten sowohl für limnische als auch terrestrische Organismen beobachtet (Hickling *et al.*, 2005; Chen *et al.*, 2011). Hierbei wurde deutlich, dass Arten den geeigneten klimatischen Bedingungen in Richtung höherer geographischer Breiten als auch in größerer Höhen ü. NN folgen (Sala *et al.*, 2000; Parmesan, 2006; Chen *et al.*, 2011).

Abgesehen von diesen empirisch erhobenen Daten, die sich neben dem hohen Zeit- und Kostenaufwand nur auf vergangene klimatische Veränderungen beziehen, können Modellprojektionen dabei helfen, den Einfluss des prognostizierten Klimawandels auf die Verbreitungsgebiete der Arten zu projizieren. Hierbei kommen GIS-gestützte ökologische Arealmodelle zum Einsatz (species distribution models, SDMs), anhand derer sich der potenzielle Einfluss des Klimawandels auf mögliche Arealverschiebungen auf dem Artniveau simulieren lässt. Die Arealmodelle basieren auf den Umweltvariablen an den Fundpunkten einer Art und können anhand von Modellalgorithmen die Vorkommenswahrscheinlichkeiten einer Art auf das gesamte Untersuchungsgebiet projizieren (Elith & Leathwick, 2009). Neben der gegenwärtigen Projektion des Verbreitungsgebietes können mit Hilfe zukünftiger Klimaszenarien, wie z.B. die des Weltklimarates IPCC, die klimabedingte Empfindlichkeit von Arten abgeschätzt werden. Hierbei stehen eine

Vielzahl an Modellalgorithmen zur Verfügung, die die spezifischen Habitatanforderungen einer Art basierend auf den Umweltvariabeln ableiten. Um die Unsicherheiten der Modellprojektionen zu reduzieren, wurde in dieser Arbeit von dem sog. „ensemble forecasting“ Gebrauch gemacht, d.h. es wurde simultan auf eine Vielzahl von Modellierungsalgorithmen mittels der BIOMOD / R –Software zurückgegriffen, deren Ergebnisse in einer Gesamtprojektion (consensus) vereint werden (Thuiller *et al.*, 2009; R Development Core Team, 2011).

*Hypothesen*

In der vorliegenden Dissertation wurde anhand von Arealmodellen untersucht, inwieweit die potentiellen Verbreitungsgebiete von Makrozoobenthosarten in Fließgewässern auf verschiedenen räumlichen Skalen vom prognostizierten Klimawandel beeinflusst werden. Zusätzlich wurde getestet, welchen Einfluss das zugrunde liegende Untersuchungsgebiet und die verwendeten Umweltvariablen auf die Modellprojektionen haben. Die Arbeit umfasst drei Studien, die sich jeweils auf eine Hypothese beziehen.

In der ersten Studie wurde die klimabedingte Empfindlichkeit von 38 Makrozoobenthosarten entlang des Flusskontinuums (Vannote *et al.*, 1980) in den deutschen Mittelgebirgen untersucht. Dafür wurde zunächst die rezente Verbreitung der Arten in einem Fließgewässernetz modelliert, die anschließend mittels zweier Klimaszenarien des IPCC in das Jahr 2080 projiziert wurden. Dabei wurde die folgende Hypothese (H1) getestet:

- *Die klimabedingte Vulnerabilität von Makrozoobenthosarten entlang des Flusskontinuums ist von ihrer Temperaturpräferenz abhängig.*

In der zweiten Studie wurde das Untersuchungsgebiet auf den gesamten europäischen Raum erweitert und die Zukunftsprojektionen der potentiellen Verbreitungsgebiete für das Jahr 2080 wurden für insgesamt 191 Makrozoobenthosarten erstellt. Dabei wurde untersucht, ob die klimabedingte Empfindlichkeit der Arten – basierend auf den Modellprojektionen – abhängig von der räumlichen Skala ist, auf der die Untersuchungen durchgeführt werden. Hierbei wurde die folgende Hypothese (H2) getestet:

- *Kalt-adaptierte Makrozoobenthosarten sowie Habitatspezialisten auf dem gesamten europäischen Raum sind einer höherer klimabedingten Vulnerabilität ausgesetzt als warm-adaptierte Arten und Habitatgeneralisten.*

In der dritten Studie wurden der Einfluss des zugrunde liegenden Untersuchungsgebietes und der Einfluss der Umweltvariablen auf die Modellprojektionen, sowie auf die Güte bezüglich der statistischen Aussagekraft der Modelle untersucht. Hierbei wurden für insgesamt 224 Makrozoobenthosarten jeweils vier verschiedene Modelldesigns angewendet, bei denen das Untersuchungsgebiet zwischen einem flächenbasierten Untersuchungsgebiet und einem Fließgewässernetz, und die Umweltvariablen zwischen Standardvariablen und korrigierten Variablen variiert wurden. Die Hypothese (H3) lautete hierbei:

- *Arealmodelle, die auf einem Fließgewässernetz und korrigierten Umweltvariablen basieren, liefern eine höhere Modellgüte bezüglich der Projektion und der Modellstatistik, als flächenbasierte Modelle mit Standard- oder unkorrigierten Variablen.*

*Ergebnisse und Schlussfolgerungen*

Die zukünftigen Modellprojektionen der ersten Studie für die Mittelgebirge haben gezeigt, dass klimabedingte Arealverschiebungen von Makrozoobenthosarten im Flusskontinuum abhängig von der Temperaturpräferenz dieser Arten sind. Für 97 bis 100% der Arten konnte mittels der Modelle ein geeignetes zukünftiges Habitat projiziert werden. Abhängig von dem Klimaszenario wurden für diese Arten jedoch gleichzeitig eine potentielle Arealverschiebung in größere Höhen um 83 bis 122 m entlang des Flusskontinuums projiziert. Für kalt-adaptierte Oberlaufarten wurde ein Verlust an geeigneten Arealen prognostiziert, wohingegen für warm-adaptierte Unterlaufarten eine Ausweitung des für sie geeigneten Areals projiziert wurde. Die Hypothese H1 wurde somit von den Modellergebnissen unterstützt.

Dieses Muster der klimabedingten Veränderungen der potentiellen Verbreitungsgebiete konnte auch in der zweiten Studie auf einer europäischen Skala beobachtet werden. Für ca. 99% der Arten konnte basierend auf den Klimaszenarien klimatisch geeignetes Areal für das Jahr 2080 projiziert werden. Neben einer allgemeinen geographischen Verschiebung der potentiellen Verbreitungsgebiete in eine nord-östliche Richtung, konnte für kalt-adaptierte Arten, sowie für Arten, die in den nördlichen Breiten Europas vorkommen, eine Reduzierung des für sie geeigneten klimatischen Areals prognostiziert werden. Gleichzeitig wurden für warm-adaptierte Arten, sowie für Arten der südlichen Breiten, ein Zuwachs an klimatisch geeigneten Arealen projiziert. Endemische Arten der Iberischen Halbinsel waren hierbei eine Ausnahme, denn zukünftigen Klimaprojektionen zufolge wurde für diese Habitatspezialisten ein starker Verlust an klimatischen Areal vorhergesagt. Die Hypothese H2 konnte somit bestätigt werden.

Die zukünftigen Projektionen der Verbreitungsgebiete auf den unterschiedlichen Skalen haben gezeigt, dass die klimabedingten Arealveränderungen einem ähnlichen Muster folgen, wie bereits beobachtete Arealverschiebungen von limnischen und terrestrischen Arten (Hickling *et al.*, 2005; Chen *et al.*, 2011). Die Modellprojektionen bekräftigen besonders die beobachtete hohe Vulnerabilität kalt-adaptierter Oberlaufarten (Daufresne *et al.*, 2007; Chessman, 2009). Infolge der reduzierten verfügbaren Fläche mit zunehmender Höhe sind diese Arten besonders von der prognostizierten Klimaerwärmung betroffen (Sala *et al.*, 2000; Bálint *et al.*, 2011; Sauer *et al.*, 2011). Hierbei ist es wichtig zu beachten, dass potentielle Konsequenzen des Klimawandels weit über mögliche Arealverschiebungen hinausgehen können. Da kalt-adaptierte Oberlaufarten in Gebirgsökosystemen oft kleine Populationen bilden, ist mit einer Reduzierung des verfügbares Habitats unter Umständen auch mit einer Verringerung der Populationsgröße oder gar mit dem Aussterben einzelner Populationen zu rechnen, welches mit einem Verlust an genetischer Diversität einhergehen könnte (Bálint *et al.*, 2011; Taubmann *et al.*, 2011). Für die Unterläufe im Flusskontinuum hingegen können neben der prognostizierten Ausdehnung des Verbreitungsgebietes von warm-adaptierten Arten zusätzlich Änderungen in der Artenzusammensetzung und Gemeinschaftsstruktur erwartet werden (Mulholland *et al.*, 1997). Darüber hinaus haben Studien gezeigt, dass eine Erwärmung der unteren Abschnitte der Fließgewässer die Etablierung von eingewanderten Arten zur Folge haben kann (Daufresne *et al.*, 2008), welches die Änderungen der Artenzusammensetzung abhängig von den Eigenschaften dieser Arten (z.B. Schlüsselart oder „ecosystem engineers“) noch weiter beeinflussen dürfte (Dudgeon *et al.*, 2006; Strayer, 2010).

Die projizierten Arealverschiebungen von Generalistenarten, d.h. Arten mit einer ausgedehnten Verbreitung im Flusskontinuum, hatten nicht den Umfang der Änderungen, die für kalt- oder warm-adaptierte Arten modelliert wurden. Die Modelle prognostizieren daher, dass diese Arten am besten gegen Änderungen klimatischer Parameter gepuffert wären. Generalistenarten tolerieren eine breite Temperaturspanne, und sind daher durch ihre ausgedehnte geographische Verbreitung charakterisiert. Dies lässt sich auf ihre Fähigkeit zurückführen, nördliche Teile Europas nach dem Pleistozän während zyklischen Vergletscherungen und Zurückweichen des Eises zu besiedeln (Bonada *et al.*, 2009; Hering *et al.*, 2009). Im Gegensatz dazu führten diese geologischen Ereignisse zu einer großen Anzahl an endemischen Arten im Mittelmeerraum (siehe z.B. Bonada *et al.*, 2009). Diese Endemiten zeichnen sich durch spezifische Habitatanforderungen aus. Dies führte dazu, dass die zukünftigen Modellprojektionen für Endemiten der Iberischen Halbinsel einen großen Verlust an klimatisch geeigneten Arealen prognostizierten. Diese Ergebnisse unterstützen das hohe Maß an Vulnerabilität von Endemiten, und untermauert die Annahme, dass der Klimawandel eine Bedrohung für die Biodiversität dieses Hotspots darstellt (Malcolm *et al.*, 2006).

Neben den ähnlichen Mustern bezüglich der Arealverschiebungen, konnte in diesen beiden Studien für die Mehrzahl der Arten ein geeignetes Habitat bzw. ein klimatisch geeignetes Areal projiziert werden. Diese Übereinstimmungen der Arealmodelle unterstützt die Beständigkeit von Modellprojektionen auf unterschiedlichen räumlichen Skalen im Hinblick auf den prognostizierten Klimawandel. Es gilt jedoch zu beachten, dass die Modellergebnisse der beiden Studien bezüglich der Genauigkeit der geographischen Verschiebungen und der potentiellen Verluste oder Ausdehnungen an geeigneten Arealen, nicht direkt miteinander verglichen werden können, um mögliche artspezifische zukünftige Habitatänderungen ableiten zu können. Vielmehr sind diese Ergebnisse hilfreich, um generelle Muster und die Richtung (d.h. Verlust oder Zuwachs an Areal) von potentiellen Änderungen in der Verbreitung von Arten zu erkennen (Araújo *et al.*, 2005). Auf der europäischen Skala wurden z.B. grob aufgelöste bioklimatische Umweltvariablen im Sinne von Whittaker *et al.* (2007) verwendet, die keine Aussagen über die genauen hydrologischen Beschaffenheiten in Flüssen und Bächen zulassen. Gleichzeitig hat die dritte Studie gezeigt, dass Modellprojektionen, die auf einem Fließgewässernetz und mit korrigierten Umweltvariablen generiert wurden, im Vergleich zu dem flächenbasierten Modelldesign mit den Standardvariablen und unkorrigierten Umweltvariablen, die Überprojektion des für die Art als geeignet klassifizierten Areals um durchschnittlich 56% reduzieren konnten. Obwohl dadurch die Hypothese H3 bestätigt wurde, ist es wichtig zu beachten, dass die Modellstatistik, welche Aussagen über die Modellgüte zulassen, sich zwischen den vier Modelldesigns nicht signifikant unterschieden: weder die TSS-Werte (true skill statistic), die sich auf das korrekt modellierte Vorkommen und Nicht-Vorkommen einer Art stützen, noch die Genauigkeit bzw. die Treffsicherheit der Projektionen (accuracy) wiesen signifikante Unterschiede auf. Dies bedeutet, dass die Evaluierung von Arealmodellen für Makrozoobenthosarten nicht allein auf der Modellstatistik beruhen darf, sondern dass ein Modelldesign mit einem Fließgewässernetz und einer genauen Auswahl an Umweltvariablen bevorzugt werden sollte. Ferner gilt jedoch auch zu beachten, dass die Anwendung dieses Modelldesigns von der räumlichen Auflösung des Untersuchungsgebietes abhängig ist, und daher für Modelle des gesamten europäischen Raums mit einer Auflösung von ca. 10 $km^2$ ungeeignet ist. Dennoch ist der Effekt der prognostizierten klimabedingten Arealverschiebungen bei beiden Modellierungsansätzen ähnlich, und unterstützt die beobachtete Vulnerabilität von Makrozoobenthosarten in Fließgewässern im Zuge des Klimawandels.

