

# Effect of biotic dependencies in species distribution models: The future distribution of *Thymallus thymallus* under consideration of *Allogamus auricollis*



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## ABSTRACT

Climate change will impact the riverine environment of aquatic organisms. However, most studies focus solely on environmental characteristics to evaluate future distribution shifts. Here, we analyse current and future distribution of the freshwater fish species *Thymallus thymallus* in relation to the caddisfly *Allogamus auricollis*. Current and future distributions of the two species were evaluated by a consensus model approach integrating seven different distribution model techniques and testing the effect of considering biotic dependence. Predictions for future distributions were calculated on the basis of the most recent representative concentration pathways (RCPs) of the IPCC for the period of the 2050s. Habitat loss and gain, distribution congruence and altitudinal shift between the two species were quantified on the basis of a full river network. The model considering biotic dependence identified the caddisfly as important variable for the distributions of European grayling, mitigating the drastic effects of climate change. Habitat loss of the grayling was attenuated by considering the distribution of the caddisfly in the distribution modelling. Strong temperature increases as well as run-off decreases led to largest habitat loss of both species (up to 70%). Our combined approach highlighted that the consideration of biotic dependencies in climate change studies improves the understanding for potential future changes of distribution patterns.

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## 1. Introduction

Climate change is expected to impact riverine ecosystems in different ways (Ficke et al., 2007). The complex mechanisms which affect the habitat of aquatic organisms induce adaption, extirpation/extinction and migration of the aquatic species. If adaption capacity is exceeded, species have to disperse to prevent extirpation and to track their habitat niche (Comte et al., 2013). Two migration pathways triggered by climate change are mostly reported: (1) upward shifts towards higher elevation and (2) northward shifts towards higher latitudes, especially if solely the climate envelope is addressed (Comte et al., 2013; Parmesan, 2006). Both transfer the suitable habitats into cold or respectively wet enough environments. Species distribution models (SDM) represent a useful tool to evaluate distribution shifts in climate change studies (Guisan and Zimmermann, 2000; Pearson and Dawson, 2003). Beside different realms (Elith and Leathwick, 2009) the

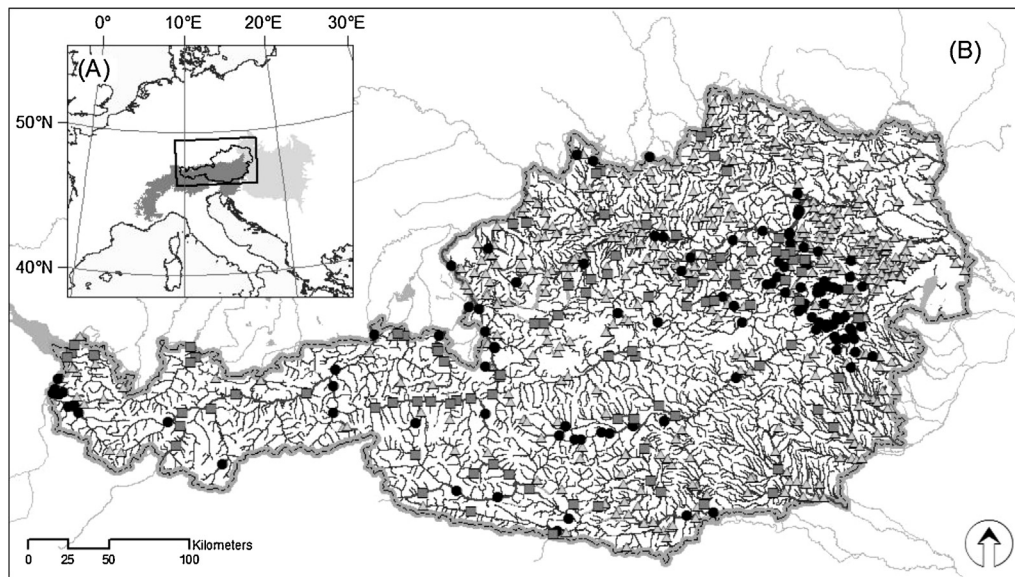
technique was also applied over different spatial extents and in various biomes of riverine ecosystems (Comte et al., 2013). However, most studies deal with single species (Elliott et al., 2015; Filipe et al., 2013) or with different species within one taxonomic group (Buisson et al., 2008). In this study we evaluate the species distributions of two taxonomic groups.

Although the hierarchical nature of riverine ecosystems has been known for a long time (Frissell et al., 1986), whole river networks are not consistently used as spatial basis for distribution models (Domisch et al., 2013; Elliott et al., 2015; Markovic et al., 2012). However, habitat characteristics are strongly related to river topography. Furthermore, the spatially explicit quantification of potential habitat losses and gains on the basis of river networks provides essential information to develop management and conservation strategies in respect of climate change impacts (e.g. Filipe et al., 2013).

Climate is a dominant factor in the ecology of stream biota (Mantua et al., 2010) as it controls discharge, through precipitation, as well as water temperature, through atmospheric energy fluxes. Over larger scales, air and water temperatures are highly correlated as energy fluxes which induce higher air temperatures also affect water temperatures (Markovic et al., 2013; Orr et al., 2014).

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**Fig. 1.** Location of investigation area in Europe (A) and species occurrences within the investigation area (B); grey rectangles: caddisfly presences, black dots: European grayling presences, light grey triangles: absences.

Both, temperature and discharge, are fundamental parts in the chemo-physical environment of aquatic organisms. Climate change is expected to increase temperatures and to impact precipitation regimes (intensity, timing and mode). The extent of those changes depends on atmospheric greenhouse gas concentrations. Accordingly, the representative concentration pathways (RCPs) of the Intergovernmental Panel on Climate Change (IPCC, 2013) constitute the latest future scenarios of plausible assumptions on economic activities, energy sources and population growth with corresponding consequences on the emission trajectories which serve as input for climate models.

