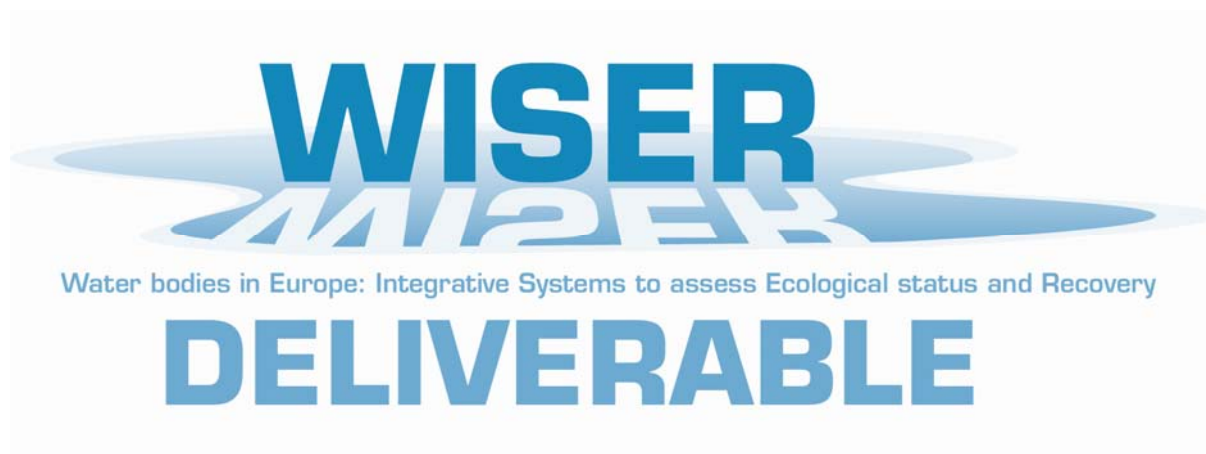


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Lead contractor: **Irstea/Cemagref**

Contributors: **Maxime Logez, Jérôme Belliard, Andreas Melcher, Helga Kremser, Florian Pletterbauer, Stefan Schmutz, Guillaume Gorges, Olivier Delaigue, Didier Pont**

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Non-technical summary

This report encompasses several studies that try to assess the consequences of climate change on the future presence/absence of fish species in European rivers. In the first part of this report we estimate the ecological preferences of fish species, such as the temperatures in which the particular species could occur. Part II uses these preferences to assess how fish species would be able to cope with future climatic conditions. These modifications have been computed for four scenarios of climate change. This part highlights the sensitivity of species preferring cool- or cold waters to climate change. Brown trout or grayling will suffer from a temperature increase and their habitat will be greatly reduced. In contrast, species living in warm rivers will benefit from the temperature increase. The third part of this report concerns a long-term study of a grayling population in the Traun River in Austria. During the last 30 years, the water temperature of this river has increased by 2.2 °C and the abundance of the grayling has sharply declined. The fourth part of this report is a case study on the whole Seine basin in France. It showed that climate change will greatly affect fish species and it could be the major factor controlling species distributions, overriding the benefits of river restoration measures.

Summary

This report, comprising four studies, attempts to assess the consequences of climate change on the distribution of 23 fish species, as well as the effects of climate change on functional assemblages. The first study aimed to estimate the ecological requirements of these species, by modelling the occurrences of fish species with environmental factors, including temperature and precipitation. The confidence intervals around the occurrence–environment relationships were also computed, to identify in which environmental conditions the predictions are more uncertain. The second aim of this study was to compare two approaches so as to compute the expected metric values. The results showed that metrics computed from the species distribution models or from models related to functional trait variability or environmental conditions give relatively similar results.

The first aim of the second study was to assess the consequences of climate change on the distribution of the 23 fish species. The logistic regressions computed in the first study were used to compute the probability of species presence under different climatic scenarios. These results demonstrated that cold- or cool-water species will be greatly and negatively affected by climate change, while warm-water species will be favoured. The uncertainty of the predicted probabilities reveal that for some species the effect of global change remains unclear, while for others only the magnitude of the response to climate change differs. These results were discussed from the perspective of river restoration and species conservation. The second aim of this study was to use the models developed to predict functional traits, so as to assess the expected drift of reference conditions. The results suggest that metrics based on species tolerance will be less represented in fish assemblages in the future, which will have important consequences on the use of current bio-assessment tools.

The third part of this report is a case study on the Traun River in central Austria. A long-term survey of more than 30 years has been conducted in a station downstream of a lake outlet flow. Owing to climate warming, the water temperature in August has increased on average by 2.2°C. In reaction to this warming, a shift of species dominance and a large decline of the grayling population were observed. This study is a good illustration of the consequences of climate change on fish assemblages and of the necessity for water managers to take into account the effect of climate change when planning restoration measures.

The fourth part of this report is a case study on the Seine basin in France. Species projections were made for the whole catchment area and demonstrate that cold-water species would be highly affected by climate change, especially in the decade of 2050–2060. Several species are predicted to be extinct up to this period, while some warm-water species are expected to expand their distributions throughout the catchment area. Human pressures were also included in the species distribution models to assess the potential effect of restoration scenarios on species distributions. The results highlight the potential benefits from these restoration measures, but mostly show that climate change will be the major factor driving species distributions, overcoming restoration measures.

CHAPTER I

Species niche and functional traits

Large scale approach: Modelling ecological niche of fish species at the European scale: species-based vs. functional traits.

Maxime Logez¹ and Didier Pont²

¹ Irstea, UR HBAN, 1 rue Pierre-Gilles de Gennes - CS 10030, F-92761 Antony, France; email: maxime.logez@irstea.fr; phone: +33 (0)4 42 66 69 86

² Irstea, UR HBAN, 1 rue Pierre-Gilles de Gennes - CS 10030, F-92761 Antony, France; email: didier.pont@irstea.fr; phone: +33 (0)1 40 96 65 52

There are three main driving forces behind the current species distribution: natural environmental conditions (Vannote et al. 1980; Junk et al. 1989; Jackson et al. 2001), species niche (Hutchinson 1957; Elliott 1994), and the anthropogenic activities that disturb or modify the functioning of the ecosystem (Ward & Stanford 1983; Poff et al. 1997). Among the environmental factors, hydromorphology and climate are the most important natural factors that control fish distribution in lotic hydrosystems (Rahel & Hubert 1991; Poff & Allan 1995; Petts & Amoros 1996; Poff et al. 1997; Wehrly et al. 2003; Caissie 2006). Anthropogenic alterations can modify the relative dominance between species, the species composition of fish assemblages (species loss, addition and/or species replacement) and local species richness (McCormick et al. 2001; Kruk & Penczak 2003; Quinn & Kwak 2003; Wang et al. 2003; Quist et al. 2005; Pont et al. 2006; Melcher et al. 2007; Pont et al. 2007; Haxton & Findlay 2008; Pont et al. 2009).

Because of their sensitivity to human disturbances and their numerous advantages, for example, their presence in almost all water bodies, well-known taxonomy, ecology and life history, food web position, etc. (Simon & Lyons 1995; Oberdorff et al. 2001), fish have long been used in bioindication studies around the world (Karr 1981; Karr et al. 1986; Karr 1991; Karr & Chu 1999, 2000; Pont et al. 2006; Pont et al. 2007) to assess the ecological status of streams (e.g. Oberdorff & Hughes 1992; Lyons et al. 1995; Hugueny et al. 1996; Hughes & Oberdorff 1999; An et al. 2002; Joy & Death 2004; Bramblett et al. 2005; Pont et al. 2009). Moreover, fish were used as a model to develop the first multi-metric index, the Index of Biotic Integrity (IBI) (Karr 1981), which has been successfully used by numerous authors. The IBI seeks to quantify a deviation between the observed assemblage attributes (both composition and structure) and assemblage attributes that are expected in the absence of human degradation. IBI statements and concepts were also used by several authors to develop other multi-metric indices (e.g. Oberdorff et al. 2001; Pont et al. 2006).

One of the main advances of the IBI was to consider that the use of several variables (also called metrics) reflecting different aspects of fish assemblages (Karr 1981; Fausch et al. 1984; Karr et al. 1986; Karr 1991) enable a better assessment of the ecological conditions of streams than considering only one assemblage attribute (Karr & Chu 1999). Ideally each metric should:

- Provide unique information on the assemblage (Karr and Chu 1999) describing the quality of a community element (Karr 1991)
- Present a specific response to human pressures (Karr & Chu 2000)
- Show varying degrees of sensitivity along a gradient of human pressures (Angermeier & Karr 1986)
- Only reflect the between-site differences in degradation (Hughes et al. 1998; Karr & Chu 1999, 2000; Oberdorff et al. 2002; Hering et al. 2006; Pont et al. 2007; Stoddard et al. 2008; Pont et al. 2009)

This last point suggests that the metric scores (mark) that are used in the index computation vary only with the level of site impairment: the difference between the observed and expected metric values results from human pressures. Since most of the assemblage attributes vary along the environmental gradient, it is necessary to control the environmental part of the variability of the metrics. Two main approaches are used to assess the effect of the environment (Roset et al. 2007):

- Type-specific approach: considering sites located in homogenous environmental conditions by either working in a small area, or on a river type, or by defining groups of sites a priori based on their environmental proximity (e.g. with cluster techniques), in order to limit the environmental difference between sites
- Site-specific approach: the expected value metrics in absence of pressure in a given site are predicted from the environmental conditions observed in this site, using predictive statistical techniques (e.g. generalized linear models; Pont et al. 2006; Logez & Pont 2011a).

Controlling the environmental variability of the metrics is of major importance to measure solely the effect of pressure with metric scores, but also to have an index with values that are comparable everywhere and in all environmental conditions encountered in the region of interest. For instance, ideally a multi-metric index (MMI) should be usable in headwater streams and lowland rivers and the MMI scores must have the same meaning (e.g. high values for good conditions and low values for bad conditions).

While numerous MMIs are mainly based on the type-specific approach (e.g. Melcher et al. 2007; Schmutz et al. 2007), recently MMIs based on the site-specific approach were developed to assess stream conditions over large areas, for example, in France (Oberdorff et al. 2002), New Zealand (Joy & Death 2002), the United States (Pont et al. 2009) and Europe (Pont et al. 2006; Pont et al. 2007). Working at the European spatial extent involves coping with a wide range of environmental conditions (Tockner et al. 2009) and a high diversity of fish faunas (Banarescu 1989, 1992; Kottelat & Freyhof 2007; Reyjol et al. 2007) that have been strongly shaped by the latest glaciations (Banarescu 1992; Hewitt 1999, 2000; Kontula & Vainola 2001; Koskinen et al. 2002; Hewitt 2004; Griffiths 2006).

Owing to the biogeographical differences observed over a large spatial extent, the use of metrics based on species composition is not relevant. In contrast, using metrics based on traits (life-history, ecological or biological), which group species with the same attributes into one variable (Usseglio-Polatera et al. 2000; Melville et al. 2006; Hoeinghaus et al. 2007; Noble et al. 2007), makes it possible to compare assemblages composed of different species pools (Reich et al.

1997; Statzner et al. 1997; Winemiller & Adite 1997; Lamouroux et al. 2002; Vila-Gispert et al. 2002a; Statzner & Moss 2004; Melville et al. 2006; Hoeinghaus et al. 2007; Logez et al. 2010). Moreover, these traits are directly or indirectly related to system functioning (Lavorel & Garnier 2002) and were successfully used in bioindication studies, especially at a large spatial extent (Pont et al. 2006; Logez & Pont 2011a).

The Indice Poisson Rivière (IPR) developed at the French national scale (Oberdorff et al. 2002) and the European indices EFI (European Fish Index) (Pont et al. 2006; Pont et al. 2007) and EFI+ (new version of the EFI) (Bady et al. 2009) were developed using only metrics based on ecological and biological traits. All these indices are predictive indices based on the reference condition approach (Bailey et al. 1998). Indeed, the expected values in absence of pressure that are compared with the observed values to compute metric scores are predicted from statistical models (Oberdorff et al. 2002; Pont et al. 2006; Bady et al. 2008, 2009). Nevertheless, the methodology used to compute the expected values of metrics based on richness (e.g. number of rheophilic species) was different. For the IPR, Oberdorff et al. (2002) used a method based on the species niche. They used models based on the relationships between environmental conditions and species presence/absence (Oberdorff et al. 2001) to predict the expected probability of the presence of species sharing the same attribute. They then aggregated these probabilities to get the expected values of a metric in a given site. Pont et al. (2006) used a different approach. Rather than modelling the species presence/absence, they directly modelled the theoretical number of species sharing a given trait in relation to the environment. This approach hypothesizes that species with similar functional traits will occur in the same environmental conditions in accordance with the predictions of the habitat filtering theories. To date, the differences between the niche and the trait approaches have not been assessed and are the objective of this study.

The spatial extent of the data set used to estimate the species niches determines the accuracy of the estimations. If the data used to calibrate the models slightly overlapped in the species distribution area, the estimated niches would only represent a small part of the species realized niche. The recent study of Barbet-Mazin et al. (2010) clearly demonstrated the importance of using data that cover the whole range of the species distribution area, for example, the extent of the climatic niche was underestimated when using a spatially restricted data set. Using a spatially restricted data set could lead to high levels of uncertainty when predicting species occurrence in environmental conditions that are rarely encountered. The levels of uncertainty associated with the species–environment relationships are rarely addressed. The recent study conducted by Grenouillet et al. (2011) showed that the uncertainty associated with fitted species occurrence varied with the environmental conditions. Therefore, it could be extremely valuable to estimate the uncertainty associated with the model's expected values so as to define the environmental conditions in which species occurrence is or is not accurately predicted.

The main objectives of this study were: (1) to estimate the species niche of 23 European freshwater species using logistic regression and slightly impacted sites located in the current species distribution area, (2) to compute the uncertainty associated with the models, (3) to assess the

reliability of the niche models along the different environmental gradients and (4) to compare the niche and traits approaches to estimate the metric expected values.

The European FAME and EFI+ projects provided the opportunity to assess the species niche at a continental scale. To our knowledge, for fresh-water fish, this type of experiment has never been conducted over such a large spatial extent. Because of the precise description of the human pressures used in the EFI+ project, we were able to select sites that were not impacted or only slightly impacted, considering various types of pressures, and to observe species absences that were not influenced by human activities. Compared to other organisms such as terrestrial plants (e.g. Hanspach et al. 2010), the fish data were collected over a smaller spatial extent and thus species occurrence could be more influenced by local pressures.

Material and methods

All the data used were collected during the European EFI+ project (contract number 044096, <http://efi-plus.boku.ac.at/>). Data were collected from national fish surveys conducted by several laboratories and governmental environmental agencies (1981–2007, 96% after 1990). The sites were sampled using electrofishing methods either by wading or by boat, depending on stream depth. All fish caught were identified at the species level. To homogenize the sampling effort between regions, only fish collected during the first pass were considered.

Species niche

Site selection

Accurately defining the site used is of major importance because all outcomes depend on the precision of the estimated relationships between species presence/absence and the environmental factors. It is necessary to select sites that reflect the realized niche of the species and to avoid “false” absence due to non-environmental factors.

Because human activities can modify the species assemblage composition, only sites that were slightly or not at all impacted were selected (Pont et al. 2005). Sites were selected based on objective criteria (Stoddard et al. 2006) following Logez and co-workers' (2011) definition of slightly impacted sites.

Sites were also selected to limit spatial autocorrelation, because spatial factors could influence the assemblage composition (Grenouillet et al. 2004) and the dependent observations are in discordance with generalized linear model (GLM) requirements (McCullagh & Nelder 1989).

To limit spatial autocorrelations, which affect the stream-fish assemblage composition and reduce the independence between sites, a grid of 0.2 decimal degrees was defined and one site per cell was randomly selected. A total of 1548 sites spread over 14 countries were selected, covering more than 4.10^6 km² (Fig. 1).

Within this global data set, for each species only the sites that were located in their distribution area were retained so as to limit the effect of biogeographical factors on species absence. For each species, the calibration data set was only composed of sites located in the main marine region where the species is considered as native (Kottelat & Freyhof 2007; Reyjol et al. 2007).

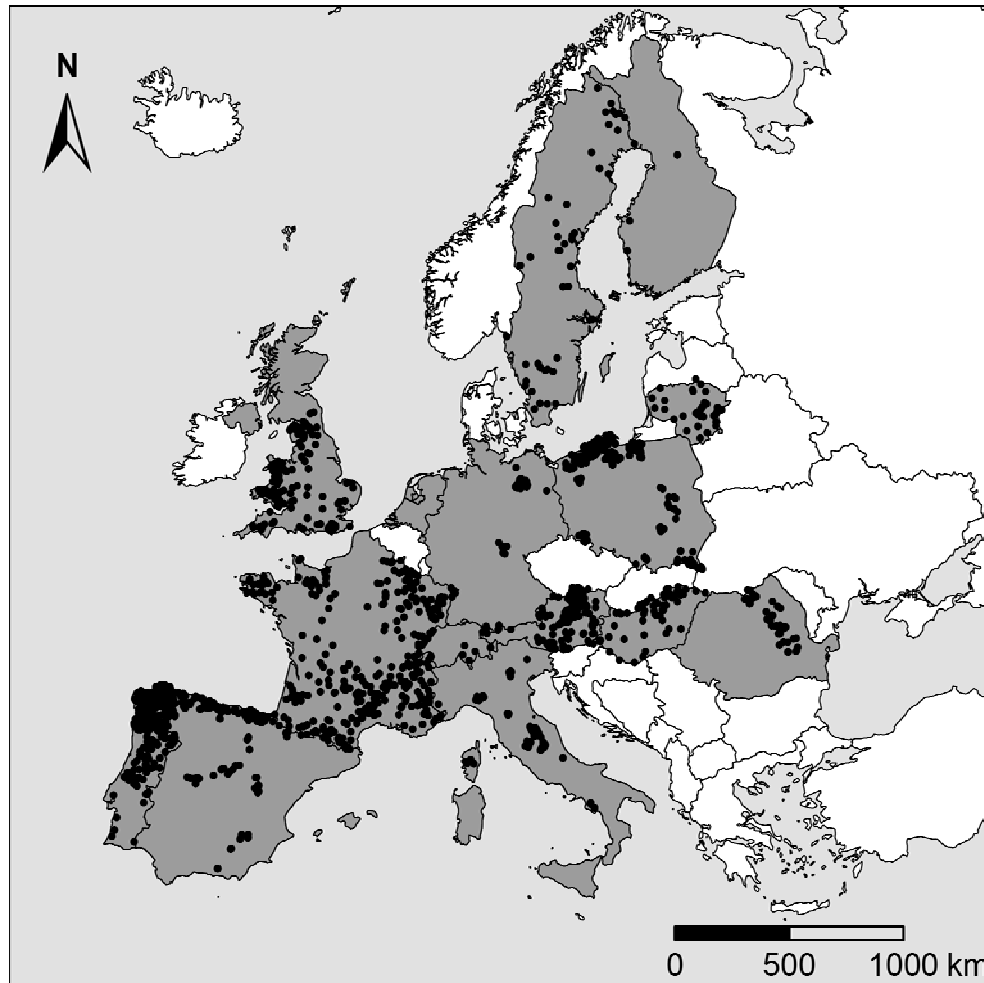


Fig. 1. Locations of the 1548 sampling sites.

Selected species

We focussed on 23 common fish species native to Europe, occurring in more than 10% of their calibration sites, to avoid rare events in the estimation of species presence (King & Zeng 2001).

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Environmental factors

To estimate the ecological niche of the 23 fish species, four environmental factors that can influence the spatial distribution of fish species were considered.

The upstream drainage area (UDA, km²) is a descriptor of the position of the stream reach along the hydrographic network (Oberdorff et al. 2001; Pont et al. 2005) and also reflects habitat diversity because stream complexity increases along the longitudinal gradient (Matthews 1998). The UDA was shown to influence the spatial distribution of freshwater fish species in Europe (Pont et al. 2005).

Stream power (STP, watt/m) is “the rate of potential energy expenditure over a reach or stream power per unit of stream length” (Gordon et al. 2004). STP reflects the hydraulicity of a stream

varying both with stream slope and discharge. The importance of hydraulicity for fish was previously demonstrated (Oberdorff et al. 2001; Pont et al. 2005; Buisson et al. 2008a), but these authors used an estimation of stream velocity based on stream width and depth. STP provides a more reliable and reproducible estimation of stream hydraulicity, because depth and width are influenced by human alterations.

STP was computed as: $STP = \rho g Q S$, with ρ the density of water (taken to 1000 kg/m³), g the acceleration due to gravity (9.81 m/s²), Q the mean annual discharge (m³/s) and S the slope (m/km). Run-off was used instead of the observed water flow to avoid any hydrological alteration induced by human activities. Q was computed as the multiplication of the UDA and of the mean annual run-off (MAR, mm/year): $Q = \frac{MAR \cdot UDA}{31536}$. MAR was estimated by first

computing the annual potential evapotranspiration (PET, mm) using Turc's formula (1954):

$$PET = \frac{P}{\sqrt{0.9 + \left(\frac{P}{L}\right)^2}},$$

with P the mean annual precipitations (in mm) and L the temperature

factor derived from the mean annual temperature (T , °C) (Turc 1954): $L = 300 + 25 * T + 0.05 * T^3$. MAR was then computed as: $MAR = P - PET$.

Temperature is a key climatic factor (Somero 1997; Begon et al. 2006) influencing fish species distribution (Matthews 1998; Wehrly et al. 2003; Pont et al. 2005; Buisson et al. 2008a). The mean air temperature in July (TJUL, °C) was used as an alias for water temperature (Allan & Castillo 2007). The thermal amplitude between July and January (TDIF) was also considered.

In addition to their ecological relevance, these factors were chosen to limit the multi-collinearity between explanatory variables in the model.

Modelling approach

Among the numerous statistical methods available to relate species occurrence to environmental conditions (Brosse et al. 2001; Austin 2007; Buisson et al. 2008a; Elith et al. 2008; Leathwick et al. 2008; Vaz et al. 2008; Chessman 2009; Hopkins & Burr 2009; Thuiller et al. 2009; Tirelli & Pessani 2009; Buisson et al. 2010), logistic regression (Hosmer & Lemeshow 2000; Collett 2002) including quadratic terms for the environmental variables is the most appropriate method with which to estimate the species niche (Hutchinson 1957; Austin 2007).

Logistic regression relates the probability of the presence of a species (p) to the environmental factors (X) through the logit function (Hosmer & Lemeshow 2000; Collett 2002):

$$\log\left(\frac{p}{1-p}\right) = \alpha + \sum_{i=1,p} \beta_i X_i \Leftrightarrow p = \frac{1}{1 + e^{-(\alpha + \sum \beta_i X_i)}},$$

with α the intercept and β_i the i^{th} coefficients

associated with the i^{th} environmental variables X_i .

To model the species niche, we used the environmental factors and their quadratic terms (except for TDIF) (Austin 2007). The complete models were as follows:

$\text{logit}(p) \sim UDA + UDA^2 + STP + STP^2 + TJUL + TJUL^2 + TDIF$. For each species the most relevant variables were selected through a stepwise procedure based on AIC (Agresti 2002).

The models' complexity would limit the observation of the relationship between a given environmental variable and the probability of species presence. Therefore, we used a graphic effect display (Fox 1987, 2003) to represent the specific marginal effect of an environmental factor on species occurrence. These graphs are drawn by computing the probability of the presence of a species along an environmental gradient. The values of the other environmental factors were fixed at their medians observed on the calibration sites where the species occurred.

Uncertainty around environment–occurrence relationships

The confidence interval (CI) was used to assess the uncertainty in the relationships between environmental factors and the probability of species presence (drawn on the graph effect display). CIs “quantify our knowledge, about a parameter of a population, based upon a random sample” (Hahn & Meeker 1991). The CI is used as an indicator of model precision (de Jong & Heller 2008) and estimates the uncertainty of the expected probability of the presence of a species in a given environment: $P(Y = 1|X)$.

CIs were first computed on the link space (around the logit; Collett 2002): $\text{CI}(\text{logit}(\hat{p}_x)) = \hat{\eta}_x \pm z_{1-\alpha/2} \cdot \text{se}(\hat{\eta}_x)$, where $z_{1-\alpha/2}$ is the upper $1-\alpha/2$ point of the standard normal distribution (α taken to 0.05), $\hat{\eta}_x$ the linear predictor (estimated logit) and $\text{se}(\hat{\eta}_x)$ its standard error. $\text{se}(\hat{\eta}_x)$ was computed using the Wald approach (Hosmer & Lemeshow 2000; Agresti 2002): $\text{se}(\hat{\eta}_x) = \sqrt{\phi \mathbf{X}'_x (\mathbf{X}'\mathbf{W}\mathbf{X})^{-1} \mathbf{X}_x}$, where ϕ is the dispersion parameter (taken to 1), \mathbf{X}_x (the environment in a given site) a vector of the matrix design \mathbf{X} and \mathbf{W} the diagonal matrix containing the estimated variance of Y . The inverse logit function was applied to the CI of the

logit to estimate the CI of the probability of presence: $\text{CI}(\hat{p}_x) = \frac{1}{1 + e^{-\text{CI}(\text{logit}(\hat{p}_x))}}$.

Species optimum

The species optimum for a given environmental factor was computed as the value for which the partial derivative was equal to zero and the second partial derivative was positive. For instance,

for TJUL the maximum was computed such that: $\frac{\partial \text{logit}(p)}{\partial Tjul} = 0 \Rightarrow \beta_1 + 2\beta_2 \cdot Tjul = 0$, where β_1

was the coefficient associated with TJUL and β_2 the coefficient associated with $TJUL^2$. The optimum was equal to $\frac{-\beta_1}{2\beta_2}$, if β_2 was positive. The estimations of the species optimum were

independent of the other environmental variables.

Species thermal niche breadth

Thermal niche breadth was defined as the minimal and maximal temperatures that a species can tolerate (Jobling 1981). These temperatures were computed such that $\text{logit}(p) = \text{logit}(c)$, where c is the probability of presence of the species which maximizes the sum of sensitivity and

specificity (Fiedling & Bell 1997). Thermal niche breadths depend on the values of the other environmental variables selected in the models. Thermal breadths were computed for 12 combinations of low-to-high STP and small-to-large UDA, while TDIF was set at the median of the calibration sites where the species was recorded.

Functional traits

Definition

A previous classification of biological and ecological traits of European fish species (Noble et al. 2007) was revised and completed during the European EFI+ and IPR+ projects (<http://efi-plus.boku.ac.at/>; the development of the new French riverine fish index). Since the 23 species studied are subsets of the 102 species recorded in the 1548 sites, we were not able to compute all metrics with the niche models and therefore we focussed on eight metrics: total richness (RICH) and seven metrics based on species trait categories (all expressed in number of species, Table 1) O2INTOL, HINTOL, RH, EURY, RHPAR, EUPAR and LITH.

The four biological and ecological traits retained were considered because of their affinity to several habitat characteristics and their sensitivity to water quality and habitat alteration (Table 1). For each trait, each species was assigned to one of the different categories. All 102 species represented in our sampling site data set are reported, providing an accurate description of the trait composition of our fish assemblages (4 traits, 7 categories).

Table 1. Description of the categories of the four biological and ecological traits considered

Trait	Categories
Tolerance to oxygen	Intolerant (O2INTOL): species requiring more than 6 mg of oxygen per litre
Tolerance to habitat degradation	Intolerant (HINTOL)
Affinity for flow velocity (habitat)	Rheophilic (RH): species preferring to live in high-flow conditions Eurytopic (EURY): species with a broad tolerance to flow conditions
Spawning habitat	(RHPAR) species preferring to spawn in running waters (EUPAR) species without clear spawning preferences
Reproduction	Lithophilic (LITH): species spawning exclusively on gravel, rocks, stones, rubbles or pebbles and with photophobic hatchlings

Species belonging to the different guilds

- O2INTOL

Table 2. List of the 9 oxyphilic species among the 23 species

<i>Alburnoides bipunctatus</i>	<i>Lota lota</i>	<i>Salmo trutta</i>
<i>Cottus gobio</i>	<i>Phoxinus phoxinus</i>	<i>Telestes souffia</i>
<i>Lampetra planeri</i>	<i>Salmo salar</i>	<i>Thymallus thymallus</i>

- HINTOL

Table 3. List of the 12 oxyphilic species among the 23 species

<i>Alburnoides bipunctatus</i>	<i>Esox lucius</i>	<i>Salmo salar</i>
<i>Barbus barbus</i>	<i>Lampetra planeri</i>	<i>Salmo trutta</i>
<i>Chondrostoma nasus</i>	<i>Lota lota</i>	<i>Telestes souffia</i>
<i>Cottus gobio</i>	<i>Rhodeus amarus</i>	<i>Thymallus thymallus</i>

- RH

Table 4. List of the 9 rheophilic species among the 23 species

<i>Alburnoides bipunctatus</i>	<i>Chondrostoma nasus</i>	<i>Salmo salar</i>
<i>Barbatula barbatula</i>	<i>Lampetra planeri</i>	<i>Telestes souffia</i>
<i>Barbus barbus</i>	<i>Leuciscus leuciscus</i>	<i>Thymallus thymallus</i>

- EURY

Table 5. List of the 10 eurytopic species among the 23 species

<i>Alburnus alburnus</i>	<i>Gobio gobio</i>	<i>Pungitius pungitius</i>
<i>Anguilla anguilla</i>	<i>Leuciscus cephalus</i>	<i>Salmo trutta</i>
<i>Cottus gobio</i>	<i>Lota lota</i>	
<i>Gasterosteus aculeatus</i>	<i>Phoxinus phoxinus</i>	

- RHPAR

Table 6. List of the 14 species spawning in running waters among the 23 species

<i>Alburnoides bipunctatus</i>	<i>Gobio gobio</i>	<i>Salmo salar</i>
<i>Barbatula barbatula</i>	<i>Lampetra planeri</i>	<i>Salmo trutta</i>
<i>Barbus barbus</i>	<i>Leuciscus cephalus</i>	<i>Telestes souffia</i>
<i>Chondrostoma nasus</i>	<i>Leuciscus leuciscus</i>	<i>Thymallus thymallus</i>
<i>Cottus gobio</i>	<i>Phoxinus phoxinus</i>	

- EUPAR

Table 7. List of the 3 species without clear spawning preference among the 23 species

<i>Lota lota</i>	<i>Perca fluviatilis</i>	<i>Rutilus rutilus</i>
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- LITH

Table 8. List of the 14 lithophilic species among the 23 species

<i>Alburnoides bipunctatus</i>	<i>Lampetra planeri</i>	<i>Salmo salar</i>
<i>Barbatula barbatula</i>	<i>Leuciscus cephalus</i>	<i>Salmo trutta</i>
<i>Barbus barbus</i>	<i>Leuciscus leuciscus</i>	<i>Telestes souffia</i>
<i>Chondrostoma nasus</i>	<i>Lota lota</i>	<i>Thymallus thymallus</i>
<i>Cottus gobio</i>	<i>Phoxinus phoxinus</i>	

Modelling approach

Owing to the nature of the metrics (count data) we used log-linear models (McCullagh & Nelder 1989; Faraway 2006) to relate metric variations to environmental conditions. Log-linear models use a non-normal distribution for the model errors, and dependent variables are linearly related to predictors through a link function (the logarithm function for the Poisson distribution; McCullagh & Nelder 1989; Cameron & Trivedi 1998). Therefore, the models have the form:

$\log(Y) = \alpha + \sum \beta_i X_i$, where Y is the dependent variable (i.e. each metric), α is the intercept, and β_i the i^{th} parameter associated with the environmental variable I . The coefficients are estimated

by maximizing the likelihood (McCullagh & Nelder 1989; Faraway 2006) rather than by ordinary least squares as done for linear models (Kutner et al. 2005; Montgomery et al. 2006).

As with the niche approach, we used the environmental factors and their quadratic terms (except for TDIF), and the most relevant variables were selected with a stepwise procedure based on AIC. The complete models were as follows:

$\log(Ns_TRAIT) \sim UDA + UDA^2 + STP + STP^2 + TJUL + TJUL^2 + TDIF$, where Ns_TRAIT is the metric considered.

The pool of species belonging to a trait category varies. To take into account these differences for each metric, the calibration sites were selected such that all species included in the metric computation belong to our pool of 23 species. For instance, among the 1548 reference sites, only the sites in which fauna was composed of one or more of the 23 species were used.

Metric expected values

Niche model

The probabilities of occurrence of all species were first estimated from the environmental conditions of the sites. Then, for the species whose distribution areas did not overlap with the main marine region that the site is located in, the probabilities of presence were set to 0. Metric expected values were obtained by summing the expected probabilities of presence of the species sharing the trait of interest. For each metric, the expected values could have been only computed on the calibration sites used for the trait approach.

Functional traits

The metric expected values were predicted from the fitted models according to the environmental conditions.

All statistical analyses were performed using the statistical software R v2.13.1 (R Development Core Team 2011).

Results

Environmental conditions

The global calibration data set (1548 sites) encompassed a large variety of environmental conditions: TJUL varied between 11.3 and 25.1°C (mean, 18.1, SD, 2.16), TDIF from 8.4 to 28.8°C (mean, 16.9, SD, 4.3), UDA from 0 to 11.5 (in log, mean, 4.5, SD, 1.8) and STP from 3.9 to 17.4 (in log, mean, 11.2, SD, 1.54).

Species niche

More than two-thirds of the 23 species were recorded in less than 25% of the sites. Gudgeon (*Gobio gobio*, L.), bullhead (*Cottus gobio*, L.), stone loach (*Barbatula barbatula*, L.) and minnow (*Phoxinus phoxinus*, L.) were the only species caught in more than 30% of the sites located in their distribution area. Brown trout (*Salmo trutta*, L.) had the highest prevalence (78.5%). The number of calibration sites varied from 385 to 1544.

Species responses to environmental factors

The great majority of species had a bell-shaped response curve along the TJUL gradient (Fig. 2), but some species had different response patterns. The estimated probability of bleak and bitterling constantly increased along the TJUL gradient, while Atlantic salmon displayed the opposite pattern. Brown trout had the most singular pattern with a sharply decreased presence only over 19°C (Fig. 2).

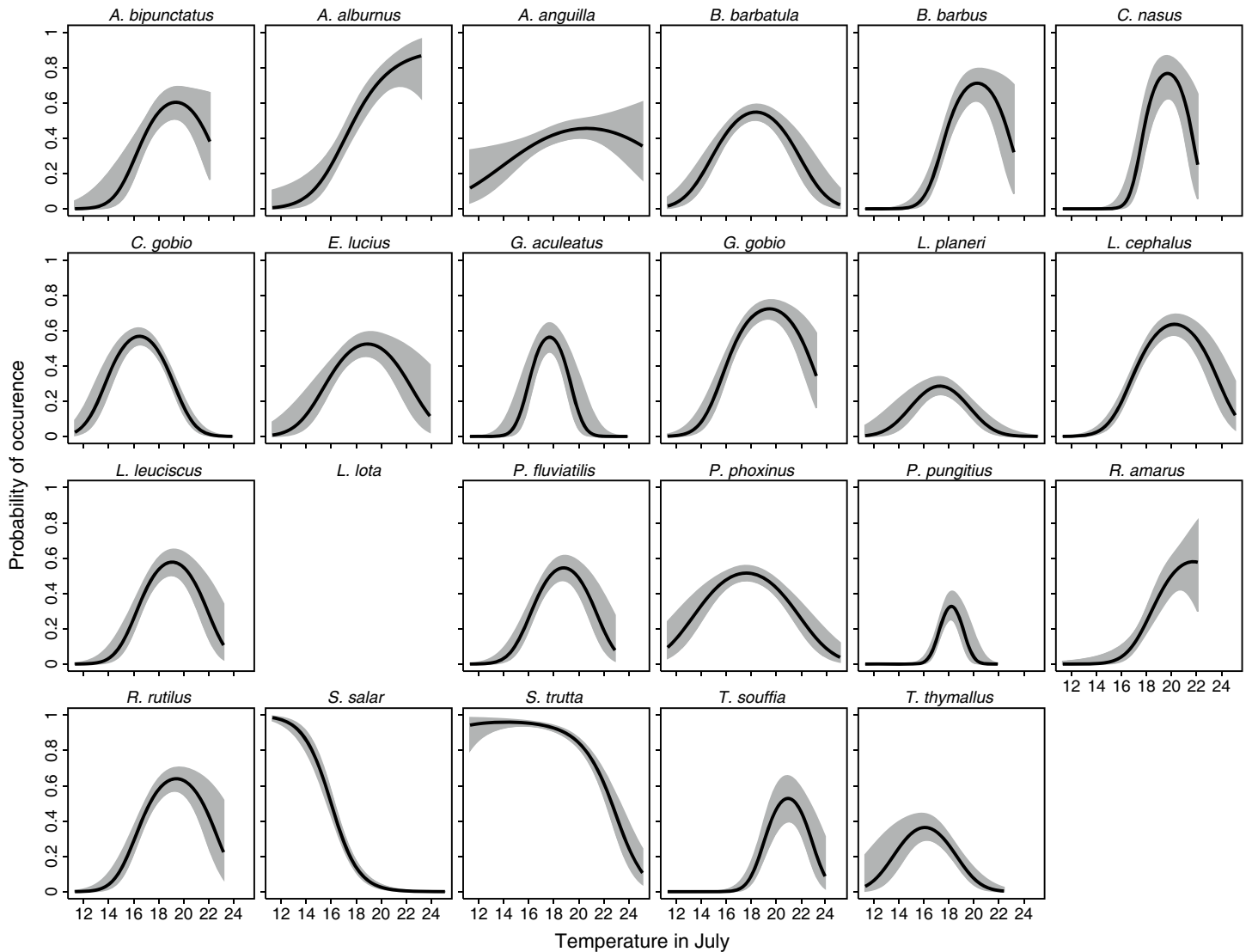


Fig. 2. Specific marginal effect of TJUL on species probability of presence. The model's expected values are in black and the CI bands are in grey.

Responses to UDA were more diverse. Spirlin, stone loach, barbel, nase, bullhead, threespine stickleback, European brook lamprey, soufie, minnow, bitterling and grayling (*Thymallus thymallus*, L.) displayed bell-shaped response curves (Fig. 3) but with different optimums and niche breadths (Table 9 and Table 10). The probability values of bleak, pike, chub (*Leuciscus cephalus*, L.), dace and roach increased along the UDA gradient. Brown trout was the only species to prefer a small-to-intermediate UDA (Fig. 3).

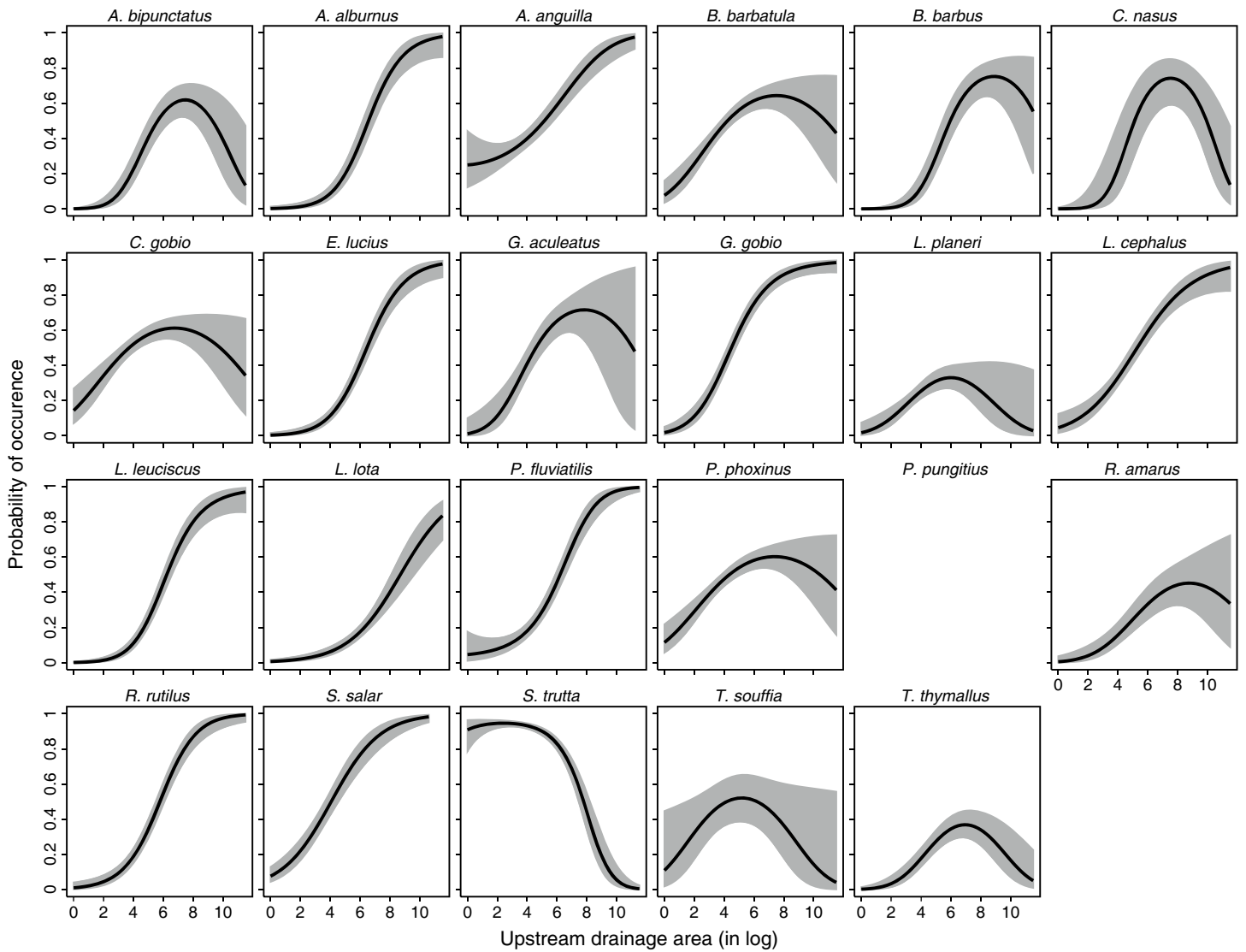


Fig. 3. Specific marginal effect of UDA on species probability of presence. The model's expected values are in black and the CI bands are in grey.

Eel, pike, threespine stickleback, European brook lamprey, ninespine stickleback, bitterling and roach were estimated to prefer low-energy streams (low STP values). In contrast, the probability of presence of nase, soufie, brown trout and grayling increased with increasing energy. The other species presented bell-shaped responses to the STP gradient with different optimums and niche breadths: stone loach and gudgeon preferred low-energy streams, whereas barbel occurred mainly in high-energy streams (Fig. 4).

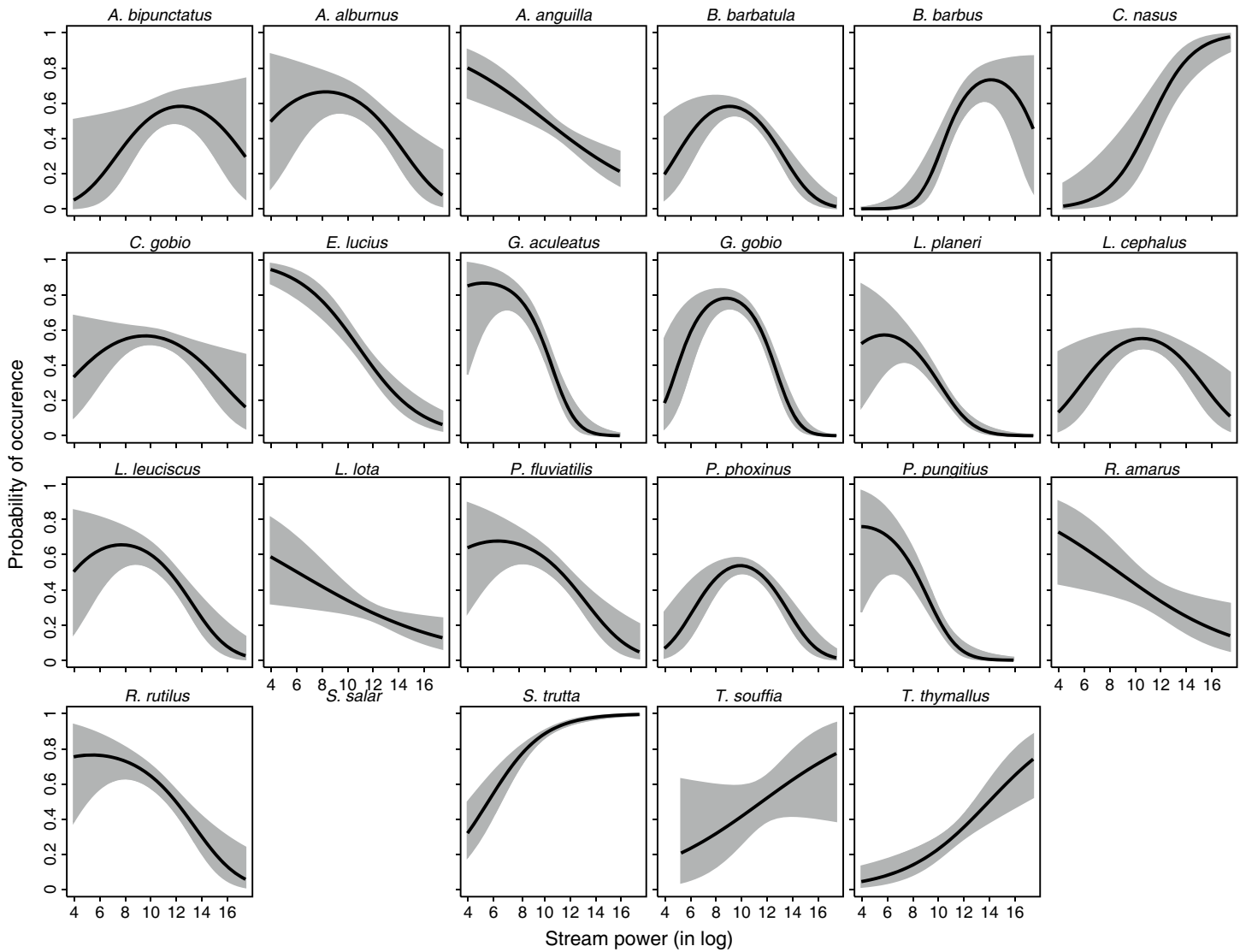


Fig. 4. Specific marginal effect of STP on species probability of presence. The model's expected values are in black and the CI bands are in grey.

The probability of species presence either increased or decreased along the TDIF gradient. Eel and Atlantic salmon preferred low thermal amplitude. Stone loach, gudgeon and brown trout responded only slightly to TDIF variations (Fig. 5).

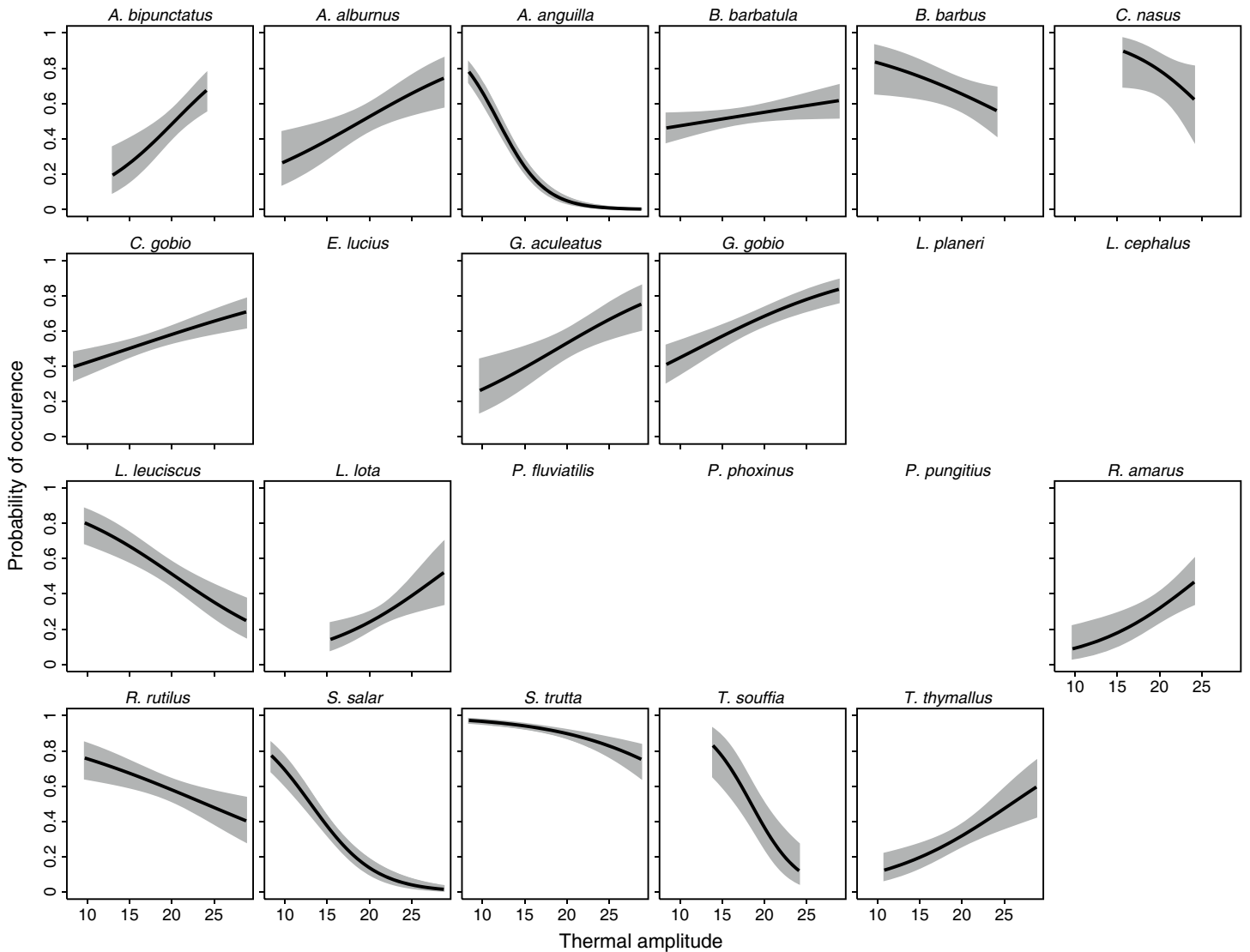


Fig. 5. Specific marginal effect of TDIF on species probability of presence. The model's expected values are in black and the CI bands are in grey.

Species niche (Tables 9 & 10)

Atlantic salmon and brown trout were clearly two cold-water species. Brown trout had one of the largest thermal niches but with a thermal tolerance dependent on the other environmental conditions. Salmon occurred in streams with a wide range of UDA, even if this species was estimated to prefer higher UDA values compared to brown trout.

Grayling (*T. thymallus*) was a cold- to cool-water species (optimum about 16°C) with a relatively narrow thermal niche, occurring in large high-energy streams.

Burbot (*L. lota*) and European brook lamprey (*L. planeri*) preferred low-energy streams. Their preference differed for UDA and TDIF (burbot in larger UDAs and more variable TDIF) as well as for TJUL (lower optimum for lamprey).

Bullhead (*C. gobio*), minnow, (*P. phoxinus*) and stone loach (*B. barbatula*) occurred mainly in cold- to cool-water streams (optimum, about 16.4, 17.6 and 18.3°C), with wide UDA ranges, but had a different STP optimum (lower for stone loach).

Threespine stickleback (*G. aculeatus*) and ninespine stickleback (*P. pungitius*) had among the narrowest thermal niches. They preferred cool water (optimum, about 17.6 and 18°C), and low-energy streams. Threespine stickleback occurred in a wide range of UDAs.

Perch (*P. fluviatilis*) and pike (*E. lucius*) were located mainly in large low-energy streams and cool to warm water, but with a narrower thermal niche for perch.

Dace (*L. leuciscus*) occurred mainly in cool to warm water and in medium to large streams.

Spiralin (*A. bipunctatus*) and roach (*R. rutilus*), both located in large rivers, preferred cool to warm temperatures (optimum about 19.4°C). Roach exhibited substantial thermal tolerance depending on the other environmental conditions, and spiralin seemed to prefer high-energy streams.

Gudgeon (*G. gobio*) occurred in cool- to warm-water streams with a large UDA but with a rather low level of energy.

Nase (*C. nasus*), chub (*L. cephalus*) and barbel (*B. barbus*) preferred large warm streams, but with different thermal niche breadths: narrower for nase and wider for barbel. Chub was more ubiquitous.

The occurrence of eel (*A. anguilla*) was mainly associated with a narrow thermal amplitude.

Soufie (*T. souffia*) occurred mainly in warm-water mid-sized streams with high TDIF.

Bitterling (*R. amarus*) and bleak (*A. alburnus*) clearly preferred warm-water streams, but with a greater thermal niche breadth and larger low-energy rivers for bleak.

Thermal niche breadth variability with other environmental conditions

For bleak, eel, pike, gudgeon, chub, perch and brown trout, the range of the thermal niche varied greatly depending on STP and UDA (

Table 10). Conversely, spiralin, nase, gudgeon, threespine stickleback, minnow, ninespine stickleback, salmon, soufie and grayling had a relatively stable thermal niche along these two gradients (Table 10).

Table 9. Estimated species optimums.

Species	TJUL	TDIF	STP	UDA
<i>A. bipunctatus</i>	19.4	–	12.3	7.5
<i>A. alburnus</i>	–	–	8.3	–
<i>A. anguilla</i>	20.6	–	–	–
<i>B. barbatula</i>	18.4	–	9.1	7.5
<i>B. barbus</i>	20.3	–	14.1	8.9
<i>C. nasus</i>	19.7	–	–	7.5
<i>C. gobio</i>	16.5	–	9.5	6.8
<i>E. lucius</i>	18.9	–	–	–
<i>G. aculeatus</i>	17.7	–	5.2	7.8
<i>G. gobio</i>	19.4	–	8.8	–

<i>L. planeri</i>	17.3	–	5.7	6
<i>L. cephalus</i>	20.3	–	10.5	–
<i>L. leuciscus</i>	19.1	–	7.7	–
<i>L. lota</i>	–	–	–	–
<i>P. fluviatilis</i>	18.8	–	6.3	–
<i>P. phoxinus</i>	17.6	–	9.9	7.4
<i>P. pungitius</i>	18.2	–	–	–
<i>R. amarus</i>	21.7	–	–	8.8
<i>R. rutilus</i>	19.4	–	5.4	–
<i>S. salar</i>	–	–	–	–
<i>S. trutta</i>	14.2	–	–	2.4
<i>T. souffia</i>	20.9	–	–	5.2
<i>T. thymallus</i>	16.1	–	–	7

Table 10. Estimated thermal niche breadths for various combinations of low to high UDA and low to high STP.