Die Studien in dieser Arbeit stützen sich im Wesentlichen auf mögliche Arealverschiebungen von Arten basierend auf zukünftigen Klimaszenarien unter der Annahme, dass die Temperaturpräferenzen der Arten konstant bleiben. Ferner wurden biotische Interaktionen oder artspezifische Migrations- und Ausbreitungsfähigkeiten nicht berücksichtigt. Die Annahme dieses Nischenkonservatismus und wie damit in diesen statistischen Modellen umgegangen werden sollte, ist eine zentrale Frage bei der Verwendung dieser Modelle (Pearman *et al.*, 2008). Dennoch sind Arealmodelle hilfreich, um erste Abschätzungen der klimabedingten Empfindlichkeit von Arten ableiten zu können. Beispiele zur erfolgreichen Anwendung der Arealmodelle beziehen sich auf unterschiedliche Forschungsgebiete im Bereich des Klimawandels, und können neben der Vorhersage von möglichen klimabedingten Arealverschiebungen von Arten auch zur Planung und Identifizierung geeigneter Schutzgebiete seltener Arten genutzt werden. Auch können die Modelle zur Untersuchung möglicher Ausbreitungswege invasiver Arten verwendet werden (Elith & Leathwick, 2009; Araújo & Peterson, 2012).

Arealmodelle liefern neben Vorhersagen von Verlusten oder Zuwachs von geeigneten Habitaten im Zuge des Klimawandels auch die Information, wo diese Veränderungen wahrscheinlich auftreten können. In Bezug auf die modellierten Arealverschiebungen in Richtung größerer Höhenlagen und / oder höherer Breiten, beruhen diese Annahmen jedoch auf Vermutungen. Ob Arten tatsächlich in der Lage sind, den erwarteten zukünftigen Verschiebungen der klimatischen Isothermen zu folgen ist ungewiss. Obwohl Studien gezeigt haben, dass z.B. terrestrische Arten zu sehr schnellen Arealverschiebungen als Reaktion des Klimawandels befähigt sind (Chen *et al.*, 2011), stellt sich die Frage, ob dies auch für Makrozoobenthosarten in Fließgewässern der Fall ist. Hier besteht jedoch noch weiterer Forschungsbedarf, da für die überwiegende Mehrheit der Arten die Autökologie und die Ausbreitungsfähigkeiten bislang unbekannt sind (Heino *et al.*, 2009; Kappes & Haase, 2011). Darüber hinaus ist es wichtig zu beachten, dass zukünftige geeignete klimatische Bedingungen nicht mit der Verfügbarkeit des künftigen geeigneten Habitats einhergehen. Letzteres wird mit hoher Wahrscheinlichkeit durch multiple Stressoren beeinträchtigt, wie z.B. die durch den Klimawandel verursachte Erwärmung und Niederschlags- und Abflussveränderungen, Änderungen der Landnutzung, Stoffeinträge, Veränderungen der Strukturgüte der Fließgewässer, oder durch Bewässerungsmaßnahmen großräumiger Agrarflächen (Ormerod *et al.*, 2010). Mögliche Strategien zur Erhaltung der Artenvielfalt in Fließgewässern sollten sich daher auf die Reduzierung dieser multiple Stressoren konzentrieren (Heino *et al.*, 2009; Ormerod *et al.*, 2010).

*Ausblick*

Die vorliegende Dissertation zeigt, dass Arealmodelle ein geeignetes und nützliches Werkzeug für die Abschätzung der klimabedingten Empfindlichkeit von Makrozoobenthosarten in Fließgewässern darstellen. Ferner konnte gezeigt werden, dass eine sorgfältige Auswahl des Modelldesigns im Hinblick auf die Reduzierung der Unsicherheiten in den Modellprojektionen von großer Bedeutung ist.

Um die Konsequenzen des Klimawandels auf Makrozoobenthosarten besser abschätzen zu können, besteht v.a. weiterer Forschungsbedarf im Bereich der Autökologie der Arten (Mulholland *et al.*, 1997). Hier sollte der Fokus auf dem Anpassungspotenzial der Organismen an neue klimatische Bedingungen (Mulholland *et al.*, 1997; Bonada *et al.*, 2007a), auf ihren Ausbreitungsfähigkeiten (Kappes & Haase, 2011), und auf ihren Reaktionen und Konsequenzen auf multiple Stressoren liegen (Ormerod *et al.*, 2010).

Für die Weiterentwicklung der Arealmodelle für diese Organismen spielt v.a. die Generierung hydrologischer Umweltvariablen eine große Rolle, da so geeignete Habitate der Makrozoobenthosarten in Fließgewässern besser charakterisiert werden können. Hier ist die Entwicklung von integrierten Modellansätzen vielversprechend (Kuemmerlen *et al.*, 2012), die basierend auf hydraulischen und hydrologischen Modellen die Eingangsvariablen für die Arealmodelle liefern.

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# Appendices

**Appendix 1** List of all 191 species used for BEMs, their taxonomic group, the number of presence records used for BEMs, the number of ecoregions where records were present for modelling, species' classification as either rare or common, life cycle (merolimnic or hololimnic), stream zonation and current preference, modelled changes of climatic suitable areas for the year 2080 under the A2a and B2a climate warming scenarios, and TSS values (CSA, changes in climatically suitable areas; TSS, true skill statistic; WA, weighted average; -, no data available for this criterion).

| Species | Taxonomic group | Presence records | Number of ecoregions | Rare species | Life cycle | Stream zonation | Current preference | CSA A2a (%) | CSA B2a (%) | TSS (WA) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Pisidium personatum* MALM 1855 | Bivalvia | 1563 | 16 | common | hololimnic | generalist | rheo to limnophil | -57.7 | -50.1 | 0.97 |
| *Esolus parallelepipedus* (MÜLLER 1806) | Coleoptera | 216 | 11 | common | merolimnic | - | rheobiont | 72.7 | 57.2 | 0.95 |
| *Hydraena lapidicola* KIESENWETTER 1849 | Coleoptera | 46 | 2 | common | merolimnic | - | rheophil | -34.3 | -27.9 | 0.99 |
| *Hydraena melas* DALLA TORRE 1877 | Coleoptera | 19 | 6 | common | merolimnic | generalist | rheo to limnophil | -79.7 | -74.0 | 0.99 |
| *Oulimnius tuberculatus* (MÜLLER 1806) | Coleoptera | 638 | 10 | common | merolimnic | - | rheo to limnophil | 30.5 | 32.9 | 0.96 |
| *Astacus astacus* (LINNAEUS 1758) | Crustacea | 471 | 13 | common | hololimnic | - | rheo to limnophil | 7.1 | 12.3 | 0.97 |
| *Crangonyx pseudogracilis* BOUSFIELD 1958 | Crustacea | 538 | 5 | common | hololimnic | - | - | -74.7 | -65.1 | 0.98 |
| *Gammarus tigrinus* SEXTON 1939 | Crustacea | 647 | 5 | common | hololimnic | river | rheo to limnophil | -86.5 | -79.9 | 0.99 |
| *Niphargus aquilex* SCHIOEDTE 1855 | Crustacea | 213 | 4 | common | hololimnic | - | - | -63.1 | -50.3 | 0.97 |
| *Orconectes limosus* (RAFINESQUE 1817) | Crustacea | 609 | 9 | common | hololimnic | river | rheo to limnophil | 70.5 | 47.9 | 0.96 |
| *Procambarus clarkii* (GIRARD 1852) | Crustacea | 154 | 6 | common | hololimnic | - | - | 236.0 | 151.3 | 0.96 |
| *Cricotopus trifascia* EDWARDS 1929 | Diptera | 29 | 7 | common | merolimnic | - | - | -95.6 | -87.8 | 1.00 |
| *Epoicocladius flavens* (MALLOCH 1915) | Diptera | 38 | 8 | - | merolimnic | - | - | -21.7 | -31.3 | 0.95 |
| *Eukiefferiella fuldensis* LEHMANN 1972 | Diptera | 24 | 2 | common | merolimnic | - | - | -83.3 | -52.5 | 1.00 |
| *Nanocladius rectinervis* (KIEFFER 1911) | Diptera | 111 | 8 | common | merolimnic | river | - | -3.0 | 8.6 | 0.98 |
| *Orthocladius holsatus* GOETGHEBUER 1937 | Diptera | 48 | 3 | common | merolimnic | - | - | -100.0 | -100.0 | 1.00 |
| *Orthocladius lignicola* (KIEFFER in POTTHAST 1915) | Diptera | 33 | 8 | common | merolimnic | - | - | -0.1 | -4.3 | 0.97 |
| *Oxycera morrisii* CURTIS 1830 | Diptera | 35 | 4 | common | merolimnic | - | - | -100.0 | -99.9 | 0.99 |
| *Ptychoptera minuta* TONNOIR 1919 | Diptera | 43 | 3 | common | merolimnic | - | rheo to limnophil | -84.7 | -70.2 | 0.99 |
| *Simulium lundstromi* (ENDERLEIN 1921) | Diptera | 16 | 4 | common | merolimnic | - | rheo to limnophil | -95.0 | -93.8 | 0.99 |

## Appendix 1 continued

| pecies | Taxonomic group | Presence records | Number of ecoregions | Rare species | Life cycle | Stream zonation | Current preference | CSA A2a (%) | CSA B2a (%) | TSS (WA) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Tvetenia discoloripes* (GOETGHEBUER in THIENEMANN 1936) | Diptera | 83 | 7 | common | merolimnic | - | - | -0.5 | 4.5 | 0.97 |
| *Baetis alpinus* (PICTET 1843) | Ephemeroptera | 216 | 11 | common | merolimnic | - | rheophil | 19.0 | 11.7 | 0.96 |
| *Baetis bundyae* LEHMKHUL 1973 | Ephemeroptera | 119 | 2 | common | merolimnic | headwater | rheophil | -93.8 | -89.8 | 0.96 |
| *Baetis fuscatus* (LINNAEUS 1761) | Ephemeroptera | 1343 | 15 | rare | merolimnic | river | rheo to limnophil | -35.0 | -32.6 | 0.88 |
| *Baetis rhodani* (PICTET 1843) | Ephemeroptera | 4692 | 19 | common | merolimnic | generalist | rheophil | -32.2 | -33.5 | 0.89 |
| *Baetis subalpinus* BENGTSSON 1917 | Ephemeroptera | 1172 | 5 | common | merolimnic | - | rheophil | -89.1 | -81.1 | 0.95 |
| *Caenis beskidensis* SOWA 1973 | Ephemeroptera | 83 | 9 | rare | merolimnic | generalist | rheophil | -19.9 | -10.1 | 0.96 |
| *Centroptilum luteolum* (MÜLLER 1776) | Ephemeroptera | 2107 | 16 | common | merolimnic | - | limnophil | -38.1 | -43.3 | 0.89 |
| *Choroterpes prati* GAINO & PUIG 1996 | Ephemeroptera | 15 | 1 | common | merolimnic | - | rheo to limnophil | -18.1 | -6.1 | 1.00 |
| *Ecdyonurus dispar* (CURTIS 1834) | Ephemeroptera | 364 | 13 | rare | merolimnic | - | rheo to limnophil | 13.5 | 17.0 | 0.96 |
| *Ecdyonurus torrentis* KIMMINS 1942 | Ephemeroptera | 323 | 9 | rare | merolimnic | - | rheo to limnophil | -14.9 | -38.3 | 0.97 |
| *Ecdyonurus venosus* (FABRICIUS 1775) | Ephemeroptera | 401 | 12 | common | merolimnic | generalist | rheo to limnophil | 4.3 | -0.8 | 0.97 |
| *Electrogena affinis* (EATON 1883) | Ephemeroptera | 28 | 8 | common | merolimnic | - | limno to rheophil | -30.1 | -58.4 | 0.98 |
| *Ephemera danica* MÜLLER 1764 | Ephemeroptera | 1697 | 15 | rare | merolimnic | generalist | rheo to limnophil | 19.7 | 19.8 | 0.93 |
| *Ephemerella aurivillii* (BENGTSSON 1908) | Ephemeroptera | 1017 | 5 | - | merolimnic | - | - | -92.4 | -83.4 | 0.94 |
| *Habroleptoides confusa* SARTORI & JACOB 1986 | Ephemeroptera | 418 | 9 | rare | merolimnic | generalist | rheo to limnophil | 5.8 | -16.7 | 0.97 |
| *Habrophlebia fusca* (CURTIS 1834) | Ephemeroptera | 201 | 10 | rare | merolimnic | - | limno to rheophil | -6.6 | -12.4 | 0.96 |
| *Heptagenia dalecarlica* BENGTSSON 1912 | Ephemeroptera | 1002 | 5 | common | merolimnic | - | rheo to limnophil | -92.4 | -82.5 | 0.96 |
| *Nigrobaetis digitatus* (BENGTSSON, 1912) | Ephemeroptera | 215 | 5 | - | merolimnic | - | - | -56.4 | -47.8 | 0.94 |
| *Paraleptophlebia submarginata* (STEPHENS 1835) | Ephemeroptera | 367 | 14 | common | merolimnic | generalist | rheo to limnophil | 14.3 | 15.0 | 0.95 |
| *Rhithrogena semicolorata* (CURTIS 1834) | Ephemeroptera | 685 | 14 | common | merolimnic | generalist | rheophil | 7.2 | -6.7 | 0.96 |
| *Serratella ignita* (PODA 1761) | Ephemeroptera | 2405 | 17 | common | merolimnic | generalist | rheo to limnophil | 27.7 | 28.2 | 0.94 |
| *Ancylus fluviatilis* O.F. MÜLLER 1774 | Gastropoda | 2536 | 17 | common | hololimnic | generalist | rheobiont | 46.2 | 37.6 | 0.95 |
| *Gyraulus albus* (O.F. MÜLLER 1774) | Gastropoda | 1742 | 14 | common | hololimnic | generalist | limno to rheophil | -22.0 | -9.7 | 0.97 |
| *Physella acuta* (DRAPARNAUD 1805) | Gastropoda | 407 | 13 | common | hololimnic | river | indifferent | 53.3 | 38.8 | 0.98 |
| *Erpobdella octoculata* (LINNAEUS 1758) | Hirudinea | 2660 | 17 | common | hololimnic | generalist | indifferent | 0.7 | -8.2 | 0.94 |
| *Calopteryx haemorrhoidalis* (VAN DER LINDEN 1825) | Odonata | 75 | 5 | common | merolimnic | - | - | 302.6 | 207.6 | 0.98 |
| *Calopteryx virgo* (LINNAEUS 1758) | Odonata | 1935 | 16 | common | merolimnic | - | rheophil | 51.9 | 35.5 | 0.96 |
| *Gomphus pulchellus* SELYS 1840 | Odonata | 226 | 9 | common | merolimnic | - | limnophil | 25.0 | 18.8 | 0.96 |