In consideration of thermally induced shifts, especially rivers with cool- or cold-water regimes are exposed to climate change impacts (Buisson and Grenouillet, 2009; Comte and Grenouillet, 2013; McCullough et al., 2009). Such lotic systems are well represented in Alpine regions where salmonids like *Thymallus thymallus* (Linnaeus, 1758) serve as flagship species (Huet, 1959). The eastern border of the Alps (Fig. 1A) delineates the distribution boundary of this species and is therefore of special interest. Although the European grayling is native to major parts of Europe (Northcote, 1995) with a diverse phylogeography (Gum et al., 2009; Meraner and Gandolfi, 2012), it has been less well studied in comparison to other members of the salmonid family (e.g. trout or salmon) (Riley and Pawson, 2010). Interestingly, effects of temperature increases were barely addressed although European grayling shows a more cold-stenothermic behaviour than brown trout (*Salmo trutta*, Linnaeus, 1758) with a lower tolerance to water temperature increases (Logez et al., 2012; Northcote, 1995).

European grayling are predatory feeders with benthic-pelagic habits. Accordingly, they are found closer to the river bed and ingest fewer aerial invertebrates (Woolland, 1988). Benthic prey received from drift or river bottom dominates the diet, with the importance of epibenthic prey increasing when drift is reduced (Syrjänen et al., 2011). The caddisfly *Allogamus auricollis* (Pictet, 1834) is an epibenthic filter feeder building dense populations in small and medium-sized rivers overlapping the distribution range of European grayling. The biomass of this caddisfly can account for up to 70% of the total benthic biomass found in these rivers (Geddes, 1981; Graf et al., 1992) which is the only limnephilid species which occurs in rivers where European grayling is found too. Their large accumulations of individuals are easily detectable

for bottom-feeding fish (Graf et al., 1992). Hence, the species seems predestined to serve as substantial prey of bottom feeding European grayling which preferably attack exposed invertebrates. Even though European grayling dynamically use the available habitat (Nykanen, 2001), they can be limited by the availability of food sources (De Crespín De Billy and Usseglio-Polatera, 2002). Predators and prey may follow divergent dispersal pathways due to climate change which may aggravate the environmental impacts, or a mutual distribution shift may attenuate the impacts.

In this study, we hypothesised that (1) European grayling and the caddisfly will suffer from severe habitat loss induced by climate change, (2) the magnitude of habitat loss will be related to the intensity of climate change, (3) the availability of adequate food sources (as indicated by the caddisfly) will play an important role in the distribution of European grayling, and (4) climate change induced habitat loss and elevational habitat shift of European grayling may be reduced by the availability of the caddisfly as prey also indicated by congruent distribution areas. Here, we evaluate distribution patterns of fish and macroinvertebrates in parallel spatially linked to a full river network. To our knowledge, this is the first study which directly links two taxonomic groups (fish and macroinvertebrates) in an SDM approach to evaluate potential habitat gain and loss in respect of climate change impacts and biotic dependencies on the extent of a full river network.

## 2. Material & methods

This study analysed data on species occurrences, river topography (local and catchment scale), and climate conditions (current, baseline and future). Hence, consistency of data in space and time was of special interest. All data used for model calibration originated from the period between 2003 and 2010. Analyses of climate change impacts are based on a comparison between baseline and future climate.

### 2.1. Study area & species occurrence

The investigation area includes all rivers with a catchment size larger than 10 km<sup>2</sup> in Austria and comprises a length of about 30,000 km covering the eastern border of the Alps and the transition to the Hungarian lowlands (Fig. 1A). Investigation units are based

on surface water bodies (SWBs,  $N=8572$ , mean length = 3.6 km,  $SD=4.0$ ) which form discrete entities in terms of typology and physical characteristics.

The species occurrences were queried from national monitoring databases. The SWB of the sampling site had to be unimpacted or low impacted by human activities. This was defined as not impacted by impoundment, water abstraction or hydropeaking and in at least moderate morphological condition according to the national water management plan (NGP, 2009). This criterion minimised the significance of human impacts on species absences (Pont et al., 2005) and thus explicitly factored out the role of human land use.

The presence-absence data for European grayling comprised 330 records (98 presences; Fig. 1B) in distinct SWBs originating from standardised electrofishing protocols. Sampling was performed during low flow conditions by wading or by boat depending on river size. The presence-absence records of the caddisfly were confined to 390 SWBs (122 presences; Fig. 1B) based on quantitative macro-invertebrate samplings. Both species were considered as 'absent' if not detected at any sampling site and as 'present' if recorded on at least one sampling site within the SWB during the observation period (2003–2010).

## 2.2. Environmental data

Independent variables for modelling were selected under consideration of their ecological relevance for species distributions. Initially, independent variables were tested by Spearman correlation ( $\rho < |0.8|$ ) to minimise collinearity. In regression based methods collinearity between independent variables must be omitted which in turn requires a pre-selection of independent variables or the use of synthetic variables (as derived from principal component analysis). Inter-correlated climatic descriptors were selected according to potential ecological significance (Logez et al., 2012).

River topographical variables quantified stream size (length of upstream network), potential flow velocity (actual river slope), and position on the upstream-downstream gradient (length of upstream network, distance to river mouth). The climate descriptors characterised the thermal and precipitation regime by mean July temperature in the upstream catchment, mean January temperature at the location of the SWB, and run-off potential calculated as the sum of annual precipitation in the upstream catchment standardised by upstream catchment size. A geographic information system (ArcGIS 10.1, ESRI 2011) was used to transfer raster information to the vector data of sampling sites respectively SWBs. Beside the local information of the investigation units (midpoint of SWB), we also considered the upper sub-catchment along the river network of each SWB to evaluate environmental variables (mean of temperature, sum of precipitation) accounting for catchment effects (Hopkins II and Burr, 2009; Kuemmerlen et al., 2014).