Species	UDA: 2.3			3.9			5.5		
	STP: 9	11.2	12.2	9	11.2	12.2	9	11.2	12.2
<i>A. bipunctatus</i>	–	–	–	–	–	–	17.4-21.4	16.6-22.2	16.5-22.3
<i>A. alburnus</i>	–	–	–	20.2-30.5	21.0-29.7	22.0-28.7	17.1-33.6	17.6-33.1	18.1-32.6
<i>A. anguilla</i>	14.6-26.7	17.1-24.2	19.2-22.1	13.2-28.1	15.0-26.3	16.0-25.2	11.5-29.8	12.9-28.4	13.7-27.6
<i>B. barbatula</i>	17.3-19.4	–	–	15.2-21.5	15.8-20.9	16.8-19.9	14.4-22.3	14.9-21.9	15.5-21.2
<i>B. barbatus</i>	–	–	–	–	–	19.0-21.5	–	17.5-23.1	17.0-23.5
<i>C. nasus</i>	–	–	–	–	–	18.8-20.5	–	17.8-21.5	17.5-21.9
<i>C. gobio</i>	15.3-17.7	15.5-17.4	16.2-16.7	14.2-18.8	14.3-18.7	14.5-18.4	13.7-19.2	13.8-19.1	14.0-18.9
<i>E. lucius</i>	–	–	–	–	–	–	15.3-22.5	17.4-20.5	–
<i>G. aculeatus</i>	17.4-17.9	–	–	15.8-19.5	–	–	15.3-20.1	16.5-18.8	–
<i>G. gobio</i>	–	–	–	16.7-22.2	18.1-20.7	–	15.2-23.7	15.9-23.0	16.9-22.0
<i>L. planeri</i>	15.6-19.0	–	–	14.2-20.4	16.8-17.8	–	13.7-20.9	15.5-19.1	–
<i>L. cephalus</i>	–	–	–	18.2-22.3	18.0-22.5	18.2-22.3	16.7-23.8	16.6-23.9	16.8-23.8
<i>L. leuciscus</i>	–	–	–	–	–	–	16.7-21.5	17.5-20.6	–
<i>L. lota</i>	–	–	–	–	–	–	–	–	–
<i>P. fluviatilis</i>	–	–	–	17.1-20.5	–	–	15.7-21.9	16.3-21.3	16.7-20.9
<i>P. phoxinus</i>	–	–	–	14.8-20.5	15.0-20.3	16.1-19.1	13.8-21.4	13.9-21.3	14.6-20.6
<i>P. pungitius</i>	16.9-19.5	–	–	16.9-19.5	–	–	16.9-19.5	–	–
<i>R. amarus</i>	19.3-24.2	20.4-23.0	–	17.6-25.9	18.1-25.3	18.4-25.0	16.7-26.8	17.2-26.3	17.4-26.1
<i>R. rutilus</i>	–	–	–	18.1-20.8	–	–	15.9-22.9	16.7-22.2	17.2-21.6
<i>S. salar</i>	16.6-16.6	16.6-16.6	16.6-16.6	17.6-17.6	17.6-17.6	17.6-17.6	18.7-18.7	18.7-18.7	18.7-18.7
<i>S. trutta</i>	9.4-19.0	7.4-21.0	6.7-21.7	9.9-18.5	7.8-20.6	7.0-21.4	12.8-15.6	9.2-19.2	8.3-20.1
<i>T. souffia</i>	20.0-21.9	19.3-22.5	19.1-22.8	19.2-22.6	18.8-23.1	18.6-23.2	19.1-22.8	18.7-23.2	18.5-23.3
<i>T. thymallus</i>	–	–	–	–	15.5-16.7	14.4-17.7	14.8-17.4	13.5-18.7	13.0-19.1

Table 10. (continue) Estimated thermal niche breadths for various combinations of low to high UDA and low to high STP.

Species	UDA: 6.9			9.2		
	STP:9	11.2	12.2	9	11.2	12.2
<i>A. bipunctatus</i>	16.5-22.2	15.9-22.8	15.9-22.9	17.1-21.6	16.4-22.3	16.3-22.4
<i>A. alburnus</i>	15.2-35.5	15.6-35.1	16.0-34.7	12.9-37.8	13.3-37.4	13.6-37.1
<i>A. anguilla</i>	9.9-31.4	11.1-30.2	11.7-29.6	7.2-34.1	8.1-33.2	8.6-32.7
<i>B. barbatula</i>	14.1-22.6	14.5-22.2	15.1-21.6	14.3-22.4	14.8-22.0	15.4-21.3
<i>B. barbus</i>	18.6-22.0	16.7-23.9	16.3-24.2	17.9-22.6	16.3-24.2	16.0-24.5
<i>C. nasus</i>	18.4-21.0	17.4-21.9	17.1-22.3	18.9-20.4	17.7-21.7	17.3-22.0
<i>C. gobio</i>	13.6-19.3	13.7-19.2	13.9-19.0	14.0-18.9	14.1-18.8	14.3-18.6
<i>E. lucius</i>	13.8-24.0	15.0-22.9	15.6-22.2	12.1-25.7	12.9-24.9	13.3-24.5
<i>G. aculeatus</i>	15.1-20.3	16.2-19.2	–	15.1-20.2	16.2-19.1	–
<i>G. gobio</i>	14.3-24.6	14.9-24.0	15.6-23.3	13.2-25.6	13.7-25.1	14.3-24.6
<i>L. planeri</i>	13.8-20.8	15.6-19.0	–	15.0-19.6	–	–
<i>L. cephalus</i>	15.9-24.6	15.8-24.7	15.9-24.6	14.8-25.7	14.7-25.8	14.8-25.7
<i>L. leuciscus</i>	15.3-22.8	15.8-22.4	16.2-21.9	14.0-24.1	14.4-23.8	14.7-23.5
<i>L. lota</i>	–	–	–	–	–	–
<i>P. fluviatilis</i>	14.7-22.9	15.1-22.5	15.4-22.2	13.2-24.4	13.5-24.1	13.7-23.9
<i>P. phoxinus</i>	13.4-21.8	13.6-21.6	14.2-21.0	13.7-21.5	13.9-21.3	14.6-20.6
<i>P. pungitius</i>	16.9-19.5	–	–	16.9-19.5	–	–
<i>R. amarus</i>	16.3-27.2	16.7-26.8	16.9-26.6	16.1-27.4	16.5-27.0	16.7-26.8
<i>R. rutilus</i>	14.8-24.0	15.3-23.5	15.7-23.2	13.3-25.5	13.7-25.1	14.0-24.9
<i>S. salar</i>	19.7-19.7	19.7-19.7	19.7-19.7	21.2-21.2	21.2-21.2	21.2-21.2
<i>S. trutta</i>	–	13.1-15.3	10.8-17.6	–	–	–
<i>T. souffia</i>	19.4-22.5	18.9-23.0	18.7-23.2	–	20.3-21.5	19.9-22.0
<i>T. thymallus</i>	14.2-18.0	13.1-19.0	12.7-19.4	–	14.0-18.1	13.5-18.6

Uncertainty

The uncertainty values associated with model estimations (confidence bands in Figs. 2–5) were generally low for TJUL, except for some species on the edge of this gradient, leading to a higher level of uncertainty for this environment. Spirlin, barbel, pike, bitterling and roach confidence bands widened once their thermal optimums were reached, implying a better precision of the model close to lower thermal limits. Grayling showed the opposite pattern (Fig. 2).

Uncertainty values associated with UDA and STP were higher (Fig. 3 & Fig. 4). The uncertainty was higher with a low STP for bleak, stone loach, lamprey and perch, and higher with a high STP for barbel. Spirlin, bullhead, soufie and to a lesser extent bitterling had high uncertainty values all along the STP gradient. For UDA, the high uncertainty values were mainly associated with large values (e.g. stone loach, barbel, bullhead, threespine stickleback, lamprey, roach and bitterling). Soufie was the only species for which the uncertainty was relatively high all along the UDA gradient.

In general, high uncertainty values for a given environmental gradient were observed when the effect of this variable on species occurrence was limited.

Niche vs. Functional traits

The number of sites that could have been used varies between metrics but still represents an important proportion of the 1548 sites (Table 11). This implies that the fish assemblages are mainly composed of one or more of the 23 species with the niche model.

Table 11. Number of sites available for each metric.

	RICH	O2INTOL	HINTOL	EURY	RH	EUPAR	RHPAR	LITH
Number of sites	899	1363	1231	1200	1062	1213	1101	1127

When comparing the metrics distribution, it appears that the expected values for RICH, EURY, RH and EUPAR are on average overestimated compared to the observed values (Fig. 6). In contrast, the medians of the observed and expected values are equivalent for O2INTOL, HINTOL, RHPAR and LITH, but the distributions of the expected values are less dispersed than for the observed values.

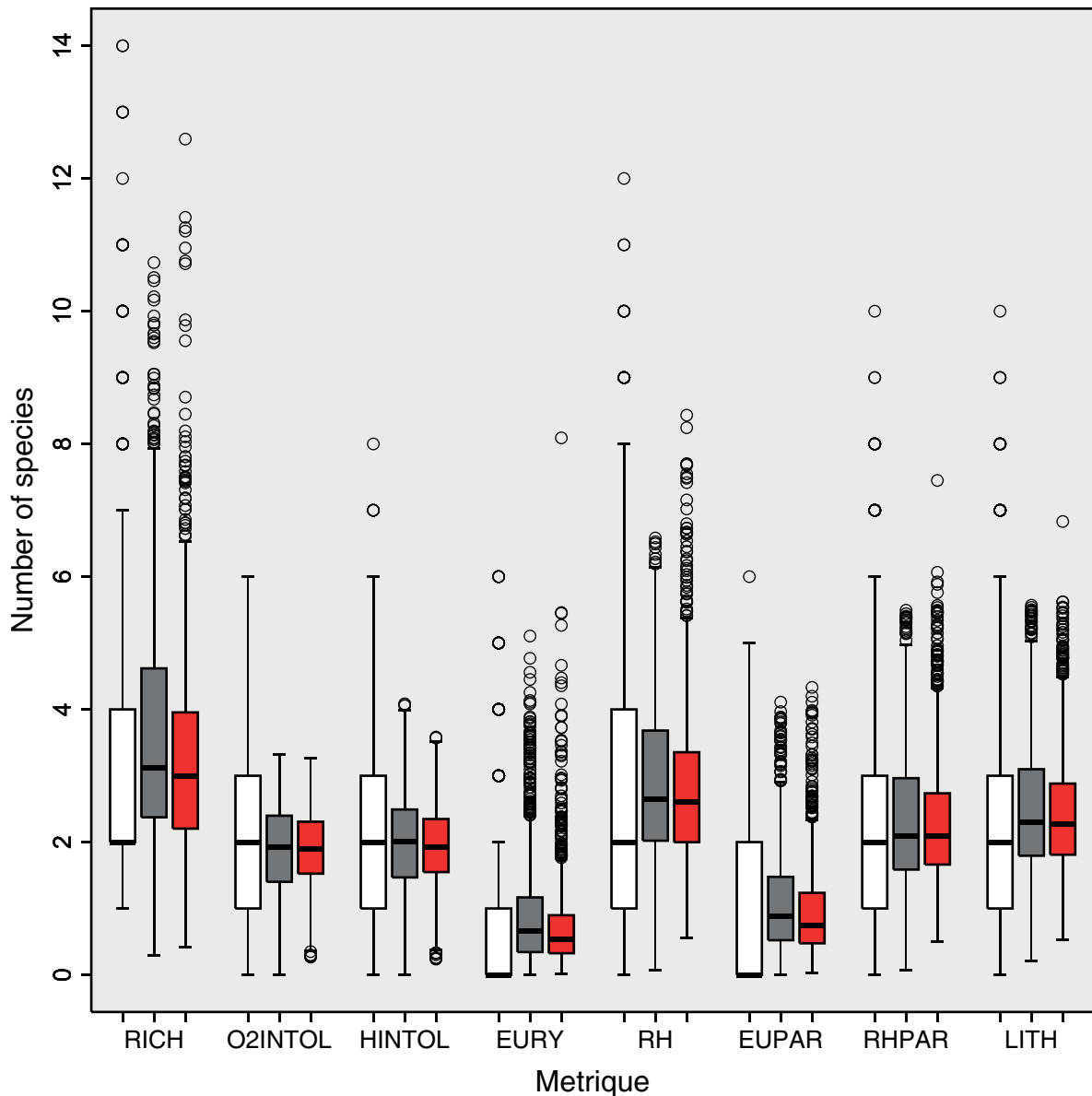


Fig. 6. Distribution of the metrics: observed (□), expected with niche model (■) and expected with trait models (■). The box boundaries represent the first and the third quartiles and the thick black bar (—) the median. Points are located outside the 1.5*interquartile range.

Pearson’s correlations between metric observed values and expected values predicted from the niche models are always higher than correlations between the observed values and expected values from the trait models, but correlations between expected values (niches and traits) are high, always greater than 0.785. Among the eight metrics, the highest correlations were observed for RICH and RHPAR, while the lowest ones were observed for O2INTOL, HINTOL and EUPAR (Table 12). Because of the large amount of data used (899–1363 sites), it is not surprising that all Pearson’s correlations are significant (p -values < 0.001).

Table 12. Pearson’s correlations between metric expected (from niche or traits models) and observed value (Obs).

	RICH	O2INTOL	HINTOL	EURY	RH	EUPAR	RHPAR	LITH
Obs vs. Niche	0.732	0.556	0.594	0.611	0.698	0.601	0.705	0.650
Obs vs. Traits	0.673	0.466	0.486	0.582	0.585	0.538	0.593	0.550
Niche vs. Traits	0.894	0.887	0.785	0.922	0.872	0.898	0.865	0.853

Niche models

The relationships between metric observed values and metric expected values computed from the niche models tend to confirm the results of the correlations (Fig. 7). Indeed, except for EURY and some extreme values, expected and observed values are closely related, as pointed out by the close relationships between the tendency curves (Loess curves) and the first bisectors (Fig. 7). Whichever metrics were considered, the low observed values tend to be overestimated, while the high observed values tend to be underestimated.

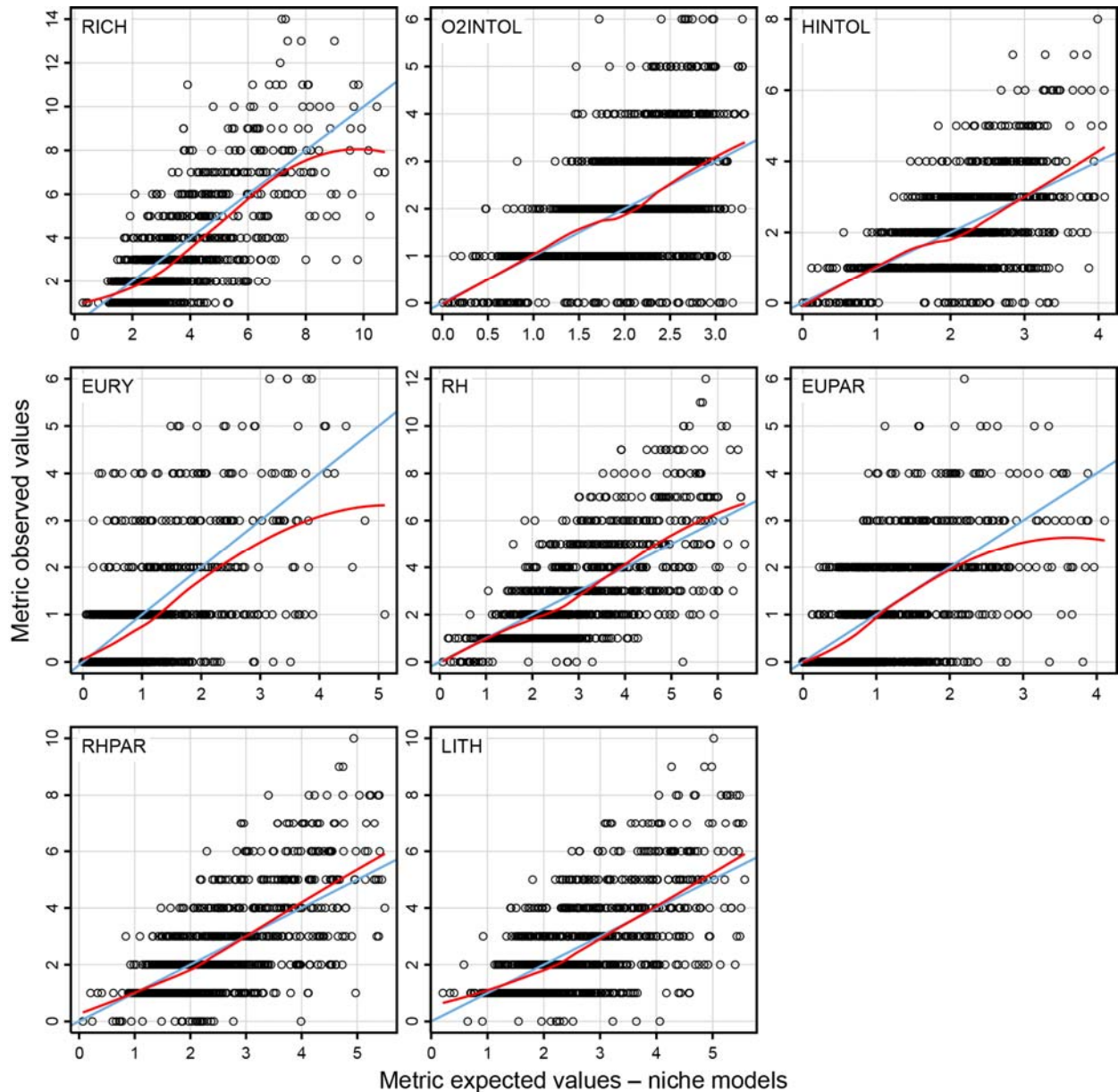


Fig. 7. Relationships between observed (y-axis) and expected values from niche models (x-axis). The blue lines represent the curve $y = x$ and the red lines represent a general trend (Loess regression curve; Hastie et al. 2009).

Trait models

The relationships between the metric observed values and metric expected values from the trait models are consistent with the patterns observed for the niche models. The over- and underestimation issues remain and seem to be somewhat more significant than with the niche models, especially for RH, EUPAR, RHPAR and LITH (Loess curves are more distinct from the first bisectors; Fig. 8). Finally, the extreme values are more marked than with the niche models.

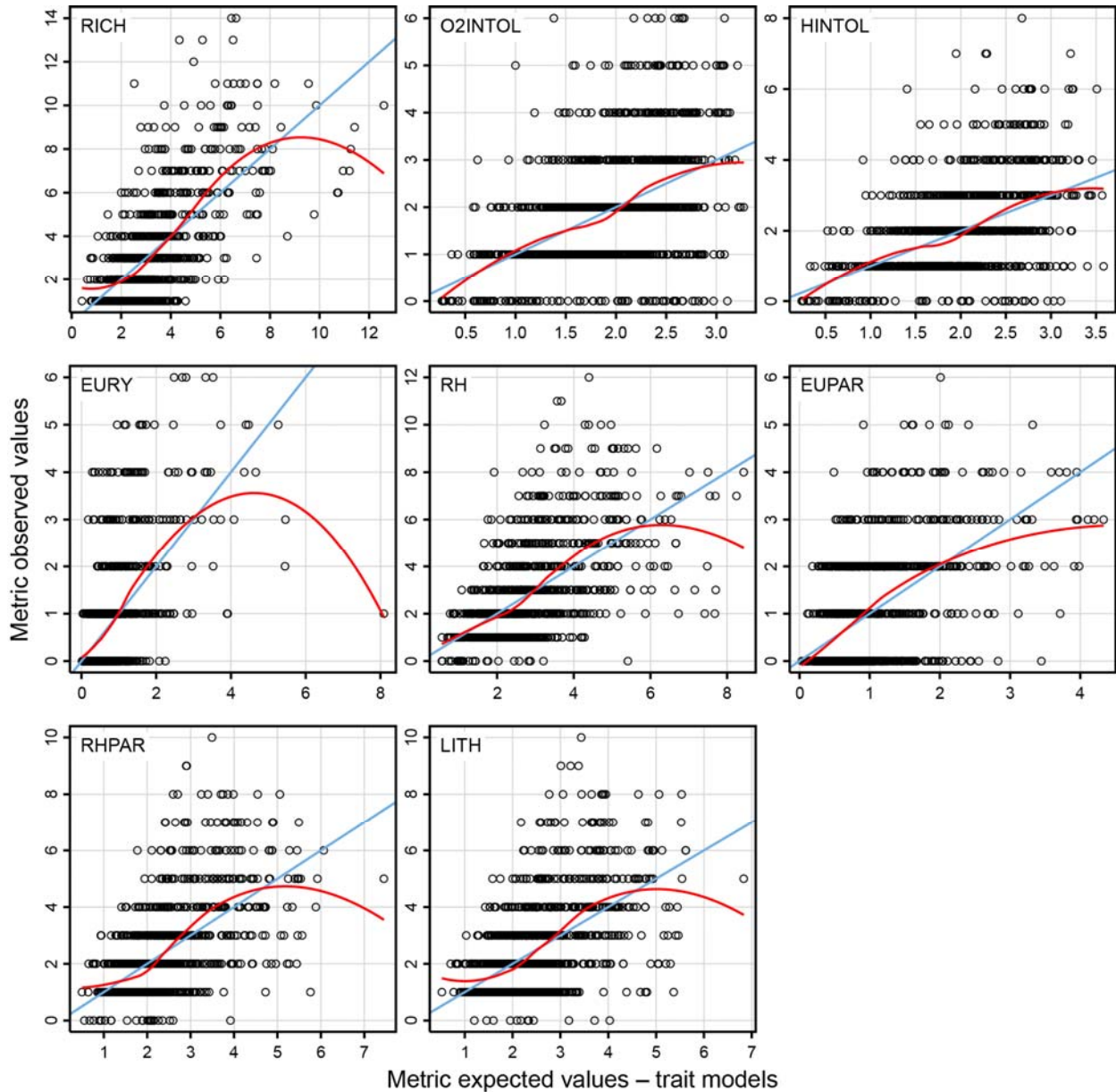


Fig. 8. Relationships between observed (y-axis) and expected values from trait models (x-axis). The blue lines represent the curve $y = x$ and the red lines represent a general trend (Loess regression curve; Hastie et al. 2009).

Niche vs. trait expected values

As revealed by Pearson's correlation coefficients (Table 12), there is a strong relationship between the metric expected values predicted from the niche models and from the trait models (Fig. 9). Overall, the relationships between the two types of metrics are linear except for the

highest values. Nevertheless, on average the expected values for RICH, EURY and EUPAR tend to be higher with the niche models than with the trait models, while this tendency is not observed for the other metrics. For EUPAR, RH and LITH a group of particular sites emerges from the scatter plots: expected values for niche models seem constant (about 0 or 1 depending on the metric), while the expected values for the trait models vary on a wider interval.

Except for RICH and EURY, the absolute differences between the metric observed values and the metric expected values are lower with niche models than with trait models (Wilcoxon sign rank tests, p -values < 0.001). Finally, the metric expected values from the niche or trait models are quite comparable.

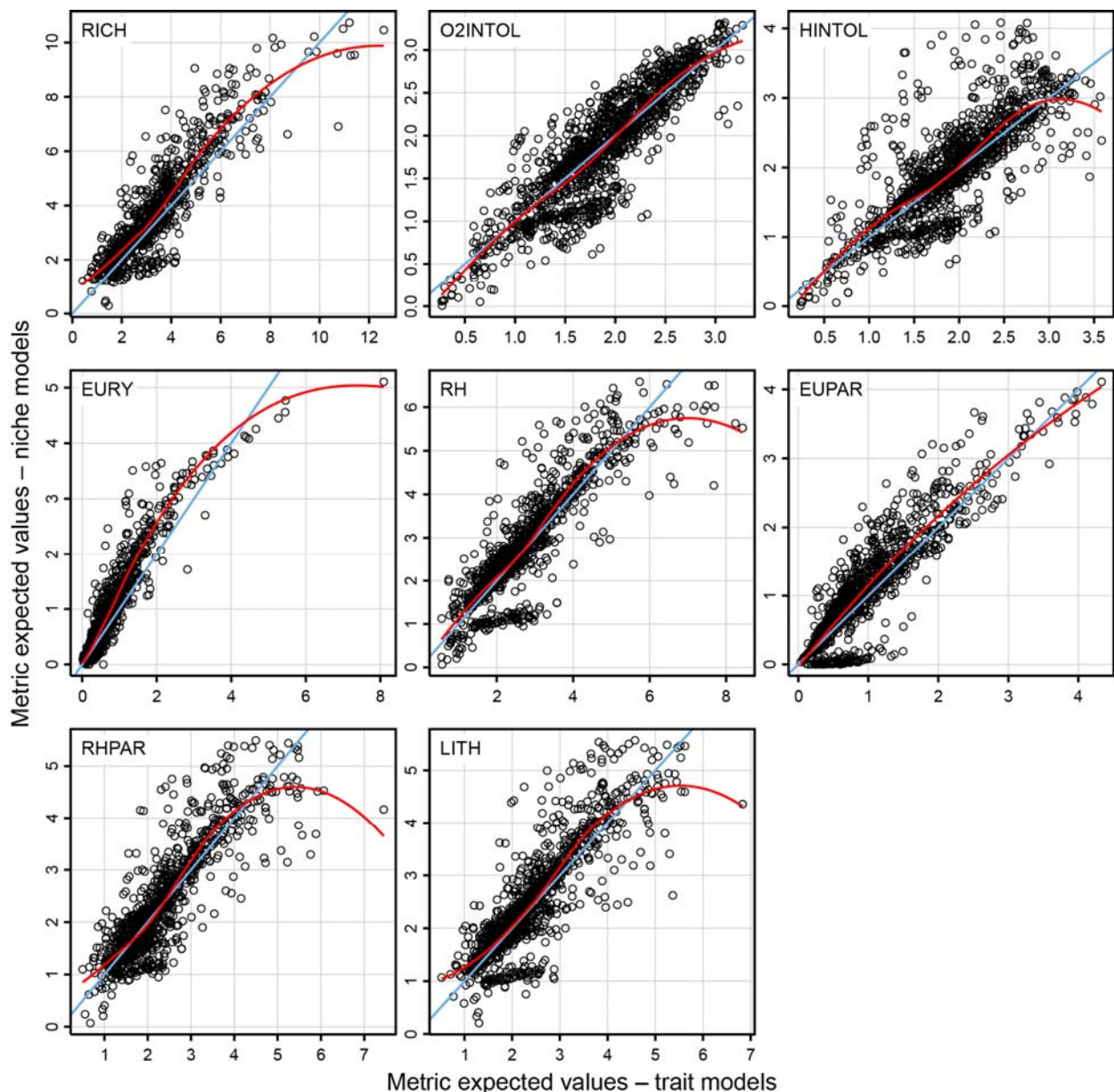


Fig. 9. Relationships between metric expected values from niche models (y-axis) and trait models (x-axis). The blue lines represent the curve $y = x$ and the red lines represent a general trend (Loess regression curve; Hastie et al. 2009).

Discussion

Species niche

These results highlight the effects of climatic factors, drainage basin and stream power on the distribution of 23 European fish species, when not considering major human alterations. Different species have very different responses to environmental gradients, and the uncertainty associated with the estimated environment–occurrence relationships varied depending on the species and the environmental conditions.

Species niche

The 23 species display very different responses to temperature, UDA and STP. As already shown (Pont et al. 2005; Buisson et al. 2008a; Hopkins & Burr 2009), both the shape of the response and the relative effect of each environmental variable differed between species, but the responses observed here were also different from those previously observed.

S. salar has a model with a high goodness of fit and the present results are consistent with previous reports. Atlantic salmon is a diadromous species that occurs in cold-water (Moyle & Herbold 1987; Rahel & Hubert 1991) and mostly fast-flowing streams, even if its preferences could change during its ontogenic development (Armstrong et al. 2003).

S. trutta has the most singular niche among the 23 species studied. The brown trout is a widespread species in Europe (Banarescu 1992; Kottelat & Freyhof 2007), occurring in various types of streams (Klemetsen et al. 2003; Lobon-Cervia 2007; Melcher et al. 2007; Parra et al. 2009; Logez & Pont 2011b). It is not surprising that this species has one of the largest niche breadths in terms of UDA and STP. The temperature range is also quite wide, but limited to cold and fresh waters. Brown trout occurrence in streams is probably more related to the spawning substrate and oxygen concentration than to hydraulic conditions (brown trout occur in lakes; L'Abée-Lund & Saegrov 1991). Salmonids have a high physiological demand for oxygen (Elliott 1994; Crisp 2000) and cold fast-flowing waters increase oxygen concentration (Allan & Castillo 2007), which could explain the brown trout's affinity for these environmental conditions (Jonsson & Jonsson 2011).

T. thymallus and *T. souffia* display similar niches, occurring mostly in medium and large streams with high energy. These species are rheophilic, living in fast-flowing streams (Gilles et al. 1998; Salzburger et al. 2003), and are stenothermal. Nevertheless, they do not occur in the same thermal ranges: grayling occurs in cold-water streams (Paquet 2002), while soufie occurs in warmer water (Gilles et al. 1998; Salzburger et al. 2003).

Burbot is known as a cold stenothermal species (Hofmann & Fischer 2002). A bell-shaped response to TJUL with a low-temperature optimum would be expected, while TJUL was not used for this species. In contrast, its occurrence increases with the annual thermal range, showing a preference for contrasted climate (continental). Burbot is a eurytopic species (Holzer 2008) that occurs mainly in large streams (Bischoff & Wolter 2001; Worthington et al. 2010), which is consistent with its increasing probability of presence along the UDA gradient. Burbot

is estimated to prefer low-energy streams, even if the species is classified as rheophilic (Oberdorff et al. 2002).

L. planeri is estimated to occur in cool temperatures with low STP and small UDA, which is consistent with previous ecology reports: it prefers cool-water streams, with larvae inhabiting fine sediment (Hardisty 1944; Holcik 1986; Keith & Allardi 2001; Maitland 2003) whose deposition occurs at low velocities (Leopold et al. 1992).

C. gobio, *B. barbatula* and *P. phoxinus* are three rhithronic species (Dussling et al. 2004), very often associated with brown trout in streams (Huet 1954; Melcher et al. 2007), preferring cool-water streams. The present results suggest that the occurrence of the bullhead in streams is mainly driven by temperature (Pont et al. 2005). While these species could also live in lakes (Utzinger et al. 1998; Zick et al. 2006; Sutela & Vehanen 2008), minnow and stone loach are also influenced by UDA and STP. The response patterns of these last two species are similar: both occur mainly in medium-sized streams with cool temperatures (Küttel et al. 2002), but minnow seemed to prefer higher-energy streams.

P. pungitius and *G. aculeatus* were both estimated to prefer small and low-energy streams, characterized by a low slope and/or low discharge (Prenda et al. 1997; Copp & Kovac 2003). This is consistent with the inverse relationship between stream power and their probability of occurrence.

The occurrences of *E. lucius* and *P. fluviatilis* are related to rivers with a large UDA, cool water and low energy. This type of river is generally characterized by floodplain development, which provides a suitable spawning habitat for pike and perch (phytophilic species) and nurseries for their juveniles (Craig 1987; Raat 1988).

L. leuciscus is considered a rheophilic species (Cowx 1988, 1989) that occurs in middle and lower reaches (Przybylski 1993) and needs a gravel substrate to spawn (Mann & Mills 1986). The niche estimated for dace partially matches these findings; its probability of occurrence is maximal in large streams with medium energy. Clough et al. (1998) observed that post-spawning dace adults seem to prefer low-flow and shallow areas.

The distribution of *A. bipunctatus* and *A. alburnus* is mainly driven by UDA and TJUL. Spirlin is a rheophilic species that occurs mainly in small and medium streams (Breitenstein & Kirchhofer 1999; Ruchin et al. 2007) and its thermal optimum is far below the bleak's thermal optimum. Bleak is a limnophilic and planktivorous species (Keith & Allardi 2001), and plankton is most abundant in open streams with substantial sunlight and slow-moving waters (Hynes 1970; Vannote et al. 1980). These conditions are mostly observed in large water bodies, in the most downstream, warmer part of rivers (Allan & Castillo 2007). This is in agreement with bleak's probability of presence increasing as UDA and TJUL increase.

G. gobio and *R. rutilus* niches are relatively close. Their probability of occurrence increases along UDA and they occur within the same thermal ranges, but their responses to STP differ. Gudgeon shows a bell-shaped response and seems to prefer intermediate STP, whereas roach prefers a low-energy stream. Gudgeon is often considered to be rheophilic, whereas roach is

more limnophilic (Mastrorillo et al. 1996; Keith & Allardi 2001; Fladung et al. 2003; Fieseler & Wolter 2006; Riffart et al. 2009).

C. nasus, *B. barbus* and *L. cephalus* are rheophilic species that have lithophilic reproduction (Roux & Copp 1996; Oberdorff et al. 2002; Holzer 2008). They exhibit different optimums along the UDA gradient (drainage area) and STP, consistent with their distribution along the longitudinal gradient (Huet 1954). Nase occurs in medium to large streams with high energy, barbel in intermediate- to high-energy streams and chub in large streams with a medium energy level. Nase's optimum for UDA is lower than that of barbel.

A. anguilla was the only species to be mainly influenced by TDIF. Eel occurrence decreases with increasing TDIF, which is probably due its migratory behaviour (Tesch 1991). Since it is a catadromous species, eel distribution is directly linked to the sea and to a weak thermal amplitude corresponding to an oceanic climate (Ward 1985). TDIF is then probably a proxy for the distance to the sea.

R. amarus occurs mainly in medium to large warm streams with low energy. It is an ostracophilic species depending on freshwater mussel occurrence for its reproduction (Heschl 1989; Smith et al. 2004). Freshwater mussel richness increases along the longitudinal gradient (Haag & Warren 1998), and bitterling is also a limnophilic and thermophilic species feeding mainly on algae (Smith et al. 2004; Van Damme et al. 2007).

Species thermal optimums

The 23 species are distributed along the entire TJUL gradient (15.4–21.9°C) according to their thermal optimums. These optimums are not directly comparable with those in the literature because the latter were estimated under laboratory conditions (Jobling 1981; Mann 1996; Küttel et al. 2002; Tissot & Souchon 2010). Nevertheless, the species ordination along the thermal gradient is consistent with the literature. Salmonids have the lowest thermal optimum followed by bullhead, European brook lamprey and stone loach, while soufie and bitterling have the highest optimums (Smith et al. 2004; Van Damme et al. 2007). The thermal optimum for bleak is probably the highest, but it could not be computed because the TJUL quadratic term was not selected. A broader data set for thermal conditions would be necessary to assess correctly the thermal niche of these warm-water species.

Uncertainty

It is highly valuable and relevant to assess and provide the uncertainty associated with the expected probability of presence of a species in a given environment. Nevertheless, and to our knowledge, confidence intervals (CIs) are rarely provided, if at all.

The accuracy of the models varies between species and environmental factors. For temperature, the relationship seems relatively accurate with a narrow CI. Several species such as spiralin, northern pike, gudgeon, barbel, nase and roach have narrow CIs up to warm temperatures, suggesting that their presence/absence is better predicted for cold- to cool-water streams. Grenouillet et al. (2011) observed a greater mismatch between predictions and the current occurrences of species in the south of France. It can be hypothesized that this is due to the

higher uncertainty in warmer temperatures and/or the species occurring in French southern streams.

From a forecasting point of view, it would be more valuable to compute the prediction interval rather than the CIs. The CI is associated with a parameter of the statistical population: the expected probability of the presence of a species in a given environment with a given level of confidence $100(1-\alpha)\%$ (Hahn & Meeker 1991). Ideally, one should expect to predict species presence/absence in new locations using the prediction interval (Hahn & Meeker 1991). Nevertheless, for logistic regression: “there is no distinction possible between confidence intervals for a future observation and those for the mean response” (Faraway 2006). This means that confidence and prediction intervals are the same for this regression (Faraway, personal communication), conversely to regular linear regression (Kutner et al. 2005). Providing the uncertainty associated with the projections using various climate scenarios would contribute towards better discussions on the predictions of the effect of climate change on large-scale species distribution.

Metric expected values: niche vs. trait models

Among the eight metrics tested here, it appears that the species niche-based metrics are better correlated to the metric observed values than the metrics based on trait models. Nevertheless, the correlations between the two types of metrics are always very high, especially for RICH, RHPAR and LITH functional traits.

Pros and cons of each method

The great advantage of the niche approach is the possibility to take into account the biogeographical differences between the various European regions (Banareescu 1989, 1992; Griffiths 2006; Reyjol et al. 2007). Most of the distribution areas of the species are known (Kottelat & Freyhof 2007) and this enables us to modulate the estimated probability of presence. Indeed, if a given species is absent in a region because of historical factors, for example, as a consequence of the last glacial period (Hewitt 1999, 2000; Kontula & Vainola 2001; Koskinen et al. 2002; Hewitt 2004), its probability of presence could be set to 0 to reflect the current situation.

With the metrics based on niche models, it is also possible to assess the relative influence of the different species in the computation of the expected values. If these metrics reveal biological impairment, it would be possible to assess which species are more impacted than others.

The main limit to this species-based approach is the necessity to model the niche of all species that could occur in a given region. When working at the European scale, it entails modelling the occurrence of more than 500 species (Kottelat & Freyhof 2007). Although we worked with a database composed of more than 14,000 sites, but only 1458 "undisturbed" sites, we were only able to model the occurrence of 23 fish species, while other authors working at the French

national scale worked with 35 species (Oberdorff et al. 2001; Buisson et al. 2008a; Buisson et al. 2010; Grenouillet et al. 2011). The low number of models available has restricted the number of metrics and sites available to compare the niche and trait approaches. Fish assemblages were selected to be composed only of members from the pool of 23 species available, so that the metric expected values could be compared with the observed values. Therefore, apart from EURY, all the metrics used in this study are characteristic of cold-water fish assemblages (Logez & Pont 2011a) and/or of small and medium streams (Logez et al. in revision). The restriction of our data set to small or medium streams is because of a greater sampling effort on these streams and our selection of sites slightly impacted or not at all. In addition, human activities increase along the longitudinal gradient of streams, which limit the number of slightly disturbed sites in the larger streams.

The choice of the model used to relate environmental conditions to species occurrence has generated an open debate, leading to several studies comparing the predictive performance of various models (Elith & Graham 2009; Grenouillet et al. 2011). We think that the most important issue is not the kind of model used (their goodnesses of fit are in general comparable, Elith & Graham 2009), but the spatial extent of the calibration data set used (Sinclair et al. 2010). If the data used to calibrate the models slightly overlap in the species distribution area, then the estimated niches would only represent a small part of the species realized niche yielding inaccurate predictions (Barbet-Massin et al. 2010). The niches estimated in this study are different to the niches estimated at the French scale by Pont et al. (2005). This pattern is particularly marked for the estimated thermal niches. With a few exceptions, we observed bell-shaped responses along thermal gradient (as in theory; Hutchinson 1957; Begon et al. 2006), while Pont et al. (2005) mostly observed monotonous positive relationships between temperature and the probability of presence.

Compared to the niche approach, the main advantage of the trait-based model is that the expected values for a given metric are directly estimated from a single model, overcoming the species-pool limitation of the niche approach. Metric expected values could be computed over a larger spatial extent, for a greater number of sites, and for assemblages composed of diverse fish faunas. For instance, the two predictive indices, EFI and its revised version EFI+, successfully used metrics based on species richness to assess the ecological status of European streams (Pont et al. 2006; Pont et al. 2007; Bady et al. 2009; Logez & Pont 2011a). Nevertheless, the use of a single model to predict metric expected values is based on a strong assumption: two communities living in similar environmental conditions without any stressors display similar attributes (e.g. number of species). In other words, it assumes there is community convergence over the region of interest (Wiens 1991; Ricklefs & Schluter 1993; Smith & Ganzhorn 1996; Bellwood et al. 2002; Lamouroux et al. 2002; Ricklefs 2006; Irz et al. 2007; Ibañez et al. 2009; Hugué et al. 2010). This assumption might be true over a restrained spatial extent, but the hypothesis could become more and more uncertain when the spatial scale is extended. A comparison of the patterns of response metric along environmental gradients between the Iberian Peninsula on the one hand and France and Belgium, on the other hand, showed some

regional specificity (Logez et al. 2010): in the same environmental conditions, the number of species for a given trait was always lower in the Iberian Peninsula than in France and Belgium. Such differences could constitute a limit to the trait approach. It could lead to an inaccurate estimation of metric expected values in reference sites and thus of the ecological conditions. In contrast, niche-based metrics should not be affected by these biogeographical differences.

Finally, SDMs and trait methods have certain advantages as well as some inconveniences, but whatever the differences between these two methods, they seem to provide comparable metric expected values even if the niche-based metrics were better correlated with the observed values.

CHAPTER II

Climate change effect on fish biological quality elements (BQEs)

Large scale approach: Potential effect of global warming on reference conditions and pressure–impact relationships: the case of fish biological quality elements including uncertainty analysis

Maxime Logez¹ and Didier Pont²

¹ Irstea, UR HBAN, 1 rue Pierre-Gilles de Gennes - CS 10030, F-92761 Antony, France; email: maxime.logez@irstea.fr; phone: +33 (0)4 42 66 69 86

² Irstea, UR HBAN, 1 rue Pierre-Gilles de Gennes - CS 10030, F-92761 Antony, France; email: didier.pont@irstea.fr; phone: +33 (0)1 40 96 65 52

Introduction

The environment, and especially climatic conditions, is the primary factor that has shaped species distributions, and thus assemblage composition and functional structure (Hutchinson 1957; Tonn et al. 1990; Schlosser 1991; Townsend & Hildrew 1994; Petts & Amoros 1996; Allan & Castillo 2007). The *niche* theory states that a species can only maintain and develop itself when environmental conditions match its ecological requirements (Hutchinson 1957; Begon et al. 2006). Several theories have linked assemblage compositions and assemblage structure (composition in traits) with environment. The theory of *habitat filtering* (Keddy 1992; Diaz et al. 1998, 1999) and the theory of *landscape filters* (Poff 1997) state that local assemblages are composed of species selected by various environmental filters from a regional species pool. Only species with an adapted suite of traits could get through the different filters. Numerous studies have supported these theories (e.g. Diaz et al. 1998, 1999).

Temperature and hydrological processes (thus precipitations) are the main environmental drivers of fish species distribution along river networks (Huet 1954; Hynes 1970; Rahel & Hubert 1991; Poff & Allan 1995; Petts & Amoros 1996; Poff et al. 1997; Pont et al. 2005; Allan & Castillo 2007). The observed and projected changes in climatic conditions (Webb & Nobilis 1995; Webb 1996; Caissie 2006; IPCC 2007; Webb & Nobilis 2007) imply modifications of the environmental conditions and thus of the habitat suitable for fish species. In response to these changes, shifts of species distributions are expected (Buisson et al. 2008a; Buisson et al. 2008b; Lassale et al. 2008; Buisson & Grenouillet 2009; Prowse et al. 2009; Britton et al. 2010; Lyons et al. 2010; Rieman & Isaak 2010; Hein et al. 2011; Wenger et al. 2011a; Wenger et al. 2011b). From the scope of conservation, it is very important to anticipate the effect of global change on species occurrences so as to evaluate the loss and/or gain of habitat that would be observed depending on the gas emission scenarios (IPCC 2007).

Human activities, by modifying the functioning of river systems, are also a main driver of species occurrences (Ward & Stanford 1983; Poff et al. 1997). Their impacts on the biota could be highly diverse, depending on the type of pressures stressing the biota and on the

environmental conditions in which they act. A reduction in species abundance, modification of species dominance, and species loss and/or gain could be some of the consequences (McCormick et al. 2001; Kruk & Penczak 2003; Quinn & Kwak 2003; Wang et al. 2003; Quist et al. 2005; Pont et al. 2006; Melcher et al. 2007; Pont et al. 2007; Haxton & Findlay 2008; Pont et al. 2009). Therefore, from a global change perspective, it would be necessary to assess which factors would have a greater effect on the presence/absence of species in the future. The Water Framework Directive stipulates that water bodies diagnosed as degraded have to be restored. It is thus a major concern for water managers to know whether climate change could weaken the planned restoration measures (Rieman & Isaak 2010). In order words, they need to assess the *risk* that the forecasted climatic conditions will overcome the effect of the restoration programmes.

In addition, if local assemblages are the results of species selection on their traits by environmental conditions (Tonn et al. 1990; Poff 1997), the assemblage functional structure should also be impacted by climate change. This should affect both impaired and reference sites. Since the first Index of Biotic Integrity, developed by Karr (1981), numerous bioassessment tools and especially multi-metric indices have used metrics based on assemblage structure in their computations. This is all the more true that the spatial extents for which these methods are designed are wide (Oberdorff et al. 2002; Pont et al. 2006; Pont et al. 2007; Logez & Pont 2011a). Species distribution limits the use of metrics based on assemblage composition when working at a large scale, whereas metrics based on traits facilitate comparisons of assemblages with different compositions. The two predictive multi-metric indices developed for European rivers (EFI and EFI+) (Pont et al. 2006; Pont et al. 2007; Bady et al. 2009) are based on fish assemblage structure. These indices are based on the reference conditions approach following the WFD requirements. Therefore, these indices compare observed assemblage structures (through several metrics) with assemblage structures that could be observed in the absence of pressures, in a given environmental condition. Metric expected values are derived from statistical models relating functional traits with environmental conditions. These models are computed on calibration sites that are slightly impacted or not at all. If assemblage structure is modified by climate change, then it could have important consequences for the use of bioassessment tools based on functional metrics. Evidence was provided of the link between assemblage structure and temperature (Logez et al. in revision), but the effect of climate change and its consequences is still an open question.

All the above-mentioned approaches are based on statistical models that relate response variables (species presence/absence, functional metric, etc.) to environmental conditions on a calibration data set. These models are always designed to predict the expected values of the response variable in new sites or in new environmental conditions. Therefore, the uncertainty associated with these predictions could vary with the environmental conditions (Collett 2002; Kutner et al. 2005; Grenouillet et al. 2011). Therefore, it would be interesting to have an estimation of the uncertainty of model predictions to calculate the reliability of the response patterns to global change. In order words, will uncertainty overcome the effect of global change?

The main objectives of this study are to assess: (1) the effect of global change on the distribution of 23 widespread European fish species, (2) the relative effect of global change and anthropogenic alterations on future species distributions, (3) the drift of reference conditions and (4) the uncertainty associated with the projections.

The EFI+ database integrating both environmental and anthropogenic factors and the data from the UK Met Office Hadley Centre for Climate Prediction and Research allowed us to test the climate change effects on riverine fish assemblages for different scenarios at the European scale.

Material and methods

All the data used, except for the forecasted climate data, were collected during the European EFI+ project (contract number 044096, <http://efi-plus.boku.ac.at/>). Data were collected from national fish surveys conducted by several laboratories and governmental environmental agencies (1974-2007, 95% after 1990). The sites were sampled using electrofishing methods either by wading or by boat, depending on stream depth. All fish caught were identified at the species level. To homogenize the sampling effort between regions, only fish collected during the first pass were considered.

Site selection

Because of the proximity of several sites and to limit the over-representation of certain regions in our data set, a grid of cells with an area of 100 km² was defined, and one site per cell was randomly selected. The data set is composed of 4543 sites distributed in 15 countries over an area greater than 4.10⁶ km² (Fig. 1).

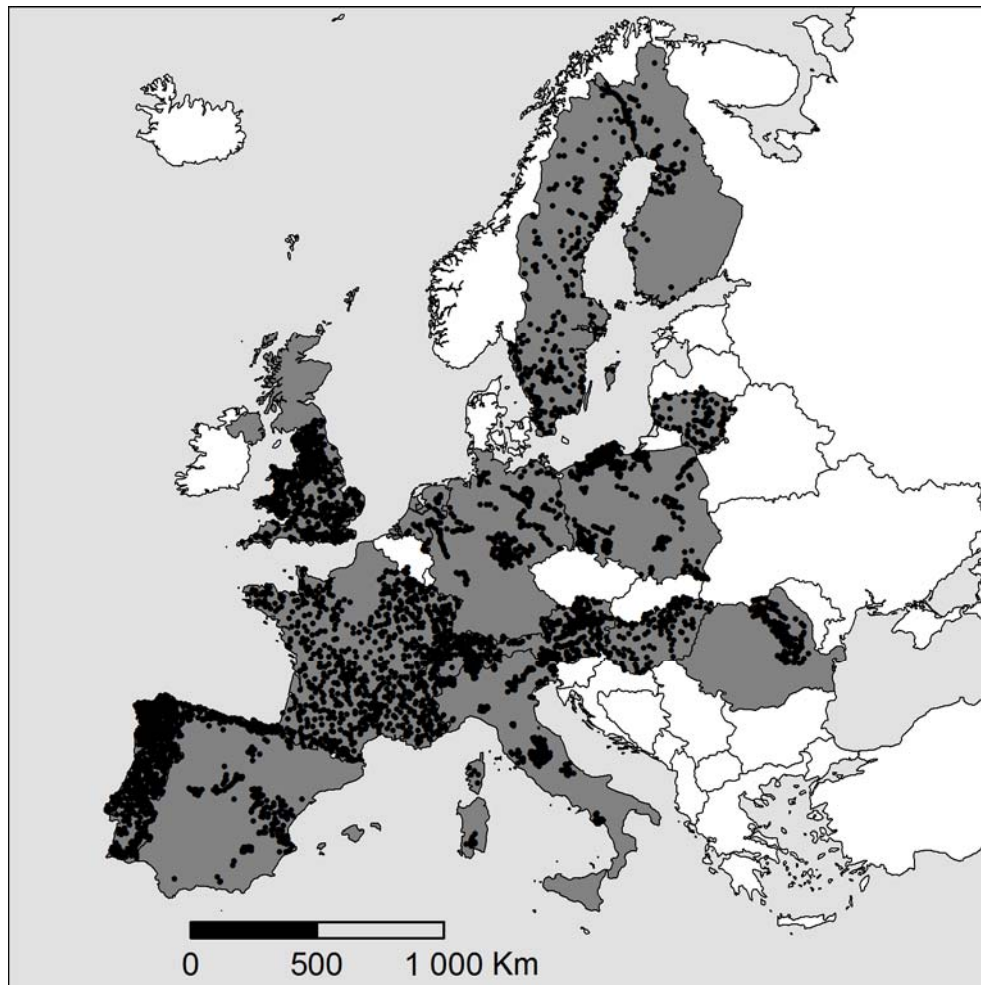


Fig. 1. Location of the 4523 sampling sites.

Climatic data

We used four different climate projections developed by the UK Met Office Hadley Centre for Climate Prediction and Research (Mitchell et al. 2004; Mitchell & Jones 2005). We average these projections for the periods 2020–2030 (referred to as 2020) and 2050–2060 (referred to as 2050). These projections are based on four different socio-economic scenarios proposed by the Intergovernmental Panel on Climate Change (Nakicenovic & Swart 2000), and used in its fourth and latest assessment report (IPCC 2007), A1FI, A2, B1 and B2. Projections were derived and averaged from three global circulation models (GCM), HadCM3 (Mitchell et al. 1998; Gordon et al. 2000), CGCM2 (Flato & Boer 2001), CSIRO-Mk2 (Hirst et al. 200; Hirst 1999).

We used the TYN SC 1.06 data-set (Mitchell et al. 2004). Data are available at a resolution of 10' x 10' grids of monthly average temperatures and monthly sums of precipitations. Four climate variables were extracted: mean air temperature in January (TJAN; cell scale), mean air temperature in July (TJUL; cell scale), annual mean air temperature (T; basin scale) and annual mean precipitations (P; basin scale). TJAN was used to compute the thermal amplitude between July and January (difference between TJUL and TJAN), TDIF. The mean annual temperature and precipitations were extracted to compute the projected stream power (STP; watt/m) (Gordon et al. 2004).

Climate change impact

Species distribution

Potential current and future distributions of species were predicted using the 23 models developed in part I of this report (Logez et al. 2011). We computed the predicted probabilities of species presence for the 4543 sampling sites. We accounted for the projected temperature and precipitation changes of the four socio-economic scenarios to predict the species distribution for the 2020–2030 and 2050–2060 time periods.

The species probabilities of occurrence were modulated according to the sampling site locations to assess the species distribution area and the potential source of colonization. For each species, if a sampling site was not located in the main marine regions where this species is currently recorded (Kottelat & Freyhof 2007; Reyjol et al. 2007), the probability of occurrence of this species was set to 0. The predicted species occurrence probabilities were derived from the occurrence probabilities that were compared with the threshold probabilities (Fiedling & Bell 1997; Buisson et al. 2008b) computed on the sites used to calibrate the models (see part I; Logez et al. 2011)

Human pressures vs. climate change

To assess the relative influence of human pressure and climate change on future species distributions we selected a data set of impacted sites. We defined a pressure gradient based on the first axis of a multivariate analysis and derived five groups of sites, from 1 (lowest level of pressure) to 5 (highest level of pressure). The data set used for this analysis was only composed of sites belonging to pressure classes 3 to 5.

First, for each species, we compared the observed occurrences with predicted presences–absences. To disentangle the effect of human pressures and model misclassifications, we computed the sensitivity (% presence correctly predicted; $TP/(TP+FA)$, Table 1) and specificity of each model (% absence correctly predicted; $TA/(FP+TA)$). These two statistics were computed with a cross-validation procedure in order to have a more realistic estimation of the error of classification made in an independent data set. Therefore, we performed a cross-validation derived from the split sampling method (Harrell 2001) by splitting the *calibration* data set into two sub-sets, train and test, containing 70% and 30% of the calibration sites, respectively. This process was repeated 10,000 times. Sensitivities and specificities were computed as the mean of the 10,000 values computed for the *test* subsets (Logez et al. accepted). Then, for each species, scenario and period, we compared the proportion of misclassified presences and absences with current observed species occurrences to assess the progression of the effect of human pressures under the various climate projections.

Table 1. Correspondence between observed species presence/absence and predicted presence/absence.