## Appendix 1 continued

| Species | Taxonomic group | Presence records | Number of ecoregions | Rare species | Life cycle | Stream zonation | Current preference | CSA A2a (%) | CSA B2a (%) | TSS (WA) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Onychogomphus uncatus* (CHARPENTIER 1840) | Odonata | 72 | 7 | common | merolimnic | - | - | 144.0 | 119.0 | 0.95 |
| *Nais alpina* SPERBER 1948 | Oligochaeta | 103 | 7 | common | hololimnic | headwater | rheobiont | 98.9 | 98.9 | 0.96 |
| *Potamothrix bavaricus* (OSCHMAN 1913) | Oligochaeta | 151 | 7 | common | hololimnic | river | limno to rheophil | -35.5 | -1.9 | 1.00 |
| *Stylodrilus brachystylus* HRABE 1928 | Oligochaeta | 21 | 6 | common | hololimnic | - | limnophil | -82.8 | -80.8 | 0.98 |
| *Amphinemura sulcicollis* (STEPHENS 1836) | Plecoptera | 1804 | 16 | common | merolimnic | - | rheophil | -49.1 | -45.4 | 0.91 |
| *Amphinemura triangularis* (RIS 1902) | Plecoptera | 198 | 13 | common | merolimnic | - | rheophil | 50.2 | 56.1 | 0.96 |
| *Brachyptera risi* (MORTON 1896) | Plecoptera | 1593 | 15 | common | merolimnic | - | rheophil | -7.1 | -14.2 | 0.90 |
| *Brachyptera seticornis* (KLAPÁLEK 1902) | Plecoptera | 379 | 12 | common | merolimnic | - | rheophil | -3.2 | -11.3 | 0.96 |
| *Capnia bifrons* (NEWMAN 1839) | Plecoptera | 249 | 17 | rare | merolimnic | - | rheo to limnophil | 31.1 | 36.1 | 0.92 |
| *Chloroperla susemicheli* ZWICK 1967 | Plecoptera | 102 | 5 | common | merolimnic | - | rheophil | -2.4 | 5.3 | 0.98 |
| *Chloroperla tripunctata* (SCOPOLI 1763) | Plecoptera | 361 | 15 | rare | merolimnic | - | rheophil | 25.5 | 18.2 | 0.95 |
| *Dinocras cephalotes* (CURTIS 1827) | Plecoptera | 590 | 17 | rare | merolimnic | generalist | rheophil | -26.6 | -26.3 | 0.91 |
| *Dinocras megacephala* (KLAPÁLEK 1907) | Plecoptera | 77 | 10 | common | merolimnic | - | rheophil | 19.9 | 30.9 | 0.97 |
| *Diura bicaudata* (LINNAEUS 1758) | Plecoptera | 418 | 13 | rare | merolimnic | headwater | rheo to limnophil | -60.9 | -58.6 | 0.92 |
| *Diura nanseni* (KEMPNY 1900) | Plecoptera | 1309 | 5 | common | merolimnic | - | indifferent | -89.1 | -79.9 | 0.95 |
| *Hemimelaena flaviventris* (PICTET 1841) | Plecoptera | 22 | 2 | common | merolimnic | - | - | -32.6 | -9.0 | 0.97 |
| *Isoperla bipartita* AUBERT 1965 | Plecoptera | 19 | 1 | common | merolimnic | - | rheophil | -67.8 | -42.3 | 1.00 |
| *Isoperla grammatica* (PODA 1761) | Plecoptera | 2022 | 19 | common | merolimnic | - | rheophil | -28.9 | -32.1 | 0.89 |
| *Isoperla lugens* (KLAPÁLEK 1923) | Plecoptera | 46 | 2 | common | merolimnic | headwater | rheophil | -24.6 | -13.9 | 0.99 |
| *Isoperla oxylepis oxylepis* (DESPAX 1936) | Plecoptera | 151 | 11 | common | merolimnic | - | rheophil | 8.9 | 30.2 | 0.96 |
| *Isoperla rivulorum* (PICTET 1841) | Plecoptera | 147 | 7 | common | merolimnic | - | rheophil | -5.0 | 1.6 | 0.98 |
| *Isoperla sudetica* (KOLENATI 1859) | Plecoptera | 33 | 3 | common | merolimnic | - | rheophil | -41.7 | 0.7 | 0.98 |
| *Leuctra aurita* NAVÁS 1919 | Plecoptera | 83 | 6 | common | merolimnic | - | rheophil | -35.2 | -25.3 | 0.97 |
| *Leuctra autumnalis* AUBERT 1948 | Plecoptera | 75 | 4 | common | merolimnic | - | rheophil | -24.4 | -9.7 | 0.98 |
| *Leuctra braueri* KEMPNY 1898 | Plecoptera | 203 | 5 | common | merolimnic | headwater | rheo to limnophil | -38.3 | -30.3 | 0.98 |
| *Leuctra fusca fusca* (LINNAEUS, 1758) | Plecoptera | 1280 | 17 | rare | merolimnic | generalist | rheophil | -7.9 | -2.8 | 0.88 |
| *Leuctra geniculata* (STEPHENS 1836) | Plecoptera | 341 | 11 | common | merolimnic | river | rheophil | 53.5 | 33.7 | 0.96 |
| *Leuctra hippopus* KEMPNY 1899 | Plecoptera | 1268 | 20 | common | merolimnic | - | rheophil | -14.2 | -17.6 | 0.89 |
| *Leuctra inermis* KEMPNY 1899 | Plecoptera | 618 | 15 | common | merolimnic | - | rheophil | -15.4 | -17.4 | 0.96 |
| *Leuctra leptogaster* AUBERT 1949 | Plecoptera | 52 | 5 | common | merolimnic | - | rheophil | 3.8 | 14.3 | 0.97 |

## Appendix 1 continued

| Species | Taxonomic group | Presence records | Number of ecoregions | Rare species | Life cycle | Stream zonation | Current preference | CSA A2a (%) | CSA B2a (%) | TSS (WA) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Leuctra nigra* (OLIVIER 1811) | Plecoptera | 1158 | 18 | common | merolimnic | headwater | limno to rheophil | -46.9 | -44.0 | 0.90 |
| *Leuctra pseudocingulata* MENDL 1968 | Plecoptera | 15 | 3 | common | merolimnic | - | rheophil | -3.8 | -10.5 | 0.96 |
| *Leuctra rauscheri* AUBERT 1957 | Plecoptera | 120 | 10 | common | merolimnic | headwater | rheophil | -27.9 | -25.9 | 0.97 |
| *Leuctra teriolensis* KEMPNY 1900 | Plecoptera | 117 | 7 | common | merolimnic | - | - | -1.8 | 6.2 | 0.98 |
| *Nemoura cinerea cinerea* (RETZIUS 1783) | Plecoptera | 2801 | 21 | common | merolimnic | generalist | limnophil | -28.1 | -24.4 | 0.88 |
| *Nemoura lacustris* PICTET 1865 | Plecoptera | 24 | 3 | common | merolimnic | - | rheo to limnophil | 89.2 | 81.3 | 0.96 |
| *Nemoura marginata* PICTET 1835 | Plecoptera | 240 | 11 | common | merolimnic | headwater | rheophil | 6.7 | 18.8 | 0.96 |
| *Nemoura mortoni* RIS 1902 | Plecoptera | 87 | 4 | common | merolimnic | headwater | rheophil | -40.1 | -25.0 | 0.97 |
| *Nemoura sciurus* AUBERT 1949 | Plecoptera | 26 | 5 | common | merolimnic | headwater | rheo to limnophil | -82.1 | -75.1 | 0.98 |
| *Nemurella pictetii* KLAPÁLEK 1900 | Plecoptera | 1251 | 17 | rare | merolimnic | generalist | limnophil | -51.1 | -42.5 | 0.89 |
| *Perla burmeisteriana* CLAASSEN 1936 | Plecoptera | 118 | 10 | - | merolimnic | - | - | 40.6 | 49.5 | 0.96 |
| *Perla grandis* RAMBUR 1842 | Plecoptera | 64 | 6 | common | merolimnic | - | rheophil | -21.3 | -9.3 | 0.97 |
| *Perla marginata* (PANZER 1799) | Plecoptera | 345 | 15 | common | merolimnic | - | rheophil | 36.3 | 32.9 | 0.95 |
| *Perla pallida* GUERIN 1838 | Plecoptera | 86 | 9 | common | merolimnic | - | rheo to limnophil | 71.1 | 69.1 | 0.96 |
| *Protonemura auberti* ILLIES 1954 | Plecoptera | 301 | 14 | common | merolimnic | headwater | rheo to limnophil | -25.3 | -14.1 | 0.97 |
| *Protonemura intricata intricata* (RIS 1902) | Plecoptera | 400 | 18 | rare | merolimnic | - | rheophil | 60.2 | 74.5 | 0.95 |
| *Protonemura meyeri* (PICTET 1841) | Plecoptera | 1200 | 15 | common | merolimnic | - | rheophil | -39.4 | -45.0 | 0.92 |
| *Protonemura montana* KIMMINS 1941 | Plecoptera | 79 | 7 | rare | merolimnic | headwater | rheophil | -43.2 | -30.4 | 0.97 |
| *Protonemura nimborum* (RIS 1902) | Plecoptera | 107 | 7 | common | merolimnic | - | rheophil | -9.4 | -1.4 | 0.97 |
| *Protonemura nitida* (PICTET 1835) | Plecoptera | 220 | 10 | common | merolimnic | headwater | indifferent | -36.1 | -27.8 | 0.97 |
| *Protonemura praecox praecox* (MORTON 1894) | Plecoptera | 279 | 13 | common | merolimnic | headwater | rheophil | 0.4 | -7.6 | 0.96 |
| *Siphonoperla torrentium torrentium* (PICTET 1841) | Plecoptera | 521 | 15 | common | merolimnic | - | rheophil | -16.3 | -10.0 | 0.97 |
| *Taeniopteryx auberti* KIS & SOWA 1964 | Plecoptera | 62 | 6 | common | merolimnic | - | rheophil | -7.4 | -10.7 | 0.97 |
| *Taeniopteryx nebulosa* (LINNAEUS 1758) | Plecoptera | 996 | 14 | rare | merolimnic | river | rheo to limnophil | -63.4 | -60.8 | 0.89 |
| *Acrophylax zerberus* BRAUER 1867 | Trichoptera | 22 | 4 | common | merolimnic | headwater | indifferent | 58.7 | 57.1 | 0.95 |
| *Agapetus delicatulus* McLACHLAN 1884 | Trichoptera | 125 | 13 | common | merolimnic | - | rheophil | 136.4 | 108.0 | 0.95 |
| *Agapetus fuscipes* CURTIS 1834 | Trichoptera | 407 | 13 | common | merolimnic | headwater | rheophil | 10.5 | 1.7 | 0.95 |
| *Agapetus incertulus* McLACHLAN 1884 | Trichoptera | 17 | 1 | common | merolimnic | - | rheophil | 31.4 | 81.1 | 0.96 |
| *Agapetus nimbulus* McLACHLAN 1879 | Trichoptera | 45 | 4 | common | merolimnic | - | rheophil | 197.0 | 135.4 | 0.97 |
| *Allogamus auricollis* (PICTET 1834) | Trichoptera | 317 | 10 | common | merolimnic | - | rheophil | -44.4 | -34.8 | 0.96 |