Three climatic data sets were implemented: (1) Current climate (2003–2010), (2) baseline climate and (3) future climate. All three conditions were described by raster surfaces with a resolution of  $1 \times 1$  km. Information on the former covers the period of species occurrences and was therefore used for model calibration. Raster describing the current climate were derived from the Integrated Nowcasting through Comprehensive Analysis (INCA) system (Haiden et al., 2011). This system combines stationary and remote sensing data to derive temperature and precipitation grids and represents the climate during the observation period in the investigation area. Data was obtained from the Central Institute for Meteorology and Geodynamics of Austria (<http://www.zamg.ac.at/cms/en>).

In order to make meaningful predictions, we implemented the second (baseline) and third (future projections) climate datasets (both available from worldclim.org). Baseline conditions were described by interpolated climate surfaces based on observation

data for the period 1950–2000 (Hijmans et al., 2005). Future climate scenarios, covering the period between 2041 and 2060 and further referred to as 2050s, were based on the most recent representative concentration pathways (RCPs) of greenhouse gases (IPCC, 2013). We analysed two RCPs (RCP 2.6 and RCP 8.5) to compare the impact of lesser and greater changes, respectively. The extent of predicted changes of temperature and precipitation also depends on the boundary conditions which differ between climate models. To cover this variability occurring within each RCP, we used the outputs of three different general circulation models (GCMs).

The combined information from all three GCMs represented statistically downscaled data (Ramirez-Villegas and Jarvis, 2010) using the worldclim-data as baseline climate. The three models were the following: The HadGEM2-ES model (Jones et al., 2011) predicting high temperature increase as well as decreasing amount of precipitation, therefore further called 'warm/dry'; the GISS-E2-R model (Schmidt et al., 2014) which predicts moderate temperature increases and relatively stable precipitation rates ('moderate/stable'), and the IPSL-CM5a-LR model (Dufresne et al., 2013) predicting warm temperatures and stable amounts of precipitation ('warm/stable').

## 2.3. Species distribution modelling

The modelling framework was based on seven modelling algorithms implemented in the BIOMOD2 package in R: (1) generalised linear models (GLM), (2) generalised additive models (GAM), (3) generalised boosting models (GBM), (4) flexible discriminant analysis (FDA), (5) classification tree analysis (CTA), (6) multiple adaptive regression splines (MARS), and (7) random forest (RF) (R Development Core Team, 2011; Thuiller et al., 2009).

The seven algorithms were used to build three ensemble models for the species distributions in total: the first for the caddisfly (called 'Allau') and the second for European grayling ('ThymEnv'), both solely based on environmental descriptors, i.e. river topography and climate. These two models were used to evaluate climate change impacts on the two species. The third model was again built for European grayling. This model ('ThymEnvAa') implemented the occurrence probability of the caddisfly as independent variable to analyse the effect of a potential biotic dependency (Fig. 2).

Presence/absence records were randomly split into a training (70%) and a test (30%) data set with 100 replications for each model type (7 techniques  $\times$  100 replications = 700 models per species). Model performance was evaluated by sensitivity (true positive predictions) and specificity (true negative predictions). Both indicators range from 0 to 1, where 0 indicates bad and 1 high performance. Models with a performance of  $<0.5$  were discarded (Allouche et al., 2006).

Relative variable importance was calculated to evaluate the relevance of the different predictors in the distribution models of the caddisfly and European grayling. Raw variable importance was calculated by a correlation between a reference prediction and a prediction where the variable was randomised. This procedure was permuted 30 times for each variable in each model. Variable importance was then calculated as  $1 - \text{mean correlation of all permutations}$ , yielding a mean importance for each variable per model run. The raw variable importance values of the predictors were then rescaled to sum up to 100, enabling a treatment as relative importance and a comparison between the algorithms.

The calibrated models were used to project species occurrences according to baseline and future climates (3 GCMs  $\times$  2 RCPs = 6 forecasts per species model) and to evaluate the persistence and shift of habitats. The occurrence probabilities, derived from each model run of all seven algorithms, were transformed into a binary digit, i.e. presence (1) or absence (0) respectively, based on a threshold maximizing the true skill statistic (TSS; sum of sensitivity plus



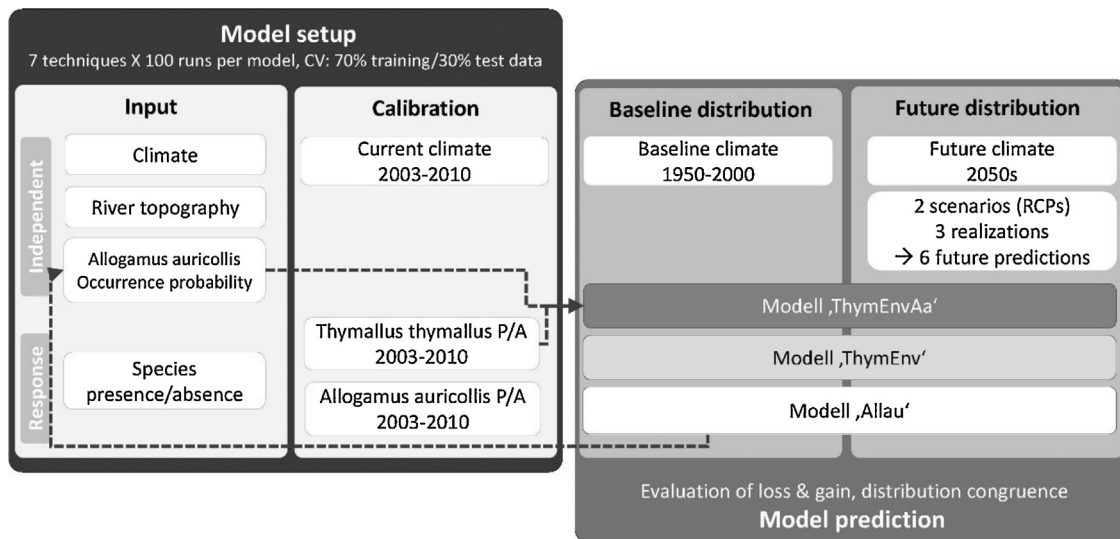


Fig. 2. Concept of the applied modelling framework to analyse current and future distributions of the caddisfly and European grayling.

specificity minus one) (Allouche et al., 2006). The binary digits of all single model runs were then summed and merged into a committee averaging, analogous to a simple vote of each run. The sum of all presence predictions (max = 700) divided by the number of models ( $N=700$ ) gave an occurrence probability (between 0 and 1) which was then transformed into the final presence or absence value for the species. This transformation was done based on a threshold of  $p=0.5$  as the transformation optimisation was already performed in the underlying model runs. Such a consensus approach has been proven to increase the accuracy of SDMs (Filipe et al., 2013; Marmion et al., 2009).