Observed	Predicted	
	Absence	Presence
Absence	True absence (TA)	False presence (FP)
Presence	False absence (FA)	True presence (TP)

Drift of reference conditions

The potential effects of climate change on the reference conditions for the functional structure of fish assemblages were assessed using the 1548 calibration sites (Fig. 1 of part I of this report).

For each of the eight metrics, local species richness (RICH), oxygen intolerant (O2INTOL), intolerant to habitat degradation (HINTOL), eurytopic (EURY), rheophilic (RH), no spawning substrate preferences (EUPAR), species spawning in running waters (RHPAR) and lithophilic species (LITH) (see Table 2 of part I of this report for the definition of each trait category), the expected value metrics were computed for the four scenarios and for both the current environmental conditions and forecasted climate conditions (2020–2030 and 2050–2060). The climate change effect was assessed by first computing the deviation between the observed and expected metric values for the current environmental conditions. The means (\bar{X}) and standard deviations of the metric deviations were computed to standardize the metrics with the formula:

$\frac{X_i - \bar{X}}{\sigma}$, with X_i the metric deviation (observed minus expected metric values). Therefore the

standardized metric values for the current environmental conditions are centred on 0 and have a standard deviation equal to 1.

For each period, the deviation between metric expected values for a given scenario and the metric observed values (for current environmental conditions) were computed and standardized using the means and standard deviations computed for the current environmental conditions (\bar{X} and σ). If climate change has an effect on reference conditions, it is expected that the distributions of standardized metrics computed for the different scenarios will depart from the distributions computed for the current environmental conditions. This was based on the assumption that in absence of climate change the assemblage compositions will not change and that the same number of species per metric would be observed.

If climate change limits the representation of the metric in fish assemblages, the deviation between metric scores would be on average positive, whereas if the climate change enhances the representation of the metrics then metric score deviations would on average shift towards negative values. Obviously, if global change has no effect on the assemblage functional structure, null metric score deviations are expected.

Uncertainty

Uncertainty associated with species distribution projections

The uncertainty associated with projections was assessed by computing the confidence interval (CI) around the predicted probability. First we computed the Wald confidence interval on the logit-scale and then applied the logit-inverse function on the confidence bounds to compute the CI of each probability of presence (Collett 2002; Faraway 2006):

$$CI(\hat{p}_x) = \frac{1}{1 + e^{-CI(\text{logit}(\hat{p}_x))}}, \text{ with } CI(\text{logit}(\hat{p}_x)) = \hat{\eta}_x \pm z_{1-\alpha/2} \cdot se(\hat{\eta}_x) \text{ and } se(\hat{\eta}_x) = \sqrt{\phi \mathbf{X}'_x (\mathbf{X}' \mathbf{W} \mathbf{X})^{-1} \mathbf{X}_x}.$$

ϕ was taken to 1 (McCullagh & Nelder 1989).

The CI provides information on the degree of knowledge of a population characteristic from a random sample (Hahn & Meeker 1991). This interval should contain the parameter's true value of the studied population (e.g. mean), with a $100(1-\alpha)\%$ level of confidence (Hahn & Meeker 1991; Scherrer 2009). Each value predicted by a logistic regression corresponds to the expectation of the response variable Y, knowing the explanatory variables X (McCullagh & Nelder 1989; Saporta 2006). Consequently, the CI associated with a prediction corresponds to the interval that should contain the average value of the probability of presence for a given environment.

In contrast, “a prediction interval for a single observation is an interval that will, with a specified degree of confidence, contain the next randomly selected observation from a population” (Hahn & Meeker 1991). This interval estimates the uncertainty associated with the prediction of a new observation remembering what has already been observed.

To evaluate the uncertainty associated with the species distribution projections, the prediction interval is more suitable. Nevertheless, for logistic regression: “there is no distinction possible between confidence intervals for a future observation and those for the mean response” (Faraway 2006). This means that confidence and prediction intervals are the same for this regression (Faraway, personal communication), conversely to regular linear regression (Kutner et al. 2005).

Therefore, CIs were computed for each site and each projection (combination of period and scenarios). The limits (lower and upper boundaries) of the CIs were derived in species presence/absence depending on the threshold probabilities (see part I). Therefore, for each species we computed the projections for the lower and upper boundaries of the CIs. If the patterns observed for the CI limits are consistent with the patterns observed for the projected probability of presence, it would suggest that the climate change effects would overcome the uncertainty associated with the projections.

Results

Climatic conditions

By 2020–2030, the mean air temperature in January will increase by 1.96°C , while this pattern will be less pronounced for July with an expected increase of 1.7°C (Table 2). The highest warming is predicted for the B1 and B2 scenarios (Table 3). The pattern predicted for 2050–2060 is inverse, with the highest warming in July but still with an important increase of temperature in January; an increase of 3°C and 2.1°C , respectively (Table 2). The highest warming is predicted with the A1F1 scenario (Table 3).

Table 2. Average monthly mean air temperatures.

	January	July
Current	1.054 (5.239)	18.113 (2.642)
2020-2030	3.013 (4.739)	19.826 (2.767)
2050-2060	3.197 (4.779)	21.085 (3.130)

Table 3. Average monthly mean air temperature predicted for the four scenario (sd).

Scenario	2020-2030		2050-2060	
	January	July	January	July
A1F1	2.946 (4.759)	19.850 (2.768)	3.586 (4.715)	21.783 (3.230)
A2	2.924 (4.747)	19.787 (2.753)	3.155 (4.755)	21.151 (3.099)
B1	3.081 (4.739)	19.825 (2.791)	2.993 (4.839)	20.674 (3.058)
B2	3.100 (4.711)	19.842 (2.754)	3.056 (4.783)	20.733 (3.002)

Climatic scenarios predict a decrease of precipitations by 2020–2030 and 2050–2060 of 16 and 8 mm, respectively (Table 4). The driest period is always predicted by the A1F1 scenario, while the highest precipitations are predicted by the B2 scenario (Table 5).

Table 4. Average precipitations on the upstream drainage area.

Current	880.271 (280.687)
2020-2030	863.617 (280.247)
2050-2060	872.076 (277.960)

Table 5. Average precipitations on the upstream drainage area predicted by the climatic scenarios.

Scenario	2020-2030	2050-2060
A1F1	860.284 (279.803)	865.629 (275.846)
A2	860.874 (280.233)	867.304 (277.742)
B1	863.175 (279.893)	871.802 (278.049)
B2	870.135 (281.058)	883.570 (280.202)

Species distribution projections

2020–2030

For the 2020–2030 period, all scenarios provide the same results for each species, except for spirilin. On the whole, all species are predicted to both disappear from some sites and to occur in new locations (Table 6 and Appendix 1). The distribution shifts vary greatly between species, but all species, except Atlantic salmon, are expected to occur in new locations and disappear from sites where they were present (Table 6).

Bleak, eel, barbel, nase, gudgeon, chub, dace, perch, ninespine stickleback, bitterling, roach and soufie are expected to experience an expansion of their distribution areas (more new occurrences than new absences). Stone loach, bullhead, northern pike, threespine stickleback, lamprey, burbot, minnow, Atlantic salmon, brown trout and grayling are expected to have a contraction of their distribution areas (Table 6).

Table 6: Match between species predicted occurrences for current climate and projected climate for the 2020–2030 period (average from the four scenarios). Absence: number of sites with species always considered absent; Presence: number of sites where species is always expected to occur; New absence: number of sites with expected population extinctions; New occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1179.5	439	132	125.5
<i>Alburnus alburnus</i>	2147.25	1534	2	432.75
<i>Anguilla anguilla</i>	2550.75	1624	73	243.25
<i>Barbatula barbatula</i>	1310.5	1739	342	238.5
<i>Barbus barbus</i>	1507.5	984	104	366.5
<i>Chondrostoma nasus</i>	703	604	144	297
<i>Cottus gobio</i>	1529	999.5	1049.5	124
<i>Esox lucius</i>	2830.5	1242.25	207.75	186.5
<i>Gasterosteus aculeatus</i>	2444.75	469.5	393.5	113.25
<i>Gobio gobio</i>	2088.25	1458.5	177.5	326.75
<i>Lampetra planeri</i>	2801.25	944.25	373.75	65.75
<i>Leuciscus cephalus</i>	1250.75	1591.25	193.75	673.25
<i>Leuciscus leuciscus</i>	1769.5	967.25	149.75	327.5
<i>Lota lota</i>	1444	951.5	45.5	10
<i>Perca fluviatilis</i>	1413.75	1439	259	397.25
<i>Phoxinus phoxinus</i>	1653	1632.5	453.5	143
<i>Pungitius pungitius</i>	2075.25	192	303	311.75
<i>Rhodeus amarus</i>	712.25	1208.25	33.75	591.75
<i>Rutilus rutilus</i>	1508.25	1476.5	215.5	459.75
<i>Salmo salar</i>	1735	766	539	0
<i>Salmo trutta</i>	2068.25	1806	629	4.75
<i>Telestes souffia</i>	690	163.25	129.75	417
<i>Thymallus thymallus</i>	2267.25	439.5	545.5	32.75

2050–2060

Compared to the 2020–2030 period, five species present divergent patterns depending on the scenarios (Appendix 1): nase, gudgeon, dace, perch and roach. For nase, dace and perch, the patterns were different between scenarios A1F1–A2 and B1–B2, while for gudgeon and roach the divergence was observed for the A1F1 scenario (Appendix 1).

For the 2020–2030 period, the distribution areas of eel, nase, dace, perch and ninespine stickleback are expected to expand, whereas for 2050–2060 they are expected to be reduced (Table 6 & Table 7). In contrast, burbot is the only species with an expected distribution contraction during 2020–2030 and a distribution expansion in 2050–2060 (Table 6 & Table 7).

The ten species that have more local extinctions than occurrences, for both periods, will face rapid extinctions between 2020–2030 and 2050–2060. This concerns the spiralin, stone loach, bullhead, northern pike, threespine stickleback, European brook lamprey, minnow, Atlantic salmon, brown trout and grayling (Table 6 & Table 7). For the seven species that have more

local apparitions than extinctions, for both periods, the patterns are more contrasting. Bleak and bitterling are the only species that are expected to have an expansion of their distribution areas between the two periods. For barbel, gudgeon, chub, roach and soufie, the number of extinctions increase faster than the number of occurrences between 2020–2030 and 2050–2060. Therefore, extinction and occurrence are more balanced, especially for gudgeon and roach (Table 7).

Table 7: Match between species predicted occurrences for current climate and projected climate for the 2050–2060 period (average from the four scenarios). Absence: number of sites with species always considered absent; Presence: number of sites where species is always expected to occur; New absence: number of sites with expected population extinctions; New occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1138.25	338.5	232.5	166.75
<i>Alburnus alburnus</i>	1806	1532.25	3.75	774
<i>Anguilla anguilla</i>	2727.5	1376.5	320.5	66.5
<i>Barbatula barbatula</i>	1243.25	1384.25	696.75	305.75
<i>Barbus barbus</i>	1454.25	846.5	241.5	419.75
<i>Chondrostoma nasus</i>	715	431.25	316.75	285
<i>Cottus gobio</i>	1510	535.25	1513.75	143
<i>Esox lucius</i>	2807.5	1023.25	426.75	209.5
<i>Gasterosteus aculeatus</i>	2430.75	275.75	587.25	127.25
<i>Gobio gobio</i>	1989.25	1220.25	415.75	425.75
<i>Lampetra planeri</i>	2793.75	665.25	652.75	73.25
<i>Leuciscus cephalus</i>	1097.25	1341.75	443.25	826.75
<i>Leuciscus leuciscus</i>	1780.25	772.75	344.25	316.75
<i>Lota lota</i>	1385.5	987.25	9.75	68.5
<i>Perca fluviatilis</i>	1383.75	1166	532	427.25
<i>Phoxinus phoxinus</i>	1628.75	1195.25	890.75	167.25
<i>Pungitius pungitius</i>	2139.5	91.25	403.75	247.5
<i>Rhodeus amarus</i>	504	1138.75	103.25	800
<i>Rutilus rutilus</i>	1484.25	1267.5	424.5	483.75
<i>Salmo salar</i>	1735	388.25	916.75	0
<i>Salmo trutta</i>	2069.25	1160.75	1274.25	3.75
<i>Telestes souffia</i>	672	104.25	188.75	435
<i>Thymallus thymallus</i>	2264.25	298.5	686.5	35.75

Species distributions

Alburnoides bipunctatus

Spirilin is expected to disappear in most of the French and Hungarian sampling sites and to appear in Austrian and Romanian sites, but also in the most northern part of its current distribution area.

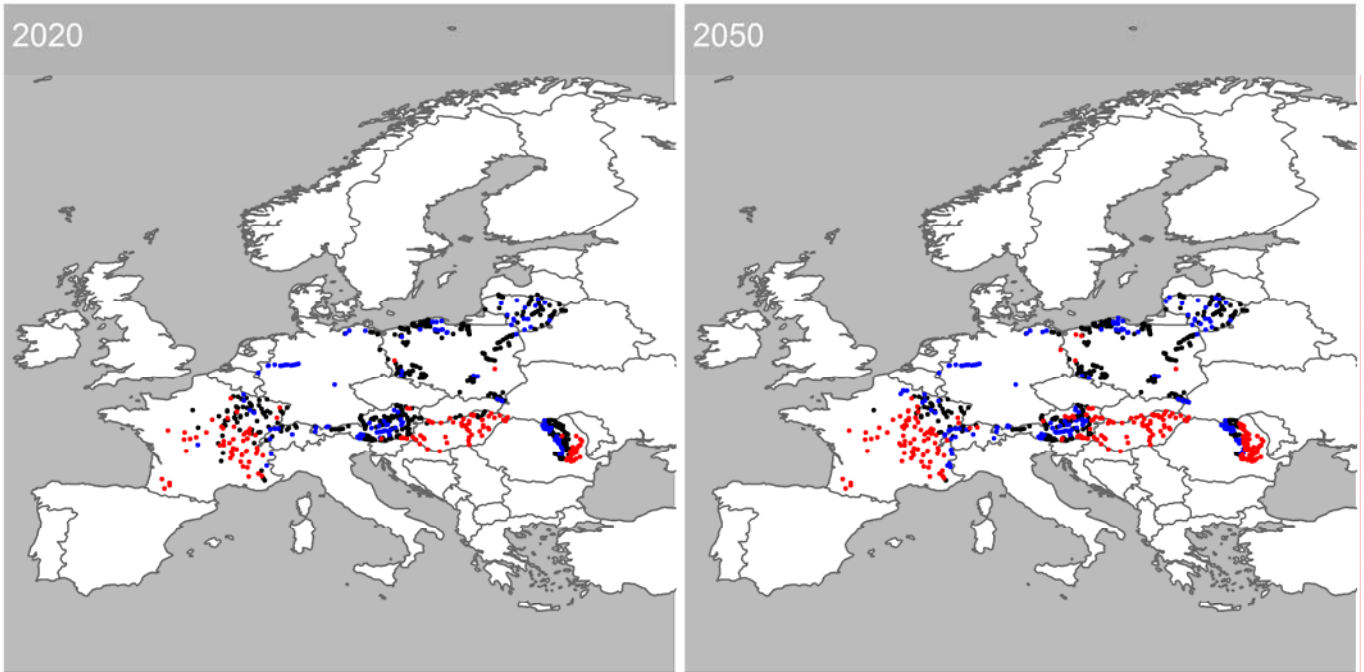


Fig. 2. Average forecasted distributions of the spirin for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Alburnus alburnus

The distribution of bleak is expected to expand almost everywhere in Europe.

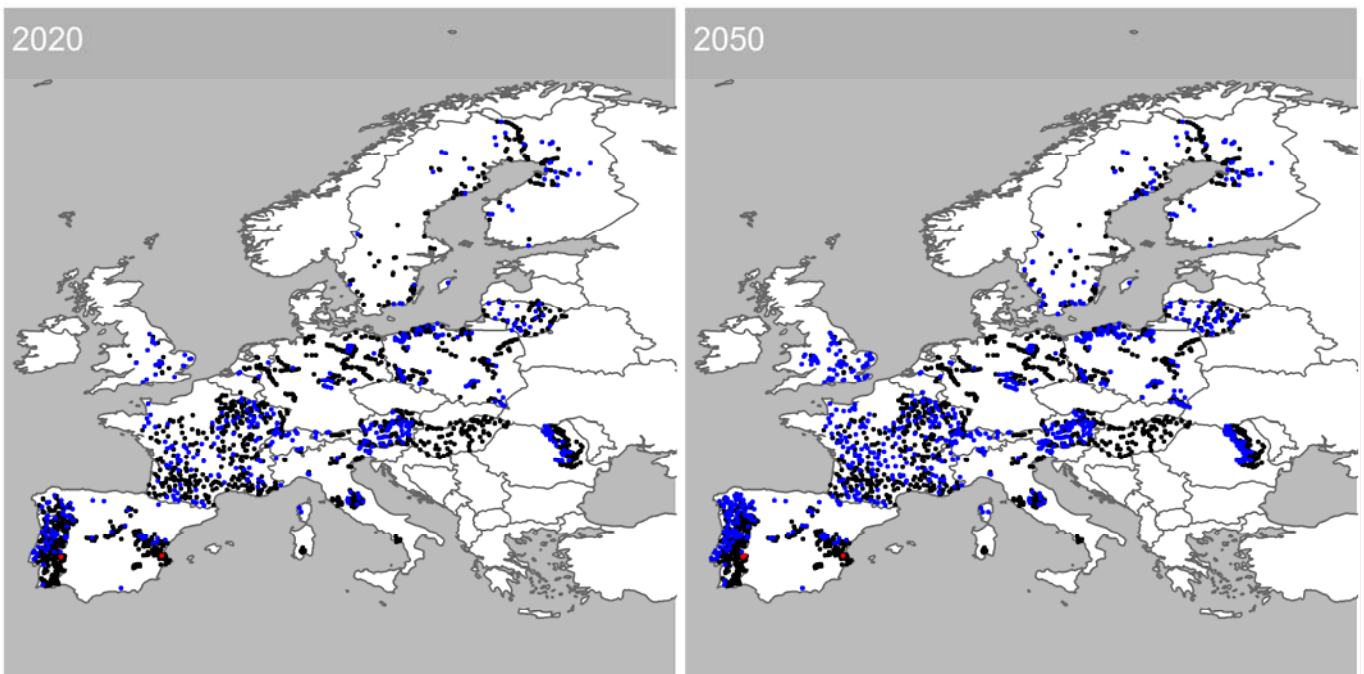


Fig. 3. Average forecasted distributions of bleak for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Anguilla anguilla

Eel is expected to disappear from numerous locations in the Iberian Peninsula and to experience a slight expansion of its distribution in Great Britain and France mainly. Its extinction will be accelerated in 2050–2060, especially in the Iberian Peninsula and France, and its local occurrence will be more rare.

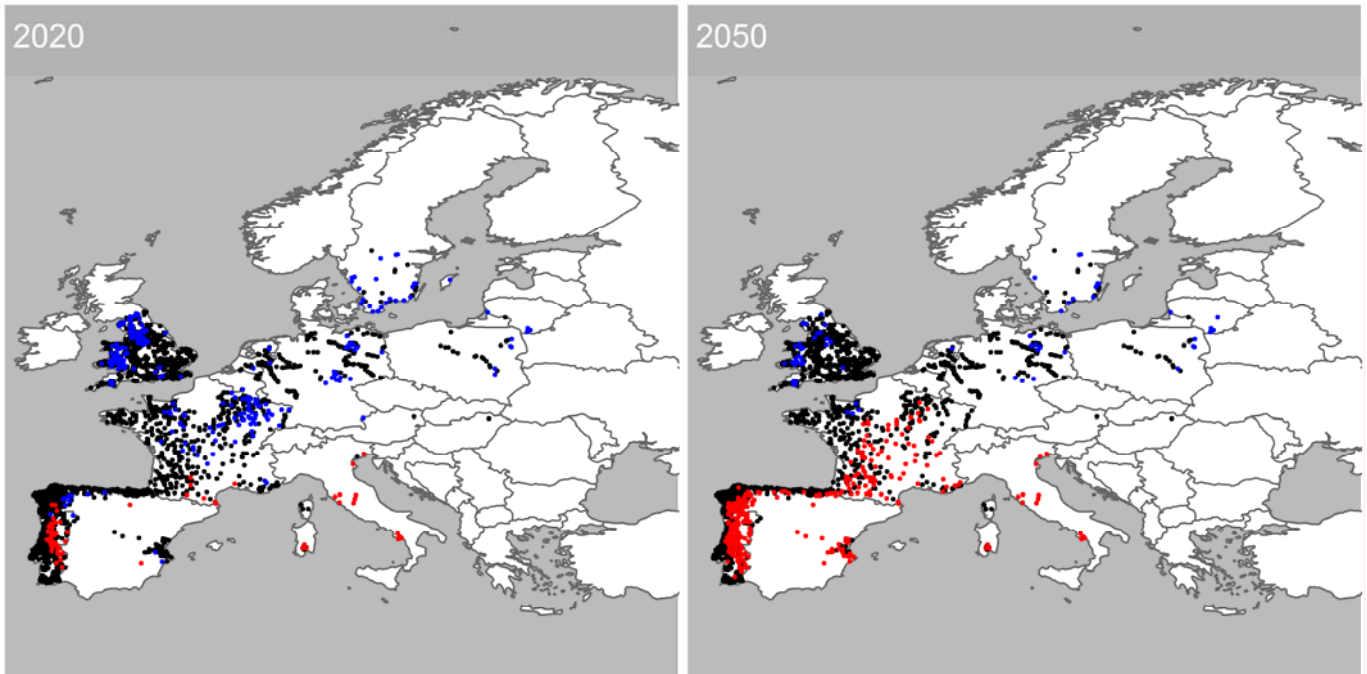


Fig. 4. Average forecasted distributions of the European eel for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Barbatula barbatula

For stone loach there is a clear shift of the distribution of this species towards northern Europe. Stone loach is expected to be almost extinct in Spanish sites. This shift occurs rapidly between the two periods.

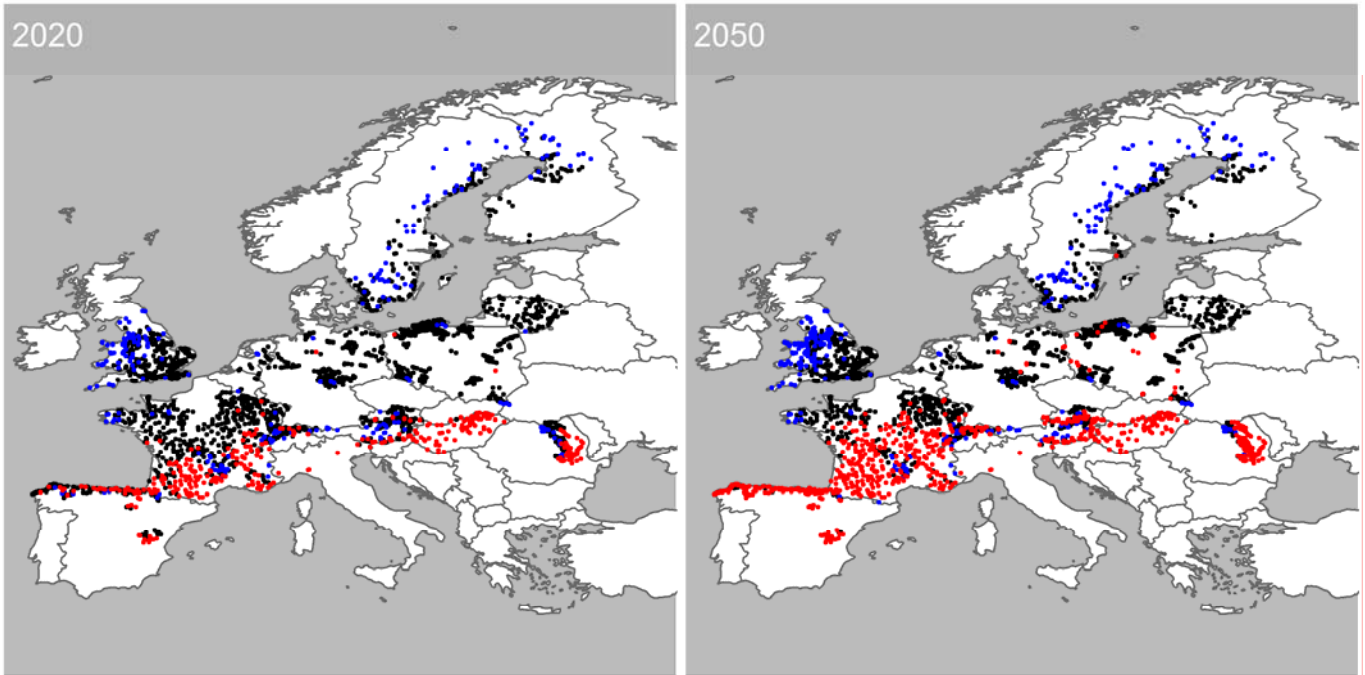


Fig. 5. Average forecasted distributions of the stone loach for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Barbus barbus

Barbel is expected to mostly disappear in the southern part of its distribution area, except in the Pyrenees, as well as in most of the Hungarian sites. At the same time, barbel is expected to occur at numerous new locations in: the northern part of France, Switzerland, Austria, England, Germany, Poland and Lithuania.

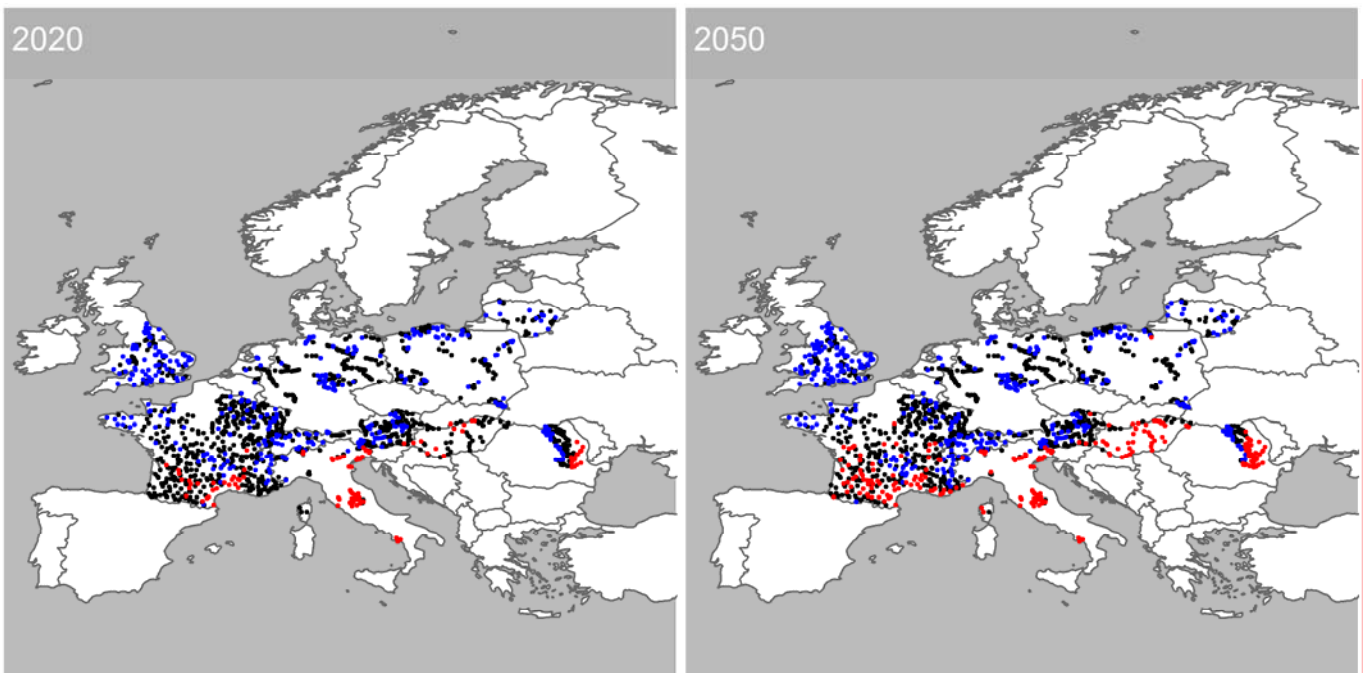


Fig. 6. Average forecasted distributions of barbel for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Chondrostoma nasus

Like many other species, nase is expected to become extinct in several southern French and Hungarian populations. The local extinctions are even more pronounced in 2050–2060, especially in France, Poland and Romania.

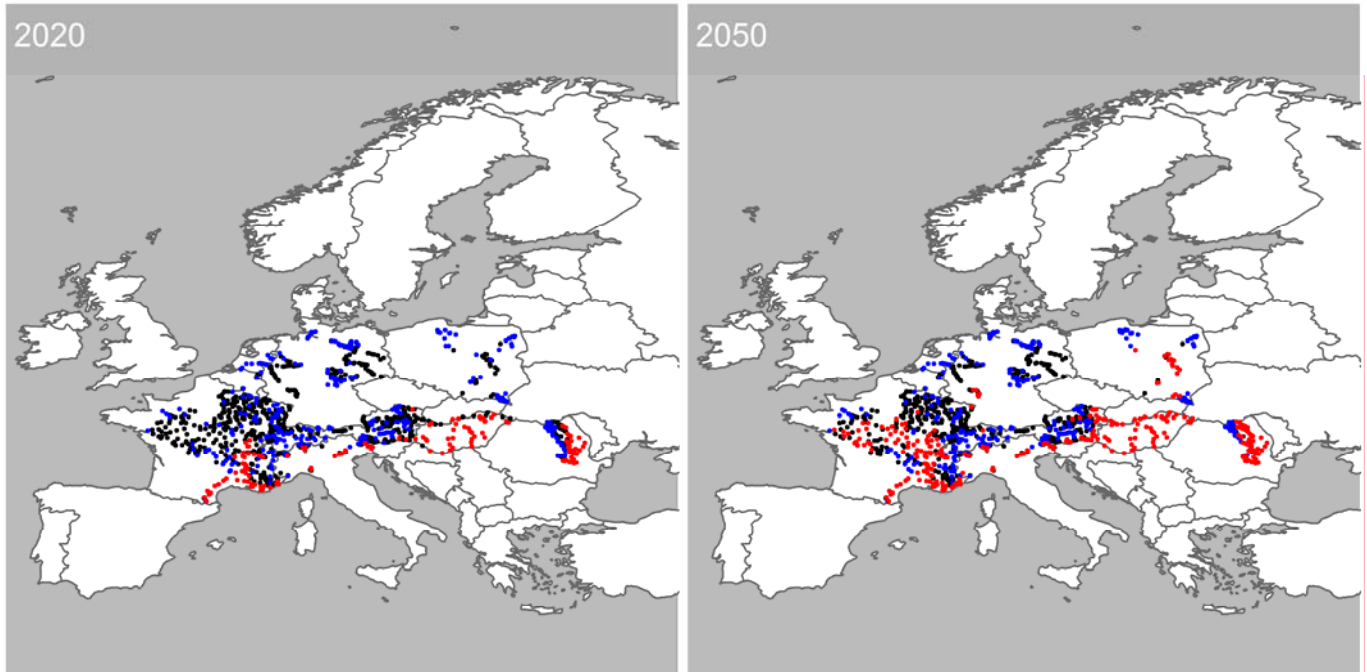


Fig. 7. Average forecasted distributions of nase for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Cottus gobio

Bullhead is expected to become extinct in a great number of populations from all 14 European countries and to remain in, or even colonize, other locations in England and Scandinavia.

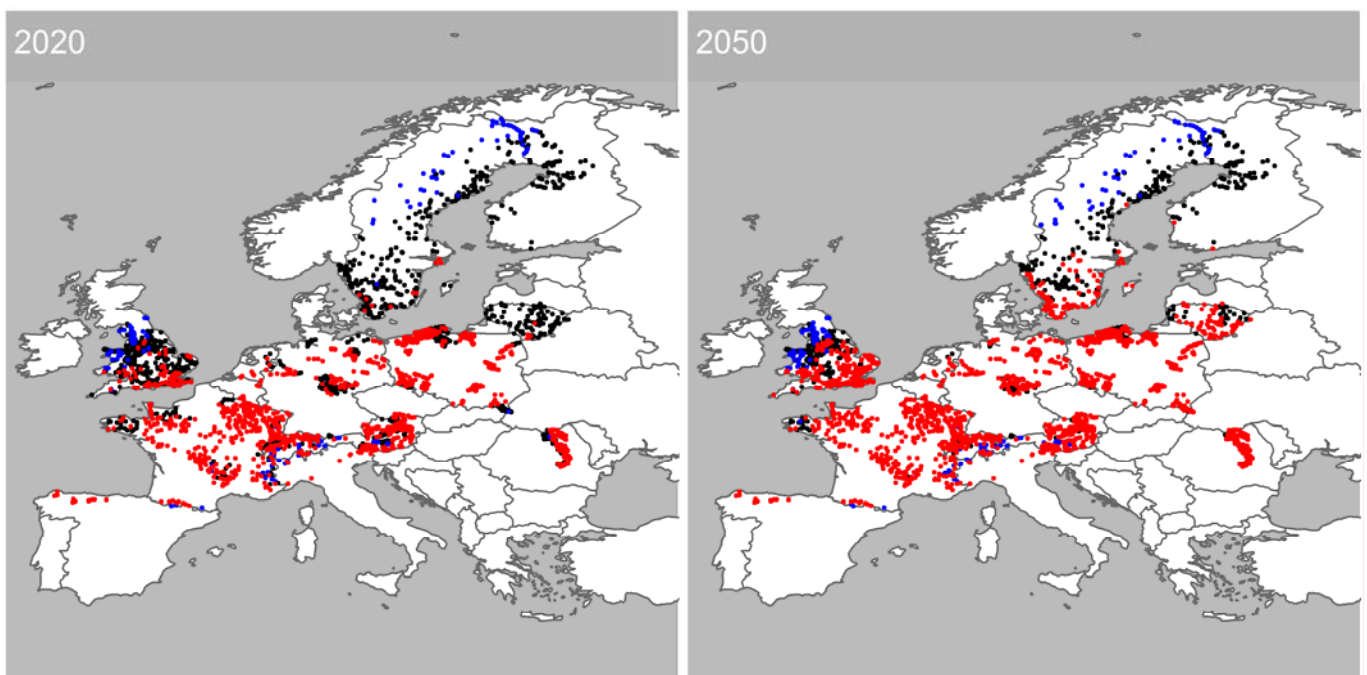


Fig. 8. Average forecasted distributions of the bullhead for t2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Esox lucius

The distribution of pike is expected to shift towards more northern locations and to mostly disappear in the Iberian Peninsula. New colonizations are expected to occur mainly in England, Germany and Scandinavia. Pike will remain quite stable in Poland and Lithuania.

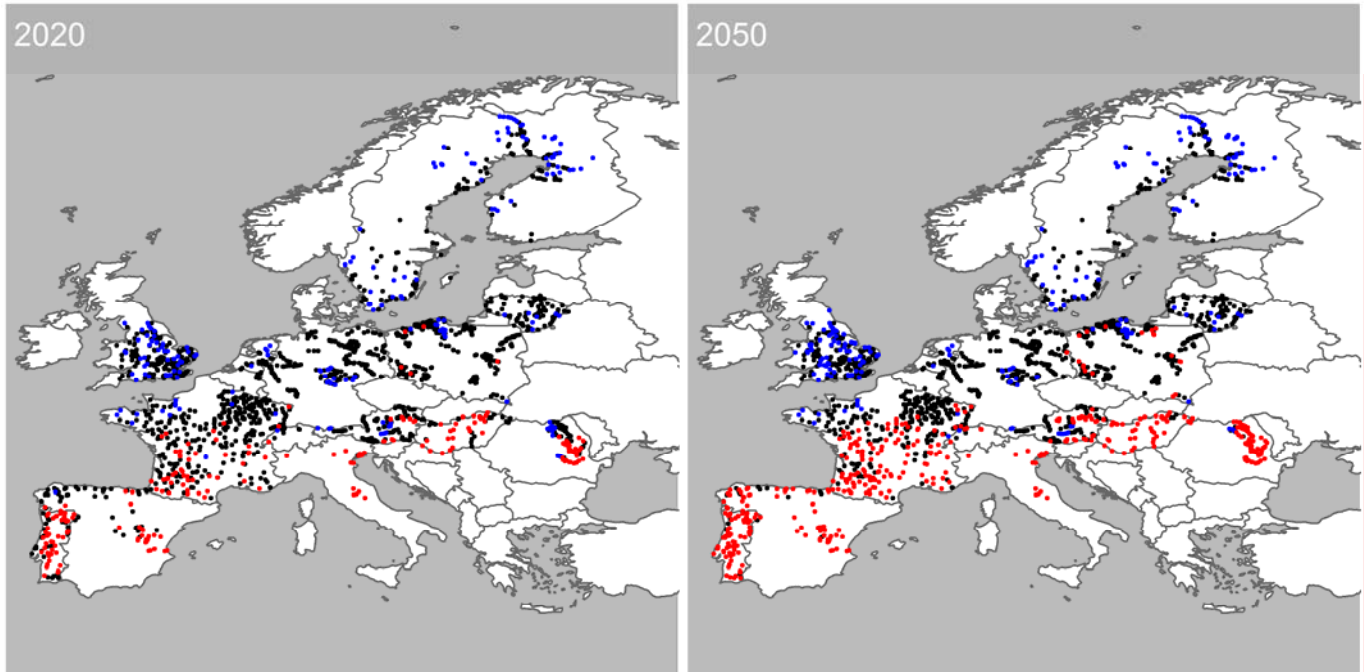


Fig. 9. Average forecasted distributions of the northern pike for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Gasterosteus aculeatus

Threespine stickleback is expected to become extinct in numerous locations and to remain or to colonize new habitats in only restricted locations (England, Sweden and Finland).

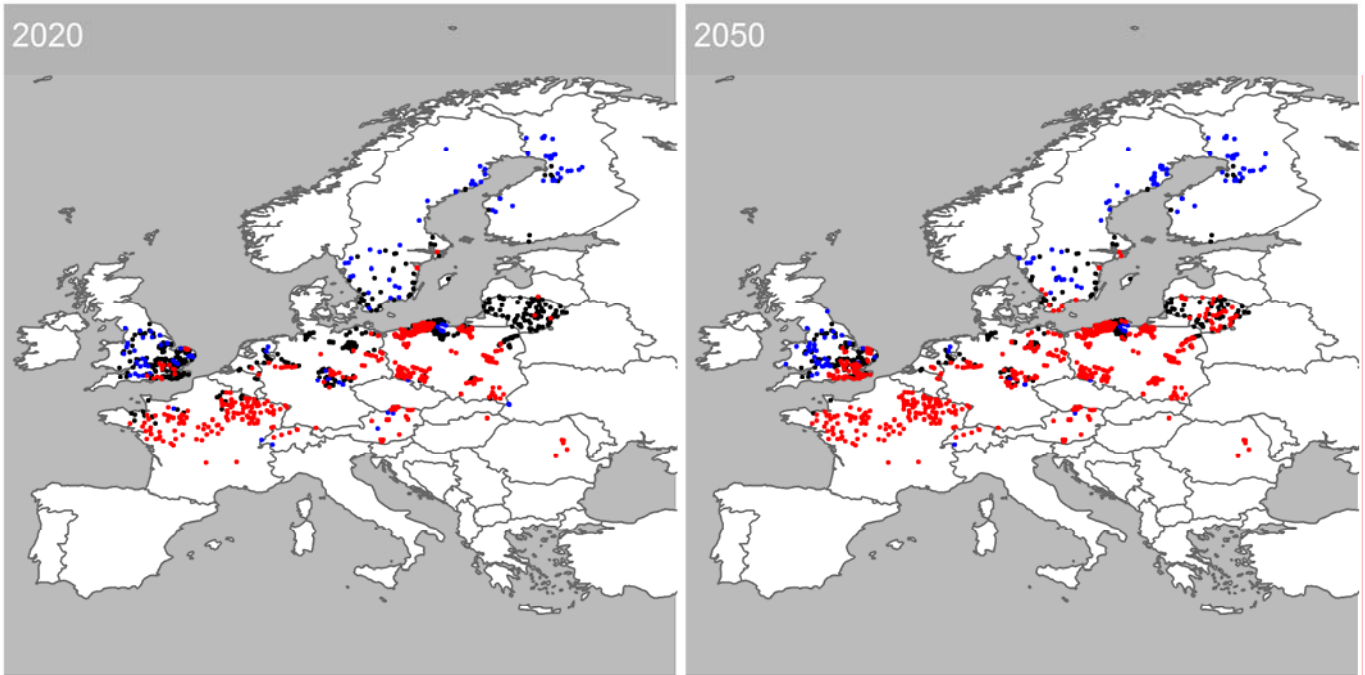


Fig. 10. Average forecasted distributions of the threespine stickleback for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Gobio gobio

Gudgeon is expected to experience a shift of its distribution to northern locations, with both rapid extinctions in the southern part of Europe and expansion in the northern part.

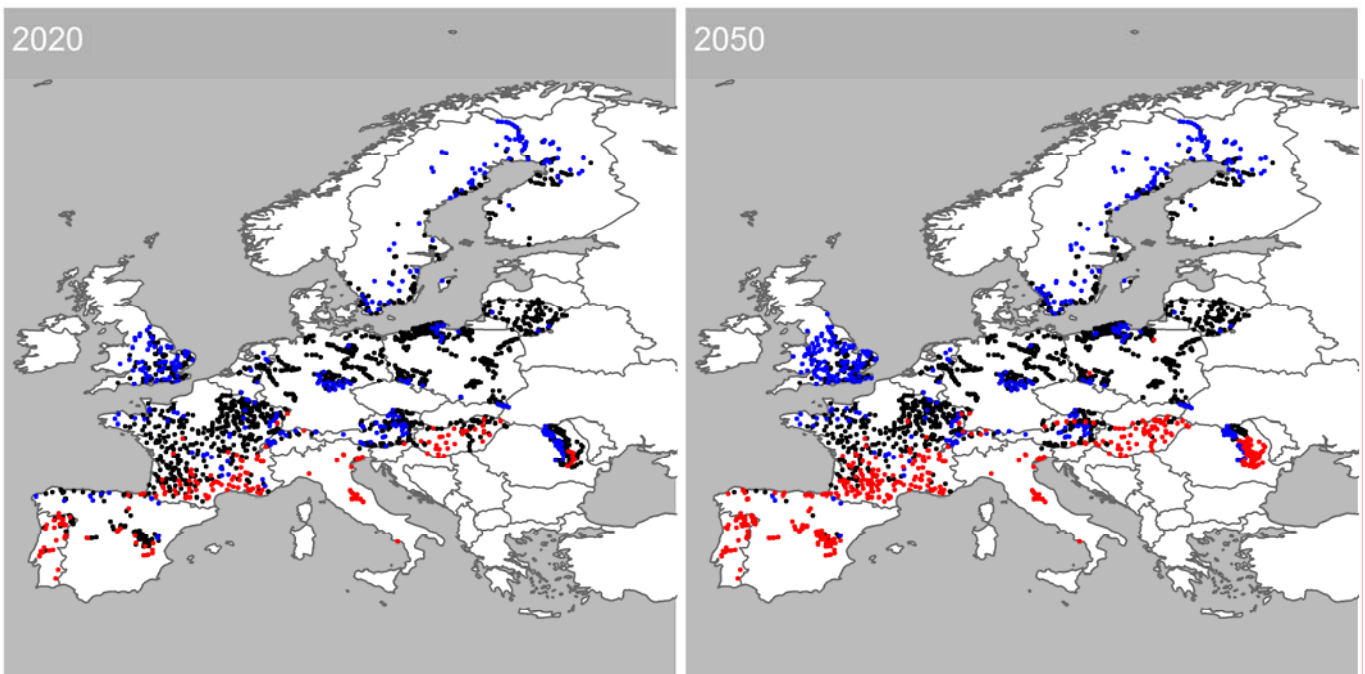


Fig. 11. Average forecasted distributions of the gudgeon for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Lampetra planeri

Lamprey is expected to experience massive extinction and to remain only in isolated areas.

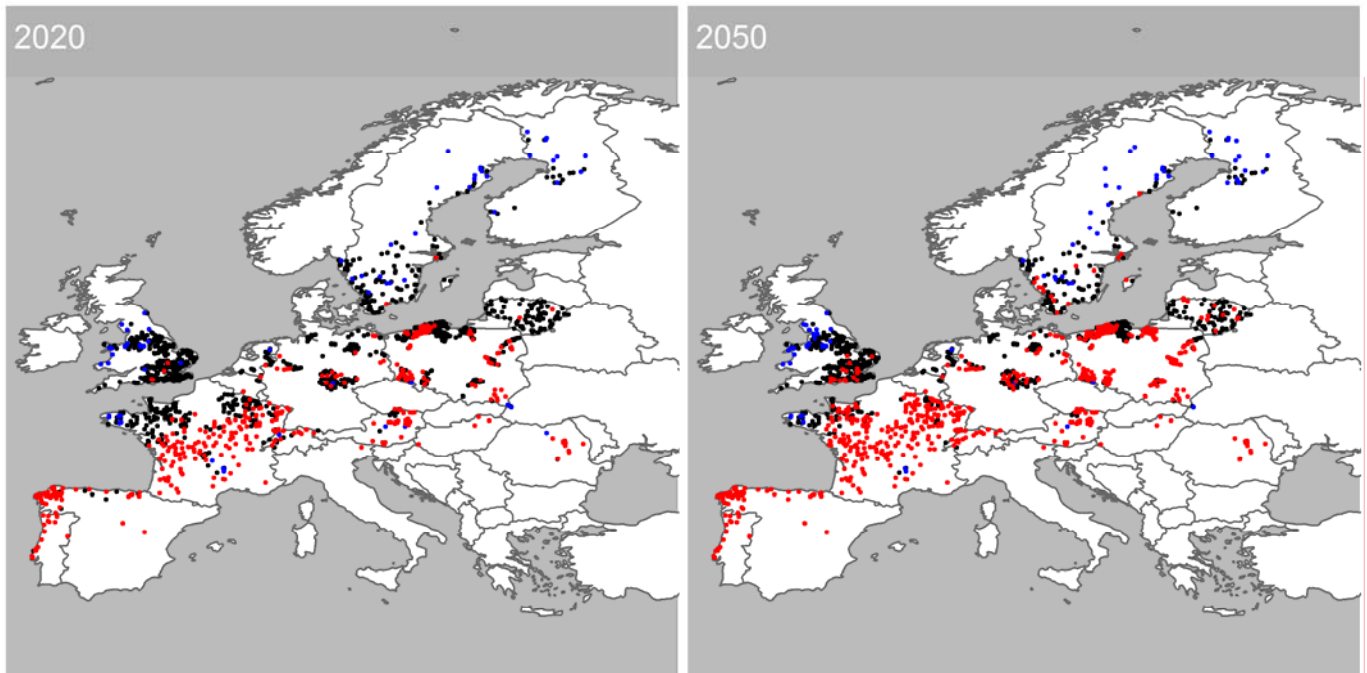


Fig. 12. Average forecasted distributions of the brook lamprey for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Leuciscus cephalus

An extinction of chub populations is expected to mostly take place in the Mediterranean part of Europe and in Hungary and Romania. Nevertheless, this species is expected to experience an expansion of its distributions in almost all countries and to colonize numerous new streams or stream reaches.

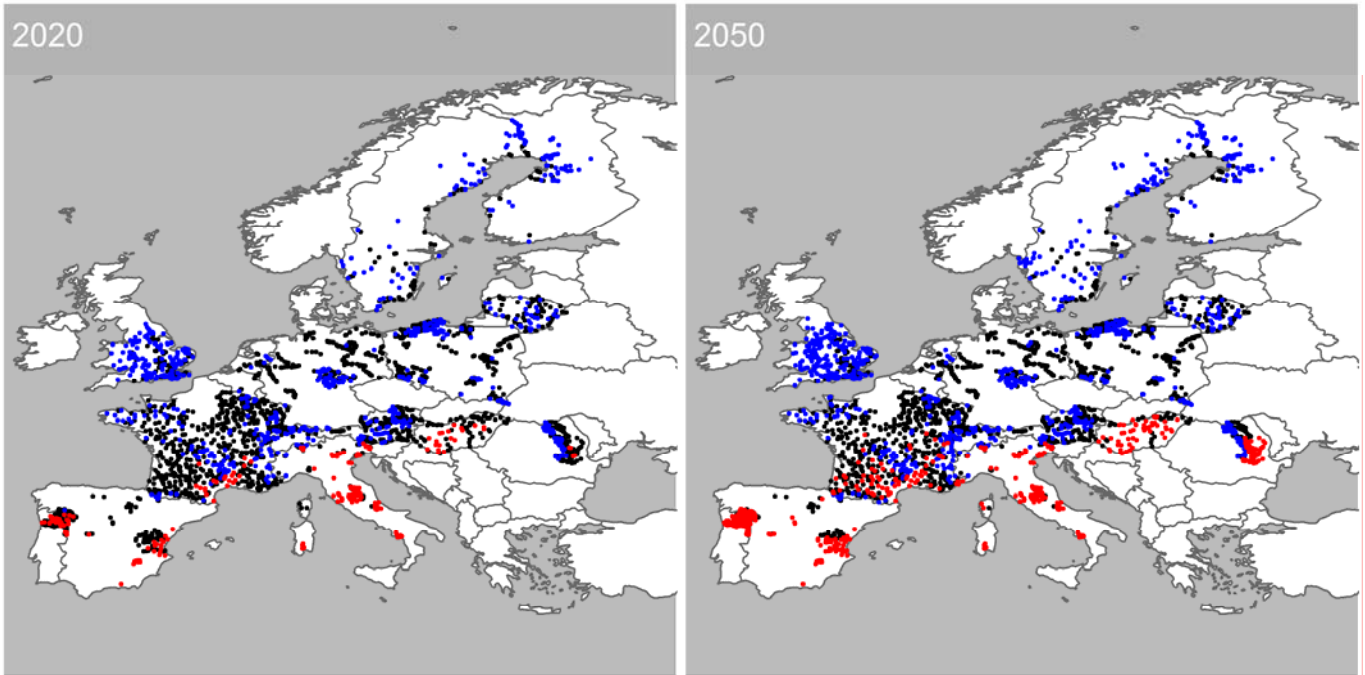


Fig. 13. Average forecasted distributions of the chub for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Leuciscus leuciscus

Dace is expected to experience an important shift of its distribution to the northern part of Europe, becoming extinct in the south of France, Hungary, Romania and likely extinct in Austria, while it will colonize numerous other locations in England, Poland and Germany.

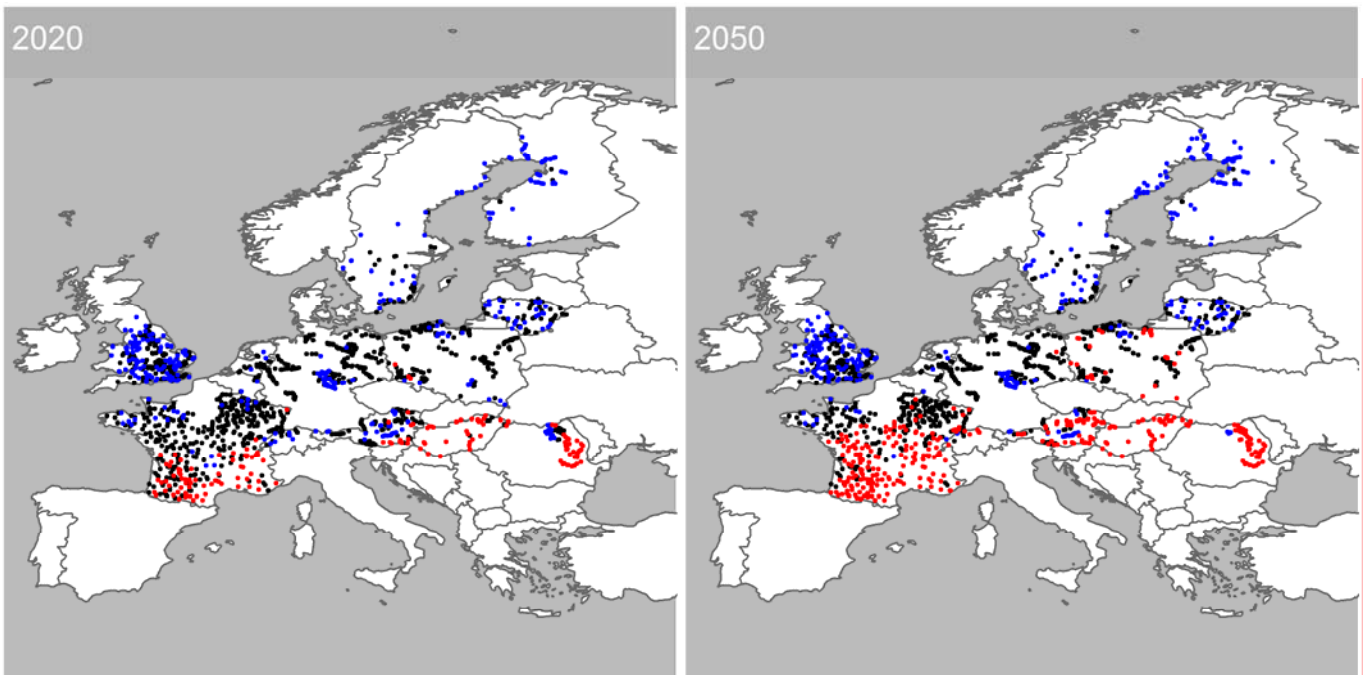


Fig. 14. Average forecasted distributions of the dace for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Lota lota

Few changes are expected for burbot in all the regions and periods considered.