## Appendix 1 continued

| Species | Taxonomic group | Presence records | Number of ecoregions | Rare species | Life cycle | Stream zonation | Current preference | CSA A2a (%) | CSA B2a (%) | TSS (WA) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Anabolia nervosa* (CURTIS 1834) | Trichoptera | 1373 | 11 | rare | merolimnic | river | limnophil | -53.5 | -45.8 | 0.95 |
| *Anomalopterygella chauviniana* (STEIN 1874) | Trichoptera | 333 | 6 | common | merolimnic | - | rheophil | -82.3 | -81.7 | 0.98 |
| *Athripsodes albifrons* (LINNAEUS 1758) | Trichoptera | 368 | 14 | rare | merolimnic | - | rheo to limnophil | 41.8 | 45.8 | 0.94 |
| *Athripsodes tavaresi* (NAVÁS 1916) | Trichoptera | 20 | 1 | common | merolimnic | - | - | -77.6 | -63.8 | 1.00 |
| *Brachycentrus montanus* KLAPÁLEK 1892 | Trichoptera | 57 | 10 | common | merolimnic | - | rheobiont | 28.4 | 42.9 | 0.95 |
| *Ceraclea dissimilis* (STEPHENS 1836) | Trichoptera | 525 | 14 | common | merolimnic | river | rheophil | 5.1 | 18.6 | 0.89 |
| *Chaetopteryx fusca* BRAUER 1857 | Trichoptera | 31 | 5 | common | merolimnic | - | rheo to limnophil | 15.4 | 22.8 | 0.98 |
| *Chaetopteryx major* McLACHLAN 1876 | Trichoptera | 38 | 6 | common | merolimnic | headwater | rheo to limnophil | -35.8 | -20.5 | 0.98 |
| *Chaetopteryx villosa villosa* (FABRICIUS 1798) | Trichoptera | 763 | 12 | common | merolimnic | generalist | rheo to limnophil | 9.8 | 11.8 | 0.94 |
| *Drusus annulatus* (STEPHENS 1837) | Trichoptera | 433 | 7 | common | merolimnic | headwater | rheophil | -58.7 | -55.3 | 0.97 |
| *Drusus discolor* (RAMBUR 1842) | Trichoptera | 103 | 9 | common | merolimnic | headwater | rheophil | -15.8 | -7.5 | 0.96 |
| *Ecclisopteryx dalecarlica* KOLENATI 1848 | Trichoptera | 110 | 8 | rare | merolimnic | generalist | rheophil | -20.1 | -12.0 | 0.95 |
| *Ecclisopteryx madida* (McLACHLAN 1867) | Trichoptera | 57 | 4 | common | merolimnic | - | rheophil | 4.4 | -2.6 | 0.97 |
| *Glossosoma conformis* NEBOISS 1963 | Trichoptera | 249 | 10 | rare | merolimnic | - | rheophil | 44.4 | 37.1 | 0.95 |
| *Glossosoma privatum* McLACHLAN 1884 | Trichoptera | 30 | 1 | common | merolimnic | - | rheophil | -78.0 | -63.1 | 1.00 |
| *Halesus digitatus digitatus* (SCHRANK 1781) | Trichoptera | 480 | 16 | common | merolimnic | - | limno to rheophil | 17.1 | 39.4 | 0.91 |
| *Halesus radiatus* (CURTIS 1834) | Trichoptera | 797 | 16 | common | merolimnic | - | limno to rheophil | 9.2 | 23.6 | 0.90 |
| *Halesus rubricollis* (PICTET 1834) | Trichoptera | 42 | 4 | common | merolimnic | headwater | rheo to limnophil | -4.1 | -1.0 | 0.98 |
| *Hydropsyche bulbifera* McLACHLAN 1878 | Trichoptera | 158 | 10 | common | merolimnic | river | rheophil | 126.5 | 116.0 | 0.94 |
| *Hydropsyche dinarica* MARINKOVIC 1979 | Trichoptera | 154 | 11 | common | merolimnic | - | rheophil | 36.7 | 20.6 | 0.96 |
| *Hydropsyche exocellata* DUFOUR 1841 | Trichoptera | 117 | 8 | rare | merolimnic | river | rheophil | 159.0 | 125.7 | 0.95 |
| *Hydropsyche fulvipes* (CURTIS 1834) | Trichoptera | 93 | 10 | rare | merolimnic | headwater | rheophil | -9.7 | -12.8 | 0.96 |
| *Hydropsyche incognita* PITSCH 1993 | Trichoptera | 329 | 10 | common | merolimnic | - | rheophil | 52.8 | 55.5 | 0.94 |
| *Hydropsyche infernalis* SCHMID 1952 | Trichoptera | 29 | 1 | common | merolimnic | headwater | rheophil | 4.1 | 23.4 | 0.99 |
| *Hydropsyche instabilis* (CURTIS 1834) | Trichoptera | 848 | 14 | common | merolimnic | - | rheophil | 75.5 | 59.3 | 0.93 |
| *Hydropsyche lobata* McLACHLAN 1884 | Trichoptera | 56 | 1 | common | merolimnic | river | rheophil | -2.3 | 10.9 | 0.99 |
| *Hydropsyche pellucidula* (CURTIS 1834) | Trichoptera | 1907 | 16 | common | merolimnic | - | rheophil | 15.7 | 9.7 | 0.88 |
| *Hydropsyche saxonica* McLACHLAN 1884 | Trichoptera | 432 | 12 | rare | merolimnic | - | rheophil | -23.3 | -13.3 | 0.92 |
| *Hydropsyche siltalai* DÖHLER 1963 | Trichoptera | 2415 | 16 | common | merolimnic | - | rheophil | -4.7 | -6.7 | 0.90 |
| *Hydropsyche tenuis* NAVÁS 1932 | Trichoptera | 92 | 7 | common | merolimnic | - | rheophil | 10.4 | 12.7 | 0.95 |

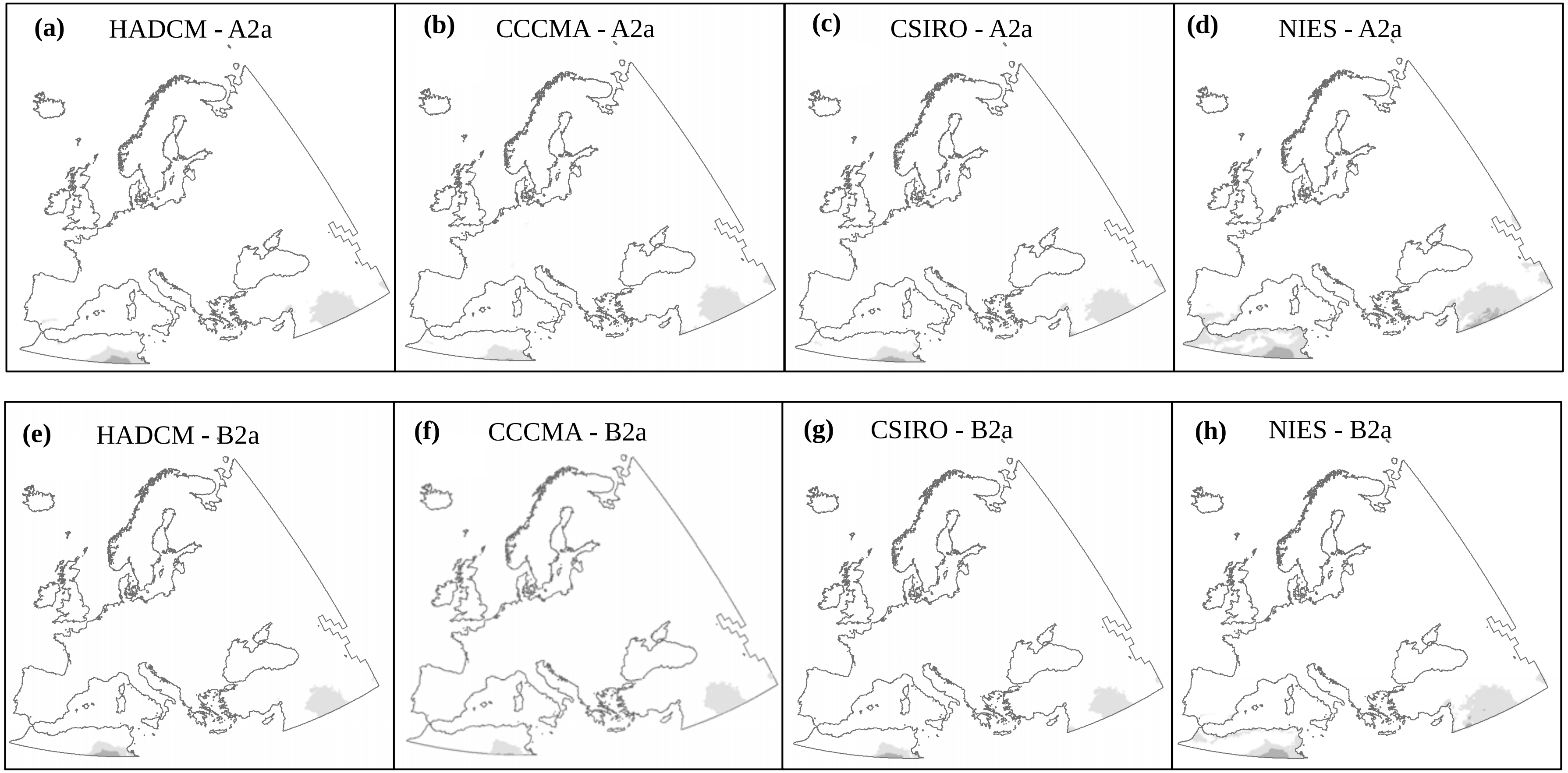
## Appendix 1 continued

| Species | Taxonomic group | Presence records | Number of ecoregions | Rare species | Life cycle | Stream zonation | Current preference | CSA A2a (%) | CSA B2a (%) | TSS (WA) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Hydroptila fuentaldeala* SCHMID 1952 | Trichoptera | 25 | 1 | common | merolimnic | - | - | -70.4 | -47.6 | 1.00 |
| *Hydroptila idefix* MALICKY 1979 | Trichoptera | 36 | 1 | common | merolimnic | - | - | -72.5 | -56.2 | 1.00 |
| *Larcasia partita* NAVÁS 1917 | Trichoptera | 19 | 1 | common | merolimnic | - | rheophil | -42.8 | -26.4 | 1.00 |
| *Lepidostoma hirtum* (FABRICIUS 1775) | Trichoptera | 2064 | 17 | common | merolimnic | - | limno to rheophil | -15.2 | -15.7 | 0.88 |
| *Limnephilus marmoratus* CURTIS 1834 | Trichoptera | 470 | 12 | common | merolimnic | - | limnophil | -3.8 | -7.2 | 0.96 |
| *Lype reducta* (HAGEN 1868) | Trichoptera | 571 | 15 | rare | merolimnic | - | indifferent | 66.4 | 55.1 | 0.91 |
| *Melampophylax melampus* (McLACHLAN 1867) | Trichoptera | 77 | 3 | common | merolimnic | - | rheophil | 35.3 | 31.4 | 0.96 |
| *Melampophylax mucoreus* (HAGEN 1861) | Trichoptera | 132 | 5 | common | merolimnic | - | rheophil | -82.6 | -78.9 | 0.97 |
| *Metanoea rhaetica* SCHMID 1955 | Trichoptera | 40 | 4 | common | merolimnic | - | rheobiont | 10.1 | 16.0 | 0.98 |
| *Micrasema longulum* McLACHLAN 1876 | Trichoptera | 134 | 6 | common | merolimnic | - | rheobiont | -70.1 | -62.1 | 0.98 |
| *Micrasema minimum* McLACHLAN 1876 | Trichoptera | 173 | 11 | rare | merolimnic | - | rheobiont | 72.6 | 65.6 | 0.94 |
| *Mystacides azurea* (LINNAEUS 1761) | Trichoptera | 1295 | 16 | common | merolimnic | river | limnophil | 56.6 | 65.5 | 0.86 |
| *Odontocerum albicorne* (SCOPOLI 1763) | Trichoptera | 1534 | 15 | common | merolimnic | - | rheophil | 46.5 | 27.4 | 0.96 |
| *Oecismus monedula monedula* (HAGEN 1859) | Trichoptera | 77 | 7 | common | merolimnic | - | rheophil | 16.8 | 6.2 | 0.97 |
| *Oxyethira archaica* MALICKY 1975 | Trichoptera | 28 | 1 | common | merolimnic | - | - | -69.7 | -55.3 | 1.00 |
| *Philopotamus ludificatus* McLACHLAN 1878 | Trichoptera | 226 | 9 | common | merolimnic | - | limno to rheophil | 34.8 | 30.5 | 0.96 |
| *Philopotamus variegatus variegatus* (SCOPOLI 1763) | Trichoptera | 149 | 9 | rare | merolimnic | - | limno to rheophil | 149.6 | 117.8 | 0.94 |
| *Plectrocnemia conspersa conspersa* (CURTIS 1834) | Trichoptera | 1098 | 15 | common | merolimnic | - | limno to rheophil | 39.9 | 46.9 | 0.90 |
| *Polycentropus excisus* KLAPÁLEK 1894 | Trichoptera | 102 | 6 | common | merolimnic | - | limno to rheophil | 234.1 | 163.3 | 0.96 |
| *Polycentropus flavomaculatus flavomaculatus* (PICTET 1834) | Trichoptera | 3080 | 18 | common | merolimnic | river | limno to rheophil | -25.9 | -28.4 | 0.86 |
| *Polycentropus telifer* McLACHLAN 1884 | Trichoptera | 46 | 1 | common | merolimnic | - | limno to rheophil | -62.8 | -45.1 | 1.00 |
| *Potamophylax latipennis* (CURTIS 1834) | Trichoptera | 611 | 16 | common | merolimnic | generalist | rheo to limnophil | -55.2 | -44.1 | 0.91 |
| *Potamophylax rotundipennis* (BRAUER 1857) | Trichoptera | 269 | 11 | common | merolimnic | - | rheo to limnophil | -51.7 | -23.9 | 0.94 |
| *Pseudopsilopteryx zimmeri* (McLACHLAN 1876) | Trichoptera | 35 | 5 | common | merolimnic | headwater | limno to rheophil | -29.2 | -41.3 | 0.98 |
| *Psychomyia ctenophora* McLACHLAN 1884 | Trichoptera | 46 | 1 | common | merolimnic | river | rheo to limnophil | -69.4 | -53.7 | 1.00 |
| *Psychomyia pusilla* (FABRICIUS 1781) | Trichoptera | 912 | 17 | common | merolimnic | river | rheo to limnophil | 108.2 | 93.9 | 0.90 |
| *Rhyacophila adjuncta* McLACHLAN 1884 | Trichoptera | 47 | 1 | common | merolimnic | - | rheobiont | -69.4 | -42.1 | 1.00 |
| *Rhyacophila aurata* BRAUER 1857 | Trichoptera | 62 | 6 | common | merolimnic | - | rheobiont | 12.6 | 18.5 | 0.97 |
| *Rhyacophila dorsalis nevada* SCHMID 1952 | Trichoptera | 17 | 1 | common | merolimnic | - | rheobiont | 33.2 | 30.5 | 0.97 |