Based on the occurrence predictions derived from the consensus models, the impact of climate change on the distribution of the caddisfly and European grayling was investigated in respect of habitat gain and loss, distribution congruence and elevational shift. Habitat 'loss' (an SWB with baseline presence and future absence) and 'gain' (an SWB with baseline absence and future presence) was calculated based on the length of SWBs and expressed as percentage. Furthermore, the congruence between the distributions of the caddisfly and European grayling was evaluated summarising the length of SWBs, where both species were predicted to occur in common and compared to the congruent distribution length of the baseline. Elevational shift of European grayling was calculated based on the mean elevation of SWBs with predicted presence. The two models ThymEnv and ThymEnvAa were compared in their range of elevation values and the differences between the two models were tested by a Kruskal–Wallis test ( $p < 0.001$ ) to show if the implementation of the predicted distribution of the caddisfly as predictor into the distribution models significantly altered the altitudinal shift induced by climate change.

Finally, the occurrence predictions of European grayling were combined into spatial explicit maps. The gain and loss of European grayling were summarised for each distribution model and each RCP, summing up to four distribution maps (Fig. 7). These maps

indicated stable habitat suitability (baseline and future presence in the SWB) as well as sensitivity of European grayling to climate change impacts represented by the number of GCMs predicting a gain respectively loss in the SWB (summarising the predicted gain or loss according to one, two or all three GCMs).

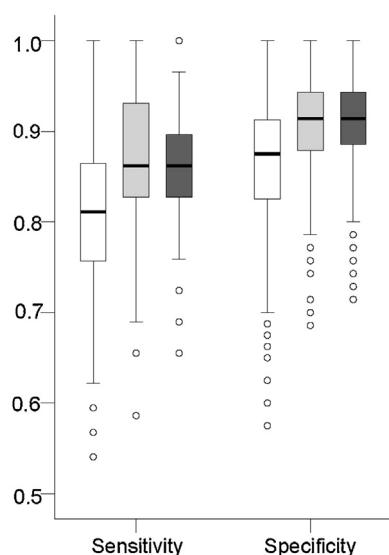
### 3. Results

The SWBs with occurrences of European grayling and the caddisfly covered a wide range of river types (Table 1). Variables dedicated to river topography showed generally smaller medians than means, indicating a prevalence of small-sized rivers which in turn reflects the expected partition of rivers in the landscape. The mean (12.8‰) and medians (5.9‰) of actual river slope reflect the topographically distinct landscape of the investigation area. The climatic variables showed more balanced distributions with small deviances between means and medians. Mean air temperature in January was around  $-1.5^{\circ}\text{C}$ . The mean temperature in July in the upstream catchment reached a maximum of  $17.2^{\circ}\text{C}$ . The run-off potential indicated rather humid conditions by a mean exceeding  $1000\text{ mm km}^{-2}$ .

The majority of models and algorithms performed well (more than 50% of models with sensitivity and specificity  $>0.8$ ) (Fig. 3), and enabled the identification of current distribution areas and the prediction of future distributions. In respect of sensitivity, model Allau performed worst (quartiles between 0.76 and 0.86). Model ThymEnv covered a comparable range but obtained higher values (quartiles between 0.83 and 0.93). In model ThymEnvAa the median of sensitivity stayed at the same level as in ThymEnv but the range shrunk (quartiles between 0.83 and 0.90). Specificity reached higher values (around 0.9) by trend in all three models (Fig. 3). Median specificity was below 0.9 for Allau and above 0.9 for ThymEnv and ThymEnvAa. The range of specificity values shrunk in model ThymEnvAa at the lower end of values.

Table 1  
River characteristics and climate descriptors for surface water bodies used for model calibration ( $N=634$ ).

| Full name                                          | Short    | Unit                | Mean   | SD    | Median | Min    | Max    |
|----------------------------------------------------|----------|---------------------|--------|-------|--------|--------|--------|
| Actual river slope                                 | Slope    | per mille           | 12.8   | 21.6  | 5.9    | 0.1    | 254.2  |
| Upstream network length                            | UpstrL   | km                  | 175.8  | 392.3 | 38.7   | 1.0    | 3877.4 |
| Distance to mouth                                  | Dmouth   | km                  | 39.5   | 80.5  | 12.3   | 0.2    | 646.3  |
| Mean temperature in January                        | TmeJan   | $^{\circ}\text{C}$  | $-1.7$ | 1.3   | $-1.5$ | $-7.0$ | 1.0    |
| Mean temperature in July in the upstream catchment | TmjJulUp | $^{\circ}\text{C}$  | 17.2   | 2.5   | 17.7   | 8.0    | 21.6   |
| Run-off potential                                  | ROpot    | $\text{mm km}^{-2}$ | 1136   | 323   | 1073   | 545    | 2226   |

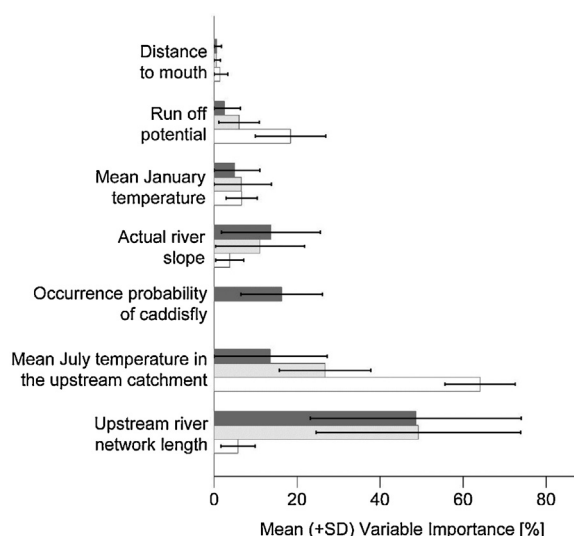


**Fig. 3.** Sensitivity and specificity of all models ( $N=700$ ) used for prediction of the caddisfly and European grayling; white box: model Allau, light grey box: model ThymEnv, dark grey box: model ThymEnvAa; bold lines represent medians, boxes indicate the inter-quartile range (IQR) and whiskers 1.5 times IQR.