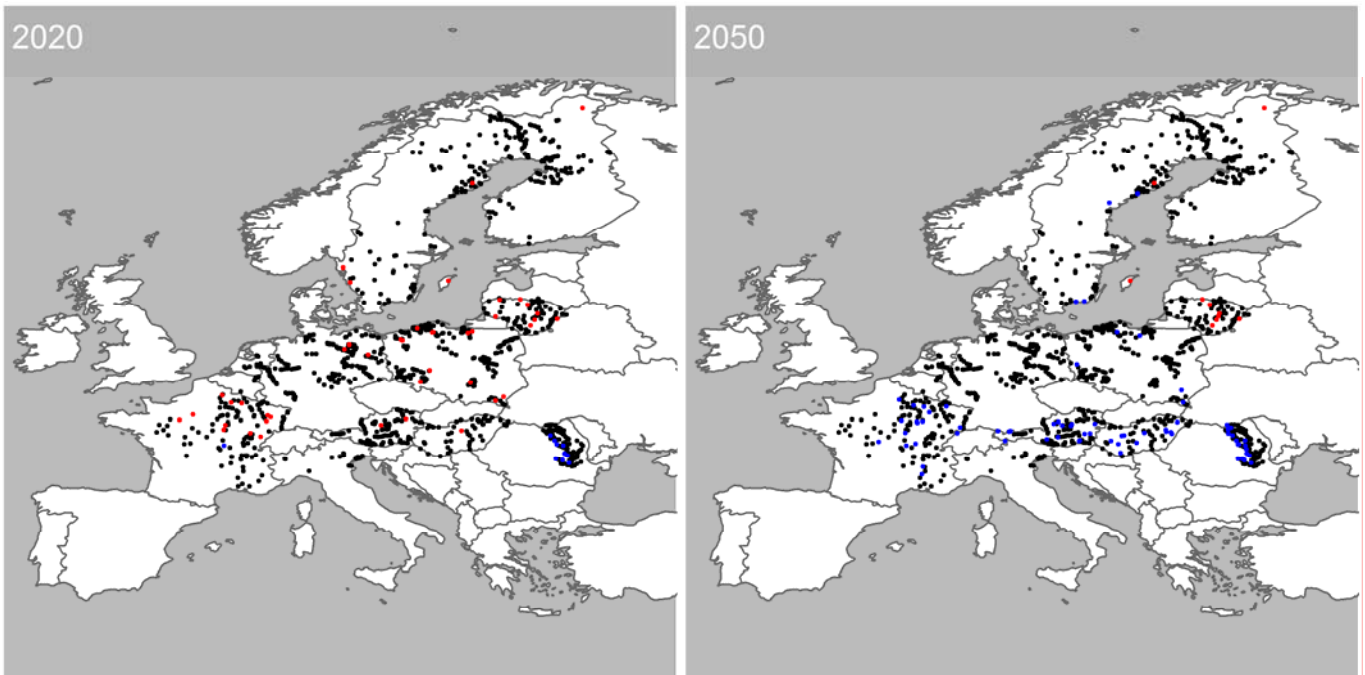


Fig. 15. Average forecasted distributions of the burbot for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Perca fluviatilis

Like many other species, perch is expected to become extinct in several southern locations and to colonize numerous northern locations. Nevertheless, the pattern is not that simple because many extinctions and colonizations are expected in Poland. Therefore, the shift of its distribution does not merely follow a south–north gradient.

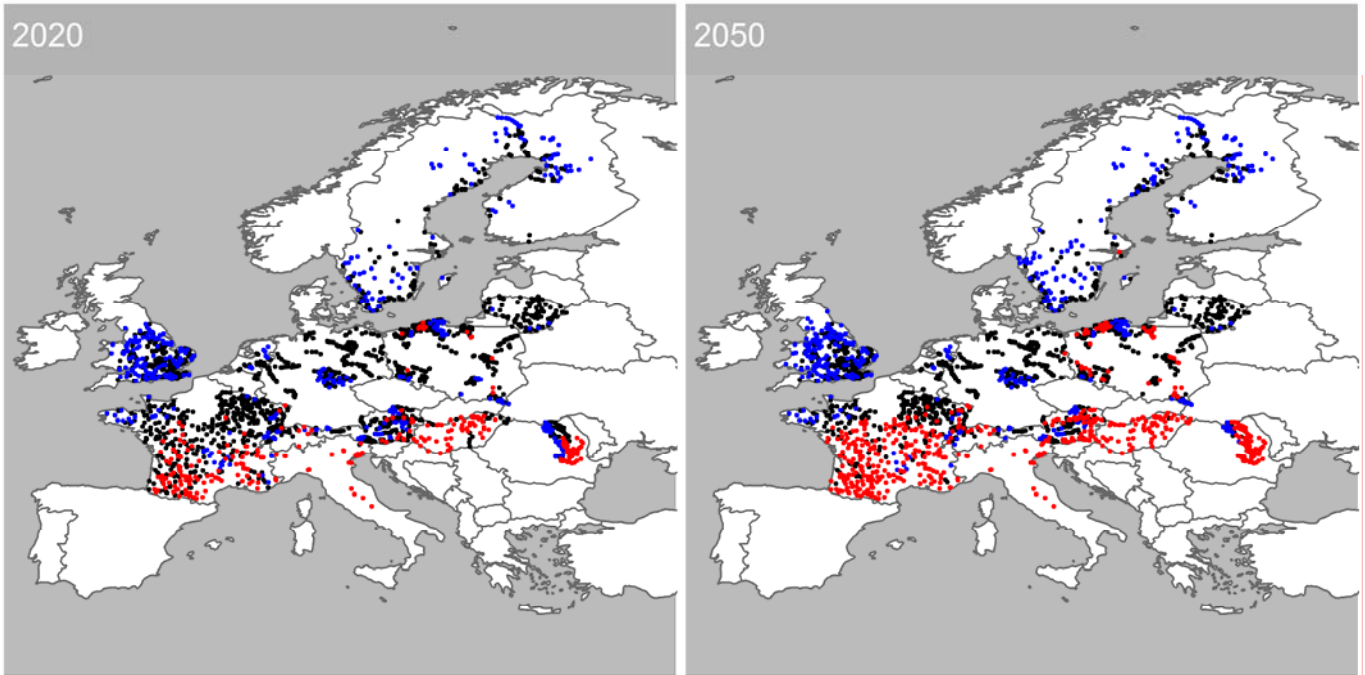


Fig. 16. Average forecasted distributions of the perch for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Phoxinus phoxinus

Like the bullhead, minnow is expected to face massive extinctions and to maintain and develop itself mostly in England and Scandinavia.

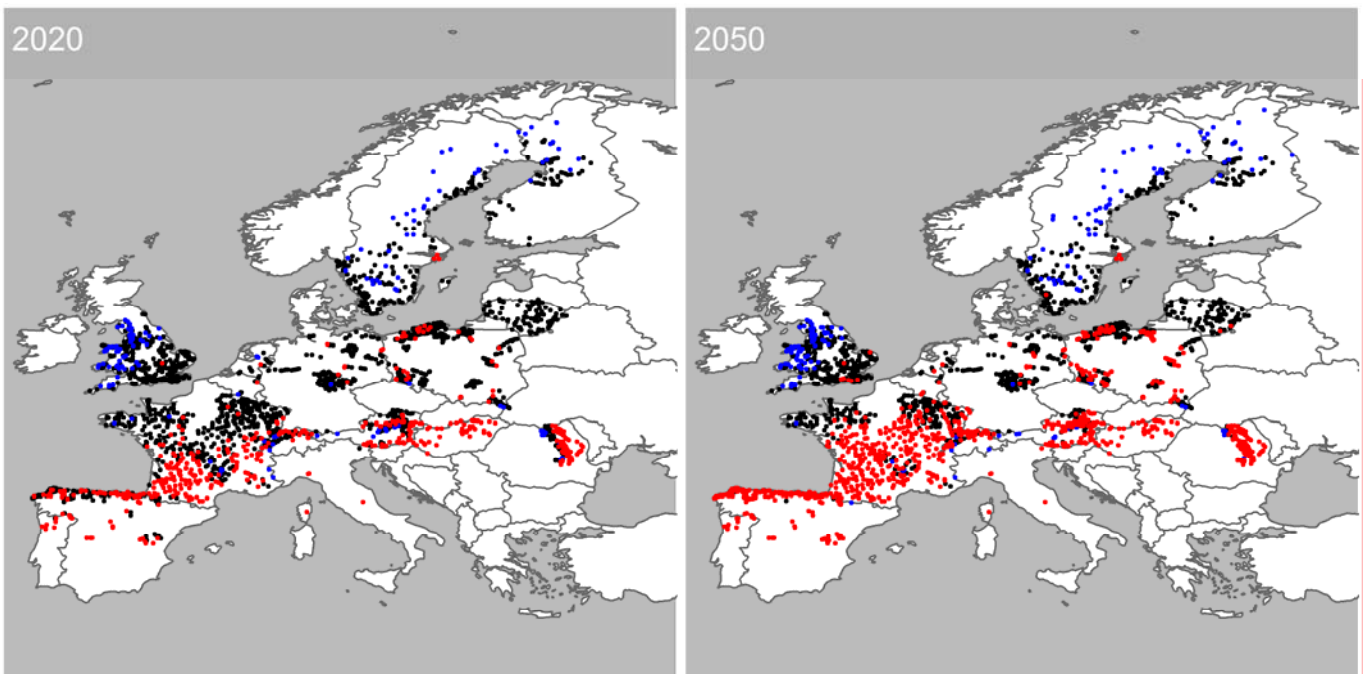


Fig. 17. Average forecasted distributions of the minnow for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Pungitius pungitius

Compared to the other species, the ninespine stickleback displays a very singular pattern. Indeed, this species is mostly expected to become extinct or to occur in new locations. Stable populations are sparse.

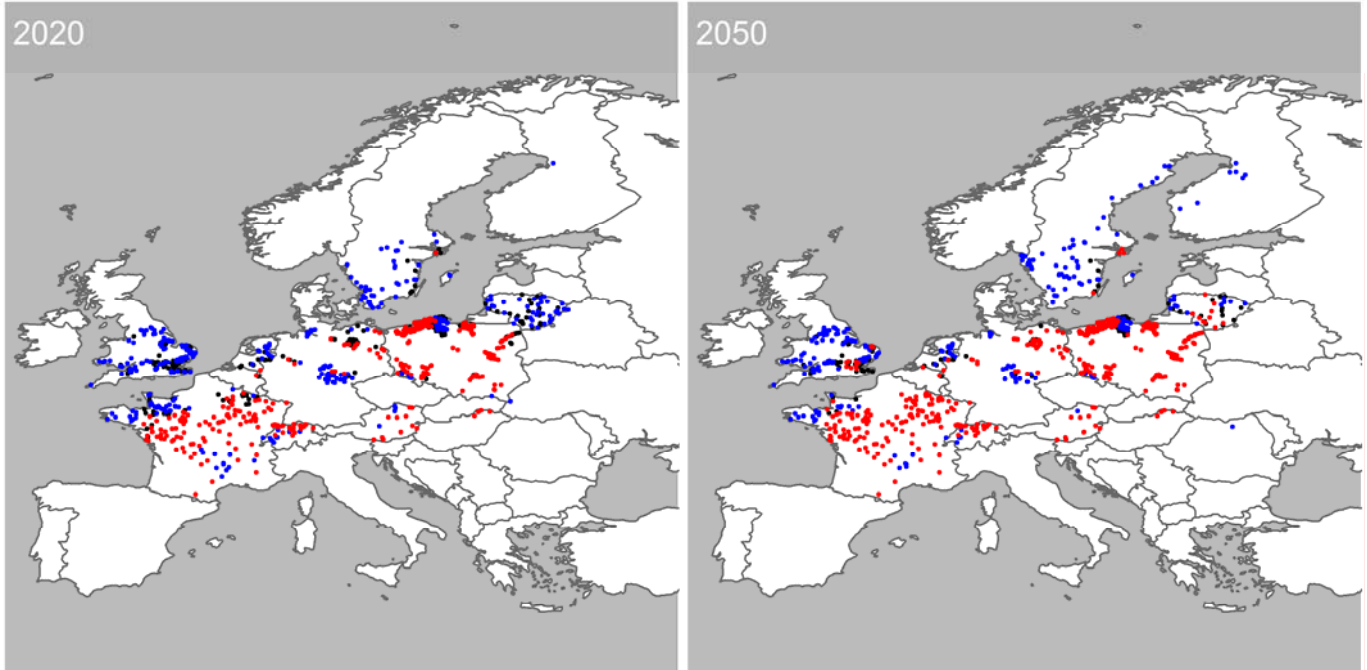


Fig. 18. Average forecasted distributions of the ninespine stickleback for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Rhodeus amarus

Along with the bleak, bitterling is the only other species that expands under climate change. Nevertheless, this species is also expected to become extinct in some Italian and Hungarian populations.

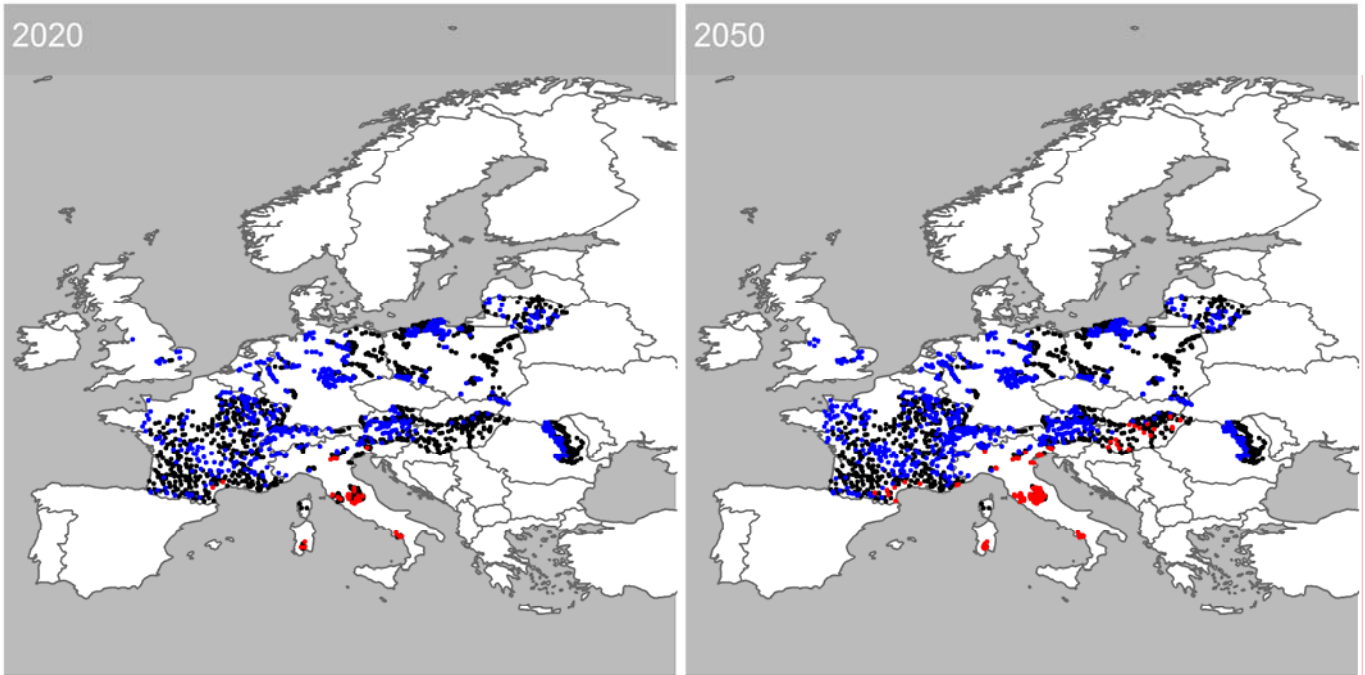


Fig. 19. Average forecasted distributions of the bitterling for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Rutilus rutilus

The pattern for roach is somewhat similar to that of perch, except that roach populations are expected to become extinct in the Iberian Peninsula and to be more stable in northern Europe.

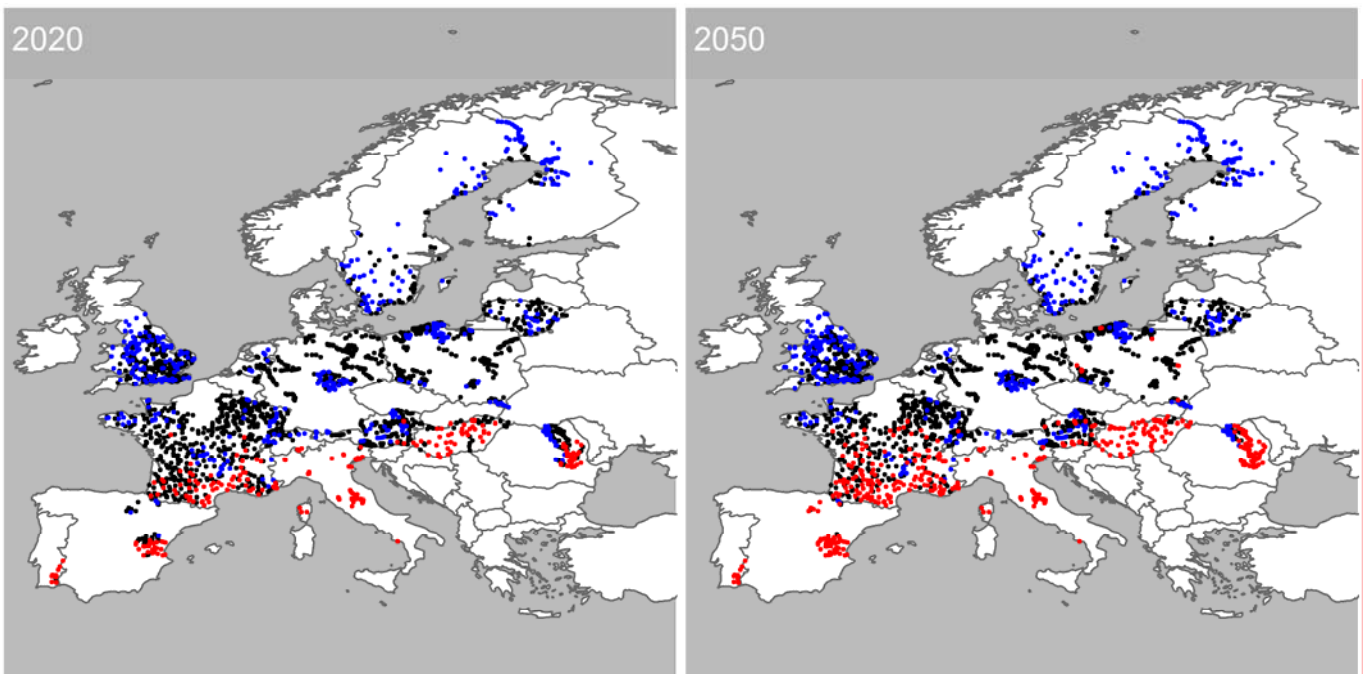


Fig. 20. Average forecasted distributions of the roach for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Salmo salar

Atlantic salmon is expected to face massive extinction all over Europe, maintaining itself mainly in the UK and some Scandinavian locations.

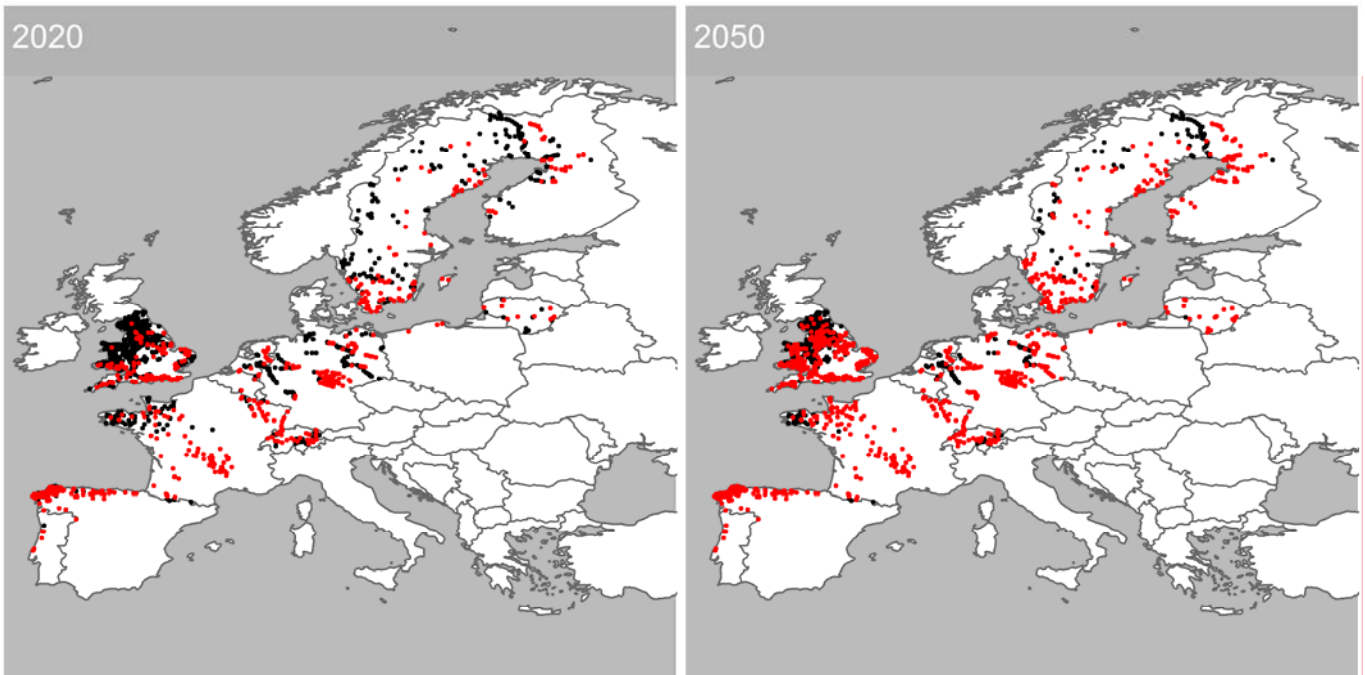


Fig. 21. Average forecasted distributions of the Atlantic salmon for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Salmo trutta

Like the salmon, brown trout is expected to experience population extinction all over Europe, but it is also expected to remain in more locations than salmon, especially in England, Scandinavia and in mountainous areas.

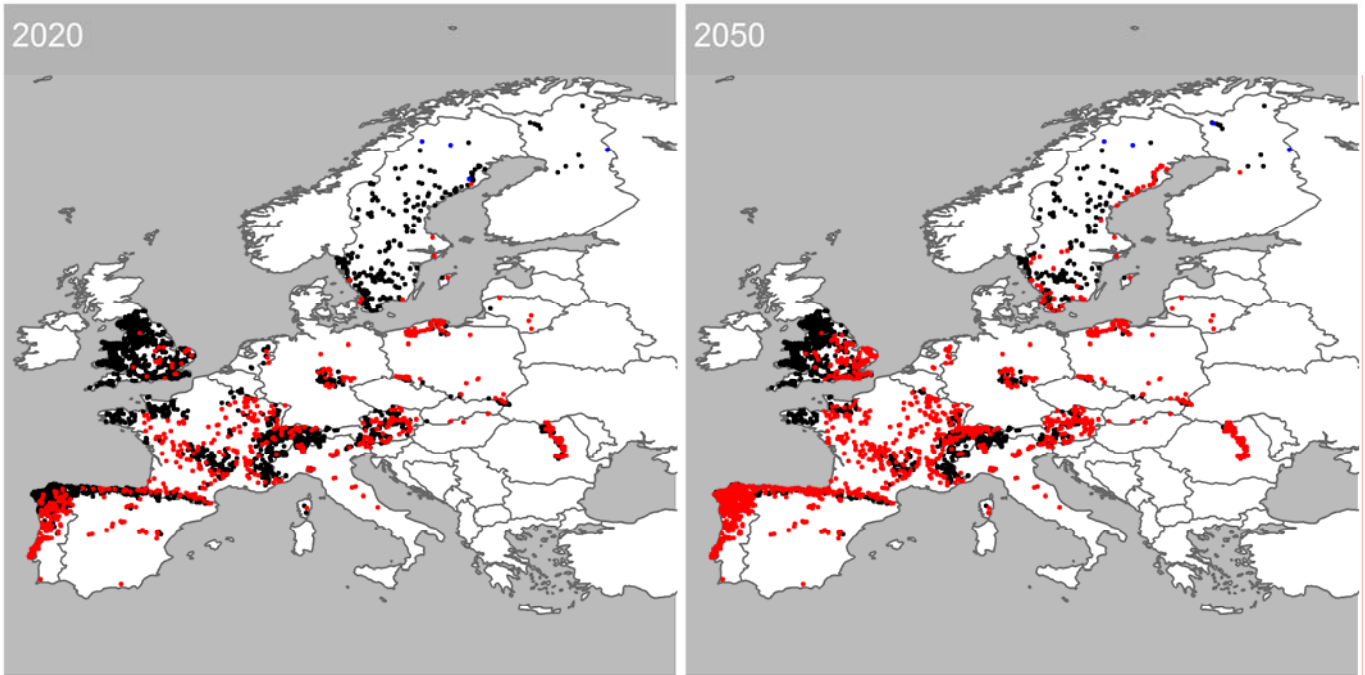


Fig. 22. Average forecasted distributions of the brown trout for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Telestes souffia

The distribution area of soufie is expected to shift towards the Alps, becoming extinct in numerous locations in Italy and in the Rhone catchment area; however, at the same time it is expected to occur newly in the north of France, Switzerland and Austria.

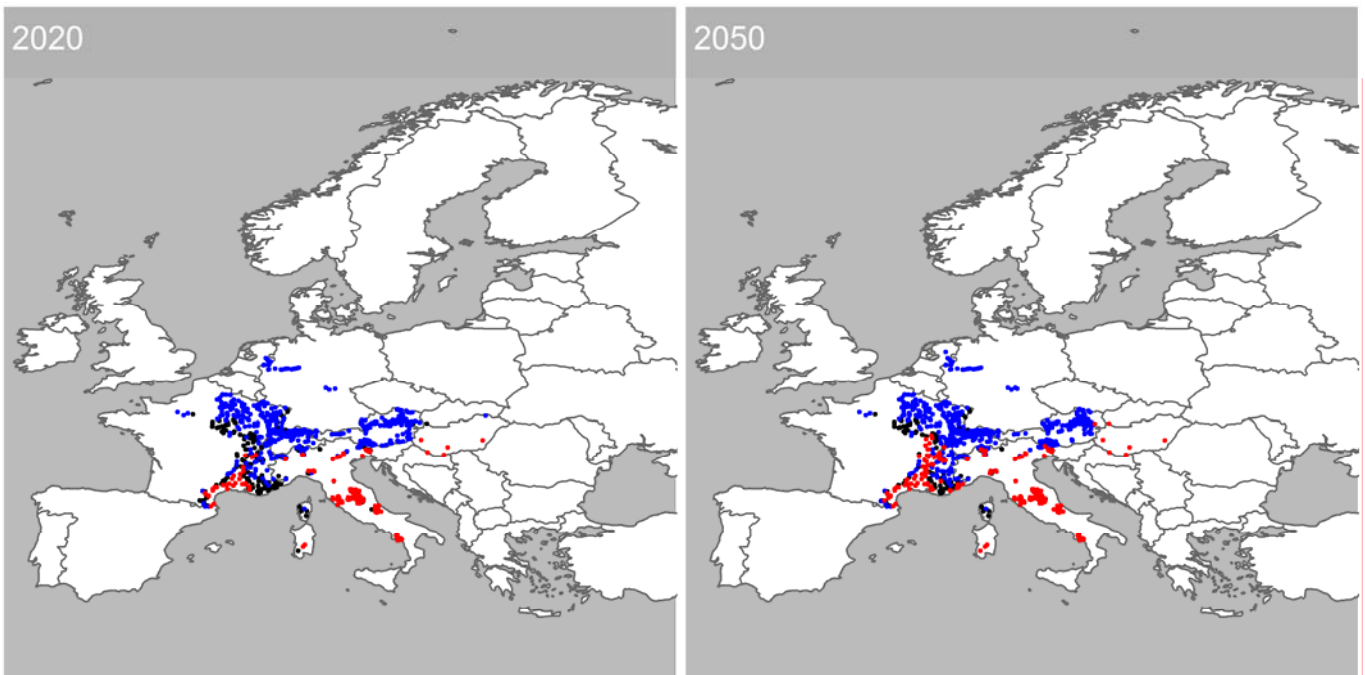


Fig. 23. Average forecasted distributions of the soufie for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Thymallus thymallus

Grayling, like the two salmonids, is expected to face massive extinctions, and to maintain itself in isolated regions of Europe, mainly in Scandinavia.

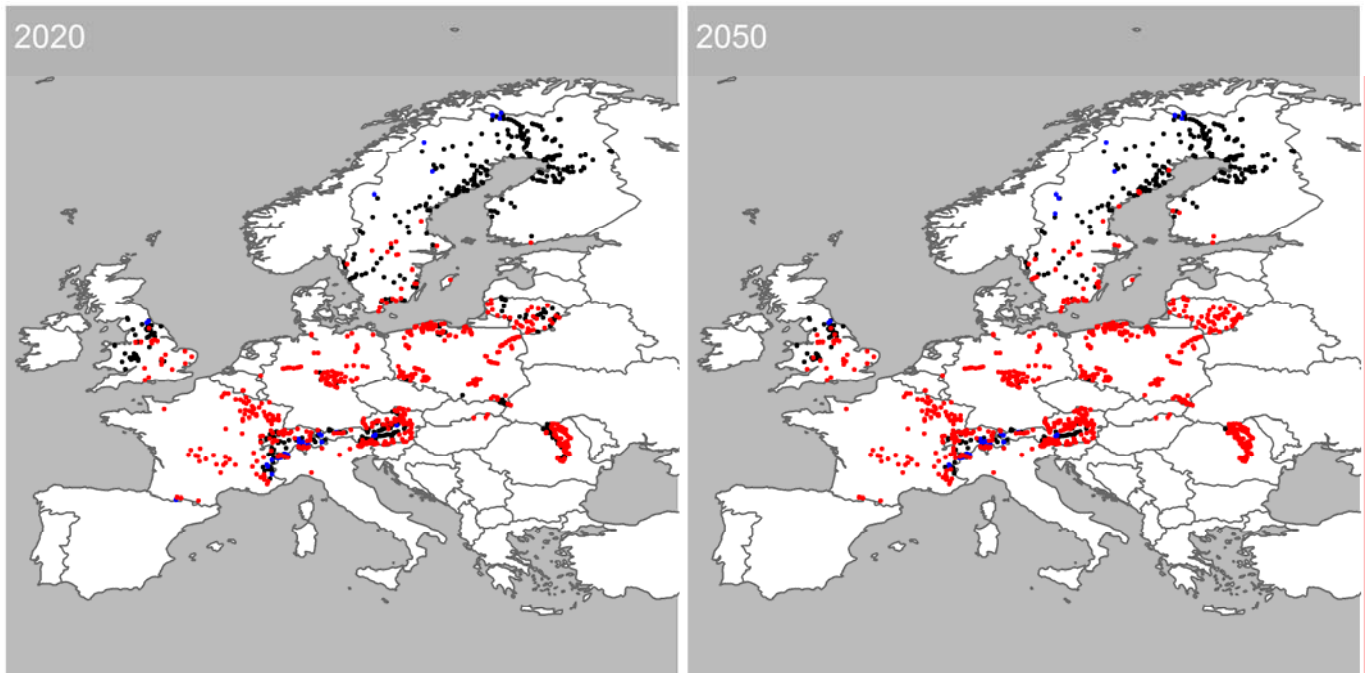


Fig. 24. Average forecasted distributions of the grayling for 2020–2030 (2020) and 2050–2060 (2050). Black dots indicate that the presence of this species is predicted for current environmental conditions and stable conditions in the future, blue dots indicate new colonization and red dots indicate population extinctions.

Climate change vs. human pressures

Comparisons between observed species presences/absences and predicted presences/absences for disturbed sites enable us to assess the effect of human pressure on species distributions. For all species, discrepancies are noted between the observed and predicted absences. The proportion of misclassification varies between species and between observed presences and absences (Table 8). For all species, except for brown trout, the number of misclassified absences is always greater than the number of misclassified presences. Nevertheless, for spiralin, sticklebacks, trout, soufie and grayling the proportion of misclassified absence is greater than for misclassified presence (Table 9).

The proportion of matching observed and predicted absences for the current environmental conditions is lower than model specificities for spiralin, bleak, eel, stone loach, barbel, nase, bullhead, northern pike, threespine stickleback, gudgeon, lamprey, chub, dace, burbot, perch, minnow, bitterling, roach, Atlantic salmon and soufie. For the other species the percentage of true-positive matches is approximately equal to model specificities. Therefore, for 20 species, we suspect that human pressures limit their presence in sites with suitable environmental conditions because the number of false presences exceeds the misclassification rate that could be expected.

The proportion of matching observed and predicted presences for the current environmental conditions is greater than model sensitivities for bleak, eel, nase, northern pike, dace, burbot, bitterling, roach and Atlantic salmon; however, the percentage of true-positive matching is lower than model sensitivities for spirlin, bullhead, threespine stickleback, European brook lamprey, ninespine stickleback and brown trout. For the other species, this percentage is approximately equal to model sensitivities. Therefore, for nine species we suppose that the environmental conditions found in the sites belonging to the “disturbed” data set limit the presence of these species. Indeed, for species such as bleak, the percentage of false absence is lower than what could be expected from the model misclassification rate (Table 9).

For climate change predictions, the results are globally comparable between scenarios for the two periods. Only the magnitudes of responses vary between scenarios. The divergent patterns of response to climate change between the four scenarios are observed for the 2050–2060 period. For bleak, dace, perch and ninespine stickleback, some scenarios predict presence or absence variation, while the patterns of response are quite stable for the other scenarios. For nase, northern pike and roach, inverse variations are predicted depending on the scenarios (Appendix 4).

The average result of the four scenarios, for each species and each period, is thus a good summary of the species responses to human pressures and climate change (Table 8). For bleak, barbel, chub, bitterling and soufie the proportion of well-classified presence decreases with climate change and is expected to be lower than model specificities for the 2050–2060 period. In contrast, European eel, stone loach, bullhead, northern pike, threespine stickleback, European brook lamprey, minnow, Atlantic salmon, brown trout and grayling display proportions of misclassified absences that increase with climate change and are expected to be higher than model specificities for the 2050–2060 period. Spirlin, nase, gudgeon, dace, burbot, perch and roach have a relatively stable proportion of well-classified absences, always lower than model specificities, while ninespine stickleback also has a stable proportion but it is always greater than its model specificity.

Concerning the proportion of misclassified presence, bleak, chub and bitterling are the only species presenting a decrease in false absence between the present and 2050–2060, with the values being lower than those expected by chance (compared with the model sensitivity). For pike, burbot, perch and roach the proportion of misclassified presences is quite stable over time and always greater than the model sensitivity, whereas for gudgeon the proportion of misclassified presences is always lower than its model sensitivity. All other species show an increase in the misclassification rates for their presences over time. Two groups can be distinguished from these results: those with proportions of well-classified presences that are always lower than the model's sensitivity values, such as barbel, and those for which the proportions of well-classified presences are greater than the model's sensitivity values for the current environmental conditions, for example the nase (Table 9 and Table 8).

Table 8: Comparison between observed species presence (Pres) or absence (Abs) in impacted sites and species projections for: current environmental conditions (Current) and 2020–2030 and 2050–2060 (averaged from the four scenarios, see Appendix 4).

Species		Current		2020–2030		2050–2060	
		Abs	Pres	Abs	Pres	Abs	Pres
<i>Alburnoides bipunctatus</i>	Abs	294	163	288.25	168.75	294	163
	Pres	27	42	30	39	38.5	30.5
<i>Alburnus alburnus</i>	Abs	592	412	469.25	534.75	370.75	633.25
	Pres	35	279	16	298	11.75	302.25
<i>Anguilla anguilla</i>	Abs	535	386	513.25	407.75	620.5	300.5
	Pres	67	401	49.75	418.25	92.5	375.5
<i>Barbatula barbatula</i>	Abs	281	395	302.5	373.5	334.5	341.5
	Pres	97	330	128.25	298.75	162.5	264.5
<i>Barbus barbus</i>	Abs	477	304	375.75	405.25	374.5	406.5
	Pres	21	189	20	190	40.75	169.25
<i>Chondrostoma nasus</i>	Abs	191	251	132	310	178.5	263.5
	Pres	3	65	14.25	53.75	37	31
<i>Cottus gobio</i>	Abs	377	472	620	229	726.5	122.5
	Pres	68	204	159	113	221.75	50.25
<i>Esox lucius</i>	Abs	604	403	643.25	363.75	708.5	298.5
	Pres	83	303	66.25	319.75	79.75	306.25
<i>Gasterosteus aculeatus</i>	Abs	602	262	674	190	740.75	123.25
	Pres	77	119	122.75	73.25	152.75	43.25
<i>Gobio gobio</i>	Abs	432	275	419.25	287.75	423.5	283.5
	Pres	135	413	130	418	154.25	393.75
<i>Lampetra planeri</i>	Abs	792	467	892.25	366.75	981	278
	Pres	26	45	38.25	32.75	48	23
<i>Leuciscus cephalus</i>	Abs	317	325	216	426	232	410
	Pres	115	392	58	449	71.25	435.75
<i>Leuciscus leuciscus</i>	Abs	404	346	351.25	398.75	414.25	335.75
	Pres	66	242	56.25	251.75	91	217
<i>Lota lota</i>	Abs	263	355	274.5	343.5	240.5	377.5
	Pres	13	75	15	73	13	75
<i>Perca fluviatilis</i>	Abs	269	348	243.5	373.5	296	321
	Pres	65	409	48	426	79.75	394.25
<i>Phoxinus phoxinus</i>	Abs	370	490	428	432	500.5	359.5
	Pres	76	222	134	164	171	127
<i>Pungitius pungitius</i>	Abs	737	154	700.25	190.75	767.25	123.75
	Pres	19	24	24.75	18.25	31.25	11.75
<i>Rhodeus amarus</i>	Abs	293	397	110	580	75.75	614.25
	Pres	12	84	3	93	1.25	94.75
<i>Rutilus rutilus</i>	Abs	267	246	220.5	292.5	250.75	262.25
	Pres	80	530	54	556	81.5	528.5
<i>Salmo salar</i>	Abs	533	447	722.75	257.25	862.75	117.25

	Pres	7	68	19.25	55.75	43.75	31.25
<i>Salmo trutta</i>	Abs	619	175	680.25	113.75	731.75	62.25
	Pres	218	379	326	271	407.25	189.75
<i>Telestes souffia</i>	Abs	242	55	145.25	151.75	165	132
	Pres	7	22	10.75	18.25	20.75	8.25
<i>Thymallus thymallus</i>	Abs	674	230	840.25	63.75	869.75	34.25
	Pres	36	83	92	27	106.25	12.75

Table 9: Proportion of matching current observed absences and predicted absences (Absence) and proportion of matching current observed presences and predicted presences (Presence), for current environmental conditions, for 2020–2030 and 2050–2060 (averaged from the four scenarios). Model specificities (% of absence correctly predicted) and sensitivities (% of presence correctly predicted) were added to establish comparisons with previous computed proportions.

Species	Absence			Spec	Presence			Sens
	Current	2020	2050		Current	2020	2050	
<i>Alburnoides bipunctatus</i>	0.6433	0.6307	0.6433	0.7818	0.6087	0.5652	0.4420	0.6883
<i>Alburnus alburnus</i>	0.5896	0.4674	0.3693	0.8263	0.8885	0.9490	0.9626	0.7847
<i>Anguilla anguilla</i>	0.5809	0.5573	0.6737	0.7465	0.8568	0.8937	0.8024	0.7450
<i>Barbatula barbatula</i>	0.4157	0.4475	0.4948	0.5104	0.7728	0.6996	0.6194	0.8033
<i>Barbus barbus</i>	0.6108	0.4811	0.4795	0.7952	0.9000	0.9048	0.8060	0.9227
<i>Chondrostoma nasus</i>	0.4321	0.2986	0.4038	0.7947	0.9559	0.7904	0.4559	0.8683
<i>Cottus gobio</i>	0.4441	0.7303	0.8557	0.5973	0.7500	0.4154	0.1847	0.8085
<i>Esox lucius</i>	0.5998	0.6388	0.7036	0.8072	0.7850	0.8284	0.7934	0.7175
<i>Gasterosteus aculeatus</i>	0.6968	0.7801	0.8573	0.7871	0.6071	0.3737	0.2207	0.8315
<i>Gobio gobio</i>	0.6110	0.5930	0.5990	0.7799	0.7536	0.7628	0.7185	0.7315
<i>Lampetra planeri</i>	0.6291	0.7087	0.7792	0.7405	0.6338	0.4613	0.3239	0.7140
<i>Leuciscus cephalus</i>	0.4938	0.3364	0.3614	0.6938	0.7732	0.8856	0.8595	0.7572
<i>Leuciscus leuciscus</i>	0.5387	0.4683	0.5523	0.8604	0.7857	0.8174	0.7045	0.7008
<i>Lota lota</i>	0.4256	0.4442	0.3892	0.7303	0.8523	0.8295	0.8523	0.7514
<i>Perca fluviatilis</i>	0.4360	0.3947	0.4797	0.6570	0.8629	0.8987	0.8318	0.8305
<i>Phoxinus phoxinus</i>	0.4302	0.4977	0.5820	0.5252	0.7450	0.5503	0.4262	0.7255
<i>Pungitius pungitius</i>	0.8272	0.7859	0.8611	0.8199	0.5581	0.4244	0.2733	0.7259
<i>Rhodeus amarus</i>	0.4246	0.1594	0.1098	0.6269	0.8750	0.9688	0.9870	0.8242
<i>Rutilus rutilus</i>	0.5205	0.4298	0.4888	0.7596	0.8689	0.9115	0.8664	0.7639
<i>Salmo salar</i>	0.5439	0.7375	0.8804	0.7756	0.9067	0.7433	0.4167	0.7995
<i>Salmo trutta</i>	0.7796	0.8567	0.9216	0.7784	0.6348	0.4539	0.3178	0.7508
<i>Telestes souffia</i>	0.8148	0.4891	0.5556	0.8408	0.7586	0.6293	0.2845	0.7695
<i>Thymallus thymallus</i>	0.7456	0.9295	0.9621	0.7409	0.6975	0.2269	0.1071	0.6976

Drift of reference conditions

For the 2020–2030 period, the different scenarios yield quite similar results (Table 10). The greatest departures from the current conditions are observed for the two intolerant metrics, O2INTOL and HINTOL, followed by RH, RHPAR and RICH. The two generalist metrics EURY and EUPAR present the slightest deviations from current environmental conditions, whatever the scenario (Table 10 & Fig. 25).

Table 10: Mean values and standard deviations (in brackets) of the deviation between standardized metrics computed for each scenario for 2020–2030 and the standardized metrics computed for the current environmental conditions. The average deviations of the four scenarios were also computed.

Metric	A1	A2	B1	B2	Average
RICH	0.151 (1.082)	0.144 (1.081)	0.150 (1.085)	0.153 (1.087)	0.150 (1.084)
O2INTOL	0.338 (1.039)	0.326 (1.038)	0.336 (1.041)	0.340 (1.041)	0.335 (1.040)
HINTOL	0.305 (1.064)	0.294 (1.062)	0.303 (1.063)	0.307 (1.064)	0.302 (1.063)
EURY	0.039 (1.033)	0.037 (1.033)	0.039 (1.035)	0.041 (1.036)	0.039 (1.034)
RH	0.235 (1.083)	0.224 (1.080)	0.233 (1.082)	0.237 (1.083)	0.232 (1.082)
EUPAR	0.091 (1.058)	0.088 (1.057)	0.095 (1.059)	0.098 (1.061)	0.093 (1.059)
RHPAR	0.194 (1.073)	0.186 (1.071)	0.193 (1.074)	0.196 (1.074)	0.192 (1.073)
LITH	0.143 (1.056)	0.135 (1.054)	0.141 (1.056)	0.143 (1.056)	0.141 (1.055)

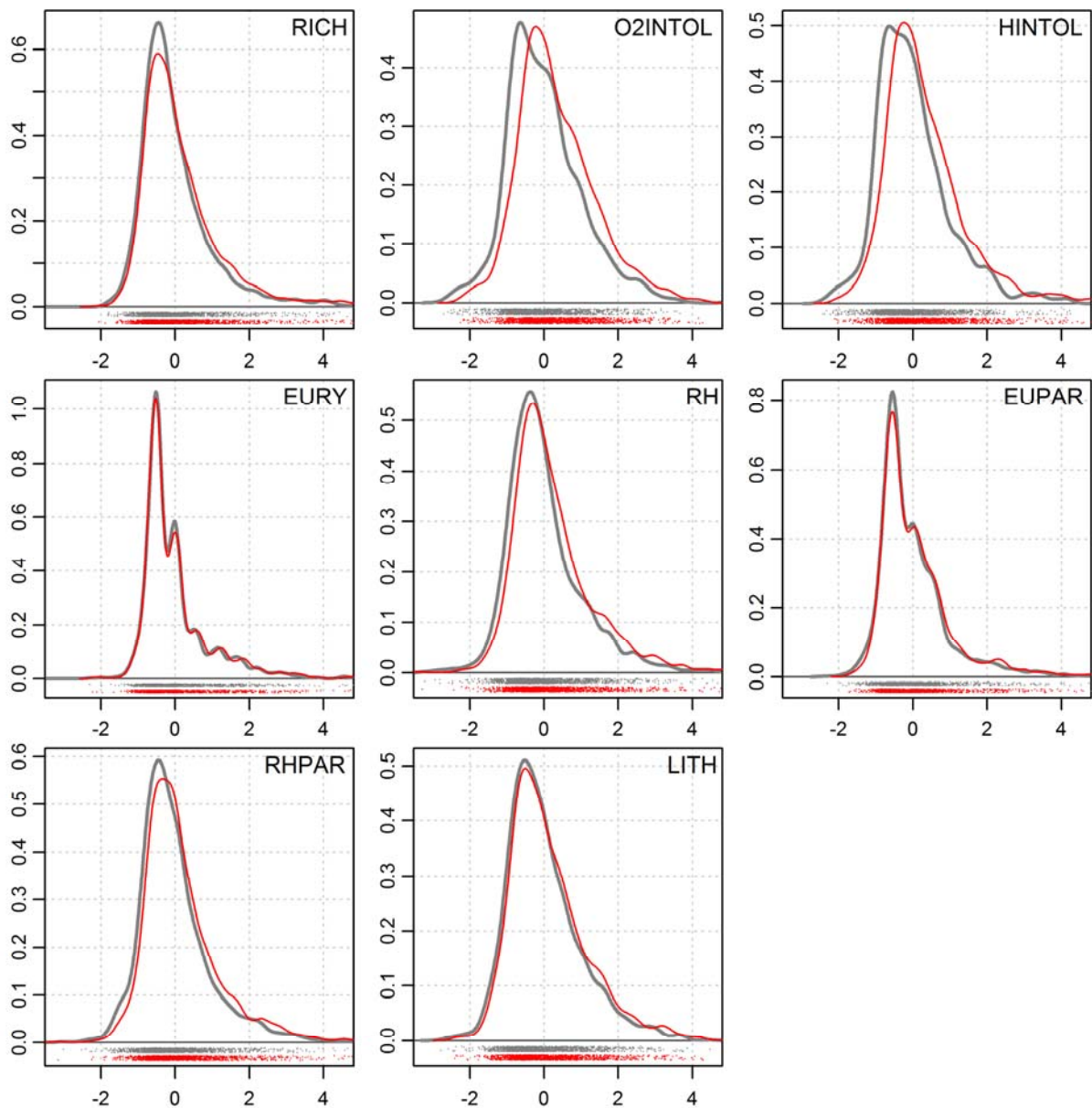


Fig. 25. Densities (kernel estimation) of the standardized metrics on the current environmental conditions (in grey) and for 2020–2030 (in red, average of the four scenarios).

The patterns observed for the 2050–2060 period are rather similar to those of the 2020–2030 period, but they are amplified (Table 11 & Fig. 26Fig.):

- All metrics display greater deviations from the current environmental conditions.
- The tolerant metrics, O2INTOL and HINTOL, have the greatest average deviations, ranging from 0.54 to 0.59.
- The lowest deviations are observed for the generalist metrics, EURY and EUPAR (average equal to 0.112 and 0.175, respectively).

The major difference concerns the high variability between the four scenarios. For all metrics, the greatest departures are observed for the A1F1 scenario, while the smallest deviations are observed for the B1 scenario.

Table 11: Mean values and standard deviations (in brackets) of the deviation between standardized metrics computed for each scenario for 2020–2030 and the standardized metrics computed for the current environmental conditions. The average deviations of the four scenarios were also computed.

Metric	A1	A2	B1	B2	Average
RICH	0.412 (1.146)	0.330 (1.128)	0.265 (1.113)	0.276 (1.117)	0.321 (1.125)
O2INTOL	0.729 (1.064)	0.606 (1.055)	0.505 (1.048)	0.520 (1.050)	0.590 (1.053)
HINTOL	0.660 (1.095)	0.551 (1.084)	0.459 (1.075)	0.473 (1.076)	0.536 (1.082)
EURY	0.152 (1.073)	0.116 (1.062)	0.088 (1.054)	0.094 (1.057)	0.112 (1.061)
RH	0.596 (1.150)	0.482 (1.128)	0.391 (1.110)	0.405 (1.114)	0.468 (1.124)
EUPAR	0.229 (1.104)	0.179 (1.090)	0.142 (1.079)	0.150 (1.083)	0.175 (1.088)
RHPAR	0.497 (1.127)	0.400 (1.111)	0.323 (1.100)	0.334 (1.100)	0.388 (1.109)
LITH	0.429 (1.114)	0.335 (1.096)	0.264 (1.082)	0.273 (1.083)	0.325 (1.093)

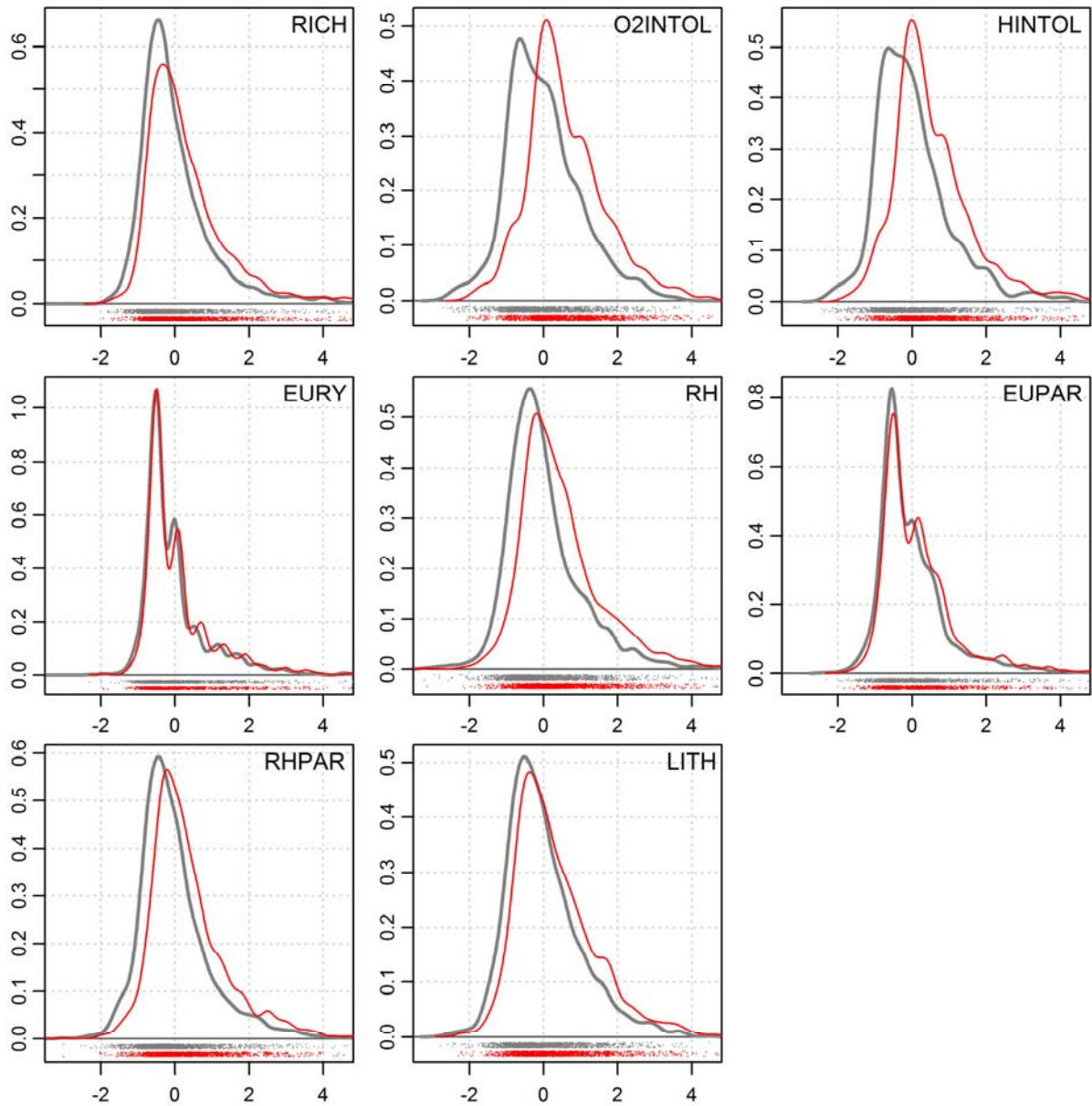


Fig. 26. Densities (kernel estimation) of the standardized metrics in the current environmental conditions (in grey) and for 2050–2060 (in red, average of the four scenarios).

The deviation between standardized metrics computed on current climate conditions and the climate forecasted for 2050–2060 will increase with increasing temperature deviation as shown in Fig. 27. A similar pattern is observed along the drainage area, with deviations increasing along the longitudinal gradient (Fig. 28). Deviations increase slightly along the deviations of thermal amplitude and stream power (Fig. 29 and Fig. 30).