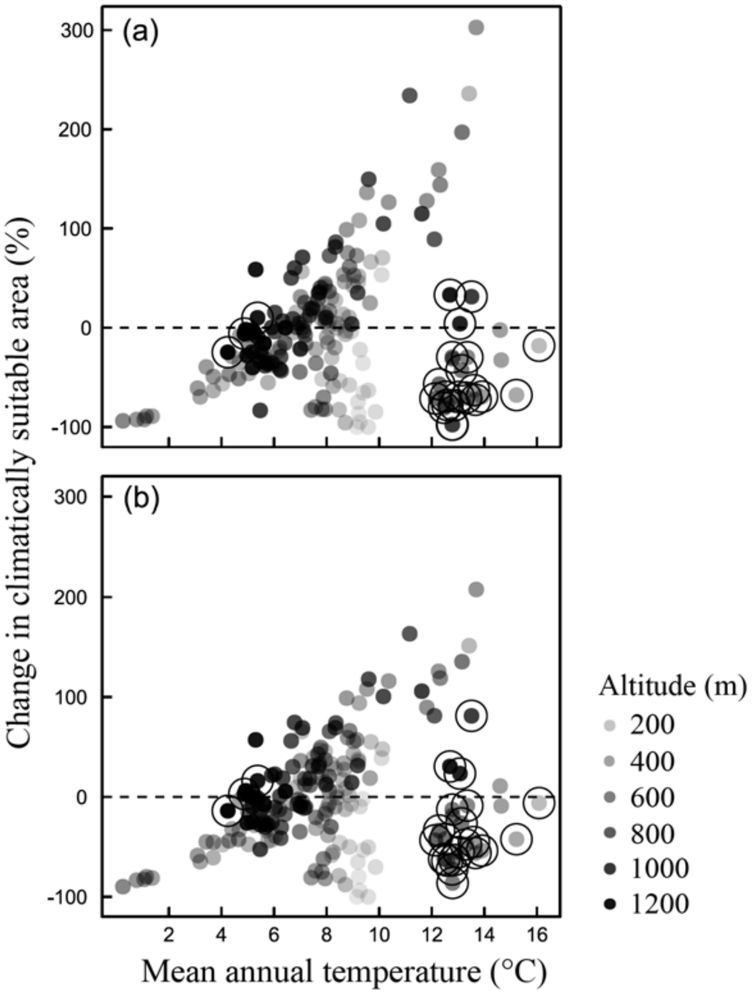
## Appendix 1 continued

| Species | Taxonomic group | Presence records | Number of ecoregions | Rare species | Life cycle | Stream zonation | Current preference | CSA A2a (%) | CSA B2a (%) | TSS (WA) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Rhyacophila glareosa* McLACHLAN 1867 | Trichoptera | 26 | 5 | common | merolimnic | - | rheobiont | 0.3 | 21.6 | 0.99 |
| *Rhyacophila intermedia* McLACHLAN 1868 | Trichoptera | 81 | 8 | common | merolimnic | headwater | rheobiont | 0.0 | 5.6 | 0.96 |
| *Rhyacophila lusitanica* McLACHLAN 1884 | Trichoptera | 38 | 1 | common | merolimnic | - | rheobiont | -29.7 | -8.7 | 1.00 |
| *Rhyacophila meridionalis* PICTET 1865 | Trichoptera | 33 | 3 | common | merolimnic | - | rheobiont | 114.9 | 105.8 | 0.95 |
| *Rhyacophila nubila* (ZETTERSTEDT 1840) | Trichoptera | 2226 | 14 | common | merolimnic | - | rheobiont | -69.6 | -64.8 | 0.89 |
| *Rhyacophila praemorsa* McLACHLAN 1879 | Trichoptera | 47 | 7 | common | merolimnic | - | rheobiont | -45.8 | -29.9 | 0.97 |
| *Rhyacophila pubescens* PICTET 1834 | Trichoptera | 103 | 8 | common | merolimnic | headwater | rheobiont | 81.5 | 69.3 | 0.95 |
| *Rhyacophila relicta* McLACHLAN 1879 | Trichoptera | 44 | 2 | common | merolimnic | - | rheobiont | -29.6 | -12.6 | 1.00 |
| *Rhyacophila stigmatica* KOLENATI 1859 | Trichoptera | 50 | 5 | common | merolimnic | headwater | rheobiont | -5.9 | 3.0 | 0.97 |
| *Rhyacophila tristis* PICTET 1834 | Trichoptera | 317 | 13 | common | merolimnic | - | rheobiont | 86.2 | 74.0 | 0.92 |
| *Schizopelex festiva* (RAMBUR 1842) | Trichoptera | 58 | 1 | common | merolimnic | headwater | - | -31.3 | -18.8 | 1.00 |
| *Sericostoma flavicorne* SCHNEIDER 1845 | Trichoptera | 153 | 9 | common | merolimnic | generalist | limno to rheophil | 61.2 | 66.2 | 0.95 |
| *Sericostoma personatum* KIRBY & SPENCER 1826 | Trichoptera | 1769 | 16 | common | merolimnic | headwater | limno to rheophil | -46.0 | -47.6 | 0.90 |
| *Sericostoma vittatum* RAMBUR 1842 | Trichoptera | 21 | 1 | common | merolimnic | headwater | - | -56.8 | -33.6 | 1.00 |
| *Silo nigricornis* (PICTET 1834) | Trichoptera | 315 | 12 | common | merolimnic | - | rheophil | 42.1 | 43.1 | 0.95 |
| *Silo pallipes* (FABRICIUS 1781) | Trichoptera | 939 | 14 | common | merolimnic | - | rheophil | -37.7 | -39.3 | 0.91 |
| *Synagapetus iridipennis* McLACHLAN 1879 | Trichoptera | 41 | 4 | common | merolimnic | headwater | rheo to limnophil | 104.9 | 100.5 | 0.95 |
| *Thremma tellae* GONZÁLEZ 1978 | Trichoptera | 47 | 1 | common | merolimnic | headwater | rheophil | -71.2 | -43.4 | 1.00 |
| *Tinodes maclachlani* KIMMINS 1966 | Trichoptera | 153 | 8 | common | merolimnic | - | rheophil | 127.9 | 89.6 | 0.96 |
| *Wormaldia beaumonti* SCHMID 1952 | Trichoptera | 20 | 1 | common | merolimnic | - | rheo to limnophil | -97.6 | -86.1 | 1.00 |
| *Wormaldia corvina* (McLACHLAN 1884) | Trichoptera | 27 | 1 | common | merolimnic | headwater | rheo to limnophil | -97.5 | -72.6 | 1.00 |
| *Wormaldia lusitanica* GONZÁLEZ & BOTOSANEANU 1983 | Trichoptera | 25 | 1 | common | merolimnic | - | rheo to limnophil | -80.6 | -62.0 | 1.00 |
| *Dugesia tigrina* (GIRARD 1850) | Turbellaria | 391 | 7 | common | hololimnic | - | limno to rheophil | -65.4 | -53.2 | 0.99 |

**Appendix 2** Non-analogue climates of the four future climate projections used for the A2a and B2a emission scenarios. Increasing intensities of grey represent a higher number of predictors whose values range beyond those of the baseline. White areas represent analogue climates, i.e. values of predictors which lie within the range of the baseline.



**Appendix 3** 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. Increasing intensity of greyscale represents increasing mean altitudes of species' presence records. Circles mark endemic species.



**Appendix 4** Stream macroinvertebrates that were modelled successfully for all of the modelling designs and were thus considered for further analyses (n=224). The species information is presented with the corresponding taxonomic group, the number of species records for calibrating the models on the entire area and number of records that fall into the study area, the accuracy in the study area, and the TSS consensus scores for each modelling design in the entire area for calibrating the models.

| | | | | Accuracy | | | TSS score | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Taxonomic group | Presence records total | Presence records study area | Landscape / Landscape masked | Stream network | Stream network corrected | Landscape / Landscape masked | Stream network | Stream network corrected |
| *Anodonta anatina* (LINNAEUS, 1758) | Bivalvia | 47 | 27 | 0.96 | 0.96 | 0.96 | 0.945 | 0.969 | 0.959 |
| *Corbicula fluminea* (O.F. MÜLLER, 1774) | Bivalvia | 67 | 46 | 1.00 | 1.00 | 1.00 | 0.991 | 0.980 | 0.977 |
| *Dreissena polymorpha* (PALLAS, 1771) | Bivalvia | 76 | 27 | 0.93 | 0.93 | 0.96 | 0.918 | 0.941 | 0.968 |
| *Pisidium amnicum* (O.F. MÜLLER, 1774) | Bivalvia | 173 | 78 | 0.99 | 1.00 | 0.97 | 0.925 | 0.920 | 0.920 |
| *Pisidium henslowanum* (SHEPPARD, 1823) | Bivalvia | 123 | 23 | 0.96 | 0.83 | 0.96 | 0.956 | 0.956 | 0.973 |
| *Pisidium nitidum* JENYNS, 1832 | Bivalvia | 107 | 35 | 1.00 | 1.00 | 1.00 | 0.980 | 0.968 | 0.974 |
| *Pisidium personatum* MALM, 1855 | Bivalvia | 26 | 19 | 1.00 | 1.00 | 1.00 | 0.984 | 0.987 | 0.968 |
| *Pisidium subtruncatum* MALM, 1855 | Bivalvia | 228 | 93 | 0.97 | 0.96 | 0.97 | 0.969 | 0.970 | 0.960 |
| *Pisidium supinum* A. SCHMIDT, 1851 | Bivalvia | 60 | 31 | 1.00 | 1.00 | 1.00 | 0.973 | 0.964 | 0.987 |
| *Sphaerium corneum* (LINNAEUS, 1758) | Bivalvia | 846 | 468 | 0.92 | 0.91 | 0.89 | 0.896 | 0.906 | 0.890 |
| *Asellus aquaticus* (LINNAEUS, 1758) | Crustacea | 1600 | 942 | 0.92 | 0.94 | 0.93 | 0.874 | 0.858 | 0.852 |
| *Corophium curvispinum* SARS, 1895 | Crustacea | 75 | 28 | 0.96 | 0.96 | 1.00 | 0.989 | 0.986 | 0.990 |
| *Dikerogammarus villosus* (SOWINSKY, 1894) | Crustacea | 139 | 50 | 0.94 | 0.94 | 0.98 | 0.962 | 0.967 | 0.973 |
| *Echinogammarus berilloni* (CATTA, 1878) | Crustacea | 67 | 50 | 1.00 | 1.00 | 1.00 | 0.995 | 0.993 | 0.993 |
| *Echinogammarus ischnus* (STEBBING, 1906) | Crustacea | 14 | 11 | 1.00 | 1.00 | 1.00 | 0.989 | 0.984 | 0.988 |
| *Gammarus fossarum* KOCH in PANZER, 1836 | Crustacea | 1237 | 922 | 0.95 | 0.97 | 0.94 | 0.912 | 0.894 | 0.898 |
| *Gammarus pulex* (LINNAEUS, 1758) | Crustacea | 2145 | 1302 | 0.91 | 0.92 | 0.92 | 0.870 | 0.854 | 0.875 |
| *Gammarus roeselii* (GERVAIS, 1835) | Crustacea | 1362 | 890 | 0.94 | 0.96 | 0.95 | 0.924 | 0.913 | 0.925 |
| *Gammarus tigrinus* SEXTON, 1939 | Crustacea | 63 | 31 | 1.00 | 1.00 | 1.00 | 0.983 | 0.983 | 0.977 |
| *Jaera istri* (VIEUILLE, 1979) | Crustacea | 83 | 29 | 0.93 | 0.93 | 1.00 | 0.982 | 0.977 | 0.994 |

## Appendix 4 continued

| | | | | Accuracy | | | TSS score | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Taxonomic group | Presence records total | Presence records study area | Landscape / Landscape masked | Stream network | Stream network corrected | Landscape / Landscape masked | Stream network | Stream network corrected |
| *Orconectes limosus* (RAFINESQUE, 1817) | Crustacea | 67 | 37 | 0.97 | 0.97 | 0.97 | 0.956 | 0.947 | 0.971 |
| *Proasellus coxalis* (DOLLFUS, 1892) | Crustacea | 191 | 137 | 0.97 | 0.96 | 0.94 | 0.949 | 0.938 | 0.936 |
| *Brillia bifida* (KIEFFER, 1909) | Diptera | 29 | 20 | 1.00 | 1.00 | 1.00 | 0.985 | 0.981 | 0.977 |
| *Chironomus obtusidens* GOETGHEBUER, 1921 | Diptera | 18 | 14 | 1.00 | 1.00 | 1.00 | 0.951 | 0.927 | 0.921 |
| *Chironomus plumosus* (LINNAEUS, 1758) | Diptera | 22 | 20 | 0.90 | 0.90 | 0.90 | 0.963 | 0.945 | 0.916 |
| *Chironomus riparius* MEIGEN, 1804 | Diptera | 44 | 36 | 1.00 | 0.97 | 0.97 | 0.960 | 0.961 | 0.964 |
| *Diamesa insignipes* KIEFFER in KIEFFER & THIENEMANN, 1908 | Diptera | 30 | 25 | 1.00 | 1.00 | 1.00 | 0.987 | 0.985 | 0.989 |
| *Microtendipes chloris* (MEIGEN, 1818) | Diptera | 32 | 24 | 1.00 | 1.00 | 0.96 | 0.992 | 0.981 | 0.958 |
| *Polypedilum convictum* (WALKER, 1856) | Diptera | 20 | 18 | 1.00 | 1.00 | 1.00 | 0.983 | 0.985 | 0.968 |
| *Prodiamesa olivacea* (MEIGEN, 1818) | Diptera | 1236 | 837 | 0.90 | 0.91 | 0.92 | 0.876 | 0.864 | 0.868 |
| *Rheocricotopus fuscipes* (KIEFFER, 1909) | Diptera | 24 | 18 | 1.00 | 1.00 | 1.00 | 0.974 | 0.978 | 0.963 |
| *Tvetenia discoloripes* (GOETGHEBUER in THIENEMANN, 1936) | Diptera | 30 | 30 | 1.00 | 1.00 | 0.97 | 0.991 | 0.992 | 0.989 |
| *Baetis alpinus* (PICTET, 1843) | Ephemeroptera | 185 | 154 | 0.96 | 0.94 | 0.97 | 0.958 | 0.957 | 0.953 |
| *Baetis buceratus* EATON, 1870 | Ephemeroptera | 98 | 63 | 0.94 | 0.92 | 0.94 | 0.913 | 0.893 | 0.968 |
| *Baetis fuscatus* (LINNAEUS, 1761) | Ephemeroptera | 555 | 392 | 0.91 | 0.88 | 0.90 | 0.896 | 0.870 | 0.914 |
| *Baetis liebenauae* KEFFERMÜLLER, 1974 | Ephemeroptera | 37 | 27 | 1.00 | 1.00 | 1.00 | 0.989 | 0.982 | 0.989 |
| *Baetis lutheri* MÜLLER-LIEBENAU, 1967 | Ephemeroptera | 395 | 302 | 0.94 | 0.96 | 0.94 | 0.929 | 0.917 | 0.924 |
| *Baetis melanonyx* (PICTET, 1843) | Ephemeroptera | 73 | 70 | 0.97 | 0.97 | 0.99 | 0.985 | 0.982 | 0.981 |
| *Baetis muticus* (LINNAEUS, 1758) | Ephemeroptera | 279 | 198 | 0.92 | 0.93 | 0.94 | 0.941 | 0.931 | 0.937 |
| *Baetis nexus* NAVÁS, 1918 | Ephemeroptera | 29 | 29 | 0.97 | 0.97 | 0.97 | 0.996 | 0.995 | 0.996 |
| *Baetis niger* (LINNAEUS, 1761) | Ephemeroptera | 142 | 109 | 1.00 | 0.99 | 0.99 | 0.977 | 0.975 | 0.975 |
| *Baetis rhodani* (PICTET, 1843) | Ephemeroptera | 2404 | 1613 | 0.90 | 0.92 | 0.89 | 0.871 | 0.844 | 0.852 |
| *Baetis scambus* EATON, 1870 | Ephemeroptera | 358 | 269 | 0.86 | 0.88 | 0.92 | 0.915 | 0.893 | 0.912 |
| *Baetis vardarensis* IKONOMOV, 1962 | Ephemeroptera | 86 | 64 | 1.00 | 0.98 | 0.97 | 0.967 | 0.953 | 0.977 |