The relative importance of the predictors highlighted differences between the caddisfly and European grayling. The river topographical variable upstream length of the river network reached the highest importance for both European grayling models and minor importance for the caddisfly model. Mean July temperature in the upstream catchment showed the highest importance for the caddisfly and was the second most important variable for European grayling (Fig. 4). Generally, river topography had less and climate higher importance for the caddisfly distribution. Mean July temperature in the upstream catchment and run-off potential were the most significant predictors of the caddisfly occurrence followed by January temperature. Mean July temperature in the upstream catchment was also the most important climatic descriptor in both European grayling models.

Future climate conditions were described by two RCPs realised through three downscaled GCMs (Table 2). January and July temperatures generally increased between baseline and RCP 2.6 and from this to RCP 8.5 in respect of means, minima and maxima. The January temperature increase was stronger for the mean values than for minima and maxima. In contrast the maxima of July temperature increased more than the means. Mean run-off potential showed a recurrent trend from RCP 2.6 to RCP 8.5 in the warm/dry realisation. In the two GCMs with stable precipitation conditions the mean of run-off potential was a bit higher and the minima and maxima were lower than in the baseline.

Predicted gain and loss showed a clear pattern for all three models. An increasing amount of loss is linked to the intensity of temperature increase and run-off decrease as described by the



**Fig. 4.** Mean relative importance (with 95% confidence interval) of independent variables per species model ( $N=700$ ); white bar: model Allau, light grey bar: model ThymEnv, dark grey bar: model ThymEnvAa.

three GCMs. Accordingly, the largest losses were predicted under warm/dry conditions. Loss in model ThymEnv was larger compared to model ThymEnvAa. Model Allau predicted the lowest gains (all  $<5\%$ ; min = 0.1%) in comparison to both European grayling models irrespective of RCP or GCM. The gain predicted by model ThymEnv ranged from 1.9% (warm/dry RCP 8.5) to 7.2% (warm/stable RCP 2.6). Model ThymEnvAa showed the same pattern in respect of minimum/maximum gains but reached a bit higher values (1.5% and 10.0%, respectively) (Fig. 5).

Distribution congruence with the caddisfly was generally higher in model ThymEnvAa than in ThymEnv. River length with congruent distributions of the two species were largest in the moderate/stable realisation. Under RCP 2.6 the length of congruent distribution was comparable to the baseline climate. The additional length of congruent distribution was largest in the warm/stable realisation and smallest in the warm/dry realisation where the absolute length of congruent distribution was smallest too (Table 3).

Comparing the mean elevation of European grayling presences, the difference between model ThymEnv and ThymEnvAa was significant in all cases ( $p < 0.001$ ) excepting the baseline and the moderate/stable realisation of RCP 2.6. In all other predictions the consideration of the caddisfly presence attenuated the upwards shift of European grayling significantly. Under warm/dry conditions in RCP 8.5, the difference of the mean elevation between the two models for European grayling presences was highest (230 m). The smallest future elevation increase was observed for moderate/stable conditions in RCP 2.6 (Fig. 6).

The distribution maps, summarising the predictions of the three GCMs in one map, revealed a common pattern of habitat suitability

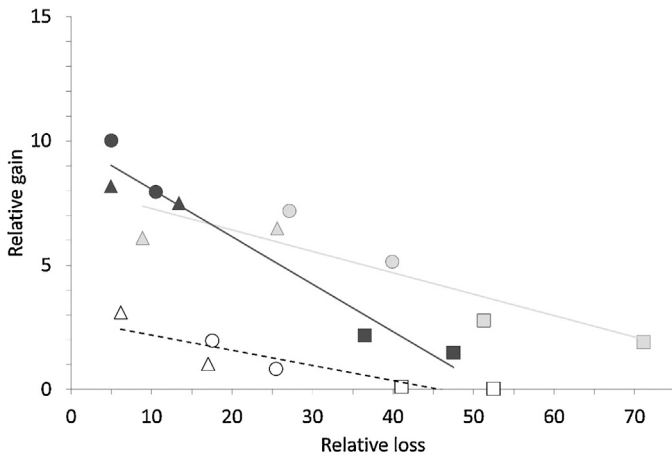
**Table 2**

Summary of climatic variables in all surface water bodies ( $N=8572$ ) for baseline and future climate; all variables are characterised by mean (minimum/maximum); TmeJan = mean temperature January, TmjulUp = mean temperature of July in the upstream catchment, ROpot = run-off potential.

|          |                 | TmeJan ( $^{\circ}\text{C}$ ) | TmjulUp ( $^{\circ}\text{C}$ ) | ROpot ( $\text{mm km}^{-2}$ ) |
|----------|-----------------|-------------------------------|--------------------------------|-------------------------------|
| Baseline |                 | −3.5 (−9.7/−0.6)              | 14.8 (3.5/20.2)                | 1367 (578/2481)               |
| RCP 2.6  | Warm/dry        | −0.5 (−6.9/3.5)               | 18.8 (7.0/24.9)                | 1333 (528/2323)               |
|          | Moderate/stable | −1.8 (−7.9/1.4)               | 15.9 (4.5/21.5)                | 1391 (561/2447)               |
|          | Warm/stable     | 0.5 (−5.9/3.8)                | 17.4 (6.1/23.0)                | 1411 (561/2475)               |
| RCP 8.5  | Warm/dry        | 0.6 (−5.9/4.7)                | 20.7 (9.0/26.7)                | 1295 (505/2303)               |
|          | Moderate/stable | −0.5 (−6.7/2.7)               | 17.0 (5.6/22.6)                | 1401 (552/2443)               |
|          | Warm/stable     | 1.4 (−4.7/4.6)                | 18.4 (6.9/24.0)                | 1392 (551/2417)               |