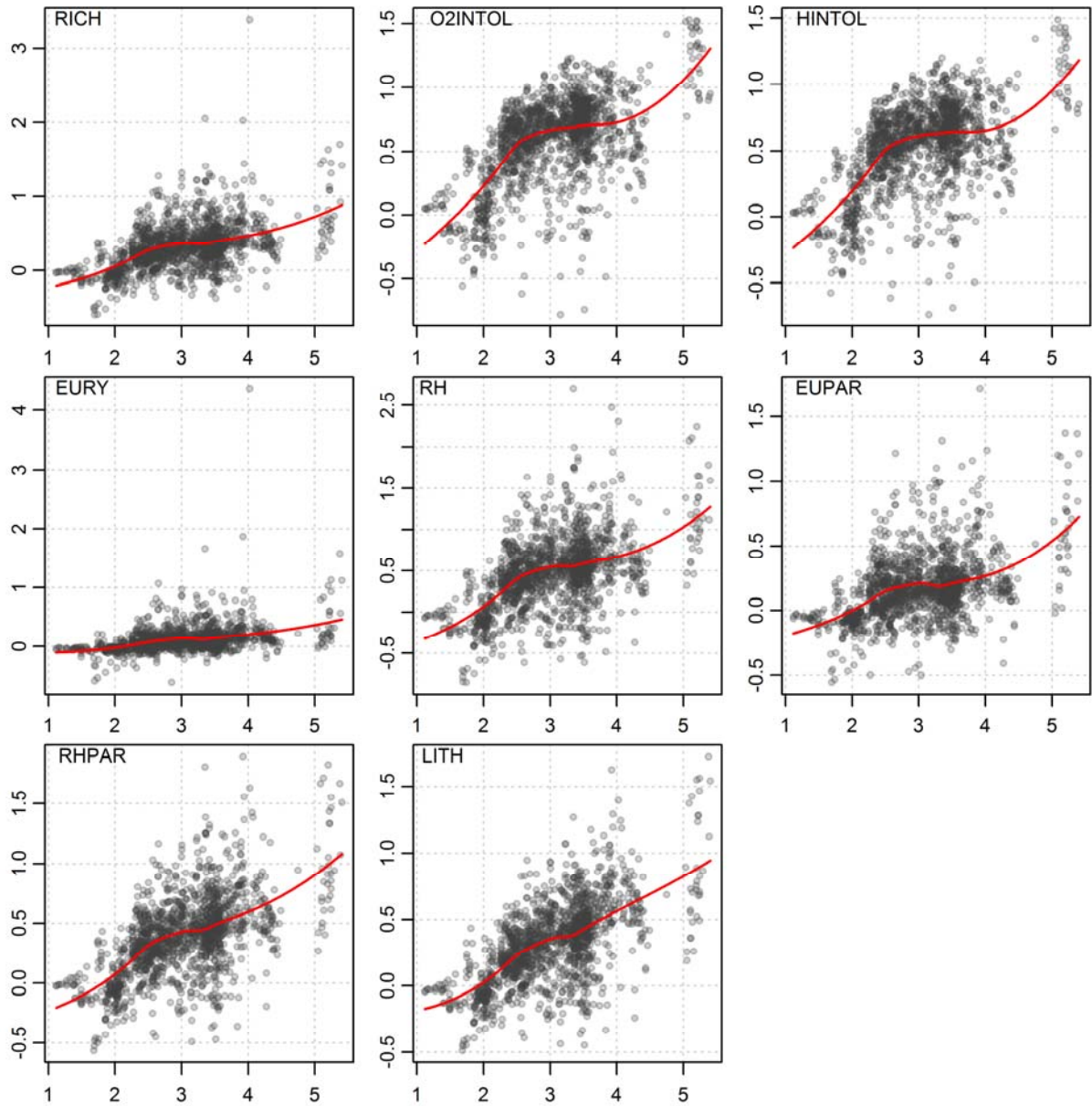


Fig. 27: Relationships between average metric deviations (y-axis) and mean air temperature deviations (x-axis) of the current climatic conditions and the climatic conditions projected for 2050–2060. Tendencies are represented by Loess curves (in red).

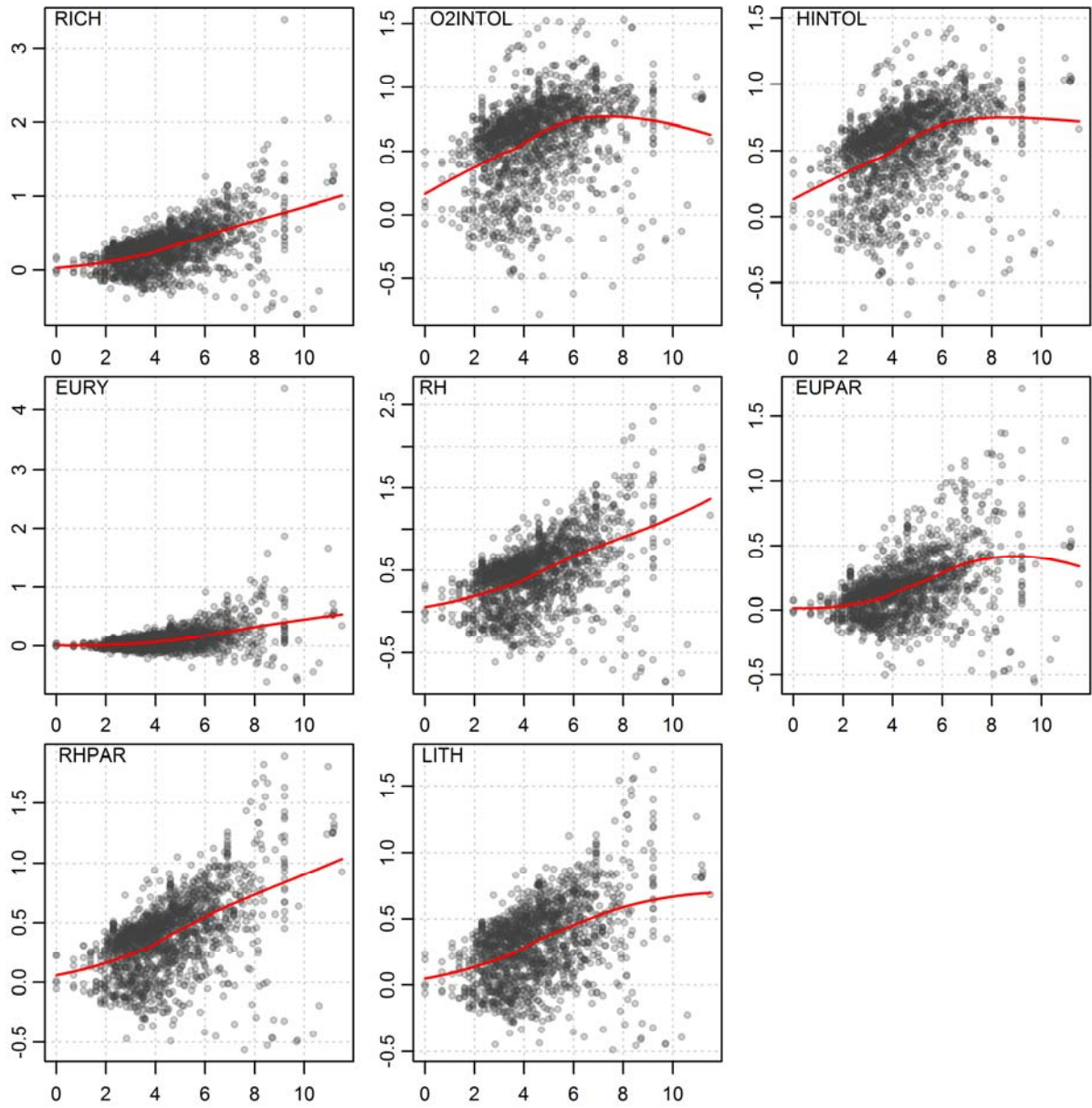


Fig. 28: Relationships between average metric deviations of the current climatic conditions and the climatic conditions projected for 2050–2060 (y-axis), and the upstream drainage area (log-transformed) (x-axis). Trends are represented by Loess curves (in red).

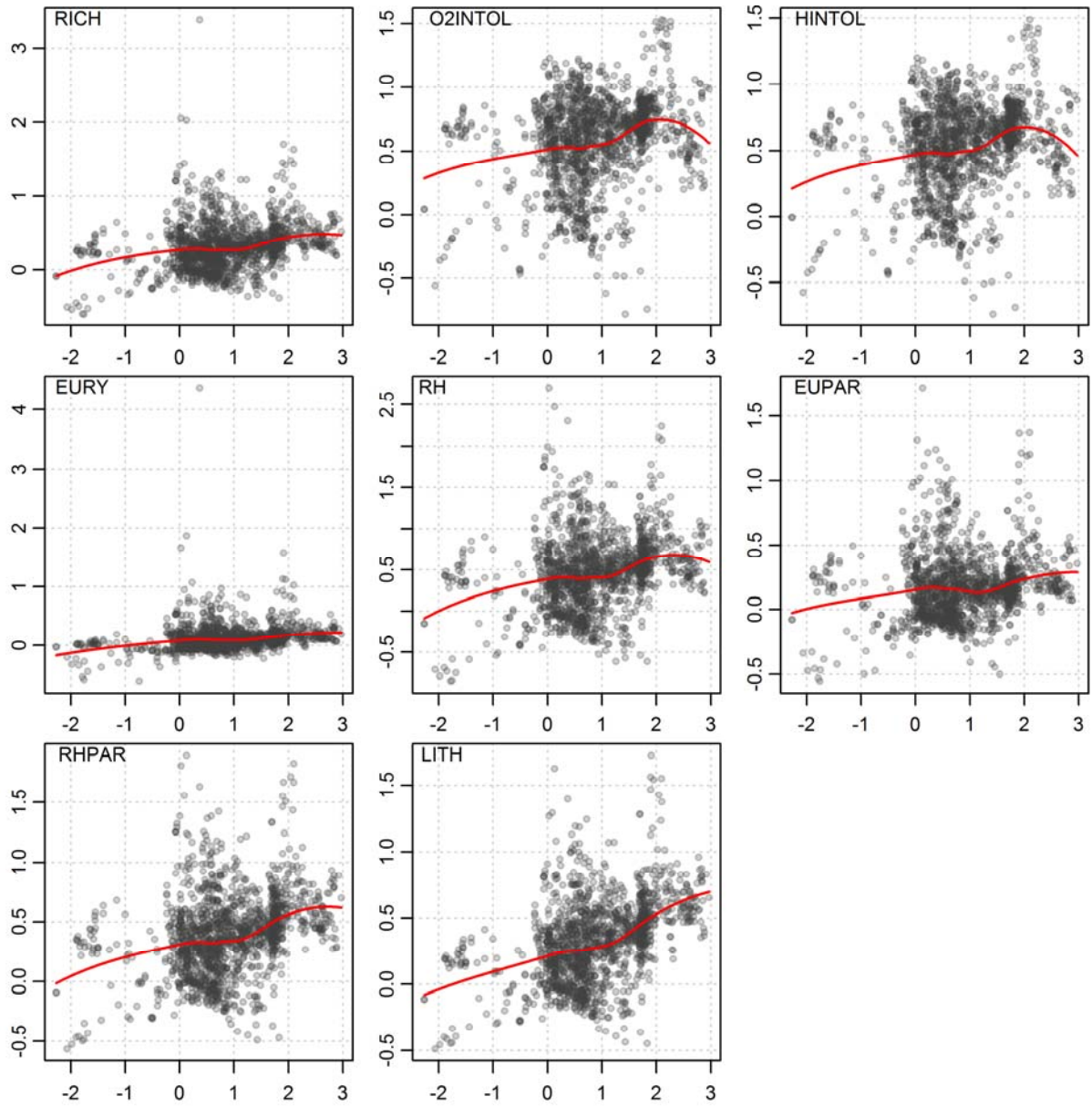


Fig. 29: Relationships between average metric deviations (y-axis) and thermal amplitude deviations (x-axis) of the current climatic conditions and the climatic conditions projected for 2050–2060. Tendencies are represented by Loess curves (in red).

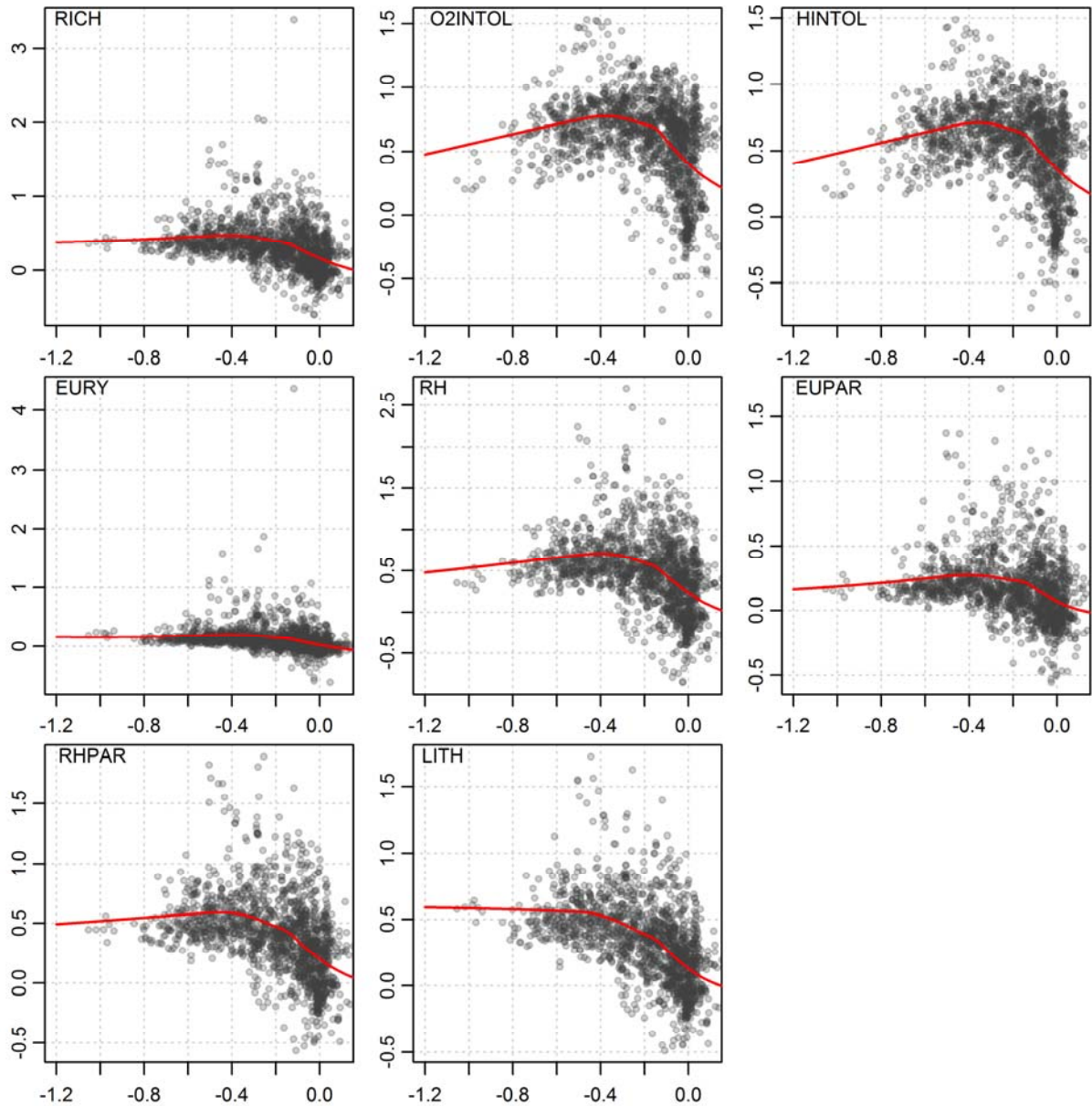


Fig. 30: Relationships between average metric deviations (y-axis) and power deviations (x-axis) of the current climatic conditions and the climatic conditions projected for 2050–2060. Tendencies are represented by Loess curves (in red; one extreme value was removed for better clarity).

Uncertainty

Uncertainty associated with species distribution projections

For the 2020–2030 period, whatever the scenario, only six species display a common pattern with the lower and upper limits of the CIs. Two species have distribution areas in expansion (difference between local new occurrences and local new extinctions): barbel and chub. In contrast, bullhead, Atlantic salmon, brown trout and grayling are expected to experience species distribution contraction with both the lower and upper limits of the CIs (Table 12).

For the 17 other species, the patterns are unclear, and they are expected to contract or expand depending on the limit of the CIs used to derive the future occurrences of species (Table 12). Some divergence can also be observed between species and scenarios. For instance, for

bitterling, with the lower limits, an expansion in its distribution area is expected with the A1F1 scenario and it is predicted to experience less suitable locations with the three other scenarios (Appendix 5).

Table 12: Number of locations that would experiences local extinction (New absence) or local occurrence (New presence), with either the lower (low) or the upper (up) limits of the confidence intervals, for 2020–2030. Values were averaged from the four scenarios (Appendix 5).

	New absence		New presence	
	low	up	low	up
<i>Alburnoides bipunctatus</i>	385.5	40.75	13	442.75
<i>Alburnus alburnus</i>	70.75	0	64.5	913
<i>Anguilla anguilla</i>	154	40.25	109.5	395
<i>Barbatula barbatula</i>	525.25	206.25	103.25	432.5
<i>Barbus barbus</i>	169.25	69.5	190.25	585.75
<i>Chondrostoma nasus</i>	367	74.75	51	547.75
<i>Cottus gobio</i>	1321.25	817	53.75	220
<i>Esox lucius</i>	361	115.25	46.75	441.25
<i>Gasterosteus aculeatus</i>	591.25	224.75	26.25	335.25
<i>Gobio gobio</i>	305.25	109.25	158	549.25
<i>Lampetra planeri</i>	601	199	10.25	216.5
<i>Leuciscus cephalus</i>	262.5	135.75	486.5	852
<i>Leuciscus leuciscus</i>	248	103.5	99	582.25
<i>Lota lota</i>	504.5	0	0	566.25
<i>Perca fluviatilis</i>	354.5	197.5	207.75	591.75
<i>Phoxinus phoxinus</i>	721.5	267.25	34.25	313.25
<i>Pungitius pungitius</i>	363.5	226.5	115.25	552
<i>Rhodeus amarus</i>	218	2	129	913
<i>Rutilus rutilus</i>	307.25	139.75	242	679.5
<i>Salmo salar</i>	643.75	444.5	0	0
<i>Salmo trutta</i>	959.25	367.25	0	26.5
<i>Telestes souffia</i>	205.25	88.25	97.25	726.5
<i>Thymallus thymallus</i>	704	350.5	11	94.75

For the 2050–2050 period, the patterns are more marked than for 2020–2030. Bleak, chub and bitterling are the only three species that are expected to experience an expansion in their distribution areas, both with the lower and upper limits of the CIs and for all scenarios considered (Appendix 5). In addition to bullhead, Atlantic salmon, brown trout and grayling, European eel, stone loach, threespine stickleback, European brook lamprey and minnow are expected to display distribution area contractions (Table 13). However, the eel is not expected to have a rapid extinction in the B1 scenario with the upper limits of the CIs (Appendix 5). For the other species, including barbel, the patterns are unclear (Table 13).

Table 13: Number of locations that would experiences local extinction (New absence) or local occurrence (New presence), with either the lower (low) or the upper (up) limits of the confidence intervals, for 2050–2060. Values were averaged from the four scenarios (Appendix 5).

	New absence		New presence	
	low	up	low	up
<i>Alburnoides bipunctatus</i>	417	145	31.75	397.75
<i>Alburnus alburnus</i>	26.5	0.25	364.25	1237.25
<i>Anguilla anguilla</i>	473.75	225.75	8.25	176
<i>Barbatula barbatula</i>	851.75	576.75	176.5	442.75
<i>Barbus barbus</i>	325.5	186.75	267.5	598.75
<i>Chondrostoma nasus</i>	527.5	208.25	84.25	487.25
<i>Cottus gobio</i>	1695.25	1336.5	78.25	215.75
<i>Esox lucius</i>	561.75	315.75	72	399.75
<i>Gasterosteus aculeatus</i>	718.5	462.25	42.25	294.25
<i>Gobio gobio</i>	484.75	354.5	299	570
<i>Lampetra planeri</i>	844.5	497.75	17.75	181.25
<i>Leuciscus cephalus</i>	502.25	392.75	660	985.25
<i>Leuciscus leuciscus</i>	431.75	257.5	150	506.5
<i>Lota lota</i>	398.5	0	0	607.5
<i>Perca fluviatilis</i>	650.5	438.5	264.5	609
<i>Phoxinus phoxinus</i>	1102.5	702.5	62	304.75
<i>Pungitius pungitius</i>	439.25	365.75	88.5	453
<i>Rhodeus amarus</i>	217.25	37.25	477.75	1005.75
<i>Rutilus rutilus</i>	525.25	347.5	306.75	669.5
<i>Salmo salar</i>	987.75	832.75	0	0
<i>Salmo trutta</i>	1511	1024.5	0	11
<i>Telestes souffia</i>	232	147.25	175.5	626.5
<i>Thymallus thymallus</i>	768.25	574	17.75	77.75

Discussion

Species distribution

Not surprisingly, projections from the species distribution models state that climate change will greatly affect the distribution of European fish species (Xenopoulos et al. 2005; Buisson et al. 2008b; Daufresne et al. 2009). These changes differ depending on the gas emission scenarios (Buisson et al. 2008b; Buisson et al. 2010), but all scenarios provide the same general pattern, only the magnitudes of response differ. On the other hand, the species responses to climate change will be highly variable.

Among the 23 species, cold- and cool-water species (salmonids and rhithronic species) will be the most negatively affected by climate change. Compared to the current situation, suitable climatic conditions for their presence would be greatly limited (Isaak et al. 2011) and lead to very high extinction rates of local populations. This is also true for most of the rhithronic species

often associated with the brown trout: bullhead, stone loach, minnow and European brook lamprey (Huet 1954).

Other species such as chub, dace and soufie will experience both local extinctions and potential colonizations (new locations with climatic conditions becoming suitable). For these species, we will observe a shift of their distribution at the catchment scale, and over their distribution areas. Compared to salmonids, these species are found in warmer temperatures (Logez et al. accepted). The greatest expansions will probably be observed for bleak and bitterling. The rise in observed (Webb & Nobilis 1995; Webb 1996; Webb & Nobilis 2007) temperature and expected temperature with global change (IPCC 2007) will generate suitable conditions in numerous locations with a current unsuitable environment. As bitterling is an ostracophilic species (Smith et al. 2004; Van Damme et al. 2007), its expansion would be associated with the distribution shift of the freshwater mussels in which this species spawns.

All these results follow the thermal preferences of these 23 fish species (Jobling 1981; Mann 1996; Küttel et al. 2002; Tissot & Souchon 2010). Species preferring cold- to cool-water temperatures will be more sensitive to global changes, even if they are relatively eurythermal such as brown trout (Logez et al. 2011), while species preferring warmer temperatures and with large thermal ranges will be less affected by climate change and may even be favoured by it. Climate change will hasten the species turnover (Buisson et al. 2008b) and modify the composition of the species assemblage (Xenopoulos et al. 2005; Graham & Harrod 2009).

These results emphasize that water managers need to take into account the potential effect of climate change. As stated by Rieman and Isaak (2010), the amount of money available for river restorations is limited and restoration measures should be prioritized according to their probability of success. Indeed, if the effect of climate change overrides the effect of human pressures that prevented fish populations to develop and maintain themselves, then whatever restoration measures are taken into account will be inefficient with regard to the underlying objectives of the restoration projects. For instance, human pressures were found to limit the distribution of Atlantic salmon. This species was observed to occur in fewer locations than expected from the environmental conditions. From a conservation point of view, and because of its patrimonial status and economic interest, managers may be tempted to make significant financial efforts towards restoring streams to support salmon populations. Nevertheless, in the northern part of Spain, along the Atlantic coast, almost all locations sampled are expected to have unsuitable environmental conditions for this species by 2020–2030 and 2050–2060. Therefore, in this area the restoration effort should be focussed on species other than Atlantic salmon, regardless of the perception of the general public. It is necessary to assess the vulnerability of local populations to climate change (Rieman and Isaak 2010). If the effects of climatic and anthropogenic factors are more balanced, the benefits of restoration measures would be notable over a period of time and then become inefficient if, for instance, temperature still continues to rise. Therefore, it would be worthwhile to integrate a concept of “durability” in restoration programmes. Durability could be defined as the time period that restoration measures would be successful considering the ecological objectives.

Even if species distributions models (SDMs) have clear limits (Sinclair et al. 2010), they can be useful decision support tools that could help to prioritize restoration actions. They could provide a valuable and relevant estimation of the vulnerability of populations to climate change and thus of the ecological success that could be expected from restoration measures. SDMs could offer information on the suitability of the habitat conditions for a given species in absence of pressures. Nevertheless, additional investigations are needed to better understand the relative influence of environmental and anthropogenic stressors on species occurrences and thus to better assess the reliability of restoration measures.

Climate change vs. human pressures

Bullhead, Atlantic salmon, grayling, threespine stickleback, European brook lamprey, minnow and brown trout are particularly affected by climate change. The percentage of matching between observed and predicted absences increases over time, exceeding model specificities. This suggests that with climate change the environmental conditions will become unsuitable, leading to a proportion of misclassified absences lower than expected by chance. At the same time the proportion of matching presences in these species decreases, and is transformed into absences by the climate change. Therefore, for these species we expect that the effect of climate change on future species distribution will override the effect of human pressures for the areas belonging to the disturbed sites data set. This is even true for bullhead, threespine stickleback, lamprey, minnow and Atlantic salmon, for which effects of human pressures were visible by limiting their occurrence in disturbed sites (proportion of well-classified presences lower than model specificities). Overall, these results are consistent with the forecasted distributions of these species. Indeed, cold- and cool-species distributions would be soundly impacted by climate change, especially because of the raising temperature. Therefore, it is not surprising that for these species, climate change is expected to have a greater impact than human pressures.

As with these seven species, eel has a proportion of well-classified presences that decreases and a proportion of well-classified absences that increases over time, but to a lesser extent. Combined with the fact that its proportion of false presences exceeds what could be expected by chance, the future distribution of eel should be comparably influenced by climate change and human pressures.

The distribution of stone loach should be influenced by both human pressures and climate change, since this species has the same patterns of variation in misclassification rates as those observed for eel.

Bleak, chub and bitterling are the only species whose proportions of matching absences increase and proportions of matching presences decrease with climate change scenarios. Therefore, for these species we should expect that climate change would greatly affect their distributions by increasing the number of sites that would have suitable environmental conditions for them. We could consider that the expected expansion of the distribution of these species will depend on their ability to cope with human pressures, as they will be able to occur in sites with moderate to high levels of pressures.

For the barbel, the proportion of false presences is high and decreases moderately over time, whereas the proportion of false absences is low but increases over time. This indicates that the occurrence of this species could be limited by human pressures in several sites of the impacted data set. The expected decrease of the proportion of matching absences and matching presences with climate change suggests that the distribution of barbel will change, and that barbel will be more susceptible to human impacts as the proportion of distributed sites with suitable environmental conditions for this species will increase.

Soufie presents the same pattern, but the proportion of well-classified absences is close to the model specificity and could thus be considered as independent of anthropogenic alterations. Moreover, the magnitude of responses for this species is far greater than the patterns observed for barbel. All these results suggest that for soufie, climate change will be the major factor affecting its future distribution.

For nase, dace and spirin, the proportion of well-classified absences are relatively constant over time and lower than their model specificities. In parallel, the proportion of well-classified presences decreases over time. For nase this latest proportion exceeds model sensitivity for the current environmental conditions and decreases steadily over time. Therefore, nase would probably be more affected by climate change, in addition to human pressure effects. These results must be interpreted with caution because this species was caught in a small number of disturbed sites. For dace and spirin, the effect of human pressures should be more important than climate change.

Gudgeon, burbot, perch and roach have constant misclassification rates for both absences and presences over time. For the current environmental conditions, all these species have a proportion of well-classified presences greater than what could be expected from model sensitivities, suggesting that environment is a limiting factor. All species have a proportion of well-classified absences lower than model specificities, suggesting that human pressures limit their occurrences in several disturbed sites. These results tend to demonstrate that human pressures would limit their potential future distribution.

For the current environmental conditions, the proportion of matching absences for the ninespine stickleback is similar to the model specificity and is constant over time, suggesting that this species is not affected by human pressures. However, the proportion of misclassified presences increases with climate change, suggesting that climate will be the major factor influencing ninespine stickleback distributions in the future.

The proportion of misclassified absences for pike is lower than the model specificity for the current environmental conditions, and it increases over time. This suggests that this species is negatively affected by human pressures and that its future distribution will be influenced by anthropogenic pressures and climate change.

As previously discussed, further work is necessary to better understand the role of the environment and human pressures on species occurrence and, more specifically, to better disentangle the hierarchy of their effects and their interactions. Indeed, in this study we were

only able to coarsely assess which factor would have the greatest effect on species occurrences, but we were not able to quantify this effect.

Drift of reference conditions

Comparisons of the means of the standardized metrics computed on the current environmental conditions and on forecasted climatic conditions show that the functional structure of fish assemblages will change. The drift of reference conditions will be related to the strength of changes in climatic conditions. On average, we expect a lower representation of the eight trait categories in the calibration sites, but climate change will not affect the different functional trait categories in a similar way. The two metrics based on species intolerance would be more affected than the others.

All these results strongly suggest that it would be necessary to revise the multi-metric indices based on functional traits (Pont et al. 2006; Pont et al. 2007; Bady et al. 2009) for assessing the ecological conditions of rivers in the future. Indices such as the European Fish Index (EFI) or its new version (EFI+) should be valid by 2020–2030, on the Water Framework Directive horizon, as the differences between standardized metrics are not so marked. Over this period, the use of these indices in their present form should probably be avoided.

From a technical point of view, the process of standardization of the metric transforming the deviation between observed and expected values to metric scores (Hering et al. 2006; Pont et al. 2006; Pont et al. 2007; Logez & Pont 2011a) would no longer be consistent. Whatever the type of transformation — normalization (Pont et al. 2006), min–max (Hering et al. 2006) — the different elements necessary for the transformation were computed on the calibration data set for current environmental conditions. Not modifying these values would lead to over- or underestimation of the metric departure from reference conditions and provide an erroneous diagnosis of river conditions for reference and impaired sites.

From a theoretical point of view, the metrics selected for integration in a multi-metric index must be representative of the region where they are applied (species pool, environment and pressures) and sensitive to human pressures (Hughes et al. 1998; Karr & Chu 1999, 2000; Hering et al. 2006; Pont et al. 2007; Pont et al. 2009).

The substantial average deviations observed between standardized metrics imply that climate change will bring an important turnover of the functional structure of assemblages. The representation of several metrics will be limited in fish assemblages, which would limit their value as future bioassessment tools. Including a metric with little or no representation in a given region would limit the discrimination between sites (Harris & Silveira 1999). Therefore, it would be necessary to take into account these functional changes by revising the set of potential metrics that could be integrated in a final index computation and in this way develop new multi-metric indices. These new indices would have to reflect the new functional structure of fish assemblages.

Among the eight metrics studied here, two would be particularly sensitive to climate change: O2INTOL and HINTOL. These two metrics, related to the intolerance of fish species, are

abundant and widespread in small to medium streams and/or in cold- to cool-water streams (Logez et al. 2011; Logez et al. in revision). Climate change will diminish their importance in these fish assemblages thereby limiting their use, although these metrics are currently widely used in bioindication studies (Bady et al. 2009; Logez & Pont 2011a). Indeed, these metrics derived from species intolerance are often among the most sensitive metrics to human pressures (Fausch et al. 1984; Oberdorff & Hughes 1992; Simon & Lyons 1995; Joy & Death 2004; Melcher et al. 2007; Vehanen et al. 2010).

It is thus possible that climate change will limit the overall sensitivity of fish assemblages to anthropogenic pressures and promote more intolerant and/or generalist species. Developing indices based on a species pool mainly composed of generalist or resistant species is a real challenge, as experienced in Mediterranean regions (Hermoso et al. 2010). Owing to the harsh environmental conditions (Gasith & Resh 1999) in which these species have evolved, numerous Mediterranean fish species are generalist or tolerant species (Vila-Gispert et al. 2002b; Clavero et al. 2004) limiting the development of multi-metric indices for these regions (Hermoso et al. 2010). For instance, the European Fish Index is poorly sensitive to human degradations in the Iberian Peninsula (Pont et al. 2007). The results of this study suggest that climate change would complicate the development of a multi-metric index in the future. This will also depend on the species that will colonize European freshwater systems and on their characteristics.

If the wish to harmonize national riverine fish indices is maintained after 2027 (end of implementation of the Water Framework Directive), these results suggest that the common index used in the inter-calibration process should also be revised. Indeed, this index is the average of two metrics derived from the sensitivity to low concentration of oxygen and to habitat degradation (Pont 2011). These results indicate that the utility of this index would be limited. One could imagine that the inter-calibration process would have to be repeated after the end of the WFD.

All the issues discussed here concerned indices based on a site-specific approach (Roset et al. 2007) and on the reference condition approach (Bailey et al. 1998). Consequences of climate change on bioassessment tools are not limited to the use of functional traits. We are convinced that indices that compare observed assemblage compositions with a theoretical composition in absence of pressures, based or not on a type-specific approach (Melcher et al. 2007) such as the successful RIVPACS (Simpson & Norris 2000; Wright et al. 2000), would face the same problems. Species distribution will be greatly modified by climate change, and thus also the assemblage composition of the reference sites. If the theoretical assemblages are not revised, this will lead to inconsistent comparisons between future observed and expected assemblages in the absence of pressures.

Uncertainty

The uncertainty associated with the probability of species occurrences was highly variable between species. For some species, the uncertainty strongly overcomes the potential effect of climate change on their future distributions. Conclusions concerning these species should thus be made with caution. Depending on which limit of the confidence intervals is considered as the

future probability of presence, we could even observe inverse patterns of response. For these species, conclusions are blurred by the uncertainty of the model prediction. Other species have clear patterns of response to the modification of the climatic conditions, but the magnitude of the responses could be highly variable.

Some authors, such as Grenouillet and Buisson, worked on other sources of uncertainty such as climatic scenarios or statistical methods (Buisson et al. 2010; Grenouillet et al. 2011), but few authors assessed the uncertainty associated with the fitted relationships between species occurrences and environmental conditions. Our results demonstrate that to forecast the future species distributions, uncertainty associated with model prediction should be taken into account so as to have an estimation of the reliability of the projections. The uncertainty values could reinforce the decisions of water managers to restore a given river or not depending on the reliability of the projections.

All the conclusions are indivisible from the data sets used in this study. These data sets could not reflect the complete reality of European rivers, either by encompassing only a fraction of the environment (Tockner et al. 2009), a fraction of the fish species that occur in Europe (Banarescu 1992; Kottelat & Freyhof 2007), or a fraction of the human pressures that stress European rivers. All conclusions are driven from samples taken at a very local scale (river segment), and it would be interesting to project species distribution over an extensive European river network to assess the potential change over all lotic European freshwater systems.

In conclusion, climate change will affect both species distribution and assemblage functional structure. These alterations will increase as the changes in climatic conditions become more consequential. Climate change would have substantial consequences on restoration plans of rivers and on the use of multi-metric indices based on functional traits. Nevertheless, the strong uncertainty associated with the results forces us to be cautious concerning these first conclusions.

CHAPTER III

Case study: Traun River, Austria

Effects of climate change on fish assemblages in terms of lakes and their outlets in Alpine areas

Andreas Melcher¹, Helga Kremser², Florian Pletterbauer³, Stefan Schmutz⁴

¹ *University of Natural Resources and Life Sciences; Department of Water, Atmosphere and Environment; Institute of Hydrobiology and Aquatic Ecosystem Management, Max-Emanuel-Straße 17; A-1180 Vienna, Austria; email: andreas.melcher@boku.ac.at; phone: +43 1 47654-5223*

² *University of Natural Resources and Life Sciences; Department of Water, Atmosphere and Environment; Institute of Hydrobiology and Aquatic Ecosystem Management, Max-Emanuel-Straße 17; A-1180 Vienna, Austria; email: helga.kremser@boku.ac.at*

³ *University of Natural Resources and Life Sciences; Department of Water, Atmosphere and Environment; Institute of Hydrobiology and Aquatic Ecosystem Management, Max-Emanuel-Straße 17; A-1180 Vienna, Austria; email: florian.pletterbauer@boku.ac.at*

⁴ *University of Natural Resources and Life Sciences; Department of Water, Atmosphere and Environment; Institute of Hydrobiology and Aquatic Ecosystem Management, Max-Emanuel-Straße 17; A-1180 Vienna, Austria; email: stefan.schmutz@boku.ac.at*

Introduction

Riverine ecosystems are affected by different anthropogenic pressures. Besides water pollution, hydromorphological alterations, connectivity disruptions and direct interferences with the fish community (e.g. fishing, stocking), climate change jeopardizes the integrity of river ecosystems (Schmutz & Mielach 2011). The rising air temperature is the best-known phenomenon of global climate change (Kromp-Kolb 2003; Matulla & Haas 2003). Since water temperature is mainly determined by heat exchange with the atmosphere, higher air temperatures lead to higher water temperatures. For rivers, there are strong correlations between water and air temperature (Hari et al. 2005; Webb & Nobilis 1997; Moshini & Stefan 1999; Solheim et al. 2010). In water bodies, water temperature is a determining factor and plays a major role in the distribution of fish species. Global climate change and local anthropogenic impacts such as factory heating emissions can result in warming water bodies and can consequently permanently modify their fish biocenoses. Most aquatic organisms (e.g. salmonids) have a specific range of temperatures they can tolerate, which determines their spatial distribution along a river or on a regional scale. Climate change could lead to the extinction of some aquatic species or at least modify their distribution in a river system or move their distribution northwards. Several indications of climate impact on the functioning and biodiversity of freshwater ecosystems have already been observed, such as northward movement, phenology changes and invasive alien species (Solheim et al. 2010). Temperature has to be considered as an environmental resource and should be increasingly important as a structuring factor of river fish assemblages, especially in regulated and degraded river systems, directly related to the loss of fluvial habitats therein (Wolter 2007).

Relevance and effects of temperature changes on fish fauna

Water temperature describes one of the most significant factors for the survival of aquatic biota (flora and fauna) of freshwater ecosystems (Armour 1991; Fry 1967, 1971; Varley 1967; Hutchinson 1976). The temperature regime influences fish populations in their migratory behaviour, egg evolution, spawning process, fertilization and growth rate as well as their metabolism, respiration and tolerance of parasites. Consequently, all spheres of life of the single fish species are strongly influenced by water temperature. Minor modifications often confine the survival of single species or life stages and consequently their occurrence and, respectively, their distribution (Jungwirth & Winkler 1984; Schmutz & Jungwirth 2003). Even a small increase in water temperature can alter the fish community composition. While excessively low temperatures cause lethargy (reduced digestion, low reaction time), temperatures above optimum levels increase metabolism (e.g. digestion) to a degree, where fish cannot find enough food for compensation, thereby exhausting their fat reserves. Eurythermic species prefer and tolerate significantly higher temperatures during summer, while temperature conditions in rivers are very similar during winter for steno- and mesothermic species (Jungwirth et al. 2003; Schmutz & Mielach 2011). Interventions in the temperature regime of a water body can lead to advantages for one species and disadvantages for another. The different temperature regimes along a river continuum in combination with temperatures preferred by fish species cause a typical distribution of fish communities which can be classified into different fish zones (Huet 1949; Schmutz & Mielach 2011).

Temperature and climate change

Selected Austrian rivers and lakes were analysed in terms of changing water temperature from 1976 to 2006 and revealed for both increasing temperatures. The difference between yearly mean water temperature and long-term mean water temperature increased at the end of the time series. Furthermore, the analyses revealed an increase of water temperature of approximately 2.5°C in rivers ($n = 30$) and 3°C in lakes ($n = 19$) in the last 30 years. The result matches the insights of Webb & Nobilis (1995, 2007), who proved a nearly 2°C increase of temperature during the 20th century for Austrian streams. The rising of water temperature is clear for lakes. Lake outflows are influenced by the lake situated upstream, and are more strongly affected by the global climate change than water sections without any impact from a lake. Therefore, if climate warming advances at the same magnitude as has occurred thus far, today's situation of lake outflows could reflect the prospective image of all stream flows.

As a result of the water-temperature analyses, summer 2001 (June, July, and August) was selected as average. The time series analyses revealed especially warm temperatures for August 2003 and rather cold temperatures for August 2005. In this period, streams warmed on average 2.5°C and lakes about 3°C.

Problems arise in this context in that migration upwards is limited through water dimensions as well as hydromorphological parameters such as slope and current velocity. Therefore it is possible that the grayling (*Thymallus thymallus*) or Danube salmon (*Hucho hucho*), both

endangered species, may become extinct in Austria in the longer term. The most quickly affected by the climate change will be species from the Epi-, Meta-, and Hyporhithral.

Case study: Traun River and Traun Lake

The whole catchment area of the Traun River ranges from almost 3000m (Dachstein) to 250m (mouth of the Danube) above sea level. The study area is located in the central part of upper Austria. We focussed on the section of Traun Lake outflow downstream where the grayling has been historically confirmed and today is almost extinct. The temperature analyses for Traun Lake revealed a mean increase of 2.2°C within the last 33 years (1976–2008) for August (Fig. 2).

Figure 3 shows the temperature curves for the three selected years, 2001, 2003, and 2005. Even in the cold year 2005 the water temperature in the outflow section was almost too warm for the grayling. The upper optimum for adults is 18°C. In the outflow section, the biomass of the grayling decreased from 68kg/ha in 1990 to 48kg/ha in 1995 and 4kg/ha in 2010. Further, the total number of fish species increased from 14 to 27 species (Fig. 4) and changed a grayling zone into a barbel zone.

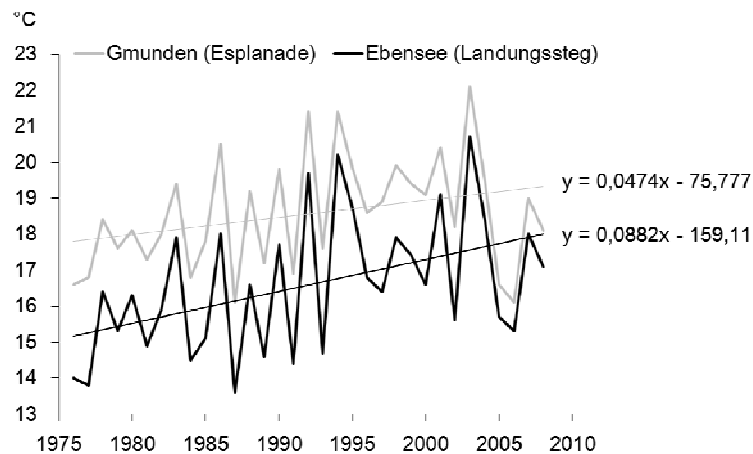


Fig. 1: Temperature trend (1976-2008) of Traun Lake for mean water temperature (°C) in August at the Gmunden and Ebensee sites

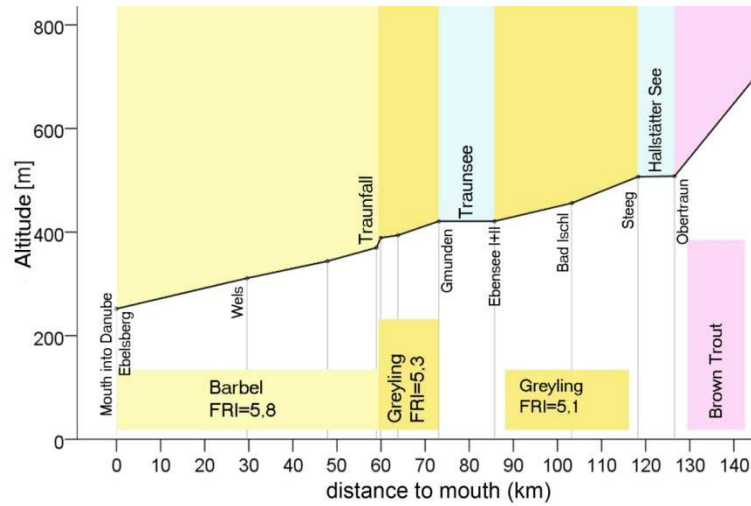


Fig. 2: Altitude trend in the catchment area of the Traun River with the fish regions (Haunschmied et. al.) together with the fish region indices (FRI) calculated following the Fish Index Austria.

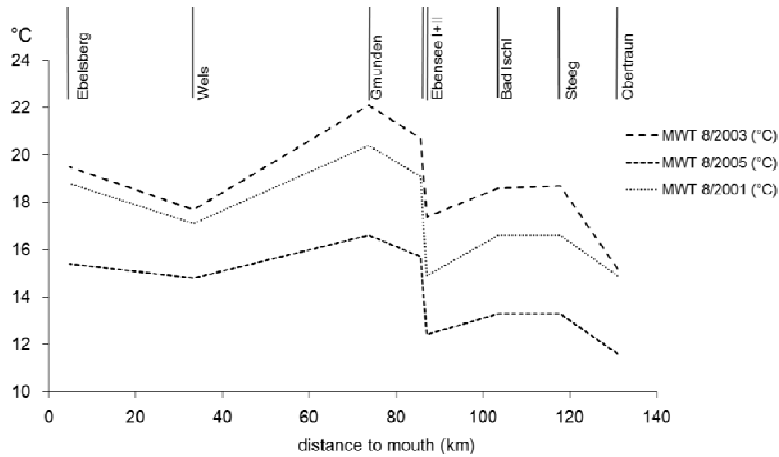


Fig. 3: Mean water temperature in August (°C) in the Traun River in 2001, 2003, and 2005.

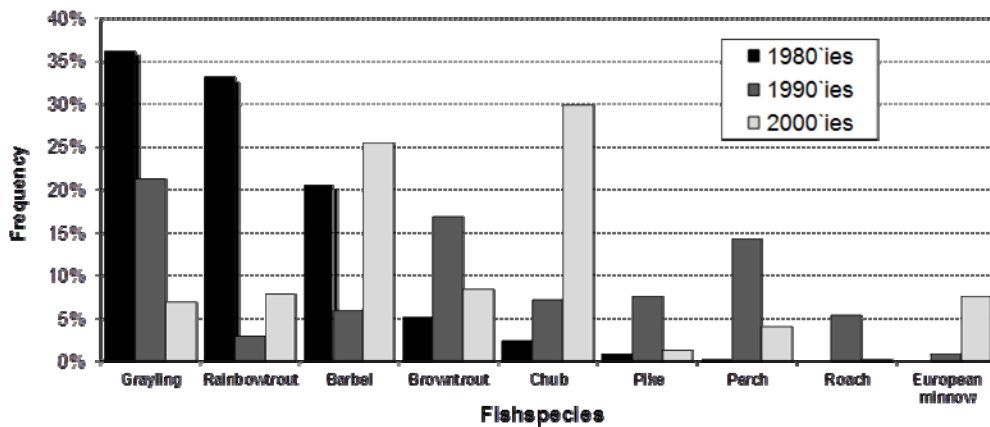


Fig. 4: Shift of species composition from the 1980s until the 2000s in the Traun River

Conclusion

For adult graylings, a temperature of 18°C is the upper optimum. At the measurement points on the Traun River, temperatures of 24°C and higher have been recorded. For the grayling, such high temperatures constitute a substantial source of stress (Küttel et al. 2002). With climate change, there is no doubt that a return to the historical fish assemblages is impossible and cannot be attained by fish stocking at the lake outflow section. The Drau River will fail to achieve the good ecological status expected by 2015 within the WFD. River management has to take into account that in areas prone to warming there must be connectivity upstream to allow species to migrate into cooler refuges.

For future research and management, one must also expect that temperature impacts are becoming increasingly significant in regulated river systems. With decreasing hydrodynamics, the significance of temperature effects will increase (Wolter 2007).

CHAPTER IV

Case study: Seine River basin

Fish assemblages of the Seine River basin: effects of climate change and reduction of human pressures

Jérôme Belliard¹, Maxime Logez², Guillaume Gorges³, Olivier Delaigue⁴, Didier Pont⁵

¹ *Irstea, UR HBAN, 1 rue Pierre-Gilles de Gennes – CS 10030, Antony, France; email: jerome.belliard@irstea.fr; phone: +33 (0)1 40 96 65 66*

² *Irstea, UR HBAN, 1 rue Pierre-Gilles de Gennes - CS 10030, F-92761 Antony, France; email: maxime.logez@irstea.fr; phone: +33 (0)4 42 66 69 86*

⁵ *Irstea, UR HBAN, 1 rue Pierre-Gilles de Gennes - CS 10030, F-92761 Antony, France; email: guillame.gorges@irstea.fr*

⁴ *Irstea, UR HBAN, 1 rue Pierre-Gilles de Gennes - CS 10030, F-92761 Antony, France; email: olivier.delaigue@irstea.fr*

⁵ *Irstea, UR HBAN, 1 rue Pierre-Gilles de Gennes - CS 10030, F-92761 Antony, France; email: didier.pont@irstea.fr; phone: +33 (0)1 40 96 65 52*

Introduction

River fish species distribution is under the control of numerous environmental variables acting at different spatial and temporal scales (Tejerina-Garro et al. 2005). Many of these environmental variables are potentially affected by human activities and on this basis are able to induce modifications in fish distribution and fish assemblage composition. For the coming decades, WFD proposes to improve ecological status of river ecosystems (and particularly fish assemblage integrity) and numerous restoration measures are being designed or implemented to achieve these objectives (Hering et al. 2004). Recent studies suggest that climate change would have major effects on riverine fish distribution (Buisson & Grenouillet 2009), which could, over the long term, challenge the present river restoration practices.

Here, considering the whole Seine River basin and using different species distribution models, we attempt to predict and compare the possible effects of climate change and restoration measures on fish species distribution and fish assemblages.

Characteristics of the Seine River basin

Natural conditions

Located in the northern part of France, the Seine River (776 km long and a catchment area covering 78 600 km²) is a quite moderate-sized European river (Fig. 1). Most of its river network flow within a vast sedimentary basin (called the Parisian Basin) composed of different geological formations, the oldest ones (Jurassic formations) located in the margins of the basin and the youngest (Tertiary formations) in its centre. Only the southern part of the basin (upper

Yonne River basin) and, to a lesser extent, its northern extremity (upper Oise River basin) flow over a metamorphic substratum (Fig. 2).

The majority of rivers flow in plains: 70% of the basin is situated at an altitude of less than 200m. Only the southern part of the basin originates at an altitude of over 600m (less than 2% of the total Seine catchment area, maximum altitude 900m). As a consequence, stream slopes are generally moderate or low (frequently < 2‰) and climate does not exhibit a strong geographical gradient.

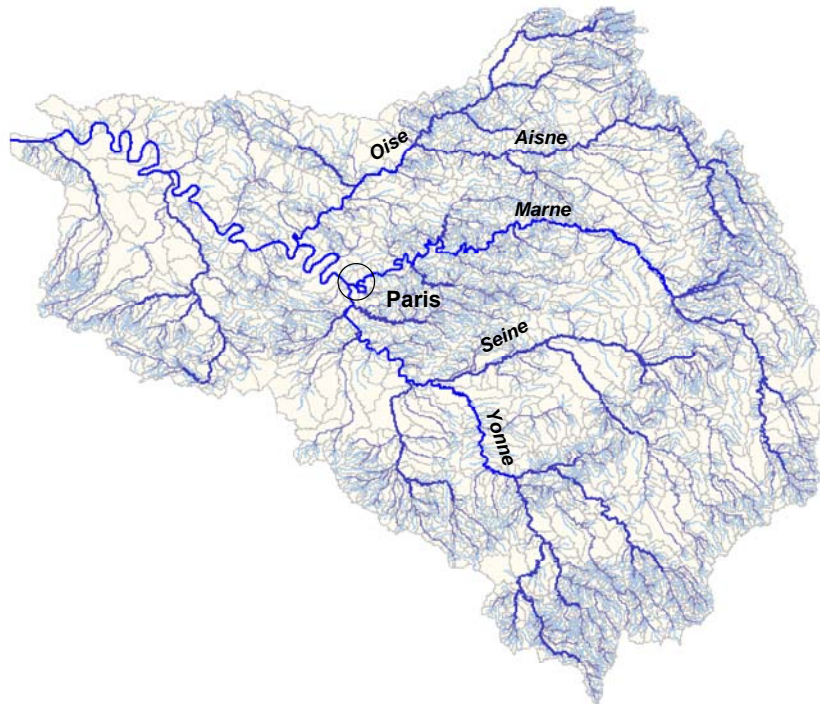


Fig. 1. Map of the river network of the Seine River basin (source PIREN-Seine AIPreshume)

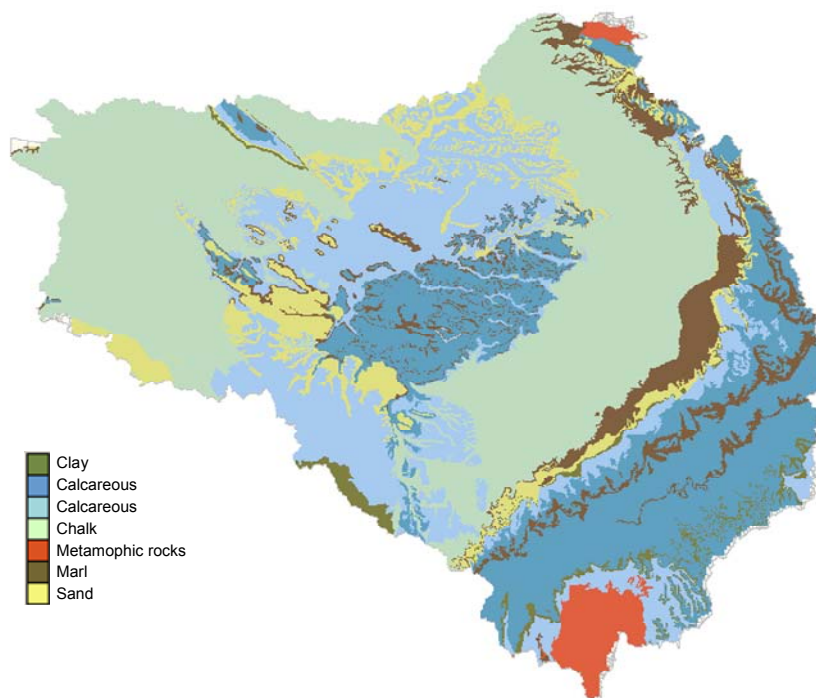


Fig. 2. Geology of the Seine catchment (source PIREN-Seine AIPreshume).

Flowing to the English Channel, the whole Seine basin experiences a typical oceanic climate. The mean annual rainfall is $750\text{mm}\cdot\text{year}^{-1}$ exhibiting weak regional variations: annual precipitations lower than $600\text{mm}\cdot\text{year}^{-1}$ are locally observed in the centre of the basin, whereas values exceeding $850\text{mm}\cdot\text{year}^{-1}$ are found in the coastal area and above all the south-eastern hills (Fig. 3). Rainfalls are quite uniformly distributed throughout the year, but river regimes exhibit a seasonal regime, with high flows in winter or early spring and low flows in summer, as a consequence of seasonal variations in evapotranspiration. The contrast between winter and summer temperatures is low in the coastal zone and reaches its maximum values in the eastern margins of the basin.