## Appendix 4 continued

| | | | | Accuracy | | | TSS score | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Taxonomic group | Presence records total | Presence records study area | Landscape / Landscape masked | Stream network | Stream network corrected | Landscape / Landscape masked | Stream network | Stream network corrected |
| *Baetis vernus* CURTIS, 1834 | Ephemeroptera | 938 | 631 | 0.90 | 0.90 | 0.91 | 0.884 | 0.864 | 0.867 |
| *Caenis horaria* (LINNAEUS, 1758) | Ephemeroptera | 161 | 47 | 0.77 | 0.70 | 0.72 | 0.923 | 0.913 | 0.929 |
| *Caenis luctuosa* (BURMEISTER, 1839) | Ephemeroptera | 266 | 158 | 0.95 | 0.93 | 0.94 | 0.905 | 0.884 | 0.915 |
| *Caenis macrura* STEPHENS, 1835 | Ephemeroptera | 116 | 78 | 0.91 | 0.91 | 0.99 | 0.948 | 0.931 | 0.964 |
| *Caenis rivulorum* EATON, 1884 | Ephemeroptera | 74 | 63 | 0.81 | 0.84 | 0.92 | 0.942 | 0.966 | 0.926 |
| *Centroptilum luteolum* (MÜLLER, 1776) | Ephemeroptera | 509 | 339 | 0.92 | 0.91 | 0.92 | 0.902 | 0.866 | 0.881 |
| *Cloeon dipterum* (LINNAEUS, 1761) | Ephemeroptera | 154 | 87 | 0.89 | 0.88 | 0.88 | 0.923 | 0.881 | 0.931 |
| *Ecdyonurus dispar* (CURTIS, 1834) | Ephemeroptera | 96 | 80 | 0.95 | 0.90 | 1.00 | 0.968 | 0.965 | 0.973 |
| *Ecdyonurus insignis* (EATON, 1870) | Ephemeroptera | 29 | 26 | 0.96 | 0.92 | 1.00 | 0.984 | 0.974 | 0.985 |
| *Ecdyonurus macani* THOMAS & SOWA, 1970 | Ephemeroptera | 29 | 24 | 1.00 | 1.00 | 1.00 | 0.991 | 0.993 | 0.988 |
| *Ecdyonurus submontanus* LANDA, 1969 | Ephemeroptera | 38 | 30 | 1.00 | 1.00 | 1.00 | 0.976 | 0.984 | 0.982 |
| *Ecdyonurus torrentis* KIMMINS, 1942 | Ephemeroptera | 285 | 238 | 0.92 | 0.96 | 0.96 | 0.953 | 0.944 | 0.946 |
| *Ecdyonurus venosus* (FABRICIUS, 1775) | Ephemeroptera | 360 | 265 | 0.90 | 0.92 | 0.94 | 0.926 | 0.907 | 0.929 |
| *Electrogena affinis* (EATON, 1883) | Ephemeroptera | 39 | 23 | 1.00 | 1.00 | 1.00 | 0.995 | 0.996 | 0.989 |
| *Electrogena ujhelyii* (SOWA, 1981) | Ephemeroptera | 58 | 52 | 0.98 | 0.96 | 0.96 | 0.977 | 0.974 | 0.982 |
| *Epeorus assimilis* EATON, 1885 | Ephemeroptera | 497 | 410 | 0.97 | 0.97 | 0.97 | 0.948 | 0.937 | 0.936 |
| *Epeorus sylvicola* (PICTET, 1865) | Ephemeroptera | 57 | 32 | 1.00 | 1.00 | 1.00 | 0.987 | 0.981 | 0.981 |
| *Ephemera danica* MÜLLER, 1764 | Ephemeroptera | 1179 | 750 | 0.90 | 0.94 | 0.91 | 0.867 | 0.851 | 0.842 |
| *Ephemera vulgata* LINNAEUS, 1758 | Ephemeroptera | 51 | 17 | 0.76 | 0.76 | 0.88 | 0.925 | 0.907 | 0.969 |
| *Ephemerella mucronata* (BENGTSSON, 1909) | Ephemeroptera | 373 | 290 | 0.94 | 0.93 | 0.96 | 0.946 | 0.935 | 0.931 |
| *Habroleptoides confusa* SARTORI & JACOB, 1986 | Ephemeroptera | 629 | 455 | 0.95 | 0.93 | 0.95 | 0.931 | 0.922 | 0.925 |
| *Habroleptoides modesta* (HAGEN, 1864) | Ephemeroptera | 14 | 13 | 1.00 | 1.00 | 1.00 | 0.999 | 0.999 | 0.995 |
| *Habrophlebia lauta* EATON, 1884 | Ephemeroptera | 429 | 337 | 0.94 | 0.93 | 0.95 | 0.938 | 0.929 | 0.933 |
| *Heptagenia flava* ROSTOCK, 1878 | Ephemeroptera | 92 | 44 | 0.89 | 0.93 | 1.00 | 0.960 | 0.961 | 0.963 |

## Appendix 4 continued

| | | | | Accuracy | | | TSS score | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Taxonomic group | Presence records total | Presence records study area | Landscape / Landscape masked | Stream network | Stream network corrected | Landscape / Landscape masked | Stream network | Stream network corrected |
| *Heptagenia sulphurea* (MÜLLER, 1776) | Ephemeroptera | 253 | 116 | 0.92 | 0.94 | 0.94 | 0.938 | 0.933 | 0.923 |
| *Oligoneuriella rhenana* (IMHOFF, 1852) | Ephemeroptera | 24 | 17 | 1.00 | 1.00 | 1.00 | 0.992 | 0.991 | 0.988 |
| *Paraleptophlebia submarginata* (STEPHENS, 1835) | Ephemeroptera | 221 | 154 | 0.97 | 0.96 | 0.94 | 0.944 | 0.933 | 0.935 |
| *Potamanthus luteus* (LINNAEUS, 1767) | Ephemeroptera | 117 | 73 | 0.97 | 0.96 | 0.99 | 0.972 | 0.960 | 0.975 |
| *Procloeon bifidum* (BENGTSSON, 1912) | Ephemeroptera | 93 | 62 | 0.95 | 0.97 | 0.97 | 0.968 | 0.962 | 0.968 |
| *Procloeon pennulatum* (EATON, 1870) | Ephemeroptera | 16 | 15 | 1.00 | 1.00 | 1.00 | 0.988 | 0.974 | 0.984 |
| *Rhithrogena diaphana* NAVÁS, 1917 | Ephemeroptera | 21 | 19 | 1.00 | 1.00 | 1.00 | 0.992 | 0.991 | 0.993 |
| *Rhithrogena germanica* EATON, 1885 | Ephemeroptera | 19 | 19 | 0.95 | 1.00 | 1.00 | 0.995 | 0.995 | 0.979 |
| *Rhithrogena hercynia* LANDA, 1969 | Ephemeroptera | 16 | 16 | 1.00 | 1.00 | 1.00 | 0.993 | 0.987 | 0.976 |
| *Rhithrogena picteti* SOWA, 1971 | Ephemeroptera | 62 | 60 | 1.00 | 1.00 | 0.97 | 0.967 | 0.967 | 0.958 |
| *Rhithrogena puytoraci* SOWA & DEGRANGE, 1987 | Ephemeroptera | 19 | 19 | 1.00 | 1.00 | 0.89 | 0.998 | 0.997 | 0.983 |
| *Rhithrogena semicolorata* (CURTIS, 1834) | Ephemeroptera | 367 | 286 | 0.94 | 0.92 | 0.93 | 0.943 | 0.933 | 0.936 |
| *Serratella ignita* (PODA, 1761) | Ephemeroptera | 1035 | 749 | 0.91 | 0.92 | 0.89 | 0.884 | 0.854 | 0.892 |
| *Torleya major* (KLAPÁLEK, 1905) | Ephemeroptera | 535 | 356 | 0.97 | 0.97 | 0.94 | 0.937 | 0.931 | 0.919 |
| *Ancylus fluviatilis* O.F. MÜLLER, 1774 | Gastropoda | 1484 | 1033 | 0.91 | 0.93 | 0.90 | 0.891 | 0.863 | 0.875 |
| *Anisus vortex* (LINNAEUS, 1758) | Gastropoda | 151 | 46 | 0.91 | 0.91 | 0.93 | 0.931 | 0.912 | 0.951 |
| *Bithynia tentaculata* (LINNAEUS, 1758) | Gastropoda | 555 | 292 | 0.95 | 0.92 | 0.93 | 0.908 | 0.881 | 0.906 |
| *Galba truncatula* (O.F. MÜLLER, 1774) | Gastropoda | 72 | 51 | 0.90 | 0.88 | 0.88 | 0.941 | 0.895 | 0.893 |
| *Lymnaea stagnalis* (LINNAEUS, 1758) | Gastropoda | 107 | 42 | 0.90 | 0.90 | 0.98 | 0.938 | 0.934 | 0.948 |
| *Physa fontinalis* (LINNAEUS, 1758) | Gastropoda | 159 | 88 | 0.93 | 0.88 | 0.97 | 0.922 | 0.934 | 0.924 |
| *Physella acuta* (DRAPARNAUD, 1805) | Gastropoda | 62 | 42 | 0.88 | 0.88 | 0.88 | 0.964 | 0.959 | 0.907 |
| *Planorbis planorbis* (LINNAEUS, 1758) | Gastropoda | 61 | 21 | 0.90 | 0.90 | 0.90 | 0.957 | 0.948 | 0.956 |
| *Potamopyrgus antipodarum* (GRAY, 1843) | Gastropoda | 754 | 483 | 0.95 | 0.95 | 0.95 | 0.902 | 0.892 | 0.886 |
| *Radix auricularia* (LINNAEUS, 1758) | Gastropoda | 62 | 37 | 0.97 | 0.97 | 0.92 | 0.961 | 0.942 | 0.957 |

## Appendix 4 continued

| | | | | Accuracy | | | TSS score | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Taxonomic group | Presence records total | Presence records study area | Landscape / Landscape masked | Stream network | Stream network corrected | Landscape / Landscape masked | Stream network | Stream network corrected |
| *Viviparus viviparus* (LINNAEUS, 1758) | Gastropoda | 59 | 26 | 1.00 | 1.00 | 1.00 | 0.994 | 0.992 | 0.989 |
| *Aphelocheirus aestivalis* (FABRICIUS, 1794) | Heteroptera | 331 | 195 | 0.96 | 0.96 | 0.91 | 0.937 | 0.911 | 0.934 |
| *Gerris lacustris* (LINNAEUS, 1758) | Heteroptera | 73 | 19 | 0.89 | 0.89 | 1.00 | 0.975 | 0.968 | 0.973 |
| *Nepa cinerea* LINNAEUS, 1758 | Heteroptera | 125 | 56 | 0.88 | 0.87 | 0.87 | 0.944 | 0.919 | 0.940 |
| *Caspiobdella fadejewi* (EPSHTEIN, 1961) | Hirudinea | 31 | 27 | 0.96 | 0.96 | 0.96 | 0.992 | 0.992 | 0.991 |
| *Dina punctata* JOHANSSON, 1927 | Hirudinea | 62 | 35 | 0.91 | 0.91 | 0.91 | 0.948 | 0.950 | 0.934 |
| *Erpobdella nigricollis* (BRANDES, 1900) | Hirudinea | 123 | 80 | 0.98 | 0.95 | 0.96 | 0.942 | 0.930 | 0.946 |
| *Erpobdella octoculata* (LINNAEUS, 1758) | Hirudinea | 1740 | 1126 | 0.89 | 0.91 | 0.93 | 0.868 | 0.839 | 0.859 |
| *Erpobdella testacea* (SAVIGNY, 1822) | Hirudinea | 16 | 10 | 1.00 | 0.78 | 0.78 | 0.961 | 0.950 | 0.802 |
| *Erpobdella vilnensis* (LISKIEWICZ, 1925) | Hirudinea | 488 | 384 | 0.92 | 0.92 | 0.94 | 0.910 | 0.894 | 0.894 |
| *Glossiphonia complanata* (LINNAEUS, 1758) | Hirudinea | 925 | 610 | 0.91 | 0.92 | 0.91 | 0.859 | 0.850 | 0.846 |
| *Glossiphonia nebulosa* KALBE, 1964 | Hirudinea | 89 | 70 | 0.97 | 0.89 | 0.91 | 0.957 | 0.932 | 0.958 |
| *Helobdella stagnalis* (LINNAEUS, 1758) | Hirudinea | 580 | 375 | 0.91 | 0.88 | 0.91 | 0.881 | 0.851 | 0.870 |
| *Hemiclepsis marginata* (O.F. MÜLLER, 1774) | Hirudinea | 43 | 29 | 0.86 | 0.86 | 0.86 | 0.963 | 0.929 | 0.914 |
| *Piscicola geometra* (LINNAEUS, 1761) | Hirudinea | 68 | 50 | 0.94 | 0.92 | 1.00 | 0.964 | 0.941 | 0.968 |
| *Theromyzon tessulatum* (O.F. MÜLLER, 1774) | Hirudinea | 108 | 83 | 0.92 | 0.90 | 0.93 | 0.961 | 0.963 | 0.967 |
| *Trocheta pseudodina* NESEMANN, 1990 | Hirudinea | 33 | 26 | 0.96 | 0.96 | 0.96 | 0.979 | 0.967 | 0.954 |
| *Atherix ibis* (FABRICIUS, 1798) | Lepidoptera | 618 | 469 | 0.91 | 0.94 | 0.93 | 0.906 | 0.888 | 0.899 |
| *Atrichops crassipes* (MEIGEN, 1820) | Lepidoptera | 62 | 46 | 0.98 | 1.00 | 1.00 | 0.978 | 0.968 | 0.975 |
| *Ibisia marginata* (FABRICIUS, 1781) | Lepidoptera | 92 | 79 | 0.95 | 0.92 | 0.92 | 0.972 | 0.964 | 0.971 |
| *Limnophora riparia* (FALLEN, 1824) | Lepidoptera | 10 | 10 | 1.00 | 1.00 | 1.00 | 0.960 | 0.929 | 0.868 |
| *Prosimulium hirtipes* (FRIES, 1824) | Lepidoptera | 25 | 21 | 1.00 | 0.95 | 1.00 | 0.985 | 0.975 | 0.967 |
| *Prosimulium rufipes* (MEIGEN, 1830) | Lepidoptera | 24 | 15 | 1.00 | 1.00 | 1.00 | 0.985 | 0.983 | 0.977 |
| *Prosimulium tomosvaryi* (ENDERLEIN, 1921) | Lepidoptera | 50 | 33 | 1.00 | 1.00 | 1.00 | 0.979 | 0.975 | 0.977 |