**Table 3**  
Length of congruent distribution of European grayling with the caddisfly under baseline and future climate condition and the difference in congruent length between model ThymEnv and ThymEnvAa.

|          |                 | Congruence length [km] |           | Additional length of congruence [km] |
|----------|-----------------|------------------------|-----------|--------------------------------------|
|          |                 | ThymEnv                | ThymEnvAa |                                      |
| Baseline |                 | 5380                   | 5470      | +90                                  |
| RCP 2.6  | Warm/dry        | 1954                   | 1971      | +17                                  |
|          | Moderate/stable | 5279                   | 5457      | +178                                 |
|          | Warm/stable     | 3908                   | 4110      | +203                                 |
| RCP 8.5  | Warm/dry        | 1156                   | 1188      | +32                                  |
|          | Moderate/stable | 4055                   | 4181      | +126                                 |
|          | Warm/stable     | 2820                   | 3141      | +321                                 |



**Fig. 5.** Relation of relative gain and loss of the caddisfly and European grayling for the six future distribution forecasts (2 RCPs  $\times$  3 GCMs) with according trend lines; white symbols/black dotted line: model Allau, light grey symbols/line: model ThymEnv, dark grey symbols/line: model ThymEnvAa; rectangles: warm/dry GCM, triangles: moderate/stable GCM, circles: warm/wet GCM.

as well as gain and loss in the distribution area (Fig. 7). SWBs with a habitat loss according to all three GCMs were primarily located in the East of the investigation area and those ones with stable habitat suitability or newly gained habitats were mainly situated in the West. By comparison, the GCMs predicted in summary less habitat loss for RCP 2.6 than for RCP 8.5, and less habitat loss for model ThymEnvAa than for ThymEnv. However, the distribution maps highlighted areas with stable habitat suitability as well as river

sections with predestined habitat loss in all four cases at which the magnitude of loss increased from ThymEnvAa RCP 2.6 to ThymEnv 8.5.

#### 4. Discussion

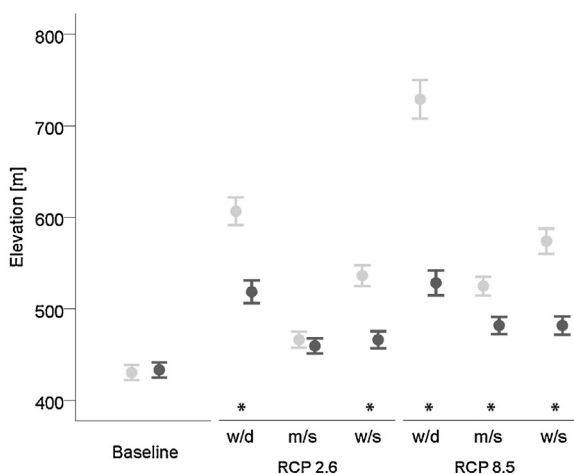
The prediction of potential distribution changes utilising SDMs offers a possibility to highlight potential future developments and to derive spatially explicit information. Our modelling framework combined biological, river topographic and climate data with high spatial resolution and maximal temporal consistency. The predictions of future distributions considered the most recent trajectories of emission pathways (IPCC, 2013). Upstream network length and July temperature in the upstream catchment were the most important variables in the ThymEnv model and were complemented by the occurrence probability of the caddisfly *A. auricollis* in the ThymEnvAa model. Predicted distributions of the caddisfly according to the model Allau were more closely related to climatic descriptors than to river topography. The predicted shrinkage of European grayling distribution was related to warming intensity and reductions of potential run-off. Consideration of the caddisfly mitigated habitat loss and augmented gains.

##### 4.1. Model performance and limitations

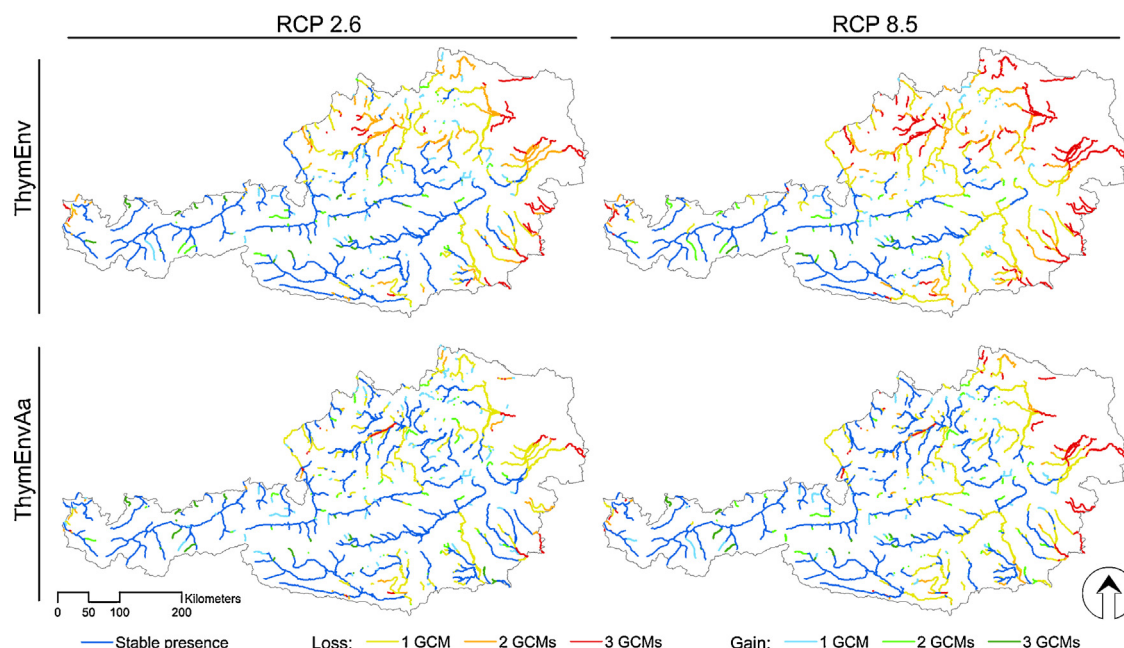
The performance of the different modelling techniques was good and satisfactory (majority of models with sensitivity and specificity >0.8). Higher specificity can be related to a prevalence of absence records in the calibration dataset and indicated higher accuracy of absence prediction which did not impede the aims of the study. Generally, the models performed worse for the caddisfly than for European grayling which could be related to the broader distribution range of the former. Nonetheless, the presence information in the occurrence data covered the distribution area of both species.