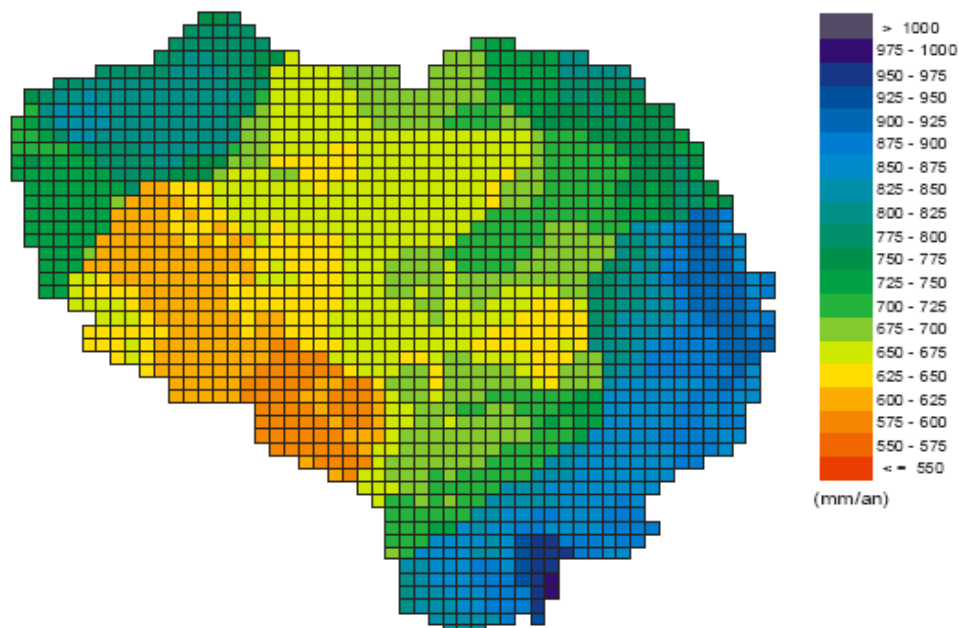


Fig. 3. Mean annual rainfall ($\text{mm}\cdot\text{year}^{-1}$) (from Ducharne et al. 2004)

Human pressures

The Seine River basin covers around 12% of the metropolitan French territory area but concentrates 23% of the French population (i.e. about 15 million inhabitants), 25% of national agricultural production and 30% of national industrial activities, reflecting a high level of human pressure.

The human population is unequally distributed: nearly 10 million inhabitants are concentrated in the city of Paris and its suburbs (i.e. 4% of the basin area) and the other large urban centres are located along the main branches of the river network; conversely the eastern part of the basin has a low population density (frequently fewer than 10 inhabitants per km^2). (Fig. 4)

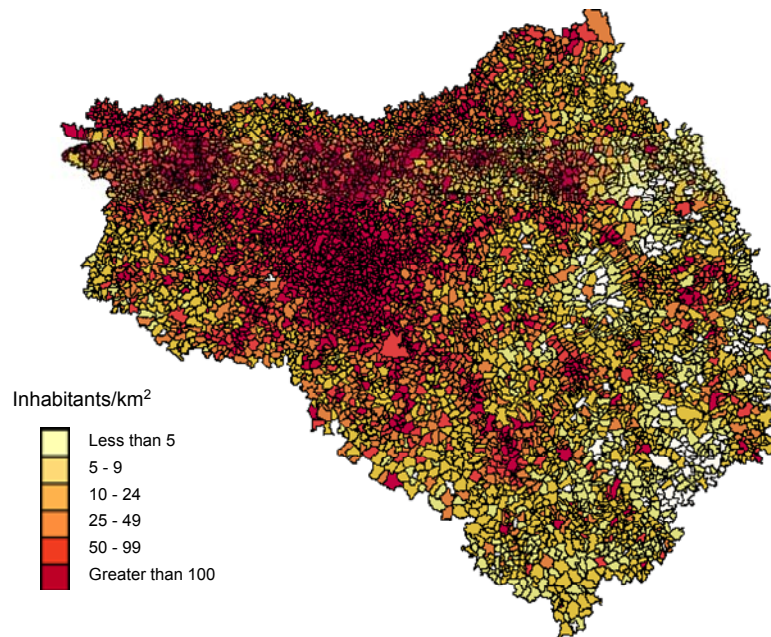


Fig. 4. Map of the population density on the Seine catchment (source PIREN-Seine AIPreshume).

A vast central zone of the Seine catchment is devoted to intensive agriculture, particularly oriented towards mass production of cereal and industrial crops. In contrast, the margins of the basin are mainly characterized by polyculture, animal farming and forestry.

The diversity and intensity of human activities induce a multiplicity of point-source and diffuse water pollution. Although organic and some toxic (particularly metal contamination) pollution have been considerably reduced during the few past decades as a consequence of wastewater treatment improvement (Billen et al. 2001; Meybeck et al. 2007), diffuse pollution (nutrients, pesticides or atmospheric pollutants) remains a major concern (Billen *et al.* 2007a; Blanchoud et al. 2007; Blanchard et al. 2007), particularly for drinking water treatment.

In addition to water quality impacts, urban concentration and agriculture activities have led to major hydromorphological modifications (channelization, reshaping, embankment, etc.), most particularly in the centre of the basin where agricultural practices are more intensive. However, even in zones nowadays considered as more "natural", rivers have frequently suffered from morphological damage because of past human activities. For example, in the southern part of the Seine basin, the Morvan, a region that is today little affected by human pressures, experienced an intensive timber floating industry for several centuries (16th–19th century) leading to a deep and long-standing morphological transformation of streams and rivers (Poux et al. 2011). Another example of an old morphological river modification concerned water mill creation from medieval times: numerous dams and barriers related to these constructions remain.

Today, the Seine River basin controls more than 50% of the national fluvial transport. This intensive navigation has implied massive modifications of the river network starting from the 17th century with construction of artificial waterways to connect the Seine catchment with the adjacent basins. The canalization of rivers themselves started in the mid-19th century and continues today. The Seine River and all its major tributaries (Yonne, Marne, Oise, Aisne) continue to be used by commercial navigation. River channelization for navigation purposes

profoundly affects channel morphology by widening and deepening channels, removing meanders, disconnecting side arms and backwaters and artificializing river banks. In addition, construction of weirs and locks to maintain a sufficient water level reduces the natural connectivity of the river network. All these morphological alterations of the fluvial ecosystem resulted in severe detrimental effects on fish populations and communities.

Nowadays, large dams and reservoirs regulate the upper reaches of the Seine River and its major tributaries (the Aube, the Marne and the Yonne). These works have a twofold objective: flood control and maintenance of minimum low-water flow. However, the predominant concern is to supply high-quality drinking water to Paris. The dams store water from December to June (by topping potential flood peaks), and then release it from July to November. Flood control by reducing lateral connectivity may greatly affect the ecosystem's functioning. For instance, in a Seine River reach upstream of Paris, spawning conditions for pike (a species preferring flooded natural grassland for spawning) were considered as optimal in 45% of the years before flood regulation; considering the present-day flood regulation operations, optimal spawning condition occurred only 15% of the years (Boët et al. 1999). Conversely, water supplies used to support flow during summer reduces the effect of pollution and thus improves life conditions for many organisms, particularly downstream of Paris.

Fish fauna

Located at the western extremity of Europe, the Seine basin is relatively isolated from the Ponto Caspian region, acting as a refuge for fish during the last glacial period. As a consequence, it has a relatively depauperate native fish fauna due to the limitation of post-glacial recolonization processes (Banarescu 1989; Reyjol et al. 2007). Considering the uncertainty on the native status of several species, it is assumed that the original fish fauna of the Seine basin included between 27 and 33 species (Boët et al. 1999).

The human impacts on the fish fauna composition date from long ago, with the first documented case the introduction of carp used for fish farming since the 13th century in artificial ponds (Hoffmann 2005), but the real transformation of the Seine fish fauna took place beginning at the end of the 18th century with the colonization of about 20 exotic species. These colonizations involve, in fact, two distinct processes. The first one results from colonization from adjacent catchments through artificial waterways built for navigation and explains, for example, the arrival of ruffe (*Gymnocephalus cernua*) and common nase (*Chondrostoma nasus*), nowadays widely distributed throughout the Seine basin. The second one, which accelerated from the second half of the 19th century, results from the direct introduction of species from different origins (Europe, North America and Asia) in order to improve fish production or to develop angling. The recent catches of new species, such as ide (*Leuciscus idus*) or asp (*Aspius aspius*), show that colonization processes persist.

In the early 19th century, many diadromous fish species were already declining in the Seine basin, but this phenomena accelerated in the second part of the 19th century because of the increase of barriers for fish migration: (1) construction of weir and lock systems for navigation purposes on the Seine and its main tributaries, (2) construction of dams in headwater catchments

in order to regulate flow and (3) heavy levels of pollution occurring downstream from Paris as a result of direct discharge of sewage into the river. This continuous decline led to the extinction of several species (sturgeon, salmon, allis shad, twaite shad, sea lamprey and smelt) during the first part of the 20th century (Belliard et al. 2009). Since the beginning of the 1970s, the water quality of the river has clearly improved and several fish passes have been established on navigation weirs allowing the return of some migratory species to the lower Seine (Rochard et al. 2007). This natural recolonization first concerned species using the estuarine part of the Seine River for spawning such as smelt and twaite shad. For the past few years, this phenomenon has also been observed for species accomplishing longer migration in freshwater such as salmon, allis shad and sea lamprey, and evidence of reproduction has recently been obtained for these three species (Belliard et al. 2009; Perrier et al. 2010).

In the end, considering all the modifications affecting the fish fauna of the Seine, 54 fish species can be currently observed in the rivers of the Seine basin. Nearly 40% (21 species) are non-native species, which illustrates the high level of human impact on the long-term evolution of the fish communities of the Seine basin.

Key points

1. The natural environmental conditions are quite homogeneous throughout the Seine basin; in particular, a large majority of rivers flow in plains and highland zones are virtually absent. In this context, we can expect a major impact of global warming on the fish species spatial distribution, especially for cold water species.
2. The Seine basin is undergoing a high level of human pressure: it covers around 12% of the metropolitan French territory area but concentrates 23% of the French population; a vast central zone is concerned by intensive agriculture. Numerous sources of water pollution (domestic, industrial and agricultural) exist; all large rivers are transformed to improve commercial navigation and reservoirs control their flow regime.
3. Some domestic and industrial pollutions have considerably regressed during the last 40 years, but non-point source pollutions remain a major problem for the basin. Conversely, restoration operations focusing on morphological or hydrological alterations are still poorly developed.
4. Nowadays, 54 fish species can be observed in the Seine basin but 40% of them are non-native. Several diadromous fish species became extinct during the first part of the 20th century. Recently, some of them have undertaken a natural recolonization of the Seine basin as a result of water quality and connectivity improvement in the lower reaches of the Seine River.

Potential species distribution and climate change

To assess the effect of climate change on fish species distribution, we used fish models calibrated at the whole European scale and predicting species occurrences from a set of environmental variables including temperature and precipitations (Logez et al. 2011; see Chapter I for more details on these models). The environmental variables included in these species distribution models are relatively independent of human pressures; consequently they

are well adapted to predicting the potential distribution of species, that is, their spatial distribution in absence of human-induced river transformations.

Species distribution models were coupled to a GIS derived from a CCM River and Catchment database giving for all European river reaches, in particular those of the Seine basin, the values of the different environmental variables used in fish models. Climate variables are available for present-day conditions but also according to different climatic scenarios (A1F1, A2, B1, B2; IPCC 2007) and periods (the decades 2020–2030 and 2050–2060) (see Chapter II for further detail). On this basis, it is possible to predict potential fish distributions considering the present climate and to simulate how these distributions could evolve under the different climate change scenarios and for the two future periods. Fish models were run for 23 species: the synthetic results are presented in Table 1.

For a given species and a given period, predicted occurrence seems quite similar between scenarios, suggesting that the evolving distribution trends are probably robust. Nine species (sculpin, three-spine stickleback, nine-spine stickleback, salmon, brown trout, grayling, and to a lesser extent stone loach and minnow) show a regular decrease. This evolution is particularly dramatic for cold-water species such as sculpin, brown trout and grayling; projections for 2050–2060 predict a quasi-disappearance of these species. Conversely, six species exhibit a clear increasing tendency (bleak, barbell, gudgeon, chub, bitterling and riffle dace (*Telestes souffia*)). The case of riffle dace stands out because the model predicts total absence in the Seine basin under present-day conditions and then a progressive colonization in 2020–2030 and 2050–2060. In fact, this species is already present in the Seine basin as a result of recent introduction from the Rhône basin.

The ten remaining species show different kinds of evolution. Some of them, such as spirlin and pike, seem quite stable between periods. Others such as common nase and roach tend to increase first and to decrease between 2020–2030 and 2050–2060.

Table 1. Species occurrence predicted on the Seine River basin considering different climate conditions (present-day conditions, four climate scenarios and two different periods). The threshold values used to distinguish between presence and absence were defined at the European scale.

Species	Current	2020–30				2050–60			
		A1	A2	B1	B2	A1	A2	B1	B2
<i>Alburnoides bipunctatus</i>	18.6	19.7	19.9	19.7	19.4	16.7	18.7	20.4	19.3
<i>Alburnus alburnus</i>	18.6	30.3	30.6	31.3	31.7	43.2	40.8	38.0	38.9
<i>Anguilla anguilla</i>	2.6	5.3	5.3	5.2	5.2	3.7	3.6	3.4	3.4
<i>Barbatula barbatula</i>	85.1	82.2	82.2	81.9	80.8	56.9	66.8	73.7	70.5
<i>Barbus barbus</i>	13.6	18.6	18.7	18.9	19.1	17.3	18.2	18.6	18.8
<i>Chondrostoma nasus</i>	11.7	21.4	21.5	21.5	21.8	14.6	16.9	18.8	17.9
<i>Cottus gobio</i>	84.5	16.3	14.6	12.1	9.3	0.4	0.2	1.7	0.7
<i>Esox lucius</i>	26.7	30.2	30.0	29.6	28.9	24.0	25.7	27.3	25.5
<i>Gasterosteus aculeatus</i>	71.9	31.2	29.7	26.3	22.4	1.7	3.0	7.4	4.2
<i>Gobio gobio</i>	58.1	68.0	68.4	68.3	68.0	60.2	64.3	67.9	66.0
<i>Lampetra planeri</i>	83.0	58.9	57.5	54.5	51.2	14.4	21.3	32.4	24.8
<i>Squalius cephalus</i>	35.0	56.6	57.2	58.1	58.9	57.5	59.4	60.2	60.5

<i>Leuciscus leuciscus</i>	16.8	20.3	20.0	19.9	19.7	14.5	15.9	16.9	16.2
<i>Lota lota</i>	21.3	19.4	19.5	19.5	19.3	22.3	22.7	22.8	21.7
<i>Perca fluviatilis</i>	50.9	58.3	57.7	56.7	55.2	30.9	37.0	44.7	40.1
<i>Phoxinus phoxinus</i>	70.5	56.2	55.9	54.7	53.3	22.4	29.6	38.7	34.0
<i>Pungitius pungitius</i>	71.0	45.1	43.5	39.4	35.6	3.7	6.0	13.7	8.8
<i>Rhodeus amarus</i>	42.0	79.4	80.3	81.3	82.3	93.7	92.4	90.8	91.4
<i>Rutilus rutilus</i>	30.8	43.6	43.4	43.2	43.3	33.9	36.1	38.3	37.1
<i>Salmo salar</i>	6.4	2.3	2.2	2.1	2.0	0.9	1.1	1.4	1.2
<i>Salmo trutta</i>	29.2	6.9	6.8	6.6	6.1	0.9	1.3	1.8	1.4
<i>Telestes souffia</i>	0.0	17.4	17.7	18.5	21.7	26.5	25.0	20.1	24.4
<i>Thymallus thymallus</i>	18.6	2.0	1.9	1.6	1.3	0.0	0.1	0.2	0.1

Different maps illustrate these possible situations considering different fish species with contrasting evolution scenarios (Figs. 5–10).

Overall, reduction of distribution related to climate warming mainly concerned headwater species. In this respect, the case of sculpin is particularly dramatic since projections predict the disappearance in the entire river network (Fig. 5) within 50 years. For headwaters, these local extinctions seem only partially compensated by the expansion of other species, probably leading to a general reduction of species richness in small rivers.

Since water temperature data was not available for most rivers, we used air temperature variables, leading to potential bias in fish distribution prediction. At a few sites, we tested the potential discrepancies between air and water temperatures and found that water temperature was 2 or 3°C lower than air temperature during summer for groundwater-fed rivers (this phenomenon seems much more pronounced for chalk streams). The potential influence of groundwater is not included in our model, so we suspect that predictions are probably too pessimistic for cold-water species. In addition, we postulate that, in the context of global warming, groundwater-fed rivers could act as refuges, to a certain extent, for some cold-water species.

Overall, those results clearly show how dramatic the effect of climate change could be on species distribution and fish assemblage composition.

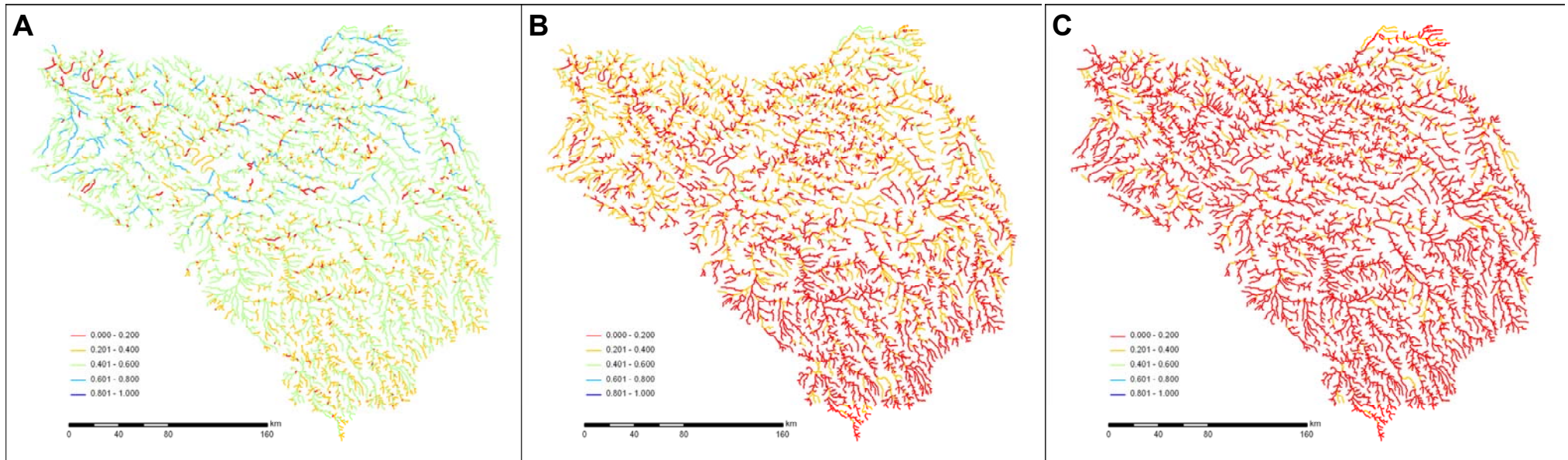


Fig. 5. Probability of presence of sculpin predicted under present-day climate conditions (A) and for the b2 climate scenario for 2020–2030 (B) and 2050–2060 (C).

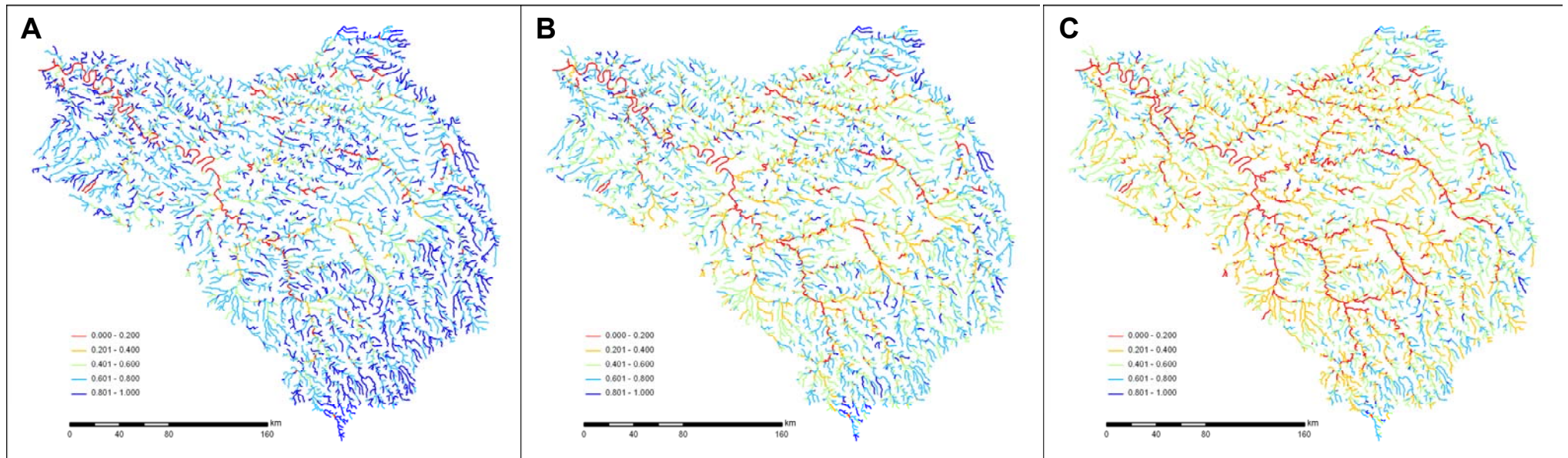


Fig. 6. Probability of presence of brown trout predicted under present-day climate conditions (A) and for b2 climate scenario for 2020–2030 (B) and 2050–2060 (C).

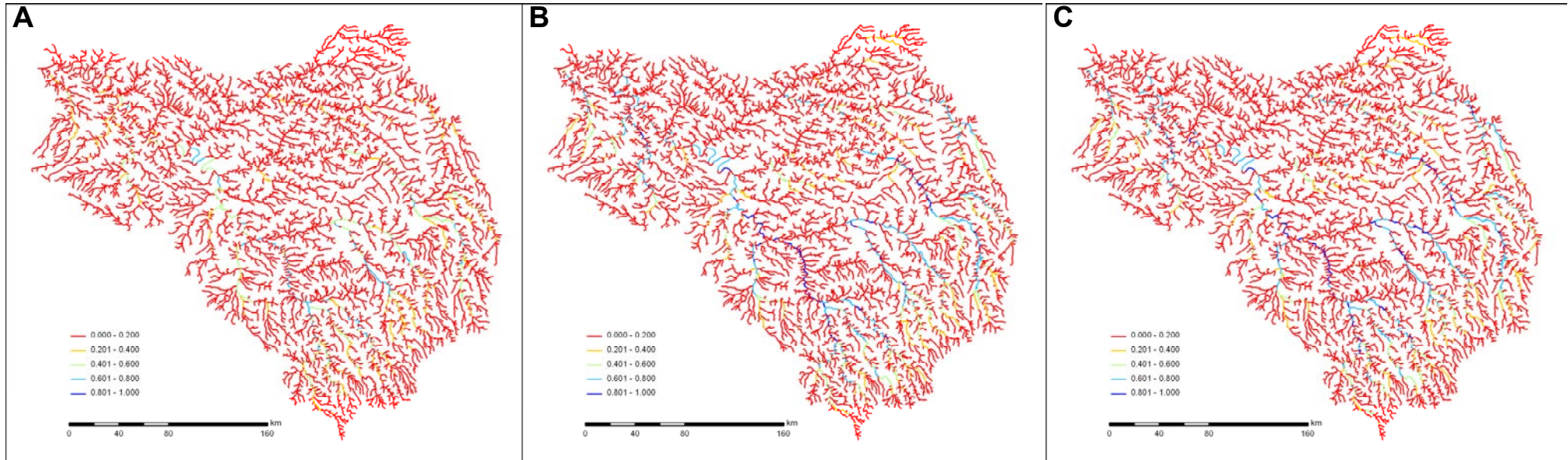


Fig. 7. Probability of presence of barbel predicted under present-day climate conditions (A) and for b2 climate scenario for 2020–2030 (B) and 2050–2060 (C)

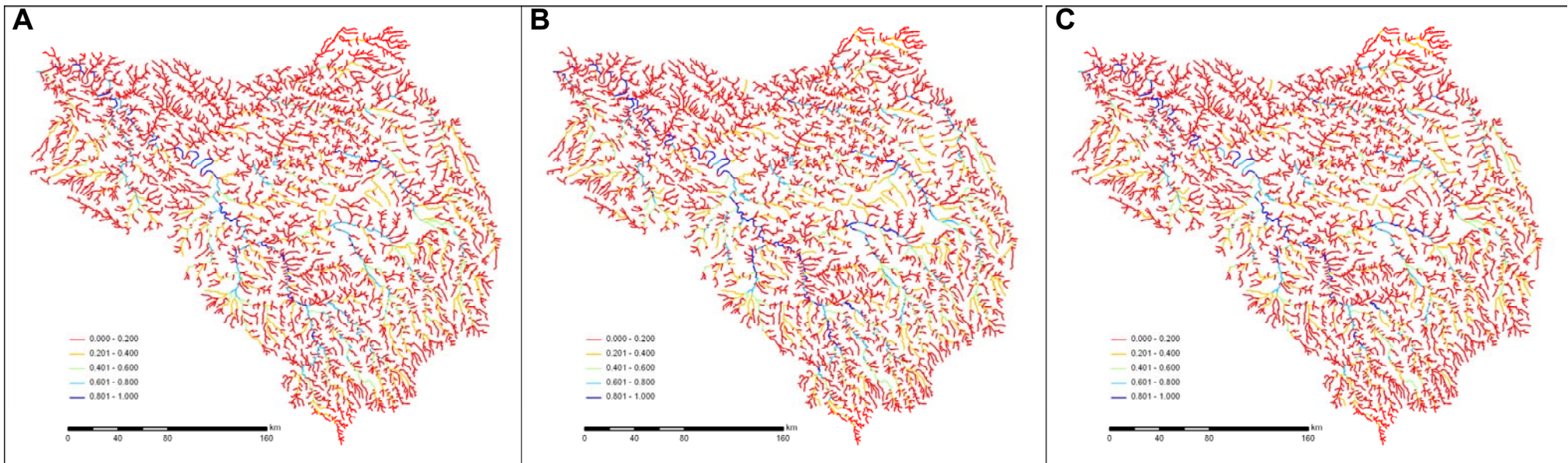


Fig. 8. Probability of presence of dace predicted under present-day climate conditions (A) and for b2 climate scenario for 2020–2030 (B) and 2050–2060 (C).

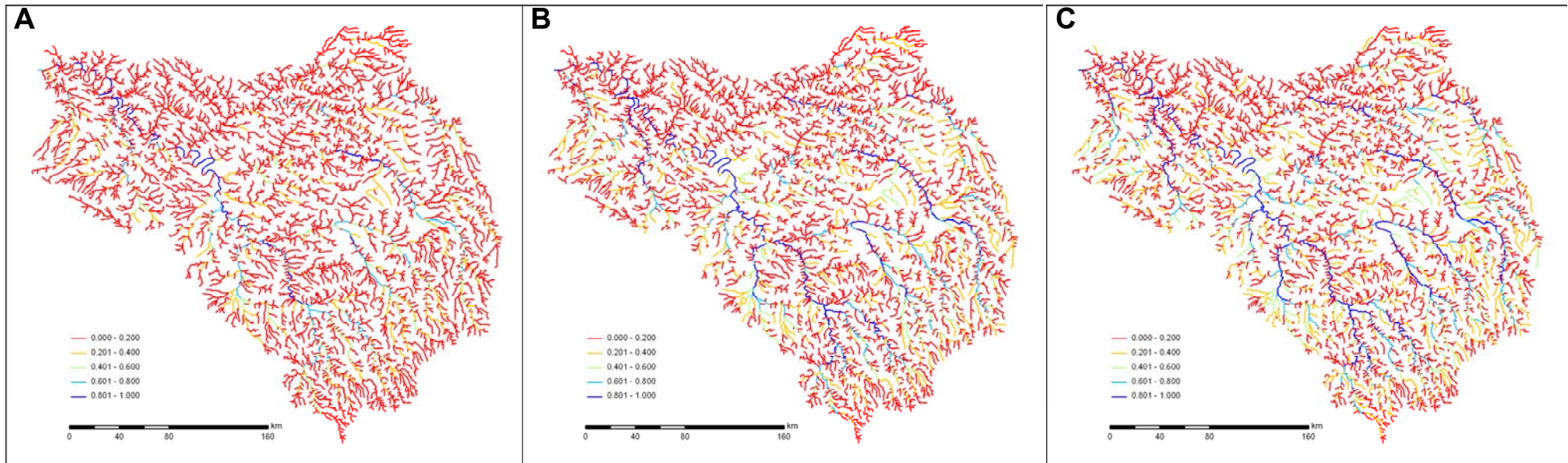


Fig. 9. Probability of presence of dace predicted under present-day climate conditions (A) and for b2 climate scenario for 2020–2030 (B) and 2050–2060 (C).

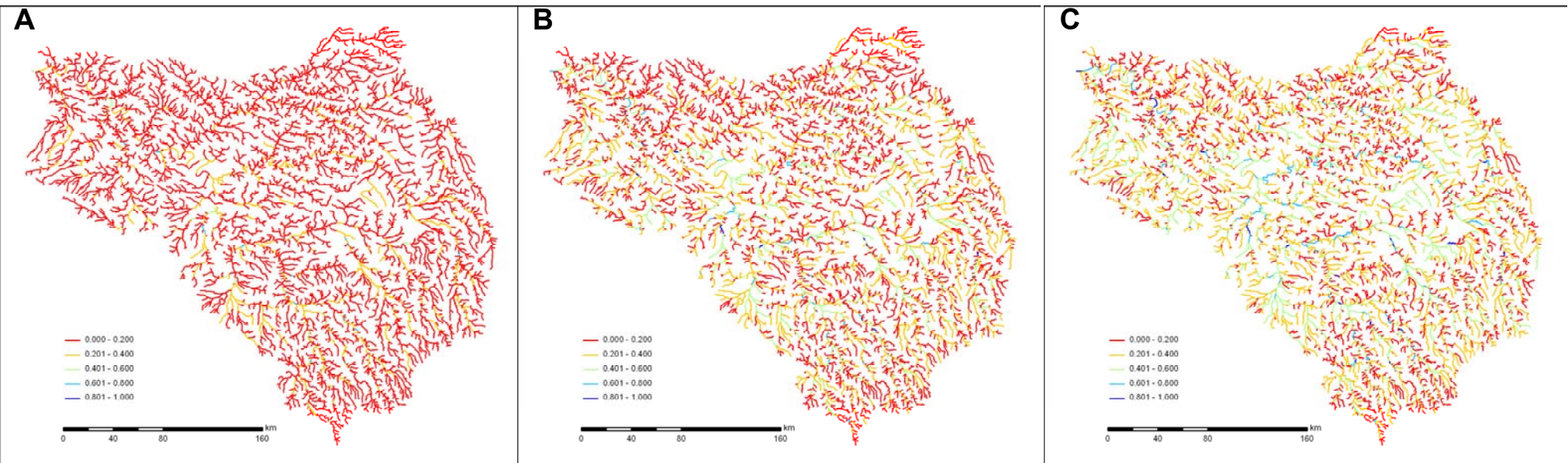


Fig. 10. Probability of presence of bitterling predicted under present-day climate conditions (A) and for b2 climate scenario for 2020–2030 (B) and 2050–2060 (C).

Species distribution and human pressures at the Seine basin scale

Introduction

This section proposes to develop predictive models of fish species presence and/or community composition At the whole Seine basin scale considering a set of environmental variables reflecting natural conditions or potentially affected by human activities. On the basis of these models and using a GIS describing environmental conditions at the river reach scale, we are able to (1) extrapolate the fish models' results at the scale of the whole Seine river network and (2) predict the potential evolution of fish distribution resulting from human pressure modifications.

Material and methods

Fish data

The fish data used to calibrate fish models were extracted from a national database developed by ONEMA grouping electro-fishing operations undertaken for ecological river monitoring. Initially, these data included 1499 fishing operations carried out between 1998 and 2007 for a given river site, several fishing operations corresponding to different dates. In the whole data set, we selected a single fishing operation for each site considering the following criteria:

- The fishing operation is as close as possible to 2000 but if possible later than 1999.
- The operation grouped a sufficient number of fish individuals ($N > 100$). This criterion was added to avoid fishing operations with an insufficient sampling effort potentially leading to the nondetection of rare species (but it was not used at sites heavily altered with very scarce fish populations).

Finally, to calibrate the models, we selected a set of 230 fishing operations, corresponding to 230 different river sites, distributed throughout the Seine River basin (Fig. 11). The majority of these sites were sampled during the 2000–2002 period.

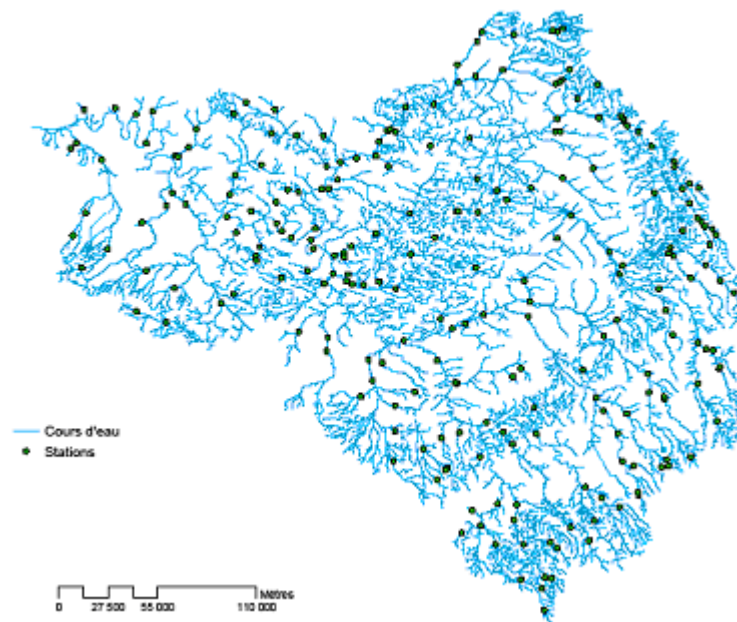


Fig. 11. Location of the 230 fish sampling sites used to calibrate species distribution models.

For each operation we had the exhaustive list of fish species caught. On the 230 sites, 43 fish species were identified, but some of them were sparsely present. Thereafter, we ran the fish models on a subset of 25 species corresponding to the most frequent fish species in the Seine catchment (presence at at least 10% of the sampling sites) (Table 2).

Environmental data set and GIS

The fish sampling sites were located on the river network on the basis of a GIS grouping a set of different layers used to produce the environmental variables thereafter used for fish modelling. Some of these layers were developed by the PIREN-Seine, a large interdisciplinary research programme on the Seine River System, jointly funded since 1989 by the French CNRS and the Water Authorities of the Seine basin (Billen et al. 2007b).

The different GIS layers were composed as follows:

- a simplified river network, derived from the national BD Carthage system (IGN), including 5163 river reaches (one reach corresponding to a part of river between two confluences);
- a digital elevation model (USGS);
- land cover from Corine Land Cover;
- geological formation (BRGM);
- river flow measurements for a set of different gauging stations (DIREN);
- water quality measurements at different river sites (RNB-AESN);
- mean monthly air temperatures for the 1954–2009 period at the scale of 3×3-km squares (Météo France).

To supplement the water quality data, we used the RIVERSTRAHLER model (Billen et al. 1994; Garnier et al. 1999) and its GIS interface SENEQUE (Rueland et al. 2007). This model

describes the biogeochemical functioning of river systems and calculates the spatial and seasonal variations of discharge and some aspects of water quality within the entire Seine River network. It accounts for the constraints set by river morphology (river slope and width), hydrometeorology, diffuse sources from the watershed, and point-source pollution from wastewater treatment plants and industries (see Billen et al. 1994 and Rueland et al. 2007 for further detail on the RIVERSTRAHLER/SENEQUE system).

We ran the RIVERSTRAHLER model based on the climatic and hydrological conditions of the year 2000. For the whole river reaches of the Seine basin, we calculated the mean values of different water quality variables for the summer period.

From the different layers and the outputs of the RIVERSTRAHLER/SENEQUE system, we generated nine environmental variables at the river-reach scale describing natural river morphology, climate and temperature conditions, water quality and some aspects of river and catchment anthropogenic transformations:

- *total catchment area* (km²) (CA). CA is frequently used as an indicator of river size, to account for upstream–downstream distribution of fish species (Oberdorff et al. 2001).
- *river slope* (‰) (SLO). This is a morphological descriptor of river conditioning, partly flow velocity, which is an important controlling factor of riverine fish distribution (Huet 1954)
- *July mean air temperature* (°C) (Tju). This variable is used as a proxy of water temperature, which is an important factor for aquatic organisms' distribution. July is considered the hottest month and consequently the most restrictive for fish distribution (Oberdorff et al. 2001).
- *difference between July mean air temperature and January mean air temperature* (°C) (ΔT). This variable accounts for temperature contrast during a year (Oberdorff et al. 2001).
- *mean oxygen concentration during July* (mg.L⁻¹) (OXY). This variable was generated with the RIVERSTRAHLER/SENEQUE model output for July considering that summer corresponds to the most restrictive period for water quality. Oxygen concentration is a crucial factor for fish distribution (Matthews et al. 1992).
- *mean ammonium concentration during July* (mg.L⁻¹) (AMMO). Like OXY, this variable was generated with the RIVERSTRAHLER/SENEQUE model output for July. Ammonium concentration potentially reflects the degree of organic pollution and may have a toxic effect for fish (Matthews et al. 1992).
- *maximum chlorophyll concentration during July* (µg.L⁻¹) (CHLO). This variable was generated with the RIVERSTRAHLER/SENEQUE model output for July. Chlorophyll concentration reflects the degree of eutrophication which may affect fish communities (Matthews et al. 1992).
- *River channelization* (yes or no) (CHE). In our case, river channelization mainly concerned channelization for navigation purposes. This has major impacts on river morphology, potentially negatively affecting fish species (Wolter et al. 2004).
- *proportion of lakes and ponds on the proximate catchment* (%) (LAK). We calculated the area of lakes and ponds present in the proximate catchment, i.e. the portion of the total catchment drained by the river reach considered. We hypothesize that lakes and ponds may act as colonization sources for some fish species (particularly warm-water

fish species) and more globally may affect river ecosystem functioning and consequently fish distributions (Falke & Gido 2004).

Before their integration into species distribution models, the environmental variables were first transformed to normalize their distribution (Table 2).

Table 2. Preliminary transformations of environmental variables before their utilization in fish models.

Variable	Transformation
CA	$\text{Log}_{10}(x)$
SLO	$\text{Log}_{10}(x + 0.1)$
Tju	No transformation
ΔT	No transformation
OXY	No transformation
AMMO	$\text{Log}_{10}(x + 0.001)$
CHLO	$\text{Log}_{10}(x)$
CHE	0 (chanelized) ; 1 (nonchannelized)
LAK	$\text{Log}_{10}(100x + 0.1)$

Species models

To predict the probability of presence of a given species ($p(x)$) as a function of an environmental variable (x), we used the logistic regression model following the expression:

$$p(x) = \frac{e^{a_0 + a_1x + a_2x^2}}{1 + e^{a_0 + a_1x + a_2x^2}}$$

For this model, the resulting response is a sigmoid (when a_2 approaches 0) or a symmetrical and bell-shaped curve, consistent with typical species responses to ecological gradients. The previous equation was extended to include more than one variable in order to take into account all the possible environmental gradients. To determine the minimum adequate set of variables for each species model, we applied stepwise procedures which automatically add and remove terms from a given model. At each step, a new parameter is added to the minimal model if it significantly reduces the unexplained deviance (see Oberdorff et al. 2001 for further detail).

Each species model provides a predicted value between 0 and 1. Intuitively, a threshold value of 0.5 is chosen to decide if the model predicts an absence (<0.5) or a presence (>0.5). In the present case, we preferred to optimize the choice of the threshold value in order to optimize the correct classifications of both presence and absence.

We used different criteria to test the accuracy of species models. The percentage of good predictions (presence and absence) is the simplest parameter to measure model achievement. To detail this aspect, we also used sensitivity (% of accurate prediction of presence) and specificity (% of accurate prediction of absence). The Kappa index (theoretical variation 0 to 1) is currently used to measure whether the rate of a model's accurate predictions is better than expected by chance. For a given model, a Kappa value greater than 0.4 is generally considered as relevant to use in a predictive way (Pont et al. 2004).

An alternative solution to assess model efficiency uses the ROC (receiver operating characteristic) curve, which is a graphical plot of the sensitivity vs. (1 - specificity).

Considering the ROC curve, the area under the curve (AUC) is frequently used as an indicator of classification accuracy (the AUC value tends to 1 for a perfect distinction between presence and absence). The AUC value is an indicator independent of the threshold value fixed to discriminate presence and absence.

For a given river reach, considering its environmental characteristics, we used each fish model to predict the probability of presence of a given species. By summing the results of all species models (or only a part of them), we were able to predict the total species richness of the fish assemblage (or a subset of it).

Results

Species models

Analysis of the 25 species models first allows one to assess the predictive efficiency of each of them (Table 3) and second to identify the major environmental factors controlling species distribution and/or assemblage composition (Table 4).

Model quality varies greatly depending on species, as illustrated by AUC values (0.708–0.917). It can be considered accurate for 16 species (AUC > 0.8). Conversely, for four species (three-spine stickleback, brook lamprey, pumpkinseed and tench), the AUC values were lower than 0.75, a sign of poor predictive ability.

For each species model, a threshold value is determined in order to maximize both sensitivity and specificity. Based on these threshold values and depending on the fish species, the percentage of accurate classifications (in terms of presence or absence) fluctuates between 63 and 86%. Globally, the Kappa index varies consistently with the AUC values. If we retain a Kappa value of 0.4 to identify reliable models, we can consider that almost all the species models could be used for predictive purposes (Table 3).

Table 3. Species occurrence, threshold probability, sensitivity, specificity, overall correct classification (OCC), kappa index (Kappa) and area under the receiver operating characteristic (ROC) curve (AUC) for the different species models.

Species	Occurrence	Threshold	Sensitivity	Specificity	OCC	Kappa	AUC
Barbel	56	0.355	0.875	0.851	0.857	0.823	0.917
Bleak	79	0.33	0.823	0.834	0.83	0.775	0.912
Bitterling	33	0.14	0.848	0.802	0.809	0.759	0.915
Brook lamprey	87	0.395	0.667	0.65	0.657	0.436	0.708
Brown trout	124	0.545	0.774	0.774	0.774	0.632	0.832
Chub	166	0.675	0.807	0.781	0.8	0.583	0.853
Common bream	39	0.155	0.718	0.66	0.67	0.497	0.778
Common nase	49	0.25	0.796	0.801	0.8	0.741	0.892
Dace	101	0.46	0.752	0.752	0.752	0.622	0.792
Eel	101	0.425	0.812	0.798	0.804	0.714	0.888
Gudgeon	150	0.67	0.68	0.663	0.674	0.374	0.754
White bream	33	0.165	0.848	0.812	0.817	0.773	0.895
Minnow	139	0.615	0.799	0.791	0.796	0.646	0.889
Nine-spine stickleback	56	0.265	0.696	0.684	0.687	0.528	0.751
Northern Pike	91	0.445	0.714	0.727	0.722	0.575	0.814
Perch	120	0.51	0.75	0.755	0.752	0.598	0.832
Pumpkinseed	31	0.165	0.71	0.714	0.713	0.593	0.727
Roach	154	0.655	0.792	0.763	0.783	0.582	0.832
Ruffe	29	0.125	0.724	0.726	0.726	0.619	0.787
Rudd	45	0.24	0.778	0.784	0.783	0.714	0.827
Sculpin	170	0.745	0.8	0.783	0.796	0.563	0.858
Spiralin	43	0.195	0.791	0.786	0.787	0.722	0.884
Stone loach	159	0.76	0.83	0.817	0.826	0.659	0.888
Three-spine stickleback	51	0.23	0.647	0.67	0.665	0.486	0.717

Table 4. Logistic models obtained for each of the 25 species.

Species	intercept	CA	CA ²	SLO	Tju	Tju ²	ΔT	ΔT ²	OXY	OXY ²	AMMO	AMMO ²	CHLO	CHLO ²	CHE	LAK	LAK ²
Barbel	-68.193	30.018	-4.39				1.062				-0.588						
Bitterling	-594.356	2.63			-2.493		78.902	-2.458							2.706	1.033	-1.084
Bleak	-66.462	2.215							13.325	-0.762			2.056				
Brook lamprey	1.701	-0.86															-0.279
Brown trout	11.52			1.599	-1.105		0.616										-0.407
Chub	-14.727	2.267					0.63										
Common bream	-433.227	1.281			43.558	-1.108											
Common nase	97.704	8.519	-1.112		-40.578	1.041	33.666	-1.008					0.89				
Dace	-21.026	5.594	-0.719				0.595								1.844		
Eel	-17.99	1.712					-1.271		7.942	-0.446	2.496	0.669					
Gudgeon	-115.583	3.567	-0.458				13.577	-4.23							1.854		
Minnow	-4.368	9.25	-1.819		-1.345		1.147						5.052	-2.074			-0.682
Northern Pike	-399.469	6.923	-0.981		39.598	-1.011					-0.395						0.635
Nine-spine stickleback	-326.736	5.298	-1.123		33.817	-0.864	-0.678										
Perch	-46.473	1.745							9.31	-0.512							0.57
Pumpkinseed	-187.871						24.068	-0.759	-0.469								
Roach	-134.032	4.674	-0.729				16.28	-0.518					1.095				0.479
Ruffe	-9.532	1.589											0.827		2.369		
Rudd	-7.425			-1.601					0.633								0.943
Sculpin	504.808	4.696	-0.952		-52.201	-1.3	0.907										
Spirilin	-22.143	2.549					1.287		-9.199	0.548					30.766		
Stone loach	-134.538	9.364	-1.914				15.235	-0.461									
Tench	-2.255			-1.204											1.308	0.431	
Three-spine stickleback	21.064	3.447	-0.587		-1.394												
White bream	-814.962	8.488	-1.143	-2.407	81.977	-2.104											

All nine environmental variables were retained, at least once, in the different species models (Table 4). Variables that were quasi-independent of human activities (i.e. CA and/or SLO) were integrated in all but one species model illustrating the species' preferences in relation to river size and/or flow velocity (see Fig. 12 for examples).

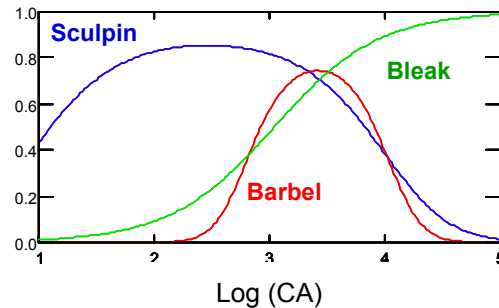


Fig. 12. Probability of presence vs. catchment area (Log-transformed) for different species.

Variables related to thermal conditions (T_{ju} and ΔT) are included in a large majority of models (20 out of 25), attesting to the importance of temperature and more broadly climatic conditions in species distribution. This situation also illustrates the potential sensitivity to climate change of the whole fish assemblages. It can be emphasized that several species such as brown trout (Fig. 13) show a clear preference for low temperatures and considerably decrease when temperature increases.

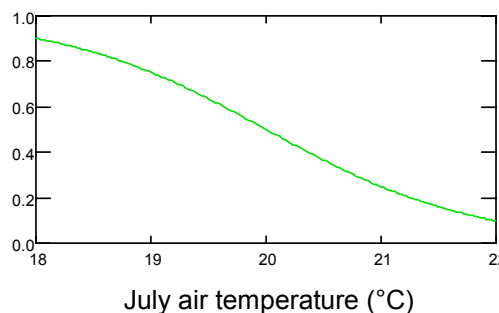


Fig. 13. Probability of presence of brown trout vs. July mean air temperature.

Variables related to water quality are included in 12 models illustrating once again the potential sensitivity of fish assemblages according to water quality degradation. For several species (bleak, roach and common nase), the probability of occurrence increases with chlorophyll concentration, suggesting that eutrophication could favour their populations.

The effect of channelization is detected for six species (bitterling, gudgeon, ruffe, spirulin, tench and dace) and always with a detrimental consequence. This adverse effect is particularly noticeable for spirulin, since this species was never noted on channelized reaches on our data set.

Abundance of lakes and ponds on the close catchment is frequently included in species models. It tends to favour species such as pike, roach, perch, rudd and tench. All these species are limnophilic and well adapted to stagnant waters. We hypothesize that for these species, lakes and ponds act as sources to colonize connected flowing waters. Conversely, brown trout and associated species (minnow, brook lamprey) tend to regress with lake abundance. This effect could result from a modification of downstream environmental conditions (water temperature

increase and water quality change) or establishment of barriers preventing fish migration and especially access to spawning grounds.

Spatial extrapolations

Fish models were built on a limited data set of 230 sites located on 208 different river reaches. Since environmental variables are available for all 5163 reaches composing our GIS, we are able to predict species occurrence for all of them and then map species distribution at the whole Seine River basin scale. To illustrate the possibilities of spatial extrapolation, we present here two examples of species prediction.

The map for minnow illustrates the case of a species located much more in upstream habitats even if it seems to avoid, to some extent, smaller streams (Fig. 14). Conversely, minnow is systematically absent from large rivers when the catchment area exceeds a few thousand square kilometres. Like several other species, minnow seems to favour a high temperature contrast between winter and summer, leading to a higher occurrence of this species in the eastern part of the basin.

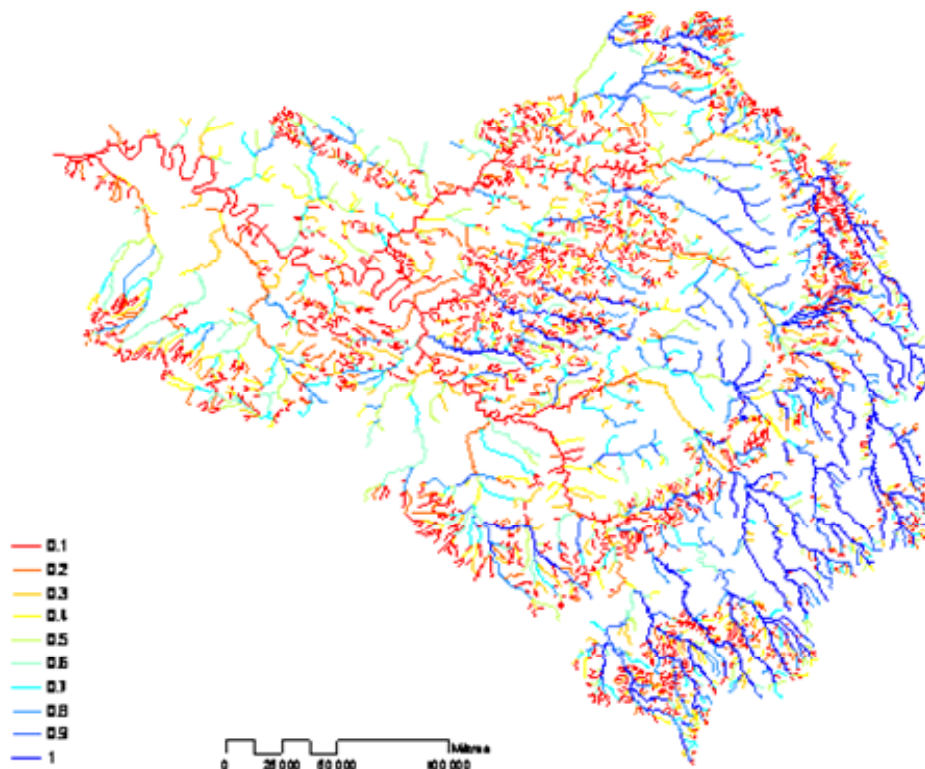


Fig. 14. Probability of presence for minnow in the Seine River network.

The map for bleak illustrates the opposite situation since this species is mainly restricted to the downstream parts of the system corresponding to a relatively low proportion of river network (Fig. 15). This species is mostly absent (or very poorly represented) in headwaters. It should be underlined that bleak seems to persist quite well in the most downstream reaches combining poor water quality and heavy morphological degradation.

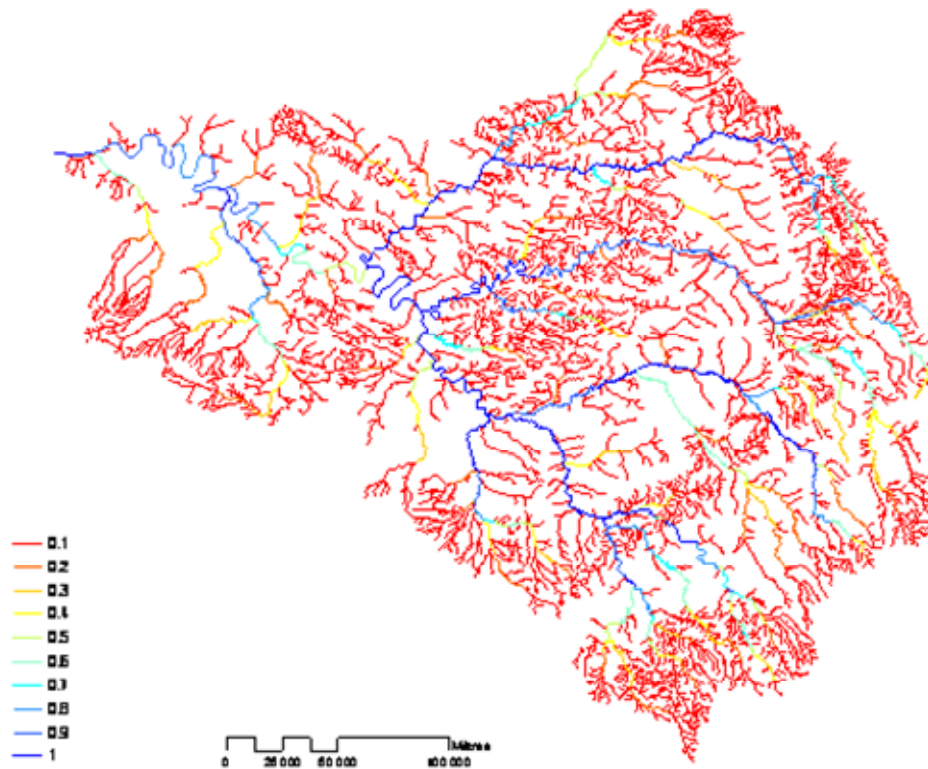


Fig. 15. Predicted probability of presence for dace in the Seine River network.