## Appendix 4 continued

| Species | Taxonomic group | Presence records total | Presence records study area | Accuracy: Landscape / Landscape masked | Accuracy: Stream network | Accuracy: Stream network corrected | TSS score: Landscape / Landscape masked | TSS score: Stream network | TSS score: Stream network corrected |
|---|---|---|---|---|---|---|---|---|---|
| *Simulium argyreatum* MEIGEN, 1838 | Lepidoptera | 59 | 55 | 0.98 | 0.98 | 0.98 | 0.984 | 0.981 | 0.984 |
| *Simulium costatum* FRIEDERICHS, 1920 | Lepidoptera | 21 | 18 | 1.00 | 1.00 | 1.00 | 0.960 | 0.960 | 0.957 |
| *Simulium cryophilum* (RUBZOV, 1959) | Lepidoptera | 97 | 79 | 1.00 | 1.00 | 1.00 | 0.986 | 0.984 | 0.981 |
| *Simulium monticola* FRIEDERICHS, 1920 | Lepidoptera | 27 | 23 | 1.00 | 1.00 | 0.96 | 0.978 | 0.969 | 0.976 |
| *Simulium ornatum* MEIGEN, 1818 | Lepidoptera | 300 | 217 | 0.94 | 0.93 | 0.94 | 0.930 | 0.905 | 0.916 |
| *Simulium reptans* (LINNAEUS, 1758) | Lepidoptera | 56 | 46 | 0.96 | 0.93 | 1.00 | 0.971 | 0.947 | 0.985 |
| *Simulium variegatum* MEIGEN, 1818 | Lepidoptera | 54 | 41 | 0.95 | 0.95 | 0.98 | 0.984 | 0.971 | 0.987 |
| *Simulium vernum* MACQUART, 1826 | Lepidoptera | 56 | 51 | 1.00 | 1.00 | 0.96 | 0.983 | 0.983 | 0.978 |
| *Sialis fuliginosa* PICTET, 1836 | Megaloptera | 300 | 229 | 0.97 | 0.94 | 0.92 | 0.908 | 0.901 | 0.884 |
| *Sialis lutaria* (LINNAEUS, 1758) | Megaloptera | 476 | 275 | 0.88 | 0.90 | 0.88 | 0.894 | 0.876 | 0.870 |
| *Sialis morio* KLINGSTEDT, 1931 | Megaloptera | 22 | 21 | 1.00 | 1.00 | 1.00 | 1.000 | 0.999 | 0.999 |
| *Sialis nigripes* PICTET, 1865 | Megaloptera | 34 | 27 | 0.93 | 0.96 | 0.96 | 0.956 | 0.942 | 0.984 |
| *Gordius aquaticus* (LINNAEUS, 1758) | Nematomorpha | 30 | 30 | 0.97 | 1.00 | 0.93 | 0.985 | 0.982 | 0.956 |
| *Calopteryx splendens* (HARRIS, 1782) | Odonata | 561 | 310 | 0.94 | 0.94 | 0.94 | 0.919 | 0.905 | 0.914 |
| *Calopteryx virgo* (LINNAEUS, 1758) | Odonata | 173 | 121 | 0.94 | 0.93 | 0.95 | 0.919 | 0.897 | 0.924 |
| *Cordulegaster boltonii* (DONOVAN, 1807) | Odonata | 51 | 45 | 1.00 | 0.98 | 0.93 | 0.976 | 0.975 | 0.959 |
| *Ischnura elegans* (VAN DER LINDEN, 1820) | Odonata | 98 | 40 | 0.98 | 0.97 | 0.97 | 0.960 | 0.968 | 0.965 |
| *Platycnemis pennipes* (PALLAS, 1771) | Odonata | 150 | 82 | 0.95 | 0.95 | 0.91 | 0.941 | 0.928 | 0.941 |
| *Eiseniella tetraedra* (SAVIGNY, 1826) | Oligochaeta | 1149 | 870 | 0.91 | 0.93 | 0.89 | 0.896 | 0.866 | 0.873 |
| *Haplotaxis gordioides* (HARTMANN, 1821) | Oligochaeta | 124 | 101 | 0.93 | 0.93 | 0.94 | 0.954 | 0.931 | 0.938 |
| *Limnodrilus hoffmeisteri* CLAPAREDE, 1862 | Oligochaeta | 133 | 95 | 0.97 | 0.98 | 0.98 | 0.986 | 0.982 | 0.981 |
| *Limnodrilus profundicola* (VERRILL, 1871) | Oligochaeta | 11 | 11 | 1.00 | 1.00 | 1.00 | 0.999 | 0.999 | 0.989 |
| *Lumbriculus variegatus* (MÜLLER, 1774) | Oligochaeta | 418 | 314 | 0.96 | 0.96 | 0.95 | 0.908 | 0.911 | 0.898 |
| *Potamothrix hammoniensis* (MICHAELSEN, 1901) | Oligochaeta | 33 | 19 | 1.00 | 1.00 | 1.00 | 0.990 | 0.993 | 0.993 |

## Appendix 4 continued

| Species | Taxonomic group | Presence records total | Presence records study area | Accuracy |  |  | TSS score |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  | Landscape / Landscape masked | Stream network | Stream network corrected | Landscape / Landscape masked | Stream network | Stream network corrected |
| *Psammoryctides barbatus* (GRUBE, 1891) | Oligochaeta | 94 | 61 | 0.97 | 0.98 | 0.95 | 0.974 | 0.973 | 0.972 |
| *Rhyacodrilus coccineus* (VEJDOVSKÝ, 1875) | Oligochaeta | 23 | 16 | 1.00 | 1.00 | 1.00 | 0.975 | 0.992 | 0.960 |
| *Stylodrilus heringianus* CLAPAREDE, 1862 | Oligochaeta | 439 | 338 | 0.96 | 0.96 | 0.93 | 0.918 | 0.895 | 0.906 |
| *Brachyptera risi* (MORTON, 1896) | Plecoptera | 411 | 307 | 0.97 | 0.98 | 0.97 | 0.943 | 0.939 | 0.935 |
| *Brachyptera seticornis* (KLAPÁLEK, 1902) | Plecoptera | 155 | 119 | 0.99 | 0.99 | 0.97 | 0.969 | 0.962 | 0.965 |
| *Chloroperla tripunctata* (SCOPOLI, 1763) | Plecoptera | 12 | 12 | 1.00 | 1.00 | 1.00 | 0.998 | 0.988 | 0.976 |
| *Dinocras cephalotes* (CURTIS, 1827) | Plecoptera | 95 | 87 | 0.89 | 0.99 | 0.92 | 0.977 | 0.972 | 0.972 |
| *Diura bicaudata* (LINNAEUS, 1758) | Plecoptera | 30 | 20 | 1.00 | 0.89 | 1.00 | 0.955 | 0.936 | 0.944 |
| *Isoperla grammatica* (PODA, 1761) | Plecoptera | 42 | 27 | 0.96 | 0.96 | 0.96 | 0.986 | 0.980 | 0.979 |
| *Leuctra braueri* KEMPNY, 1898 | Plecoptera | 17 | 16 | 1.00 | 1.00 | 1.00 | 0.995 | 0.993 | 0.974 |
| *Leuctra geniculata* (STEPHENS, 1836) | Plecoptera | 196 | 170 | 0.96 | 0.96 | 0.96 | 0.958 | 0.946 | 0.957 |
| *Nemurella pictetii* KLAPÁLEK, 1900 | Plecoptera | 47 | 39 | 1.00 | 1.00 | 1.00 | 0.964 | 0.958 | 0.974 |
| *Perla marginata* (PANZER, 1799) | Plecoptera | 180 | 142 | 0.92 | 0.94 | 0.96 | 0.969 | 0.965 | 0.960 |
| *Perlodes microcephalus* (PICTET, 1833) | Plecoptera | 48 | 38 | 0.97 | 0.97 | 1.00 | 0.982 | 0.971 | 0.984 |
| *Hypania invalida* (GRUBE, 1860) | Polychaeta | 36 | 26 | 1.00 | 1.00 | 1.00 | 0.978 | 0.983 | 0.973 |
| *Ephydatia fluviatilis* (LINNAEUS, 1758) | Porifera | 45 | 23 | 0.96 | 0.95 | 1.00 | 0.911 | 0.878 | 0.990 |
| *Spongilla lacustris* (LINNAEUS, 1758) | Porifera | 35 | 19 | 0.95 | 0.95 | 0.95 | 0.977 | 0.981 | 0.988 |
| *Trochospongilla horrida* WELTNER, 1893 | Porifera | 13 | 12 | 1.00 | 1.00 | 1.00 | 1.000 | 1.000 | 1.000 |
| *Adicella reducta* (McLACHLAN, 1865) | Trichoptera | 82 | 68 | 1.00 | 1.00 | 1.00 | 0.944 | 0.937 | 0.958 |
| *Agapetus fuscipes* CURTIS, 1834 | Trichoptera | 70 | 59 | 0.98 | 0.98 | 0.98 | 0.956 | 0.943 | 0.955 |
| *Agapetus ochripes* CURTIS, 1834 | Trichoptera | 46 | 31 | 0.97 | 1.00 | 1.00 | 0.975 | 0.967 | 0.987 |
| *Allogamus auricollis* (PICTET, 1834) | Trichoptera | 110 | 88 | 0.93 | 0.95 | 0.98 | 0.966 | 0.949 | 0.968 |
| *Annitella obscurata* (McLACHLAN, 1876) | Trichoptera | 36 | 36 | 0.97 | 0.97 | 0.97 | 0.964 | 0.957 | 0.968 |
| *Anomalopterygella chauviniana* (STEIN, 1874) | Trichoptera | 495 | 417 | 0.94 | 0.94 | 0.96 | 0.942 | 0.933 | 0.935 |