SDMs are subject to different uncertainties and limitations. A fundamental uncertainty may originate from data-wise inconsistency, e.g. differences in the observation period of biological and environmental variables. Here, we aimed to minimise data-wise inconsistency through adequate spatial resolution and maximal temporal consistency of the calibration data to improve accuracy of the modelling framework. In contrast to several other studies (Chu et al., 2005; Domisch et al., 2013; Elliott et al., 2015), we considered river topography, represented by upstream network length, river slope and distance to the mouth, already in the basic species models. The use of different descriptors of the riverine environment is highly important in analyses dealing with stream biota (Jähnig et al., 2012; Domisch et al., 2015), a fact reflected by the assigned variable importance.

The evaluation of future distribution patterns in our study was based on a free migration scenario. Even though barriers exist in the investigation area, this assumption can be underpinned as plausible



**Fig. 6.** Error bars for mean elevation ( $\pm 90\%$  confidence interval) of European grayling distribution comparing the distribution models and future climate conditions; light grey: model ThymEnv; dark grey: model ThymEnvAa; asterisks indicate significant differences tested with Kruskal–Wallis-test ( $p < 0.001$ ).



**Fig. 7.** Distribution map of European grayling indicating stable presence, gain and loss on the river network in the investigation area summarising three circulation models in the 2050s according to the models ThymEnv (upper panel) and ThymEnvAa (lower panel) and two RCPs (left: RCP 2.6, right: RCP 8.5); colour coding see legend at the figure bottom; stable absences are not shown.

by the following arguments. Both species are able to migrate and to follow their habitat niche along the riverine network: European grayling in the water and the caddisfly through aerial dispersal in their adult life-stage. Moreover, dispersal can be seen as a function of time, which permits plausibly to assume that a species will be sooner or later able to move to an adequate position in the river network (Radinger and Wolter, 2014). The consideration of barriers would also introduce additional uncertainty into the modelling framework which would be not quantifiable. This uncertainty originates from different aspects. The ability of fish species to pass barriers differs not only among but also within a species and their life stages (Cote et al., 2008). The consideration of barriers in current distributions would in turn imply that this factor has to be considered for future predictions too. However, it is not reasonably assessable how longitudinal connectivity will evolve in the future. Hence, this would introduce additional uncertainties, which cannot be sufficiently handled on this scale. The prediction period (2050s) comprises a temporal scale which potentially includes a bulk of pathways, how connectivity in the river network will look like. The possibilities range from full connectivity as postulated by the water framework directive (WFD) to highly reduced connectivity due to increased hydro power production.

#### 4.2. Ecological relevance

The applied modelling framework identified descriptors playing a vital role in driving the distributions of the caddisfly and the European grayling. We found an importance of both, climatic and river topographic variables for the distribution of European grayling without a clear precedence of one over the other. In contrast, Filipe et al. (2013) described such a precedence for brown trout which prefers cold and rapidly flowing waters. The length of the upstream river network, as descriptor of river size, and July temperature, characterising the thermal conditions, showed their importance accompanied by slope, representing the available energy budget in the river. This is in line with Huet (1959) who reported wider, rapidly flowing streams with cool and well oxygenated water as suitable habitat for European grayling. Also,

a narrow thermal preference of European grayling, with critical water temperatures below 4 °C and above 18 °C, is known from literature (Crisp, 1996; Logez et al., 2012) and in line with the findings of our modelling framework. Additionally, model ThymEnvAa assigned notable importance to the occurrence probability of the caddisfly.

Temperature is a crucial factor in the physico-chemical setting of riverine environments (Pletterbauer et al., 2015). Temperature has direct (e.g. metabolism) and indirect (e.g. oxygen solubility) effects on ectothermic aquatic organisms and their life stages (Pörtner and Farrell, 2008). In most cases, not the lethal effects of high temperatures affect species, but sublethal effects which play a vital role for growth or reproduction. Hence, sublethal effects of temperature serve as guiding factors as species tend to optimise their energetic position in their riverine environment. However, temperature is not the only trigger for movements as other factors like stream-flow, turbidity, availability of canopy and food have their effects on behaviour too (McCullough et al., 2009). Our approach furthermore considered the thermal processes in the upstream catchment which poses a clear advantage to local information alone.

Caddisflies, as epibenthic filter feeders, meet two important criteria to serve as prey for European grayling: they are easily detectable, and build very dense populations (Graf et al., 1992; Waringer, 1989). The distribution models supported the wide distribution range of the caddisfly in the investigation area, and therefore its potential availability as food source for all life-stages of bottom feeding European grayling (Northcote, 1995). Moreover, the results strengthened the hypothesis that the potential availability of adequate food sources, indicated by the occurrence of the caddisfly, plays a vital role in the distribution of European grayling. Furthermore, the availability of food sources also reduced the upwards altitudinal shift of predicted adequate European grayling habitats.