By summing the results of the 25 species models, we were able to predict the assemblage species richness. The map of species richness (Fig. 16) illustrates an original feature of the Seine basin: the species richness tends to increase from sources to intermediate river reaches in accordance with the classical model observed for other basins and to reach maximum values for large rivers only slightly impacted by human activities. Conversely, assemblage species richness tends to decrease more downstream with anthropogenic pressure intensification to reach lower values in the Seine River downstream of Paris (Boët et al. 1999).

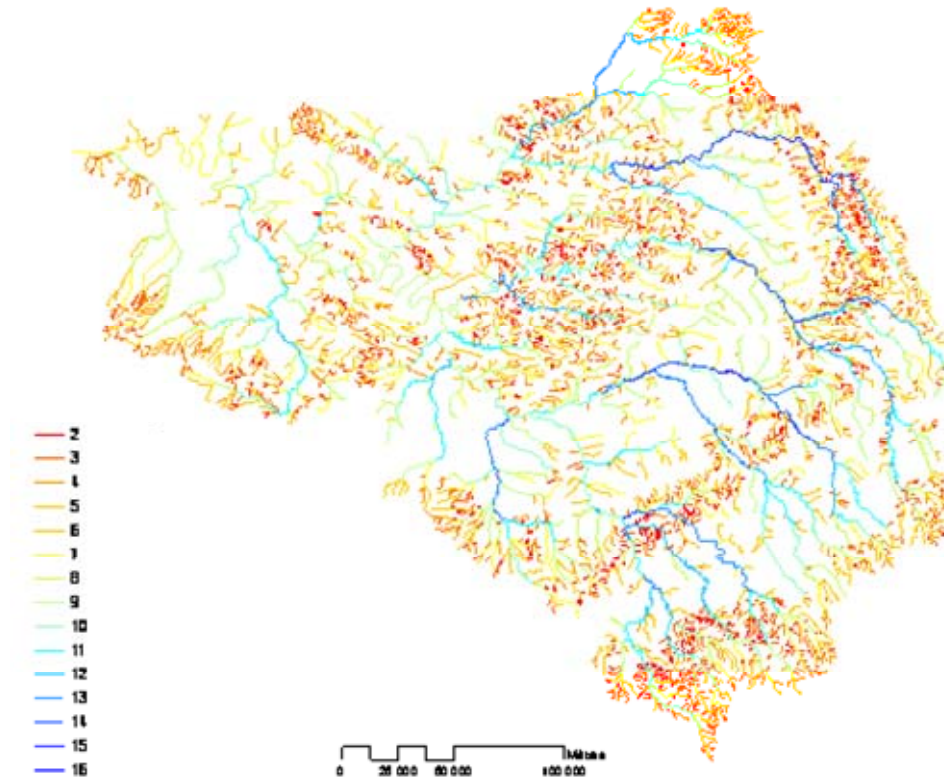


Fig. 16. Predicted species richness of the fish assemblage in the Seine River network.

Tests of restoration scenarios

Using species models, we are able to assess how modification of environmental conditions could affect species distribution and fish assemblage composition. Here we discuss three types of hypotheses related to river restoration and their possible consequences on fish assemblages: (1) limitation of channelization, (2) water quality improvement and (3) creation of ponds in order to reduce non-point source pollution (Blankenberg et al. 2006). We have to keep in mind that the scenarios tested hereafter are not totally realistic but are much more widely used to assess the scale of fish assemblage modifications that can be expected.

River channelization remediation

We saw above that river channelization negatively affects several fish species (bitterling, gudgeon, ruffe, spirlin, tench and dace) and consequently we can expect a spreading of their distribution with channelization remediation. However, it should be emphasized that channelization taken into account in fish models essentially concerns channelization for navigation purposes, which in turn goes along with reduced length of river network. For reaches used for commercial navigation, measures to reduce negative impacts (e.g. reconnection of side arms and improvement of habitat river banks) can be imagined, but this does not radically change river habitat deterioration and substantial fish assemblage improvements cannot be expected. Further, several projects plan to channelize new waterways (particularly for the Seine and Oise rivers) in order to promote fluvial transport, which will inevitably negatively impact some fish species.

For smaller rivers, the consequences of river channelization remediation are more uncertain. Some remediation measures such as re-meandering also reduce river slope and potentially negatively impact certain rheophilic species and positively impact limnophilic ones.

Overall, for the Seine river basin, we do not expect major effects of channelization remediation on fish assemblages, either because remediation possibilities are severely restricted for navigated reaches or because channelization in fact concerns a limited length of the total river network.

Water quality improvement

To test the possible effect of water quality on fish assemblages, we tested two scenarios and their consequences on model predictions. In the first scenario, we hypothesize a general reduction of organic pollution leading to an increase of oxygen concentration and a decrease of ammonium concentration. We assumed that oxygen concentration is higher than 8 mg.L^{-1} (for rivers with catchment area under 5000 km^2) or 6 mg.L^{-1} (for large rivers with catchment area over 5000 km^2) and that ammonium concentration is lower than 0.5 mg.L^{-1} for all river reaches (when these threshold values have already been achieved for a given reach, we used the present-day water conditions for model predictions). In the second scenario, we hypothesize a reduction of eutrophication on the whole basin scale assuming that chlorophyll concentration never exceeds $10 \mu\text{g.L}^{-1}$.

To assess the possible consequences of water quality improvement on fish assemblages, we looked at the total fish species richness predicted by the models (Table 5).

Whatever the scenario, the effect on species richness predictions seems very limited, raising two different observations. First, total species richness is a very synthetic indicator and even if total species richness is relatively constant, this may in fact hide modifications in terms of species composition. Second, the Seine River basin has experienced a considerable reduction of organic pollution during the past few decades and opportunities to continue reducing this pollution are probably limited. Therefore, the reference year used for water quality assessment (2000) presents a relatively acceptable situation for oxygen ammonium and chlorophyll for the whole Seine basin. Moreover, we emphasize that water quality variables are derived from model predictions and it is very likely that, locally, some pollution sources were missed in the RIVERSTRAHLER/SENEQUE system.

It is interesting to note that, even if their effects are very low (keeping in mind that this study investigates more than 5000 river reaches), both organic pollution and eutrophication reduction lead to a decrease of species richness, suggesting that a moderate pollution level may favour some fish species.

Table 5. Percentage of river reaches vs. prediction of fish assemblage species richness considering (1) the present-day environmental condition, (2) a scenario of organic pollution reduction and (3) a scenario of eutrophication reduction.

Species richness	Present-day conditions	Reduction of organic pollution	Reduction of eutrophication
2	0.1317	0.1365	0.1317
3	0.2179	0.2189	0.2179
4	0.1321	0.13	0.1321
5	0.103	0.1007	0.103
6	0.0854	0.086	0.0856
7	0.079	0.0788	0.0798
8	0.0581	0.0566	0.0591
9	0.042	0.0418	0.0424
10	0.0498	0.05	0.0546
11	0.0416	0.0413	0.0383
12	0.0238	0.0238	0.0263
13	0.0201	0.0201	0.018
14	0.0122	0.0124	0.0108
15	0.0031	0.0031	0.0002

Creation of ponds on headwater catchments

The creation of ponds on headwater catchments is currently proposed as a possible solution to reduce non-point source pollution, particularly from agriculture. Indeed, ponds seem to favour the denitrification process and reduce pesticide flux to adjacent river systems by stocking or degrading molecules. We tested a scenario corresponding to a general creation of ponds on small catchments. We hypothesize that for all river reaches draining a catchment smaller than 300 km², ponds account for 5‰ of the total catchment area; in other words, this means that for 10 km² of land, 0.5 ha of ponds are present (for territories where pond areas are already greater than 5‰, we have retained the actual values). The other environmental variables remained unchanged to run fish models.

Considering this new environmental condition, we looked at the potential consequences on fish assemblages and more specifically on species richness of limnophilic fish vs. typically headwater species (brown trout, sculpin, minnow, stone loach and brook lamprey). Widespread implantation of ponds on headwaters would lead to a clear colonization of small streams by limnophilic species. Thus, three reaches out of four for which models predict an absence of limnophilic species under present-day conditions would be colonized by one or more species (Fig. 17 & Fig. 18).

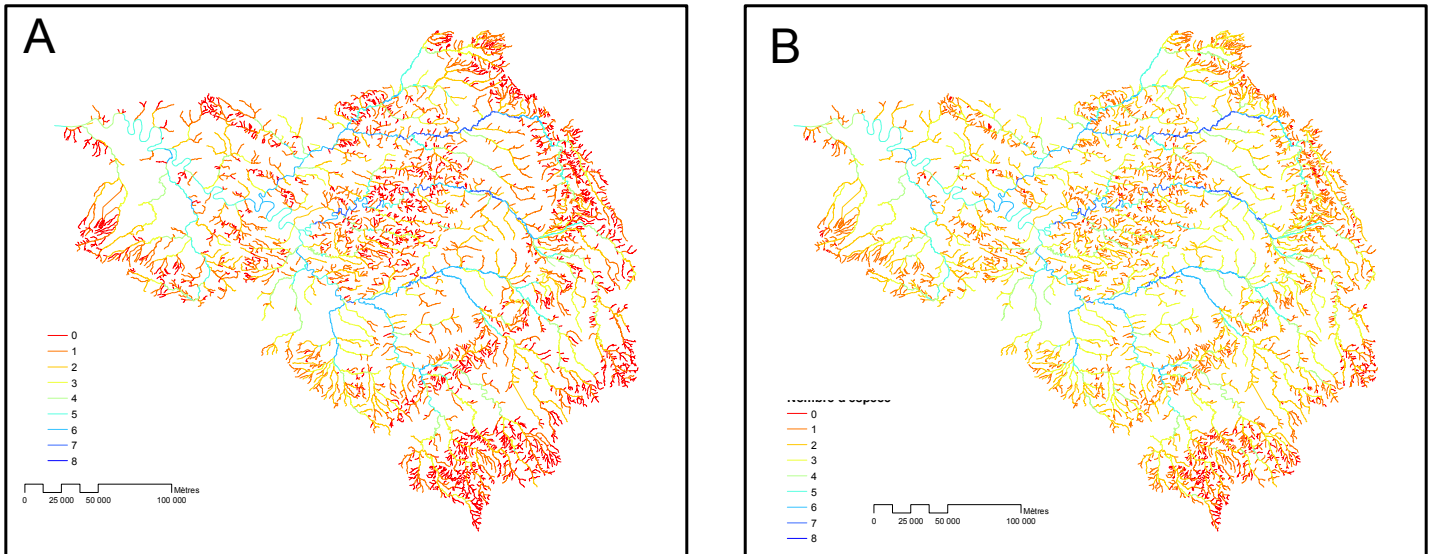


Fig. 17. Predicted species richness of limnophilic fish considering present-day environmental conditions (A) and a widespread implantation of ponds on headwater catchments.

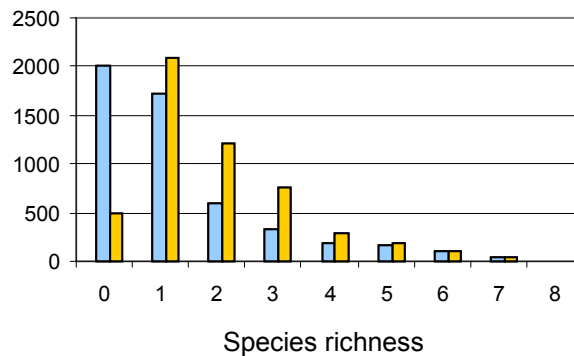


Fig. 18. Number of river reaches vs. predicted species richness of limnophilic fish considering present-day environmental conditions (blue bars) and a widespread implantation of ponds on headwater catchments (orange bars).

Conversely, widespread implantation of ponds would go with a reduction of typical headwater species, with a much greater reduction for reaches that currently host richer assemblages for this type of species (60% reduction of situations with four species and increasing situations with only one or two species) (Fig. 19 & Fig. 20).

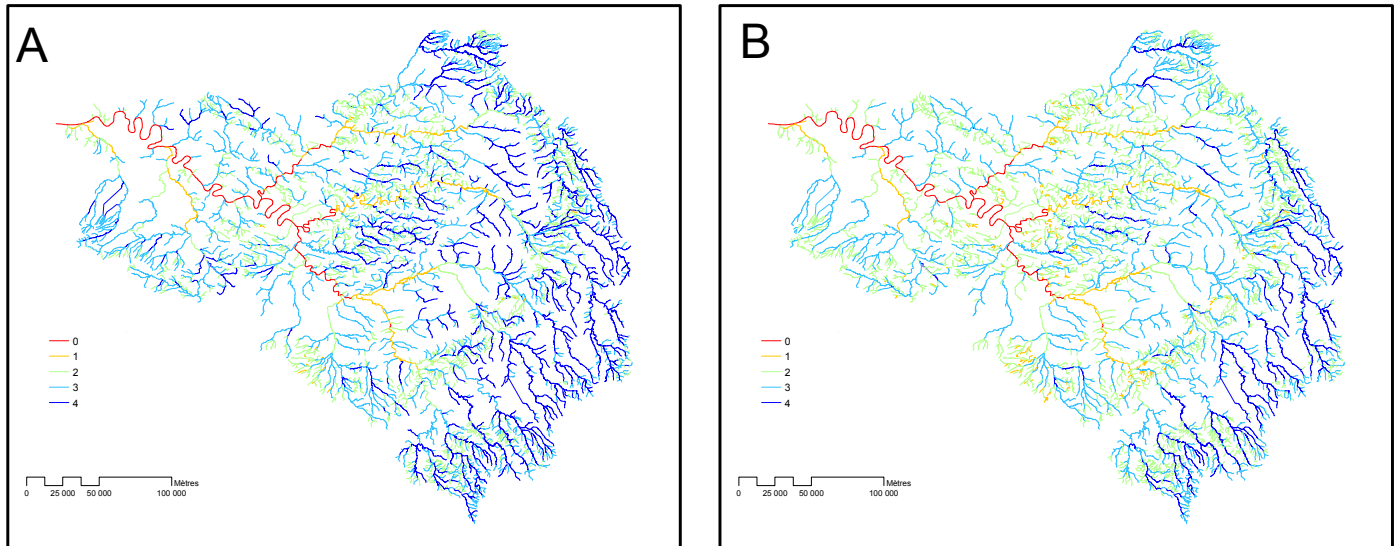


Fig. 19. Predicted species richness of headwater fish considering present-day environmental conditions (A) and a widespread implantation of ponds on headwater catchments.

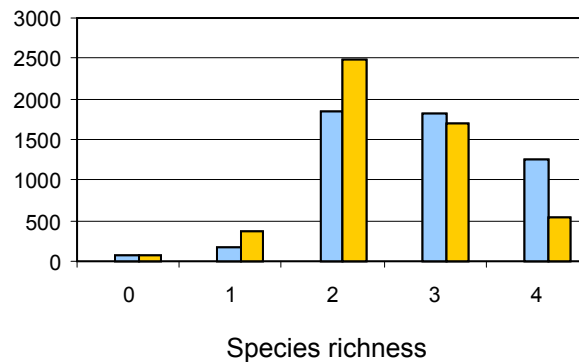


Fig. 20. Number of river reaches vs. predicted species richness of headwater fish considering present-day environmental conditions (blue bars) and a widespread implantation of ponds on headwater catchments (orange bars).

Overall, the models' predictions suggest that a widespread implantation of ponds on headwater catchments could have important consequences for fish assemblage composition in small streams.

Main conclusions

1. Regardless of the scenario considered, fish models predict a dramatic modification of most species distribution on the Seine River basin.
2. For nine species (out of 23 species studied), models predict a more or less significant decline of their distribution area. For some species such as grayling or sculpin, for the decade 2050–2060, this could lead to a total extinction on the whole Seine basin in terms of its natural environmental homogeneity. This decline basically concerned cold-water and/or headwater fish species.
3. Conversely, according to model predictions, six species could extend their distribution area on the Seine basin. However, in upstream rivers it seems that possible colonizations of new

species would not compensate for headwater species local extinction, leading to a probable reduction of species richness in fish assemblages.

4. Compared to climate change impacts, human pressure reductions that we have tested (river channelization remediation, pollution reduction and creation of ponds on headwater catchment to reduce agricultural impacts) seems to have relatively little effect on fish assemblages.

5. River channelization has potential detrimental effects on several species. However, because channelization actually concerns a limited length of the Seine River network and is generally related to essential human activities (e.g. commercial navigation), we believe that river channelization remediation would have a limited and local effect on fish assemblages.

6. We tested different scenarios of water quality (organic pollution eutrophication) improvement, and their effects on fish species richness are very limited and concern a small number of river reaches. The fact that present water quality is globally acceptable on a large part of the Seine basin explains this situation. It is noteworthy that reduction of organic pollution or eutrophication leads to a (limited) reduction of fish species richness, suggesting that a limited level of pollution may benefit some species.

7. Construction of ponds in the catchment headwaters, in order to reduce agricultural impacts, is the measure with the greatest potential to affect fish assemblages (but we did not integrate the consequences of associated water quality modifications). We predict a decline of typical headwater species and jointly colonization of small streams by limnophilic species.

CHAPTER V

Synthesis

Species niche and functional traits

Diverse responses to environmental gradients

The 23 European fish species presented contrasting responses to the four environmental gradients considered: mean air temperature in July, thermal amplitude between July and January, stream power (integrating precipitations), and upstream drainage area. The main factors driving species occurrences are upstream drainage and temperatures in July. The influence of stream power is also important, even if lower than the other two factors (this varies between species) and the influence of the thermal amplitude on species occurrence is relatively low.

In accordance with species niche theory, most of the species presented bell-shaped response curves along the thermal gradients, but with different optima and thermal tolerance ranges. The species ordination along the thermal gradient is consistent with species' optima found in the literature. Salmonids (brown trout and Atlantic salmon) prefer cold water streams and cyprinids prefer warmer conditions, especially bitterling and bleak, which have the highest thermal optima. The response patterns to the other environmental gradients showed greater contrast for the other environmental factors but were mostly consistent with the known ecology of the 23 fish species.

Uncertainty around environment–occurrence relationships

There is empirical evidence that the uncertainty around environment–occurrence relationships varies between species and between the environmental factors considered. Uncertainty around species' thermal preferences is in general low, except on the edge of the thermal gradients. Higher uncertainty values are observed along the other environmental gradients, especially for stream power. These results demonstrate the relevance of assessing uncertainty associated with model predictions, especially when projecting future species distribution.

Species niche-based and trait-based metrics are very similar

There is strong empirical evidence that metric values derived from the niche species models and metric values predicted from models relating functional traits to environmental conditions are relatively similar. Both approaches have their pros and cons, but using trait models enables one to predict the functional structure of fish assemblage at a very large scale whatever the biogeographical variations between the different European regions.

Climate change impact on fish BQE

Climate change

The four climatic scenarios predict different magnitudes of climate change, but the predicted patterns are consistent. For the 2020–2030 period, the greatest changes are predicted with the B2 scenario, while for 2050–2060 the greatest changes are predicted with the A1F1 scenario. For

the 2020–2030 period, the greatest increase in temperature will be observed in January, while it will be observed for July for the 2050–2060 period. For precipitations, the 2020–2030 period would be the driest period compared to the current conditions and to the projections for 2020–2030.

Projected species distributions: which will benefit from climate change?

All scenarios provide the same pattern of species responses to climate change, only the magnitudes of these responses differ. There is clear evidence that cold-water species will be considerably negatively affected by climate change, whereas some warm-water species will benefit. Indeed the stream sections with suitable environmental conditions will be greatly reduced for species such as Atlantic salmon and grayling, whereas bitterling and bleak will occur in many more reaches. For species with intermediate thermal preferences, the response patterns are more contrasted, with environmental conditions becoming either suitable or unsuitable. For these species, a shift in their distribution is expected, both at the watershed scale and over their distribution area.

Climate change or human pressures?

The projections highlight that climate change would be the major threat for cold-water species, even if the effects of human pressures cannot be neglected. These conclusions are supported by the Traun River case study in Austria and by the Seine basin case study. The Traun River case study clearly demonstrated the shift of assemblage composition due to increasing water temperatures during the last three decades. The fish assemblage was historically dominated by the grayling, which sharply declined over this period and was replaced by species with warmer thermal tolerances such as barbel. The Seine basin case study highlights that water quality improvement would lead to more suitable habitats for intolerant species, but that climate change effects would overwhelm the potential benefits of such restoration measures. For instance, environmental conditions would become much more favourable for salmonids with water quality enhancement, but the increase of temperatures predicted from the different gas emission scenarios will lead to limiting conditions for these species. This study also reflects the contrast between economic development and biological conservation. Indeed, environmental conditions could be enhanced for some species with channelization remediation; in this basin several projects plan to channelize new waterways to promote fluvial transport. The two studies illustrate the need to take into account climate change before planning restoration measures to reintroduce or sustain wild populations of fish. Except for water cooling, no restoration measures could help the conservation of the grayling in the section of the Traun River studied or in the Seine basin.

For some species, it is obvious that both climate change and human pressures will influence their future distribution, but it was not really possible to prioritize these two effects. Under undisturbed conditions, some species are projected to expand their distribution. Therefore, these species should find suitable climatic conditions in impaired areas in which their occurrences could be limited by anthropogenic stressors. Additional research is necessary to better assess the

relative influence of environment and human activities on species occurrence and thus on their future distribution.

SDMs: useful tools when uncertainty is provided

There is clear evidence that species distribution models could be useful tools for water managers, especially to help them prioritize the restoration actions depending on the probability of presence of a given species in the future. Nevertheless, for some species the uncertainty associated with the predictions is too great to have a clear understanding of what would happen to their distribution. Therefore, it could be highly recommended to associate uncertainty with the projections such that water managers could have an indication on the reliability of these predictions and thus on the risk and/or probability of the success of restoration actions.

Climate change impacts on the use of multimetric indices based on functional traits

In addition to local species composition; the functional structure of fish assemblages will be modified by climate change. The shift in the magnitude of the reference conditions will depend of functional traits; traits based on species tolerances will be the most severely affected. These shifts clearly indicate that over the period of the Water Framework Directive it will be necessary to revise the multimetric indices based on functional traits, which are commonly used now, such as the European Fish Index. Some of the metrics included in these indices would not be represented in future fish assemblages. This is especially true for metrics based on species intolerance, which are widely used due to their responses to human degradation. Therefore, the index scores will be computed on metrics that will become naturally absent or only slightly represented, leading to inconsistent assessment of stream ecological conditions. Moreover, if the wish to intercalibrate indices is maintained over the Water Framework Directive, it would also be necessary to revise the common index used for this process. Indeed, this index is a combination of metrics based on species intolerance, which is expected to be strongly affected by climate change.

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Appendices

Appendix 1: Match between potential and projected species distributions

2020–2030

Scenario A1F1

Table 6: Match between species predicted occurrences for current climate and projected climate under the A1F1 scenario for 2020–2030. Absence: number of sites with species always considered absent; presence: number of sites where species is always expected to occur; new absence: number of sites with expected population extinctions; new occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1179	440	131	126
<i>Alburnus alburnus</i>	2137	1534	2	443
<i>Anguilla anguilla</i>	2573	1612	85	221
<i>Barbatula barbatula</i>	1307	1719	362	242
<i>Barbus barbus</i>	1510	983	105	364
<i>Chondrostoma nasus</i>	701	603	145	299
<i>Cottus gobio</i>	1526	994	1055	127
<i>Esox lucius</i>	2829	1237	213	188
<i>Gasterosteus aculeatus</i>	2444	481	382	114
<i>Gobio gobio</i>	2082	1455	181	333
<i>Lampetra planeri</i>	2802	946	372	65
<i>Leuciscus cephalus</i>	1243	1594	191	681
<i>Leuciscus leuciscus</i>	1776	960	157	321
<i>Lota lota</i>	1442	953	44	12
<i>Perca fluviatilis</i>	1415	1437	261	396
<i>Phoxinus phoxinus</i>	1653	1612	474	143
<i>Pungitius pungitius</i>	2075	195	300	312
<i>Rhodeus amarus</i>	704	1210	32	600
<i>Rutilus rutilus</i>	1506	1474	218	462
<i>Salmo salar</i>	1735	754	551	0
<i>Salmo trutta</i>	2069	1769	666	4
<i>Telestes souffia</i>	689	161	132	418
<i>Thymallus thymallus</i>	2267	443	542	33

Scenario A2

Table 7: Match between species predicted occurrences for current climate and projected climate under the A2 scenario for 2020–2030. Absence: number of sites with species always considered absent; presence: number of sites where species is always expected to occur; new absence: number of sites with expected population extinctions; new occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1177	446	125	128
<i>Alburnus alburnus</i>	2155	1534	2	425
<i>Anguilla anguilla</i>	2555	1621	76	239
<i>Barbatula barbatula</i>	1310	1753	328	239
<i>Barbus barbus</i>	1512	986	102	362
<i>Chondrostoma nasus</i>	709	605	143	291
<i>Cottus gobio</i>	1529	1020	1029	124
<i>Esox lucius</i>	2835	1250	200	182
<i>Gasterosteus aculeatus</i>	2448	485	378	110
<i>Gobio gobio</i>	2090	1472	164	325
<i>Lampetra planeri</i>	2803	958	360	64
<i>Leuciscus cephalus</i>	1261	1599	186	663
<i>Leuciscus leuciscus</i>	1776	969	148	321
<i>Lota lota</i>	1441	958	39	13
<i>Perca fluviatilis</i>	1415	1445	253	396
<i>Phoxinus phoxinus</i>	1652	1653	433	144
<i>Pungitius pungitius</i>	2074	195	300	313
<i>Rhodeus amarus</i>	717	1211	31	587
<i>Rutilus rutilus</i>	1520	1482	210	448
<i>Salmo salar</i>	1735	777	528	0
<i>Salmo trutta</i>	2068	1810	625	5
<i>Telestes souffia</i>	702	166	127	405
<i>Thymallus thymallus</i>	2267	449	536	33

Scenario B1

Table 8: Match between species predicted occurrences for current climate and projected climate under the B1 scenario for 2020–2030. Absence: number of sites with species always considered absent; presence: number of sites where species is always expected to occur; new absence: number of sites with expected population extinctions; new occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1180	436	135	125
<i>Alburnus alburnus</i>	2150	1534	2	430
<i>Anguilla anguilla</i>	2539	1630	67	255
<i>Barbatula barbatula</i>	1315	1745	336	234
<i>Barbus barbus</i>	1506	984	104	368
<i>Chondrostoma nasus</i>	699	607	141	301
<i>Cottus gobio</i>	1532	996	1053	121
<i>Esox lucius</i>	2831	1243	207	186
<i>Gasterosteus aculeatus</i>	2445	466	397	113
<i>Gobio gobio</i>	2092	1457	179	323
<i>Lampetra planeri</i>	2801	941	377	66
<i>Leuciscus cephalus</i>	1255	1583	202	669
<i>Leuciscus leuciscus</i>	1770	972	145	327
<i>Lota lota</i>	1449	947	50	5
<i>Perca fluviatilis</i>	1416	1439	259	395
<i>Phoxinus phoxinus</i>	1656	1636	450	140
<i>Pungitius pungitius</i>	2077	192	303	310
<i>Rhodeus amarus</i>	713	1206	36	591
<i>Rutilus rutilus</i>	1504	1478	214	464
<i>Salmo salar</i>	1735	776	529	0
<i>Salmo trutta</i>	2067	1825	610	6
<i>Telestes souffia</i>	682	163	130	425
<i>Thymallus thymallus</i>	2269	437	548	31

Scenario B2

Table 9: Match between species predicted occurrences for current climate and projected climate under the B2 scenario for 2020–2030. Absence: number of sites with species always considered absent; presence: number of sites where species is always expected to occur; new absence: number of sites with expected population extinctions; new occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1182	434	137	123
<i>Alburnus alburnus</i>	2147	1534	2	433
<i>Anguilla anguilla</i>	2536	1633	64	258
<i>Barbatula barbatula</i>	1310	1739	342	239
<i>Barbus barbus</i>	1502	983	105	372
<i>Chondrostoma nasus</i>	703	601	147	297
<i>Cottus gobio</i>	1529	988	1061	124
<i>Esox lucius</i>	2827	1239	211	190
<i>Gasterosteus aculeatus</i>	2442	446	417	116
<i>Gobio gobio</i>	2089	1450	186	326
<i>Lampetra planeri</i>	2799	932	386	68
<i>Leuciscus cephalus</i>	1244	1589	196	680
<i>Leuciscus leuciscus</i>	1756	968	149	341
<i>Lota lota</i>	1444	948	49	10
<i>Perca fluviatilis</i>	1409	1435	263	402
<i>Phoxinus phoxinus</i>	1651	1629	457	145
<i>Pungitius pungitius</i>	2075	186	309	312
<i>Rhodeus amarus</i>	715	1206	36	589
<i>Rutilus rutilus</i>	1503	1472	220	465
<i>Salmo salar</i>	1735	757	548	0
<i>Salmo trutta</i>	2069	1820	615	4
<i>Telestes souffia</i>	687	163	130	420
<i>Thymallus thymallus</i>	2266	429	556	34

2050–2060

Scenario A1F1

Table 10: Match between species predicted occurrences for current climate and projected climate under the A1F1 scenario for 2050–2060. Absence: number of sites with species always considered absent; presence: number of sites where species is always expected to occur; new absence: number of sites with expected population extinctions; new occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1159	270	301	146
<i>Alburnus alburnus</i>	1662	1530	6	918
<i>Anguilla anguilla</i>	2733	1242	455	61
<i>Barbatula barbatula</i>	1230	1171	910	319
<i>Barbus barbus</i>	1439	734	354	435
<i>Chondrostoma nasus</i>	739	291	457	261
<i>Cottus gobio</i>	1527	321	1728	126
<i>Esox lucius</i>	2803	917	533	214
<i>Gasterosteus aculeatus</i>	2454	176	687	104
<i>Gobio gobio</i>	1991	1106	530	424
<i>Lampetra planeri</i>	2799	509	809	68
<i>Leuciscus cephalus</i>	1048	1207	578	876
<i>Leuciscus leuciscus</i>	1778	666	451	319
<i>Lota lota</i>	1364	985	12	90
<i>Perca fluviatilis</i>	1404	996	702	407
<i>Phoxinus phoxinus</i>	1634	986	1100	162
<i>Pungitius pungitius</i>	2201	45	450	186
<i>Rhodeus amarus</i>	433	1081	161	871
<i>Rutilus rutilus</i>	1483	1122	570	485
<i>Salmo salar</i>	1735	275	1030	0
<i>Salmo trutta</i>	2071	882	1553	2
<i>Telestes souffia</i>	681	67	226	426
<i>Thymallus thymallus</i>	2263	238	747	37

Scenario A2

Table 11: Match between species predicted occurrences for current climate and projected climate under the A2 scenario for 2050–2060. Absence: number of sites with species always considered absent; Presence: number of sites where species is always expected to occur; new absence: number of sites with expected population extinctions; new occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1137	340	231	168
<i>Alburnus alburnus</i>	1785	1533	3	795
<i>Anguilla anguilla</i>	2719	1351	346	75
<i>Barbatula barbatula</i>	1243	1369	712	306
<i>Barbus barbus</i>	1450	841	247	424
<i>Chondrostoma nasus</i>	720	418	330	280
<i>Cottus gobio</i>	1508	477	1572	145
<i>Esox lucius</i>	2806	1012	438	211
<i>Gasterosteus aculeatus</i>	2438	253	610	120
<i>Gobio gobio</i>	1984	1215	421	431
<i>Lampetra planeri</i>	2793	652	666	74
<i>Leuciscus cephalus</i>	1076	1337	448	848
<i>Leuciscus leuciscus</i>	1778	756	361	319
<i>Lota lota</i>	1373	988	9	81
<i>Perca fluviatilis</i>	1384	1145	553	427
<i>Phoxinus phoxinus</i>	1627	1170	916	169
<i>Pungitius pungitius</i>	2150	81	414	237
<i>Rhodeus amarus</i>	475	1140	102	829
<i>Rutilus rutilus</i>	1479	1258	434	489
<i>Salmo salar</i>	1735	370	935	0
<i>Salmo trutta</i>	2068	1104	1331	5
<i>Telestes souffia</i>	668	102	191	439
<i>Thymallus thymallus</i>	2267	291	694	33

Scenario B1

Table 12: Match between species predicted occurrences for current climate and projected climate under the B1 scenario for 2050–2060. Absence: number of sites with species always considered absent; presence: number of sites where species is always expected to occur; new absence: number of sites with expected population extinctions; new occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1127	374	197	178
<i>Alburnus alburnus</i>	1898	1533	3	682
<i>Anguilla anguilla</i>	2733	1458	239	61
<i>Barbatula barbatula</i>	1256	1507	574	293
<i>Barbus barbus</i>	1466	908	180	408
<i>Chondrostoma nasus</i>	701	511	237	299
<i>Cottus gobio</i>	1505	715	1334	148
<i>Esox lucius</i>	2810	1086	364	207
<i>Gasterosteus aculeatus</i>	2413	354	509	145
<i>Gobio gobio</i>	1990	1285	351	425
<i>Lampetra planeri</i>	2791	766	552	76
<i>Leuciscus cephalus</i>	1142	1418	367	782
<i>Leuciscus leuciscus</i>	1794	836	281	303
<i>Lota lota</i>	1406	988	9	48
<i>Perca fluviatilis</i>	1379	1267	431	432
<i>Phoxinus phoxinus</i>	1630	1319	767	166
<i>Pungitius pungitius</i>	2100	126	369	287
<i>Rhodeus amarus</i>	554	1168	74	750
<i>Rutilus rutilus</i>	1490	1352	340	478
<i>Salmo salar</i>	1735	472	833	0
<i>Salmo trutta</i>	2068	1337	1098	5
<i>Telestes souffia</i>	669	123	170	438
<i>Thymallus thymallus</i>	2264	340	645	36

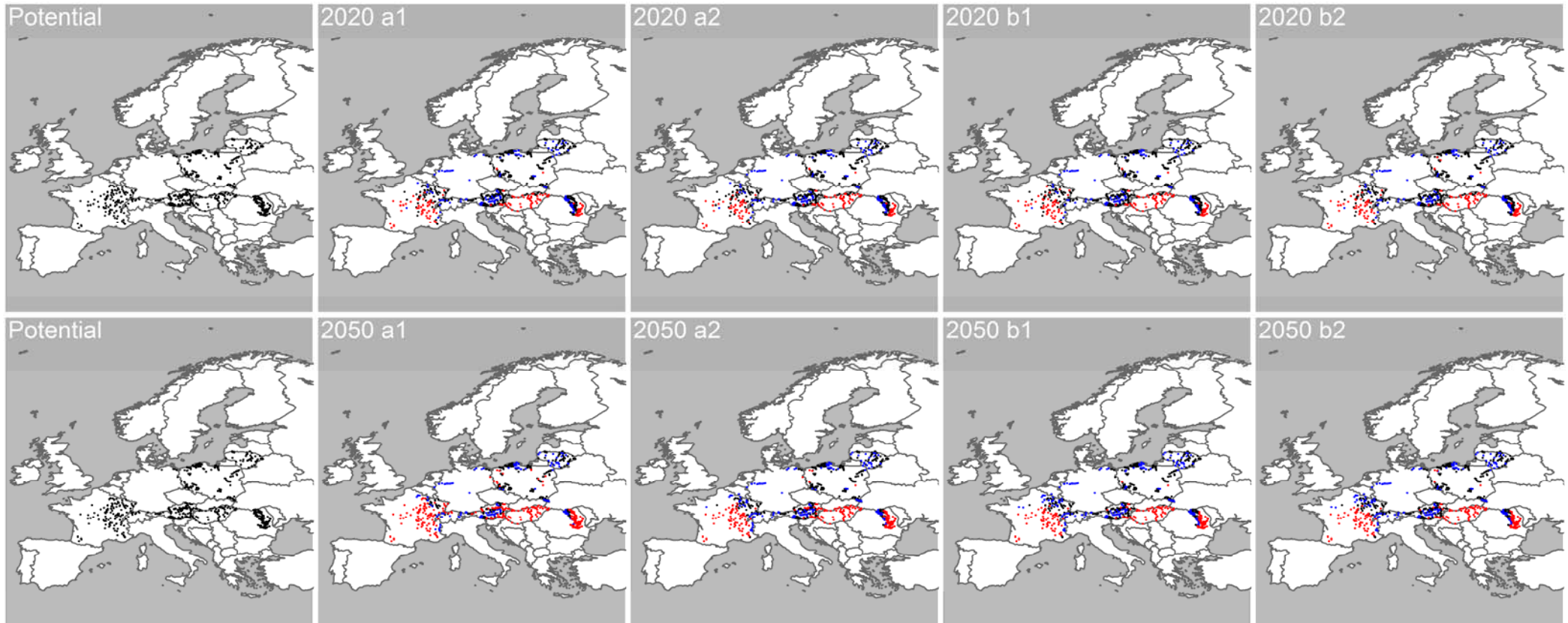
Scenario B2

Table 13: Match between species predicted occurrences for current climate and projected climate under the B2 scenario for 2050–2060. Absence: number of sites with species always considered absent; presence: number of sites where species is always expected to occur; new absence: number of sites with expected population extinctions; new occurrence: number of sites with expected population colonization.

Species	Absence	Presence	New absence	New occurrence
<i>Alburnoides bipunctatus</i>	1130	370	201	175
<i>Alburnus alburnus</i>	1879	1533	3	701
<i>Anguilla anguilla</i>	2725	1455	242	69
<i>Barbatula barbatula</i>	1244	1490	591	305
<i>Barbus barbus</i>	1462	903	185	412
<i>Chondrostoma nasus</i>	700	505	243	300
<i>Cottus gobio</i>	1500	628	1421	153
<i>Esox lucius</i>	2811	1078	372	206
<i>Gasterosteus aculeatus</i>	2418	320	543	140
<i>Gobio gobio</i>	1992	1275	361	423
<i>Lampetra planeri</i>	2792	734	584	75
<i>Leuciscus cephalus</i>	1123	1405	380	801
<i>Leuciscus leuciscus</i>	1771	833	284	326
<i>Lota lota</i>	1399	988	9	55
<i>Perca fluviatilis</i>	1368	1256	442	443
<i>Phoxinus phoxinus</i>	1624	1306	780	172
<i>Pungitius pungitius</i>	2107	113	382	280
<i>Rhodeus amarus</i>	554	1166	76	750
<i>Rutilus rutilus</i>	1485	1338	354	483
<i>Salmo salar</i>	1735	436	869	0
<i>Salmo trutta</i>	2070	1320	1115	3
<i>Telestes souffia</i>	670	125	168	437
<i>Thymallus thymallus</i>	2263	325	660	37

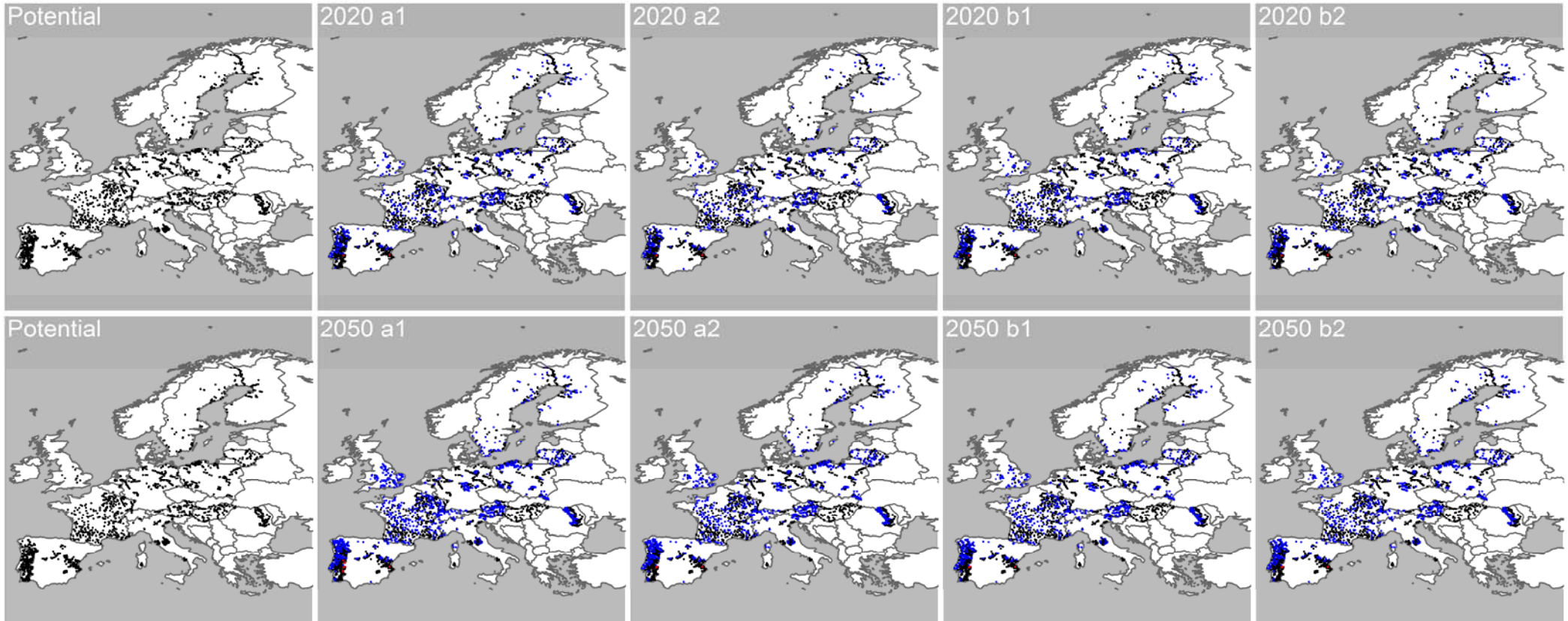
Appendix 2: Projections of species distributions for 2020–2030 and 2050–2060, under four global change scenarios.

Alburnoides bipunctatus



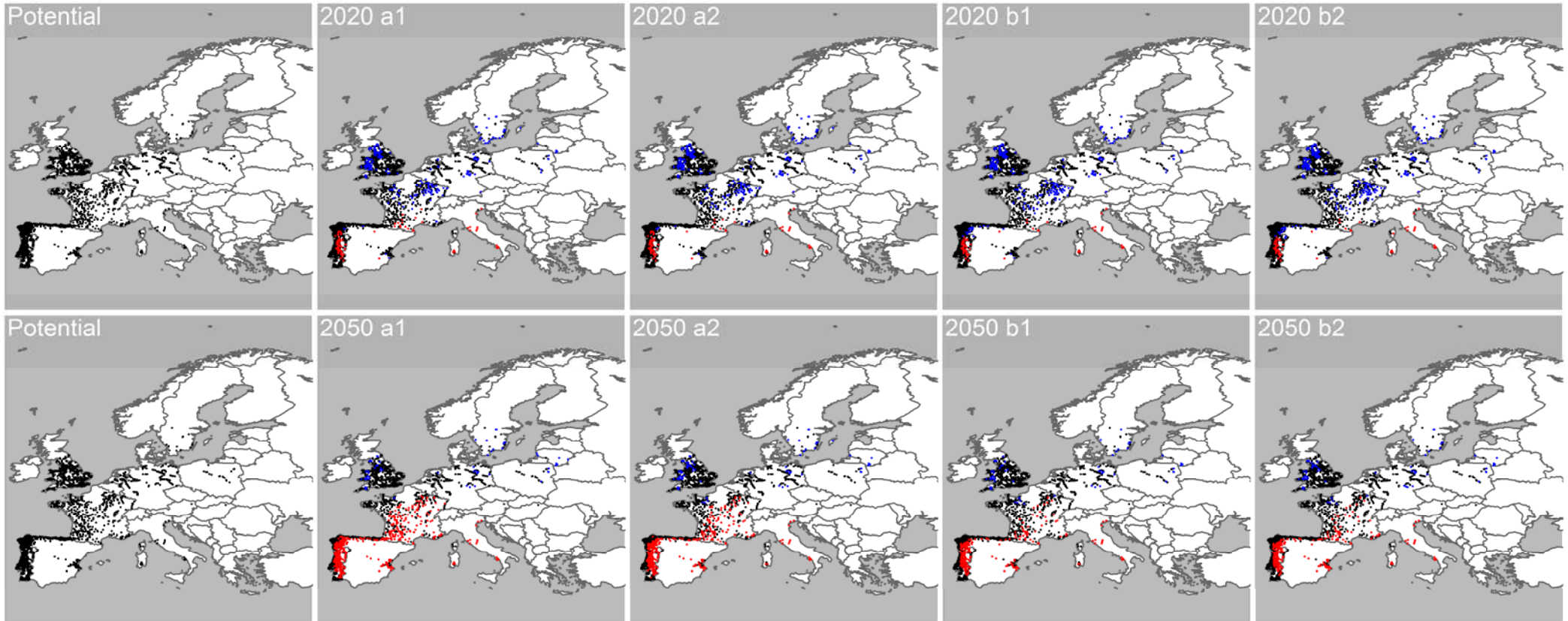
Predicted distributions of spirlin for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Alburnus alburnus



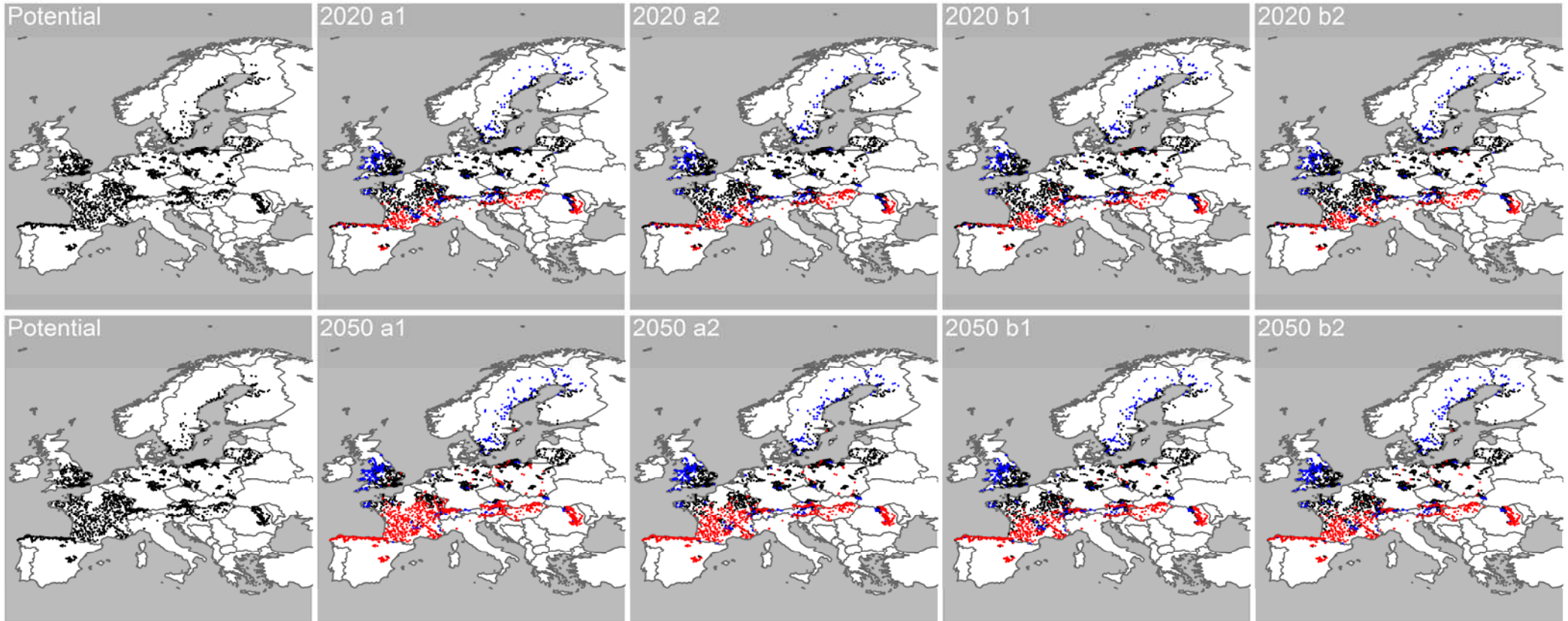
Predicted distributions of bleek for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent a disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Anquilla anquilla



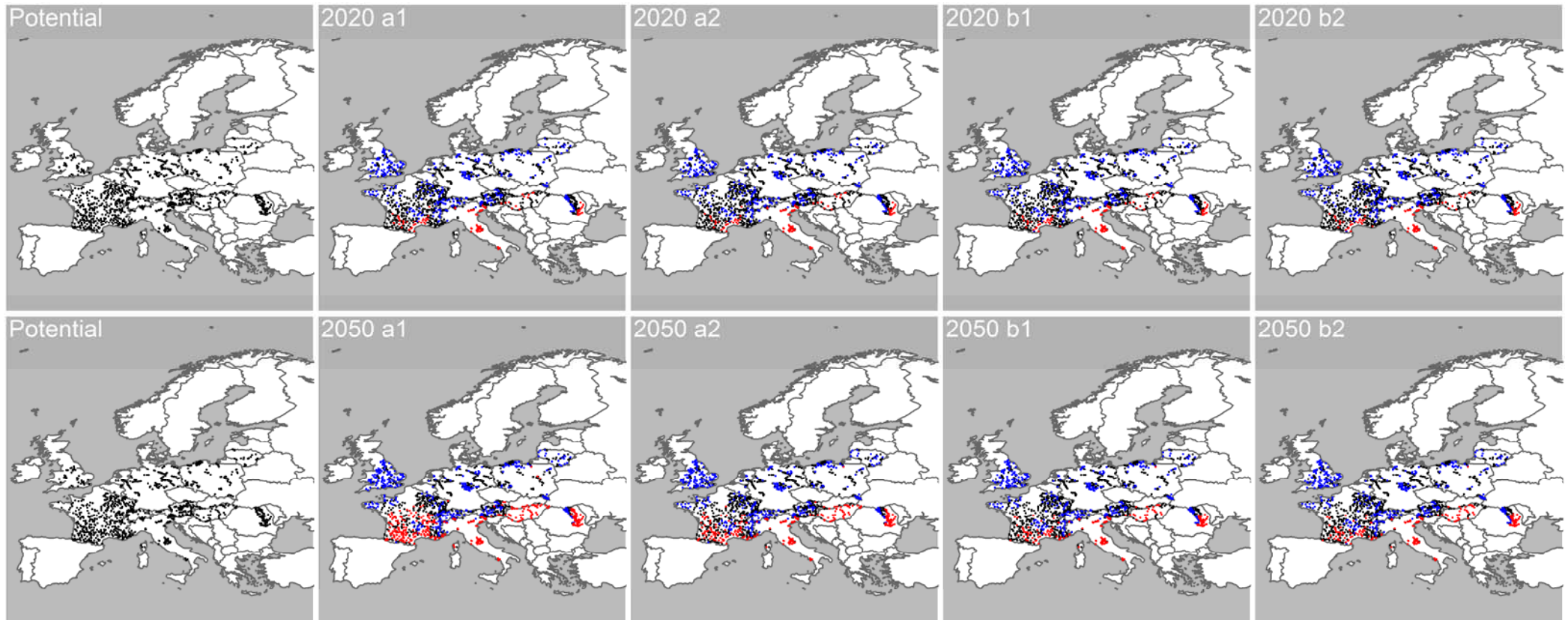
Predicted distributions of European eel for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent a disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Barbatula barbatula



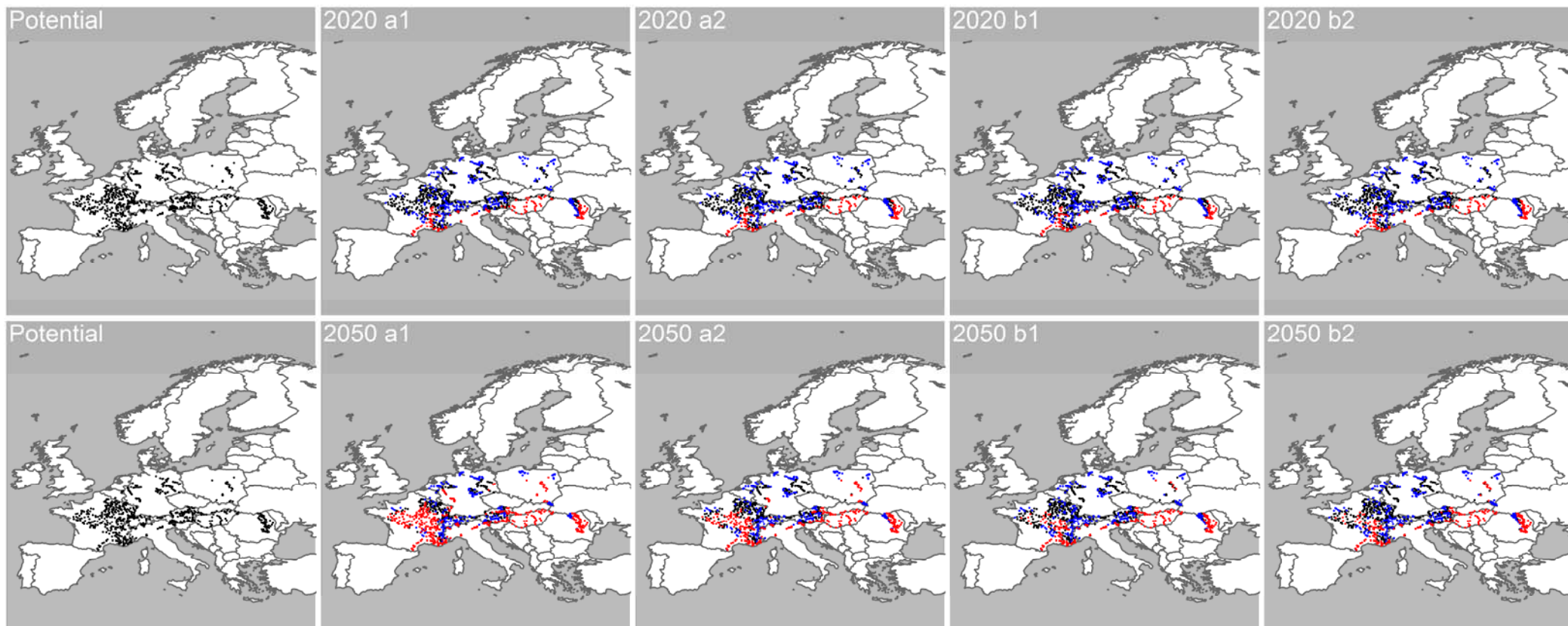
Predicted distributions of stone loach for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Barbus barbus