## Appendix 4 continued

| Species | Taxonomic group | Presence records total | Presence records study area | Accuracy | | | TSS score | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Landscape / Landscape masked | Stream network | Stream network corrected | Landscape / Landscape masked | Stream network | Stream network corrected |
| *Athripsodes albifrons* (LINNAEUS, 1758) | Trichoptera | 136 | 103 | 0.98 | 0.98 | 0.96 | 0.960 | 0.955 | 0.944 |
| *Athripsodes cinereus* (CURTIS, 1834) | Trichoptera | 277 | 171 | 0.94 | 0.95 | 0.94 | 0.918 | 0.894 | 0.924 |
| *Brachycentrus subnubilus* CURTIS, 1834 | Trichoptera | 145 | 93 | 0.97 | 0.99 | 0.95 | 0.944 | 0.930 | 0.960 |
| *Ceraclea annulicornis* (STEPHENS, 1836) | Trichoptera | 26 | 18 | 1.00 | 1.00 | 1.00 | 0.970 | 0.971 | 0.987 |
| *Ceraclea dissimilis* (STEPHENS, 1836) | Trichoptera | 98 | 49 | 1.00 | 0.96 | 0.88 | 0.949 | 0.919 | 0.938 |
| *Chaetopterygopsis maclachlani* STEIN, 1874 | Trichoptera | 22 | 21 | 1.00 | 1.00 | 1.00 | 0.996 | 0.996 | 0.986 |
| *Cheumatopsyche lepida* (PICTET, 1834) | Trichoptera | 158 | 94 | 0.97 | 0.96 | 0.98 | 0.951 | 0.935 | 0.958 |
| *Cyrnus trimaculatus* (CURTIS, 1834) | Trichoptera | 144 | 102 | 0.90 | 0.91 | 0.91 | 0.951 | 0.934 | 0.946 |
| *Drusus annulatus* (STEPHENS, 1837) | Trichoptera | 206 | 163 | 0.98 | 0.98 | 0.96 | 0.950 | 0.936 | 0.949 |
| *Ecclisopteryx dalecarlica* KOLENATI, 1848 | Trichoptera | 52 | 42 | 0.98 | 0.98 | 0.95 | 0.981 | 0.968 | 0.967 |
| *Ecclisopteryx madida* (McLACHLAN, 1867) | Trichoptera | 35 | 28 | 0.96 | 0.96 | 0.96 | 0.981 | 0.982 | 0.984 |
| *Glossosoma boltoni* CURTIS, 1834 | Trichoptera | 28 | 27 | 1.00 | 1.00 | 1.00 | 0.989 | 0.985 | 0.993 |
| *Glossosoma conformis* NEBOISS, 1963 | Trichoptera | 79 | 63 | 0.98 | 0.95 | 0.97 | 0.975 | 0.966 | 0.966 |
| *Goera pilosa* (FABRICIUS, 1775) | Trichoptera | 236 | 173 | 0.97 | 0.94 | 0.94 | 0.906 | 0.888 | 0.923 |
| *Halesus radiatus* (CURTIS, 1834) | Trichoptera | 299 | 153 | 0.98 | 0.98 | 0.94 | 0.927 | 0.910 | 0.897 |
| *Halesus tesselatus* (RAMBUR, 1842) | Trichoptera | 48 | 29 | 1.00 | 1.00 | 1.00 | 0.978 | 0.976 | 0.947 |
| *Hydropsyche bulbifera* McLACHLAN, 1878 | Trichoptera | 45 | 22 | 1.00 | 1.00 | 1.00 | 0.991 | 0.987 | 0.987 |
| *Hydropsyche dinarica* MARINKOVIC, 1979 | Trichoptera | 143 | 126 | 0.98 | 0.98 | 0.93 | 0.966 | 0.961 | 0.962 |
| *Hydropsyche fulvipes* (CURTIS, 1834) | Trichoptera | 19 | 19 | 1.00 | 1.00 | 1.00 | 0.979 | 0.988 | 0.992 |
| *Hydropsyche guttata* PICTET, 1834 | Trichoptera | 14 | 14 | 0.93 | 1.00 | 0.93 | 0.969 | 0.964 | 0.940 |
| *Hydropsyche incognita* PITSCH, 1993 | Trichoptera | 305 | 244 | 0.93 | 0.94 | 0.90 | 0.925 | 0.904 | 0.933 |
| *Hydropsyche instabilis* (CURTIS, 1834) | Trichoptera | 444 | 357 | 0.92 | 0.92 | 0.95 | 0.917 | 0.905 | 0.900 |
| *Hydropsyche pellucidula* (CURTIS, 1834) | Trichoptera | 700 | 457 | 0.90 | 0.91 | 0.91 | 0.872 | 0.835 | 0.876 |
| *Hydropsyche saxonica* McLACHLAN, 1884 | Trichoptera | 262 | 180 | 0.95 | 0.94 | 0.93 | 0.913 | 0.898 | 0.925 |

## Appendix 4 continued

| | | | | Accuracy | | | TSS score | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Taxonomic group | Presence records total | Presence records study area | Landscape / Landscape masked | Stream network | Stream network corrected | Landscape / Landscape masked | Stream network | Stream network corrected |
| *Hydropsyche siltalai* DÖHLER, 1963 | Trichoptera | 1442 | 990 | 0.91 | 0.92 | 0.90 | 0.886 | 0.859 | 0.868 |
| *Hydropsyche tenuis* NAVÁS, 1932 | Trichoptera | 39 | 35 | 0.97 | 0.94 | 0.94 | 0.988 | 0.988 | 0.987 |
| *Lepidostoma hirtum* (FABRICIUS, 1775) | Trichoptera | 517 | 375 | 0.91 | 0.91 | 0.95 | 0.911 | 0.890 | 0.910 |
| *Limnephilus lunatus* CURTIS, 1834 | Trichoptera | 324 | 115 | 0.91 | 0.92 | 0.86 | 0.929 | 0.921 | 0.905 |
| *Limnephilus marmoratus* CURTIS, 1834 | Trichoptera | 21 | 20 | 1.00 | 1.00 | 0.95 | 0.985 | 0.981 | 0.978 |
| *Lithax niger* (HAGEN, 1859) | Trichoptera | 33 | 25 | 1.00 | 1.00 | 1.00 | 0.967 | 0.941 | 0.971 |
| *Lype phaeopa* (STEPHENS, 1836) | Trichoptera | 20 | 19 | 1.00 | 1.00 | 1.00 | 0.975 | 0.960 | 0.958 |
| *Lype reducta* (HAGEN, 1868) | Trichoptera | 105 | 66 | 0.94 | 0.91 | 0.86 | 0.970 | 0.956 | 0.930 |
| *Micrasema longulum* McLACHLAN, 1876 | Trichoptera | 147 | 112 | 0.98 | 0.98 | 0.99 | 0.963 | 0.956 | 0.961 |
| *Micrasema minimum* McLACHLAN, 1876 | Trichoptera | 91 | 67 | 0.99 | 0.99 | 0.99 | 0.983 | 0.980 | 0.979 |
| *Molanna angustata* CURTIS, 1834 | Trichoptera | 67 | 23 | 0.96 | 0.96 | 1.00 | 0.957 | 0.942 | 0.961 |
| *Mystacides azurea* (LINNAEUS, 1761) | Trichoptera | 341 | 271 | 0.94 | 0.92 | 0.94 | 0.917 | 0.910 | 0.907 |
| *Mystacides nigra* (LINNAEUS, 1758) | Trichoptera | 99 | 66 | 0.92 | 0.91 | 0.94 | 0.955 | 0.924 | 0.963 |
| *Odontocerum albicorne* (SCOPOLI, 1763) | Trichoptera | 390 | 304 | 0.95 | 0.95 | 0.95 | 0.934 | 0.918 | 0.921 |
| *Oecetis notata* (RAMBUR, 1842) | Trichoptera | 32 | 21 | 0.86 | 0.86 | 0.90 | 0.952 | 0.935 | 0.928 |
| *Oecetis testacea* (CURTIS, 1834) | Trichoptera | 63 | 53 | 0.96 | 0.96 | 0.91 | 0.966 | 0.958 | 0.978 |
| *Philopotamus ludificatus* McLACHLAN, 1878 | Trichoptera | 39 | 32 | 1.00 | 1.00 | 1.00 | 0.977 | 0.961 | 0.982 |
| *Psychomyia pusilla* (FABRICIUS, 1781) | Trichoptera | 381 | 261 | 0.93 | 0.93 | 0.91 | 0.921 | 0.897 | 0.918 |
| *Rhyacophila evoluta* McLACHLAN, 1879 | Trichoptera | 119 | 102 | 0.99 | 0.99 | 0.98 | 0.973 | 0.969 | 0.970 |
| *Rhyacophila nubila* (ZETTERSTEDT, 1840) | Trichoptera | 329 | 257 | 0.97 | 0.96 | 0.97 | 0.928 | 0.931 | 0.950 |
| *Rhyacophila obliterata* McLACHLAN, 1863 | Trichoptera | 62 | 50 | 1.00 | 0.98 | 0.98 | 0.951 | 0.942 | 0.951 |
| *Rhyacophila pubescens* PICTET, 1834 | Trichoptera | 11 | 10 | 0.90 | 0.90 | 0.90 | 0.978 | 0.992 | 0.967 |
| *Rhyacophila torrentium* PICTET, 1834 | Trichoptera | 28 | 26 | 1.00 | 1.00 | 1.00 | 0.983 | 0.986 | 0.954 |
| *Rhyacophila tristis* PICTET, 1834 | Trichoptera | 77 | 63 | 0.97 | 1.00 | 1.00 | 0.972 | 0.957 | 0.970 |

## Appendix 4 continued

| Species | Taxonomic group | Presence records total | Presence records study area | Accuracy | | | TSS score | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Landscape / Landscape masked | Stream network | Stream network corrected | Landscape / Landscape masked | Stream network | Stream network corrected |
| *Sericostoma flavicorne* SCHNEIDER, 1845 | Trichoptera | 57 | 57 | 1.00 | 1.00 | 0.98 | 0.988 | 0.984 | 0.982 |
| *Sericostoma personatum* KIRBY & SPENCER, 1826 | Trichoptera | 162 | 126 | 0.98 | 0.97 | 0.97 | 0.965 | 0.951 | 0.956 |
| *Silo pallipes* (FABRICIUS, 1781) | Trichoptera | 311 | 237 | 0.97 | 0.97 | 0.96 | 0.949 | 0.937 | 0.935 |
| *Silo piceus* (BRAUER, 1857) | Trichoptera | 194 | 153 | 0.91 | 0.92 | 0.95 | 0.947 | 0.940 | 0.944 |
| *Tinodes rostocki* McLACHLAN, 1878 | Trichoptera | 33 | 27 | 1.00 | 1.00 | 1.00 | 0.974 | 0.977 | 0.985 |
| *Dendrocoelum lacteum* (O.F. MÜLLER, 1774) | Turbellaria | 210 | 158 | 0.97 | 0.94 | 0.95 | 0.940 | 0.908 | 0.933 |
| *Dugesia gonocephala* (DUGES, 1830) | Turbellaria | 716 | 555 | 0.94 | 0.91 | 0.92 | 0.905 | 0.882 | 0.889 |
| *Dugesia lugubris* (SCHMIDT, 1861) | Turbellaria | 116 | 85 | 0.89 | 0.91 | 0.92 | 0.946 | 0.917 | 0.954 |
| *Dugesia polychroa* (SCHMIDT, 1861) | Turbellaria | 16 | 15 | 1.00 | 1.00 | 0.93 | 0.997 | 0.996 | 0.989 |
| *Dugesia tigrina* (GIRARD, 1850) | Turbellaria | 86 | 69 | 0.91 | 0.89 | 0.95 | 0.967 | 0.957 | 0.968 |
| *Polycelis felina* (DALYELL, 1814) | Turbellaria | 120 | 109 | 0.95 | 0.94 | 0.96 | 0.978 | 0.980 | 0.980 |
| *Polycelis nigra* MUELLER, 1774 | Turbellaria | 88 | 77 | 0.83 | 0.78 | 0.81 | 0.949 | 0.932 | 0.881 |

**Appendix 5** Pairwise percent (± standard deviations) of overlapping grid cells classified as suitable between all combinations of the four modelling designs.

| | **Landscape** | **Landscape masked** | **Stream network** |
|---|---|---|---|
| **Landscape masked** | 51 ± 20% | | |
| **Stream network** | 45 ± 5% | 93 ± 7% | |
| **Stream network corrected** | 36 ± 6% | 74 ± 15% | 77 ± 15% |

# Author contributions

### Chapter 1

### Climate-change winners and losers: stream macroinvertebrates of a submontane region in Central Europe

*Sami Domisch, Sonja C. Jähnig, Peter Haase (2011). Freshwater Biology 56, 2009–2020*

S.D., S.C.J. and P.H. conceived the research. S.D. conducted the research, analysed the data, and wrote the manuscript. All authors discussed the results and commented on the manuscript. S.C.J. and P.H. contributed equally to the study. Two anonymous referees commented on the manuscript.

### Chapter 2

### How would climate change affect European stream macroinvertebrates' distributions?

*Sami Domisch, Miguel B. Araújo, Núria Bonada, Steffen U. Pauls, Sonja C. Jähnig, Peter Haase. Submitted to Global Change Biology*

S.D., S.C.J. and P.H. conceived the research. S.D. conducted the research, analysed the data and wrote the manuscript. M.B.A., N.B., and S.U.P. contributed species data. All authors discussed the results and commented on the manuscript. S.C.J. and P.H. contributed equally to the study.

### Chapter 3

### Choice of study area and predictors affect species distribution models of stream macroinvertebrates

*Sami Domisch, Mathias Kuemmerlen, Sonja C. Jähnig, Peter Haase. Submitted to Freshwater Biology*

S.D., M.K., S.C.J. and P.H. conceived the research. S.D. conducted the research, analysed the data, and wrote the manuscript. All authors discussed the results and commented on the manuscript. S.C.J. and P.H. contributed equally to the study.

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## Erklärung

Ich erkläre hiermit, dass ich mich bisher keiner Doktorprüfung unterzogen habe.

Frankfurt am Main, den ................................ ………………………………..............
(Unterschrift)

## Eidesstattliche Versicherung

Ich erkläre hiermit an Eides Statt, dass ich die vorgelegte Dissertation über

**Species distribution modelling of stream macroinvertebrates under climate change scenarios**

selbständig angefertigt und mich anderer Hilfsmittel als der in ihr angegebenen nicht bedient habe, insbesondere, dass alle Entlehnungen aus anderen Schriften mit Angabe der betreffenden Schrift gekennzeichnet sind.
Ich versichere, nicht die Hilfe einer kommerziellen Promotionsvermittlung in Anspruch genommen zu haben.

Frankfurt am Main, den ............................... …..............……………………………..
(Unterschrift)

# *Curriculum Vitae*

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| Since 2009 | Senckenberg Research Institutes and Natural History Museums, Biodiversity and Climate Research Centre (BiK-F), Frankfurt, Germany: PhD research under the supervision of Prof. Dr. P. Haase and Dr. S. Jähnig |
| 2007-2008 | Marine Station of the Alfred-Wegener-Institute for Polar and Marine Research, AWI, Helgoland, Germany: Diploma thesis under the supervision of Dr. M. Molis: „Effekte des eingewanderten Japanischen Beerentangs *Sargassum muticum* (Yendo) Fensholt auf die Diversität und Struktur makrobenthischer Gemeinschaften im Helgoländer Felswatt“ (“Effects of *Sargassum muticum* on the structure and diversity of macrobenthic rocky shore communities at Helgoland”) |
| 2005-2007 | Carl von Ossietzky Universität Oldenburg, Germany: Advanced studies in biology, main focus: Ecology, Zoology, Plant physiology, Marine biodiversity |
| 2001-2005 | Technische Universität Kaiserslautern, Germany: Basic studies in biology |
| 2000 | Reifeprüfung at the Deutsche Schule Helsinki, Finland |

## Publications

*Articles*

Bálint, M., Domisch, S., Engelhardt, C.H.M., Haase, P., Lehrian, S., Sauer, J., Theissinger, K., Pauls, S.U., Nowak, C. (2011). Cryptic biodiversity loss linked to global climate change. *Nature Climate Change*, 1, 313–318

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*Further publications*

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## Poster presentations

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