Our analyses focused on the biological relationship between European grayling and the caddisfly. The distribution models indicated that predicted habitats of the caddisfly may shrink in the upstream sections of the rivers. If this species may completely disappear as food source for European grayling, this gap in the



nutrition resources have to be filled by other taxa. However, the taxon included in our analyses represents the only limnephilid species with mass occurrences inhabiting the river sections where European grayling occurs (Graf et al., 1992). Other limnephilids are scarce in larger rivers and hide in discrete habitats like organic patches. The caddisfly in our analyses lives right at the surface of the substrate until pupation (Waringer, 1989). It is an opportunistic species which switches occasionally from shredding and grazing to filter feeding. This remarkable flexibility might be one reason for its high abundance. In summary, this caddisfly possesses distinct traits which in turn impedes a reasonable prognosis which macroinvertebrate species may succeed into the habitats, which may be lost for the caddisfly due to climate change impacts. Although another species may follow, it is still unclear, if this species will then also fit into the diet of European grayling.

The congruence analyses revealed that the implementation of the predicted distributions of the caddisfly as predictor led to smaller losses and larger gains in future climates. Larger congruent distribution areas were directly related to stable run-off potential. This variable, which characterised the available amount of water in the river, emerged as important factor for future distributions. Even though studies exist, which incorporated hydrological predictors (Bond et al., 2011; Kuemmerlen et al., 2012), hydrological characteristics are still not considered in all studies investigating climate change impacts in riverine environments (e.g. Filipe et al., 2013). Run-off potential as implemented in this study summarised the available amount of water in the upstream catchment under consideration of the catchment area, hence giving a plausible estimate of mean future hydrologic conditions. However, detailed information, how climate change will affect hydrology in rivers is still scarce especially in respect of hydrologic variability. Therefore, we implemented different GCMs into our approach to illustrate this variability. Two out of the three GCMs indicated stable respectively slightly increasing run-off volumes on average. This is in line with expected climate change effects in the alpine realm (IPCC, 2013). Nonetheless, minima were decreasing indicating the probability of drier condition in some regions in the future. The third GCM indicated decreasing run-off potential. In combination with increasing temperature this future path of climate led to highest habitat loss and lowest gain. Accordingly, the results indicated that the magnitude of climatic changes, i.e. intensity of warming and decrease in available run-off respectively, played a vital role for the amount of suitable habitats in the future.

#### 4.3. Implications for conservation and management

The results clearly indicated the shrinkage in the predicted distribution of European grayling and the caddisfly, underlining the need for conservation and management strategies to sustain the occurrence of these species in their native range. The use of SWBs as spatial unit for the analyses highlighted areas with different needs for conservation and management as they are used for WFD assessment too.

The prediction of future distributions indicated dramatic habitat loss, especially if warming is accompanied by run-off reductions, underlining highly important conservation implications. The predicted distribution maps (Fig. 7) delineated three zones of SWBs with distinct management and conservation needs: (1) SWBs which are expected to steadily feature suitable habitat conditions, (2) SWBs at risk of losing currently available adequate habitats, and (3) SWBs which will contain adequate habitats in the future. The first zone can serve as core area for European grayling occurrence. Therefore, the conservation of vital populations in this area has highest priority. Accordingly, the condition of European grayling populations should be monitored and further human-induced impacts avoided to maintain suitable habitats and to prevent

habitat deterioration. In the second zone, different levels of risk for the extirpation of European grayling were indicated by the number of GCMs revealing habitat loss. In this zone, mitigation measures to halt the increase of climate change induced impacts are most important. Potential mitigation measures represent the enhancement of riparian shading to reduce warming, and the restoration of morphological heterogeneity which can reduce impacts of less discharge. The third zone comprises the future potential for the distribution of European grayling. In order to be able to develop the full potential of this zone the connectivity must be enhanced. Accordingly, the connectivity to the first zone is key to enable the dispersal of European grayling to this zone. Beside the provision of migration facilities to overcome barriers, species translocation may represent a further option to compensate for the impact of barriers (Thomas, 2011).

According to post-glacial colonisation routes, the Danube basin confines a distinct genetic lineage of European grayling (Gum et al., 2009; Sušnik et al., 2001) which can even be subdivided into further lineages (Meraner and Gandolfi, 2012). Our investigation area encompasses the Eastern distribution margin in the Alps of the Danubian lineage which may therefore serve as last refugium in respect of future climate change. In turn, the information on the persistence of potential habitats gains importance (Weiss et al., 2002). Fragmentation of habitats counteracts the ability of the species to track its adequate habitat—not only physically by fragmenting the river continuum but also by selecting for less migratory genotypes which undermine the resilience against climate change (Junge et al., 2014).

Working with different scenarios and realisations is not to predict an exact future, but to better understand alternative pathways (IPCC, 2013). The usage of two RCPs and three GCMs underlined the potential variability of climate change impacts, which should enable the identification and development of adequate management decisions for different areas where the species may extirpate or newly occur in the future. In turn, robust management decisions encompass far more information including species' ecology, monitoring and validation of models, evaluation of biological responses, strategies for conservation and their implementation into policies, and finally to ensure the conservation efforts (Vörösmarty et al., 2010).

Species distribution modelling approaches such as this study represent a basic step to investigate climate change impacts and to identify changes in distribution patterns. Further research should investigate small-scale processes to identify factors and the magnitude of the factors which trigger species to disperse. Such dispersal can only be monitored by field studies potentially verifying the results of SDMs. Another important aspect is temporal stability of the habitat shift which can provide additional insights how climate change will impact future distributions. In summary, future research on climate change impacts should focus on the integration of information from different scales, e.g. large- and medium-scale spatial explicit information (as derived from SDMs) and small-scale process-based information derived from mesohabitat, in-field investigations.

This study underlined that climate change will alter riverine habitats of fish as well as macroinvertebrates, therefore inducing shifts of potential habitats. However, beside the variability of climate change, the results emphasised that biotic interactions played a crucial role for the predicted distributions of European grayling.

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