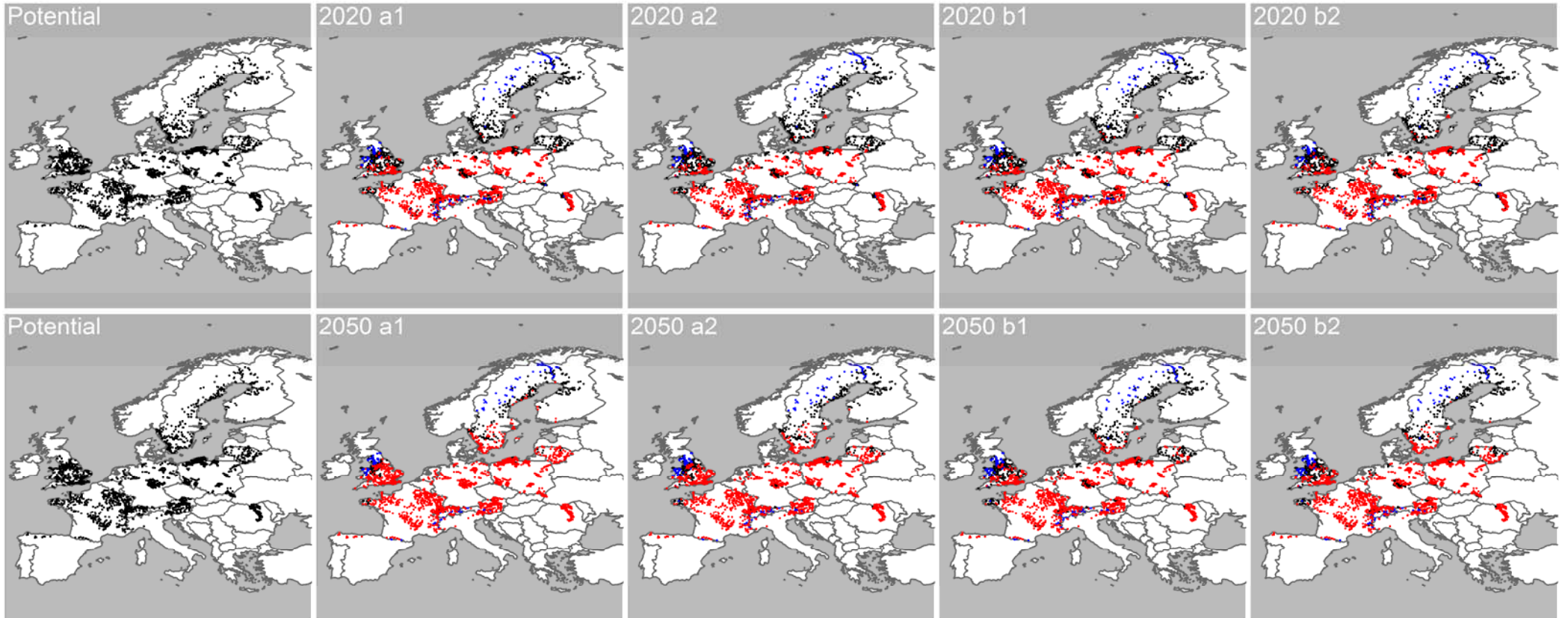
Predicted distributions of barbel for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Chondrostoma nasus



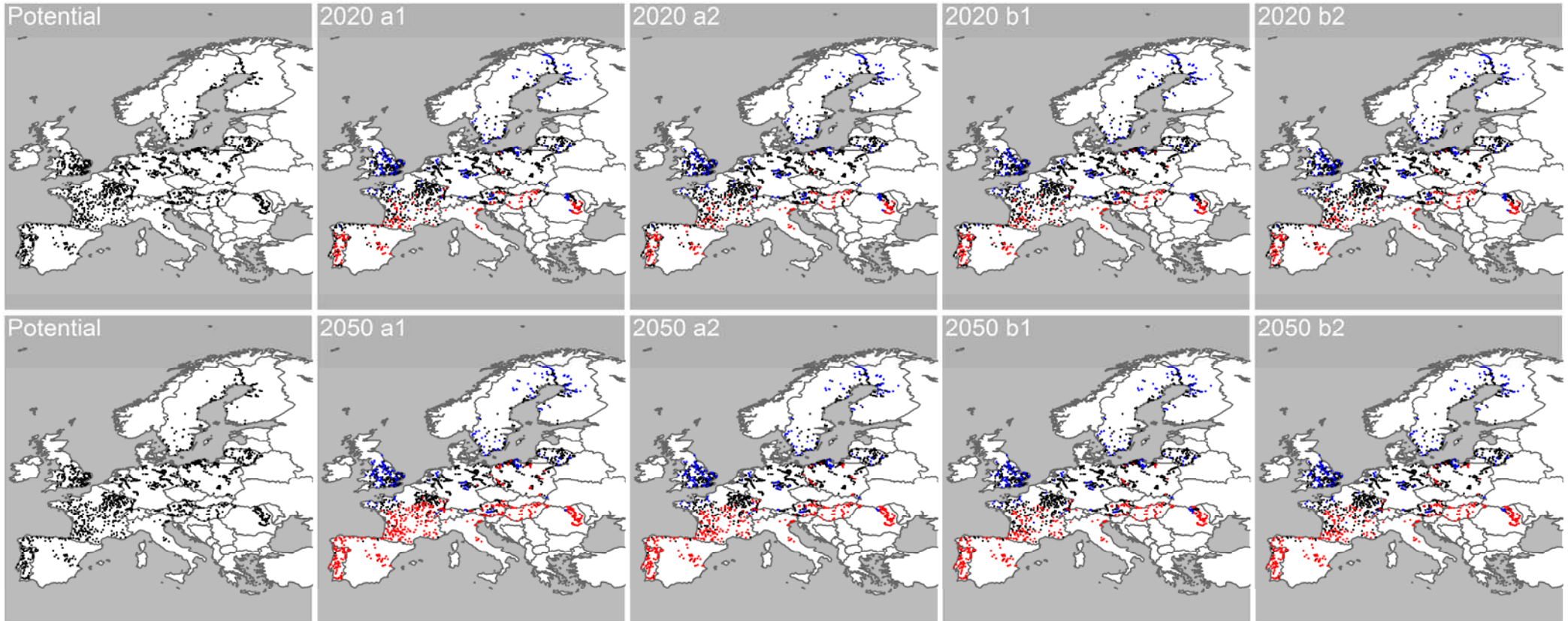
Predicted distributions of nase for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Cottus gobio



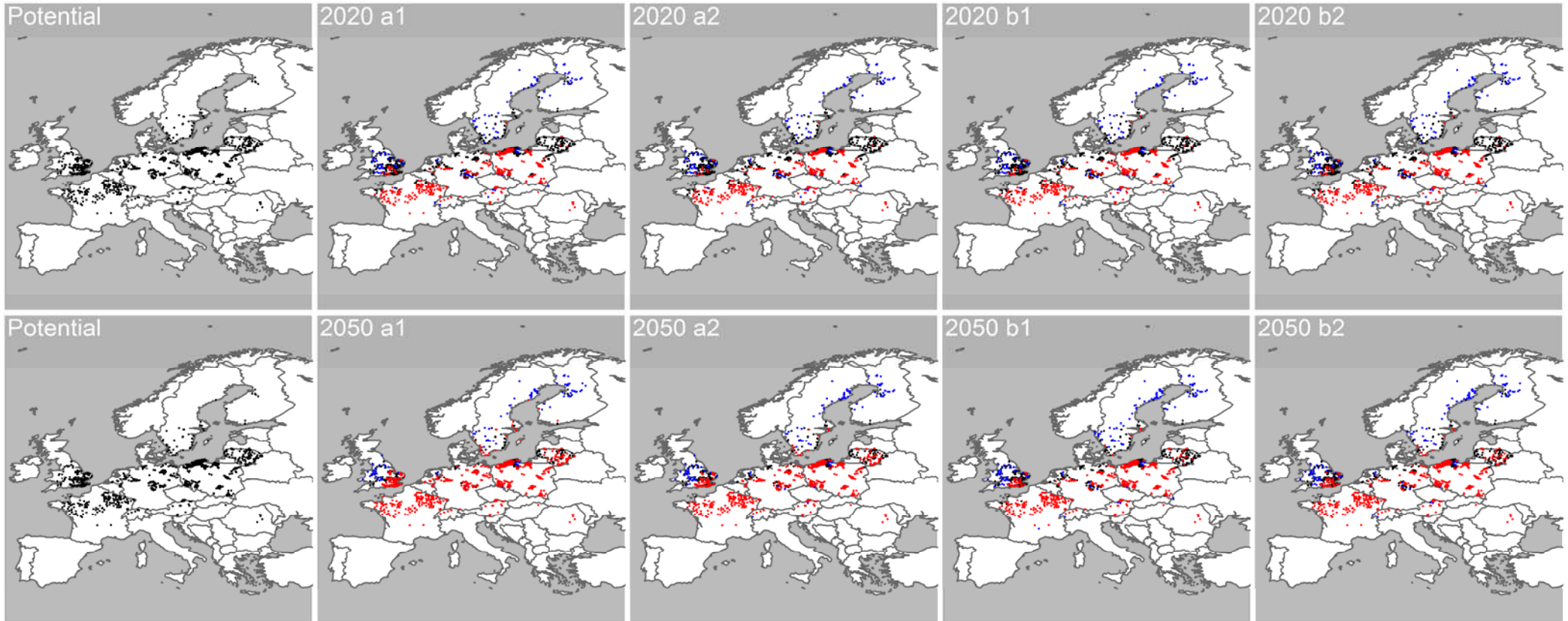
Predicted distributions of bullhead for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Esox lucius



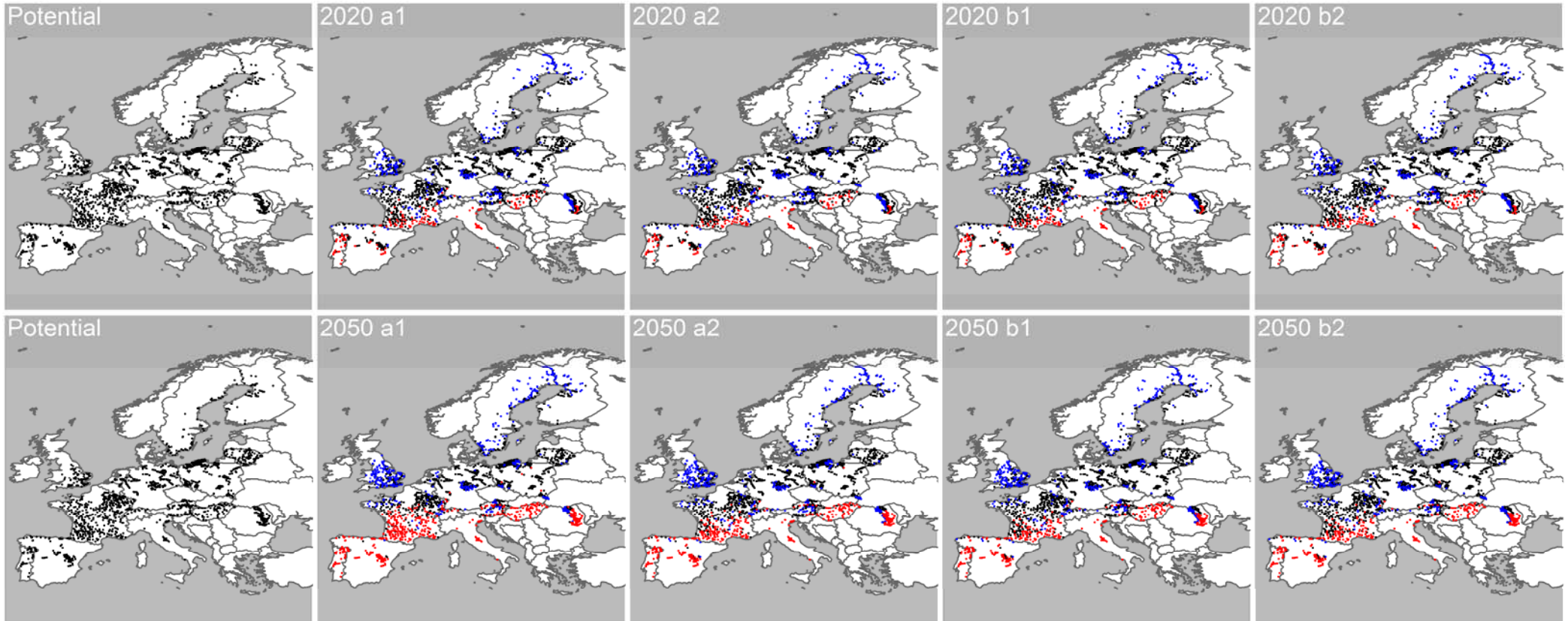
Predicted distributions of northern pike for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Gasterosteus aculeatus



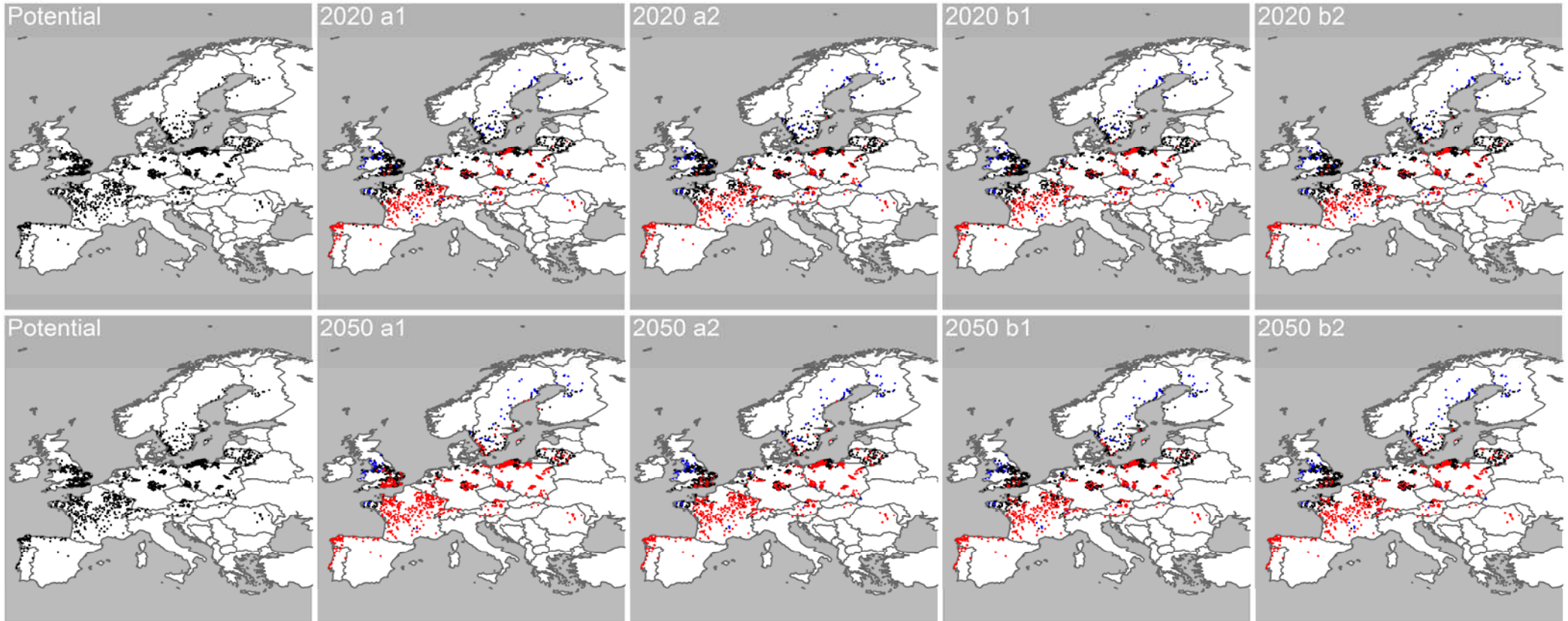
Predicted distributions of threespine stickleback for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Gobio gobio



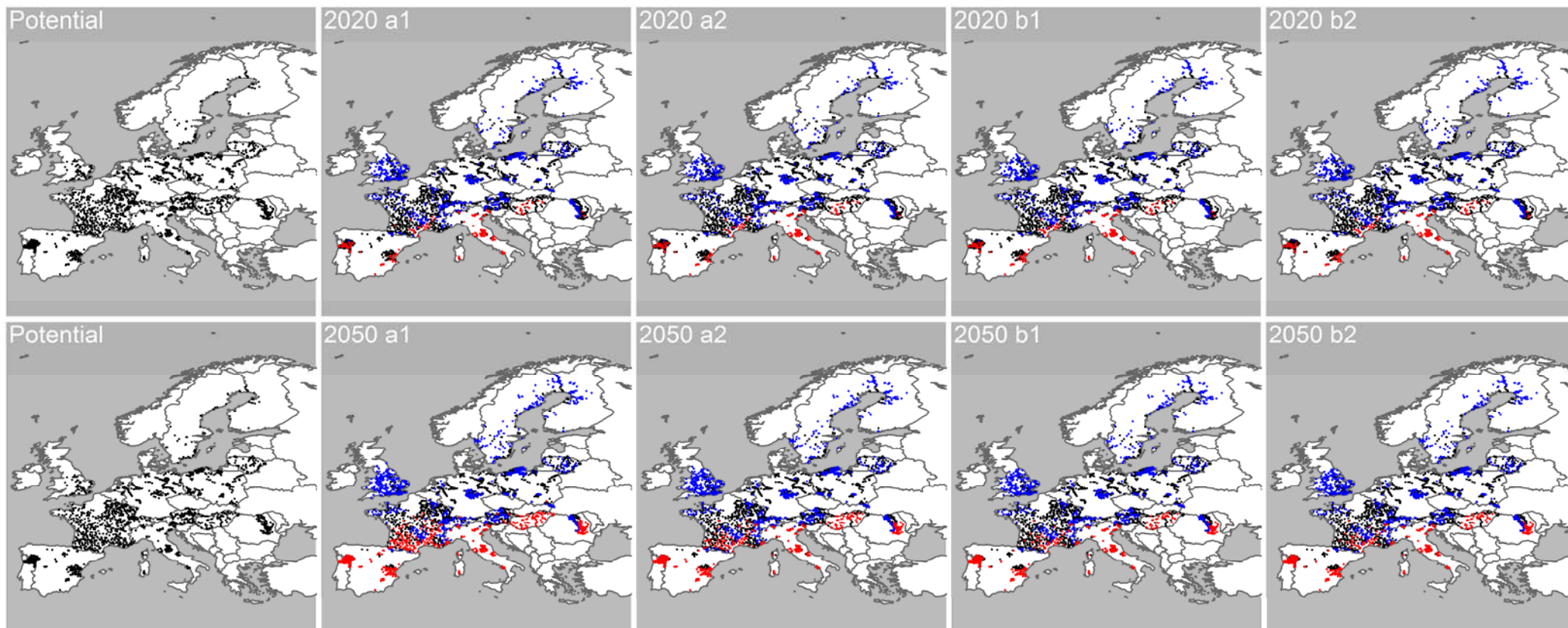
Predicted distributions of gudgeon for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Lampetra planeri



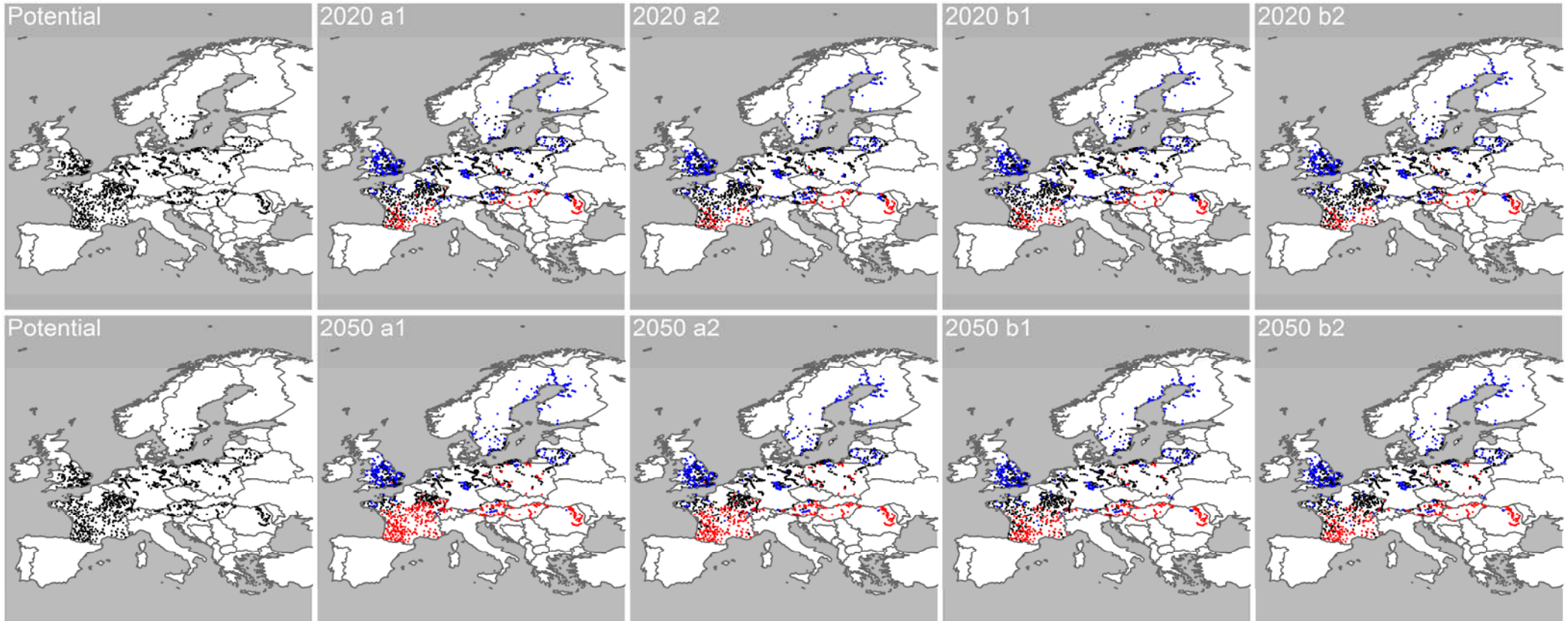
Predicted distributions of European brook lamprey for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Leuciscus cephalus



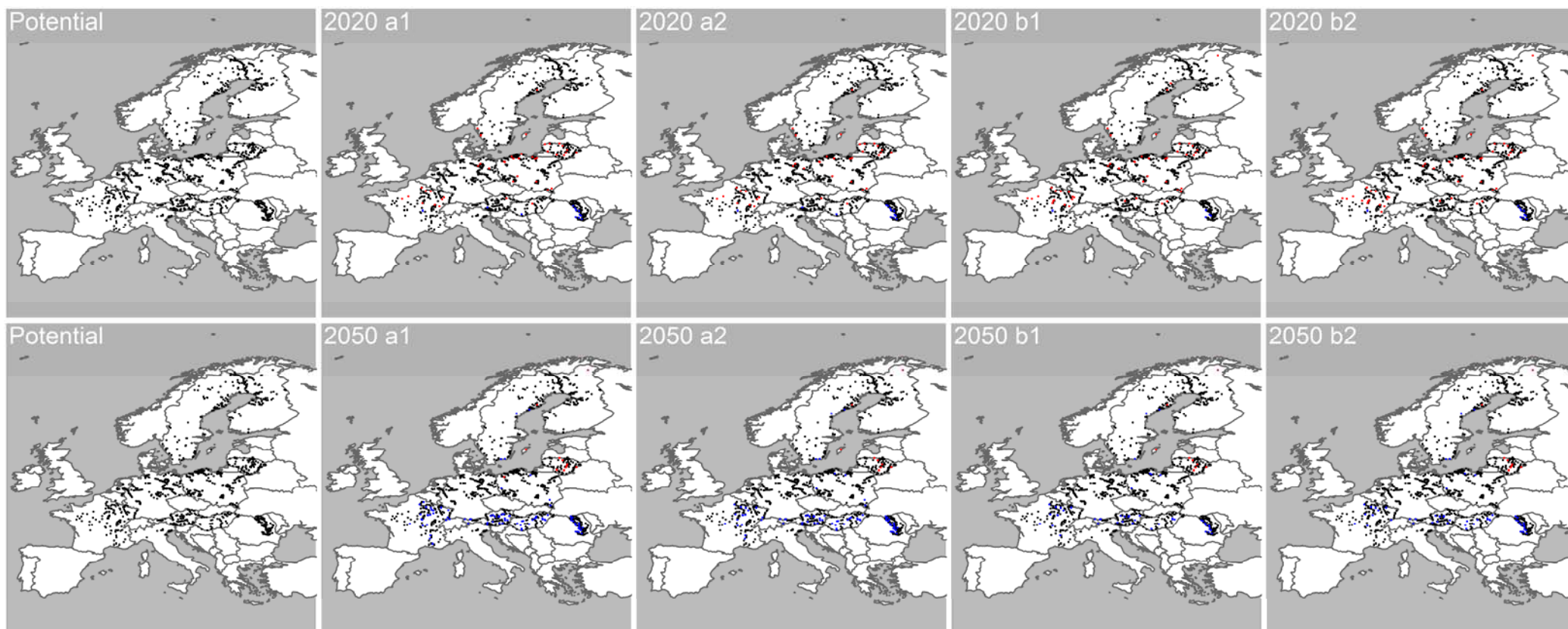
Predicted distributions of chub for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Leuciscus leuciscus



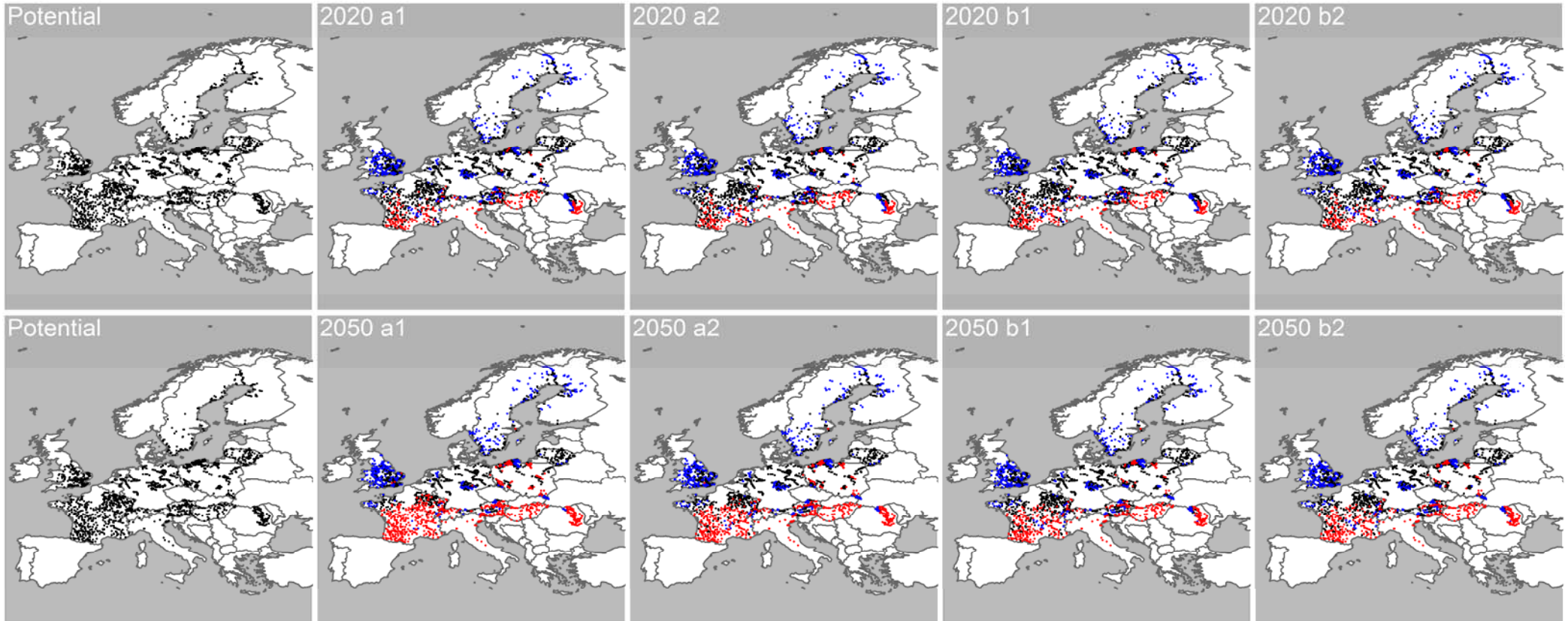
Predicted distributions of common dace for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Lota lota



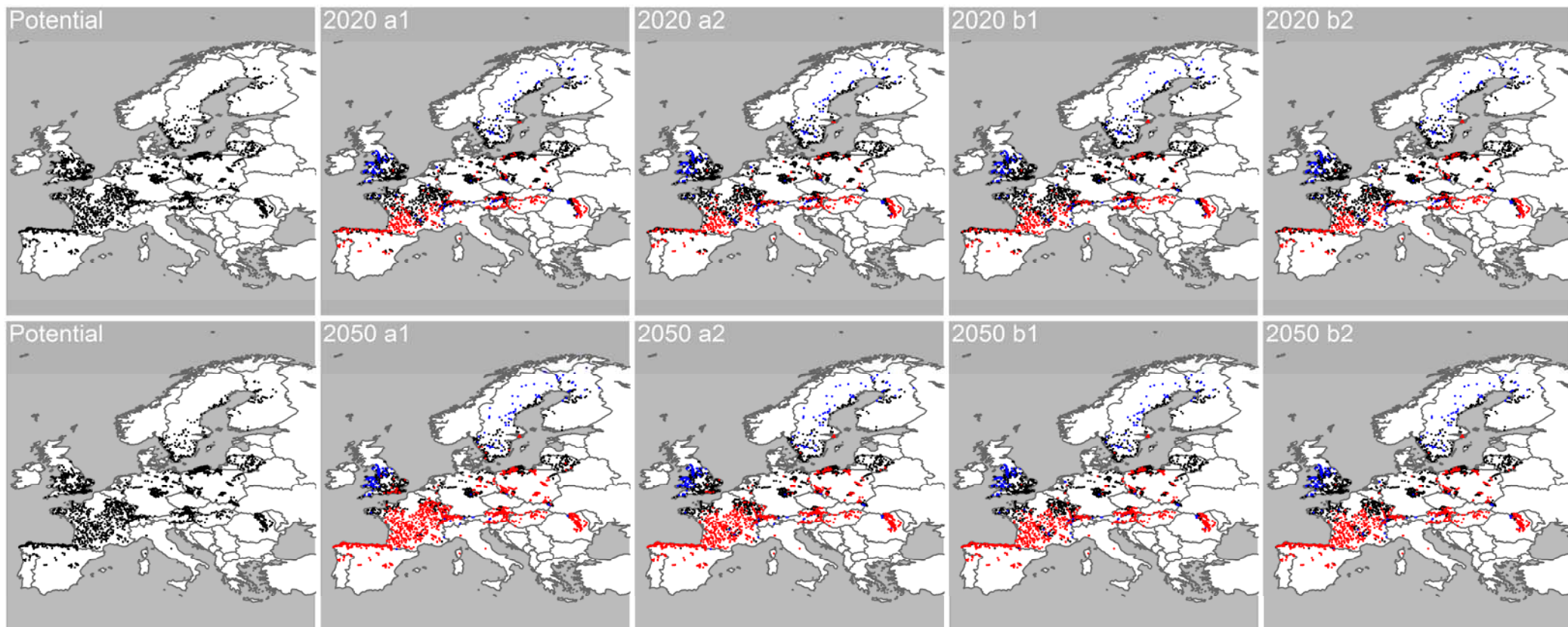
Predicted distributions of burbot for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Perca fluviatilis



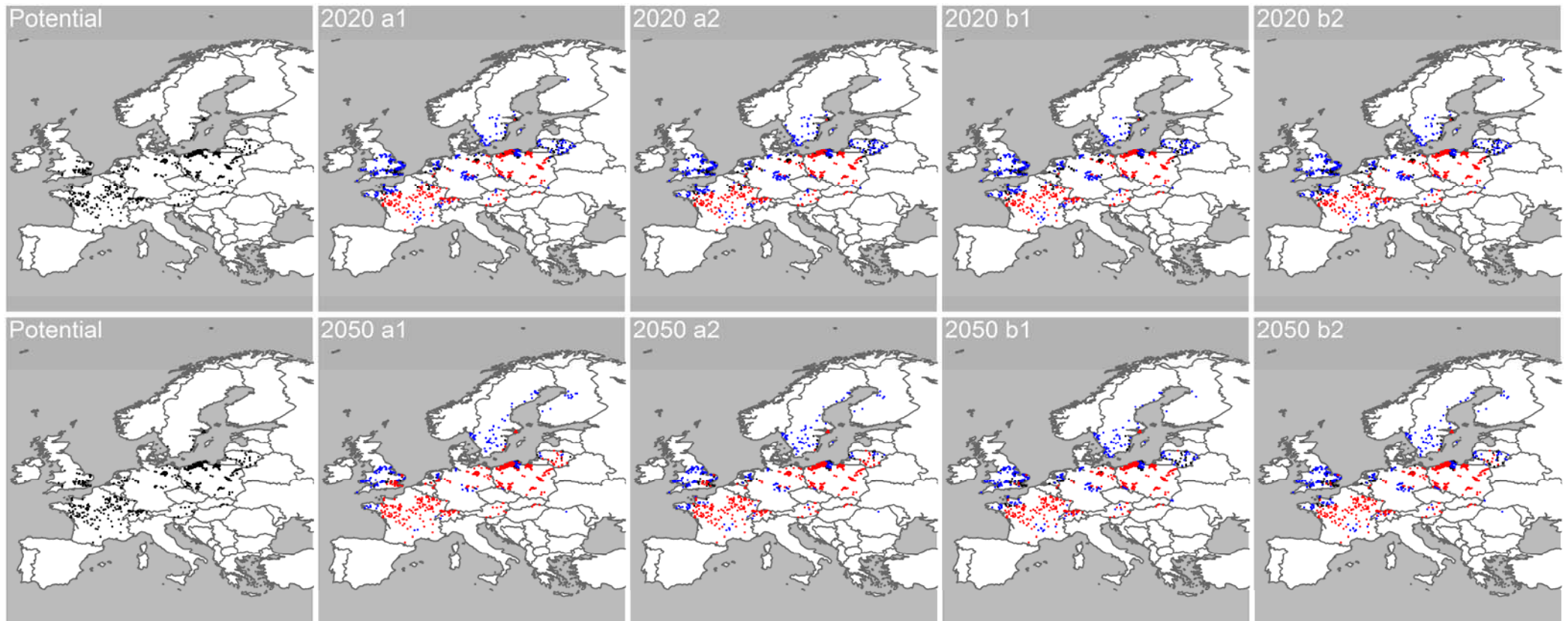
Predicted distributions of perch for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Phoxinus phoxinus



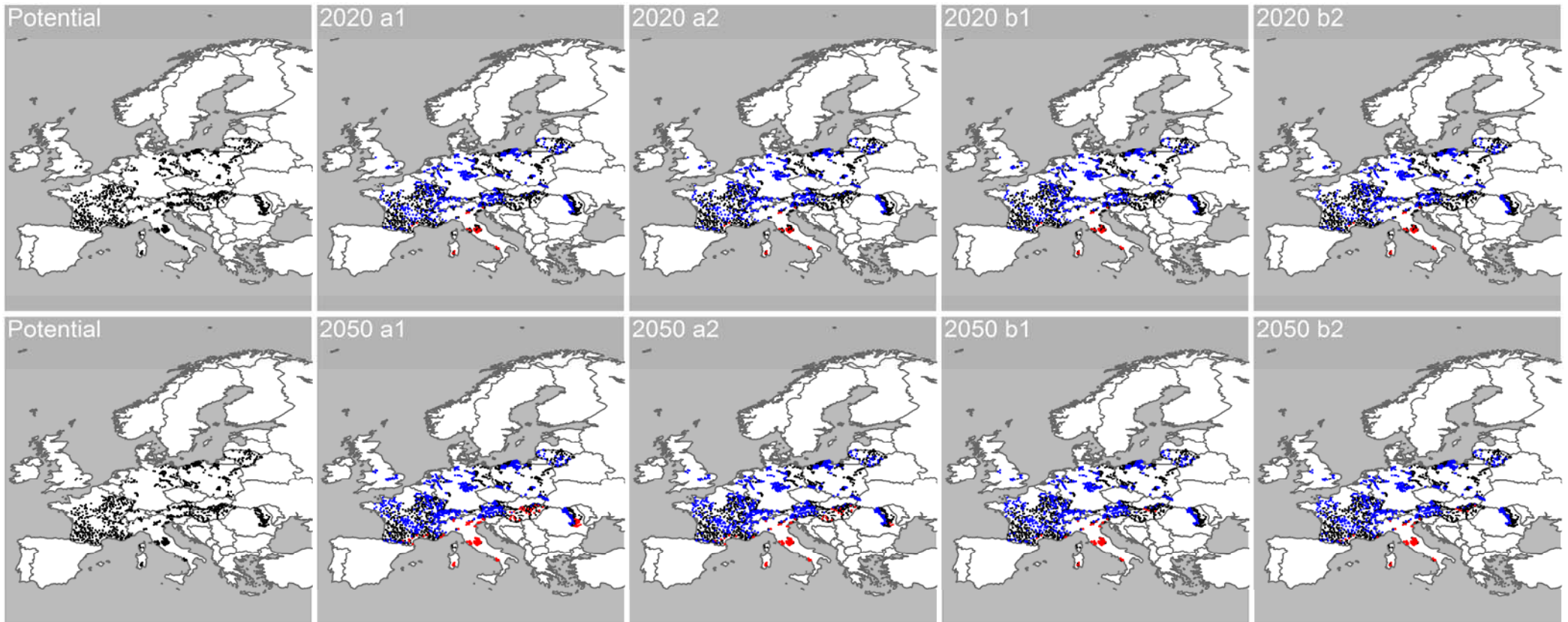
Predicted distributions of minnow for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Pungitius pungitius



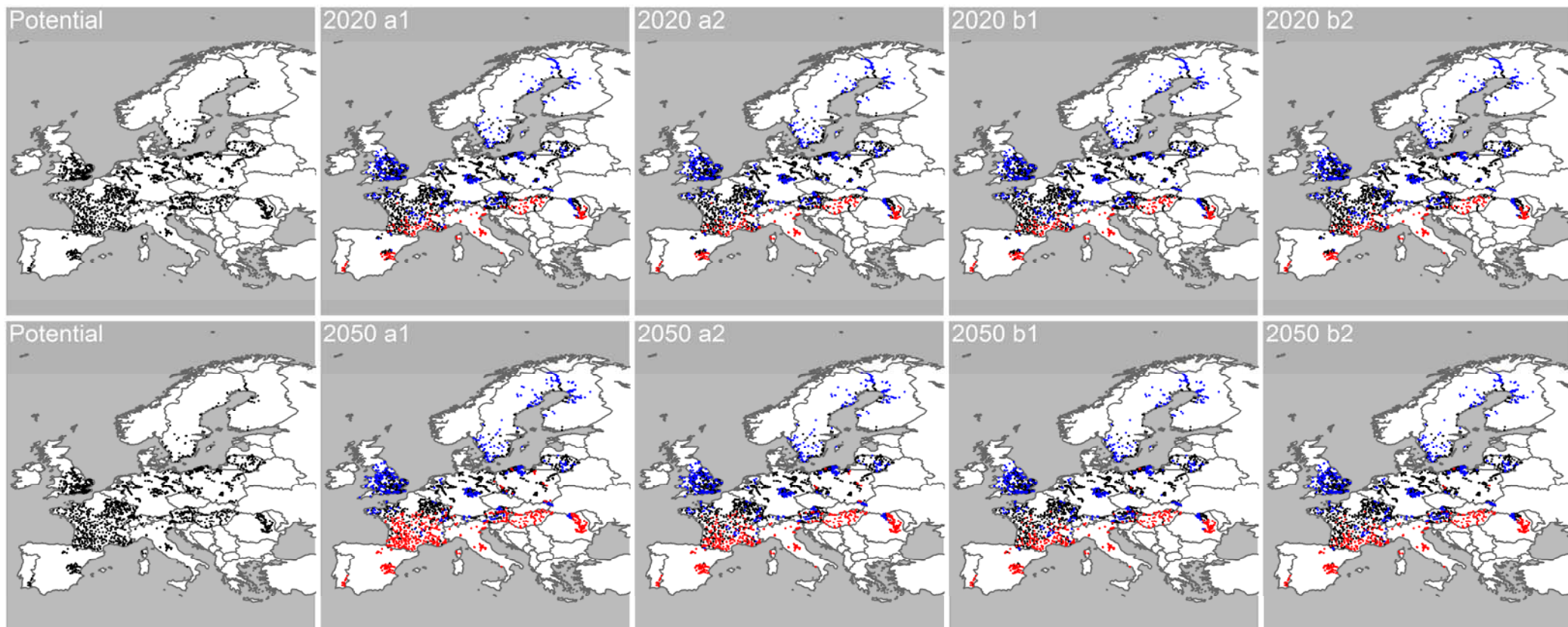
Predicted distributions of ninespine stickleback for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Rhodeus amarus



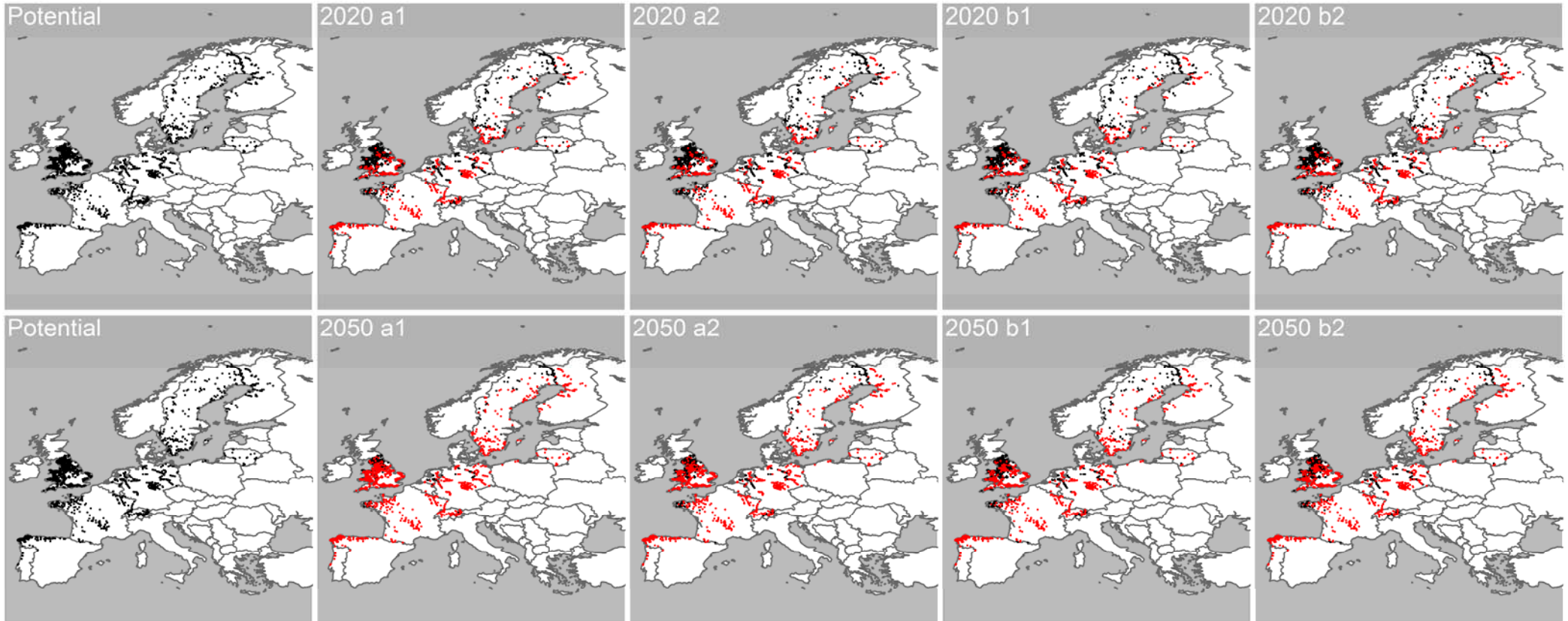
Predicted distributions of bitterling for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Rutilus rutilus



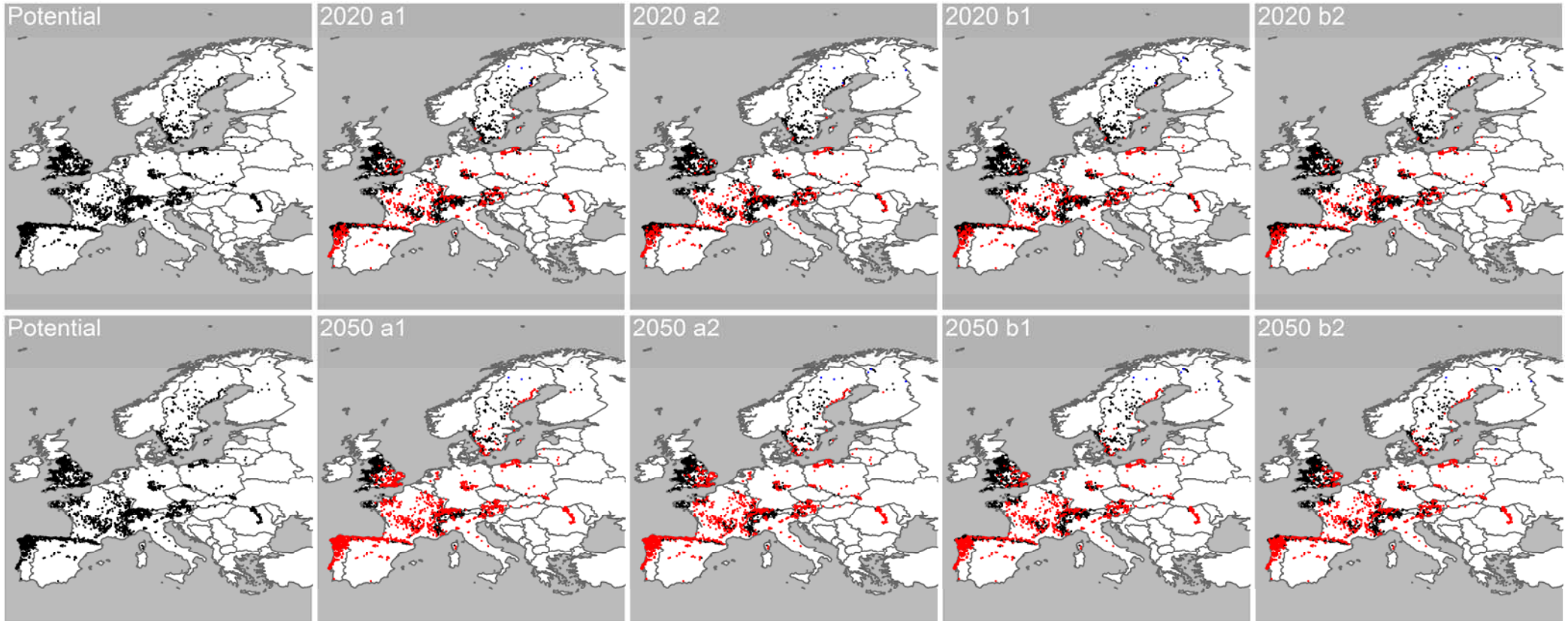
Predicted distributions of roach for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Salmo salar



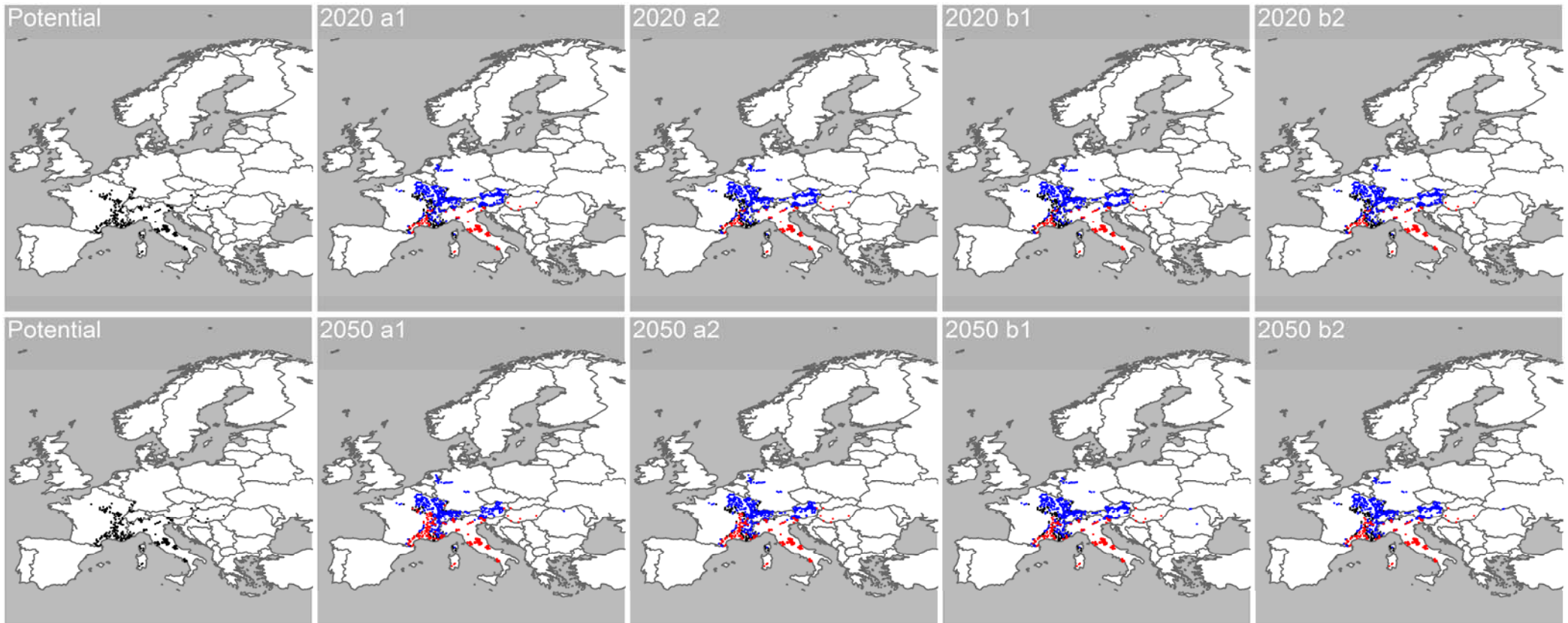
Predicted distributions of Atlantic salmon for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Salmo trutta



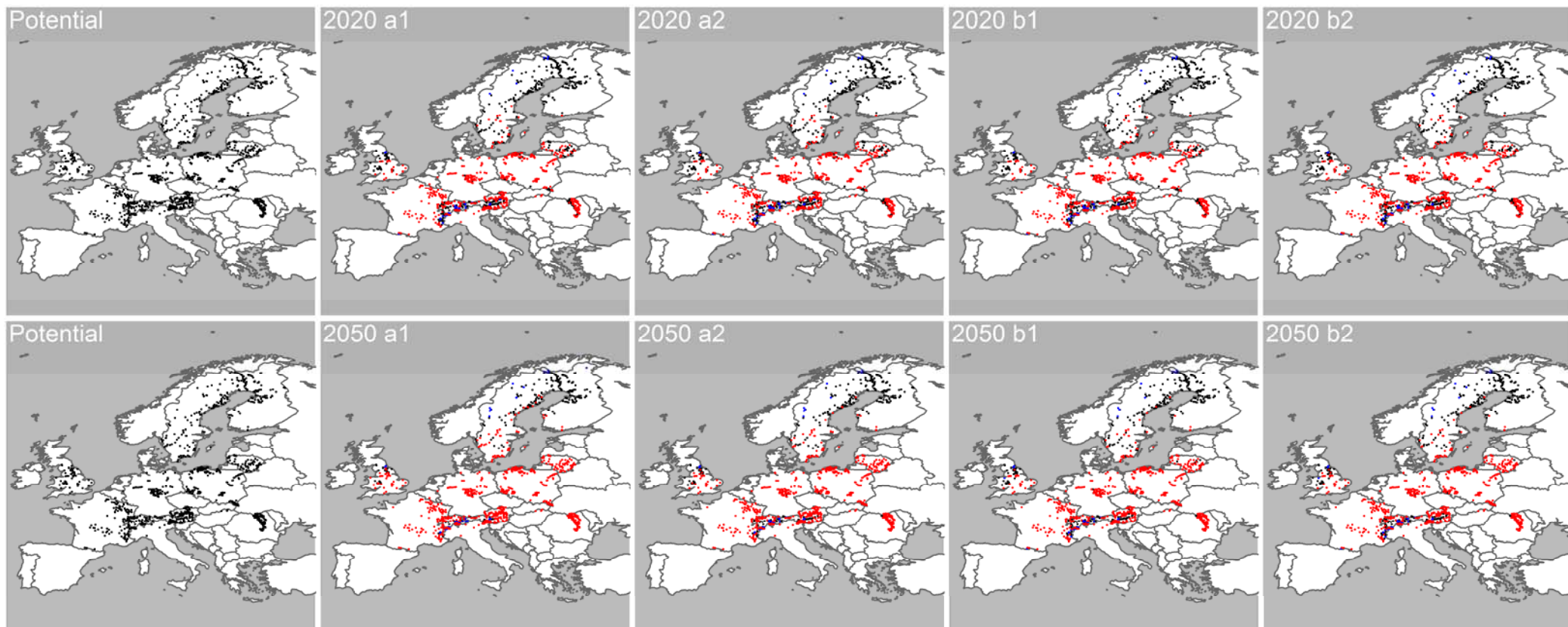
Predicted distributions of brown trout for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Telestes souffia



Predicted distributions of soufie for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Thymallus thymallus

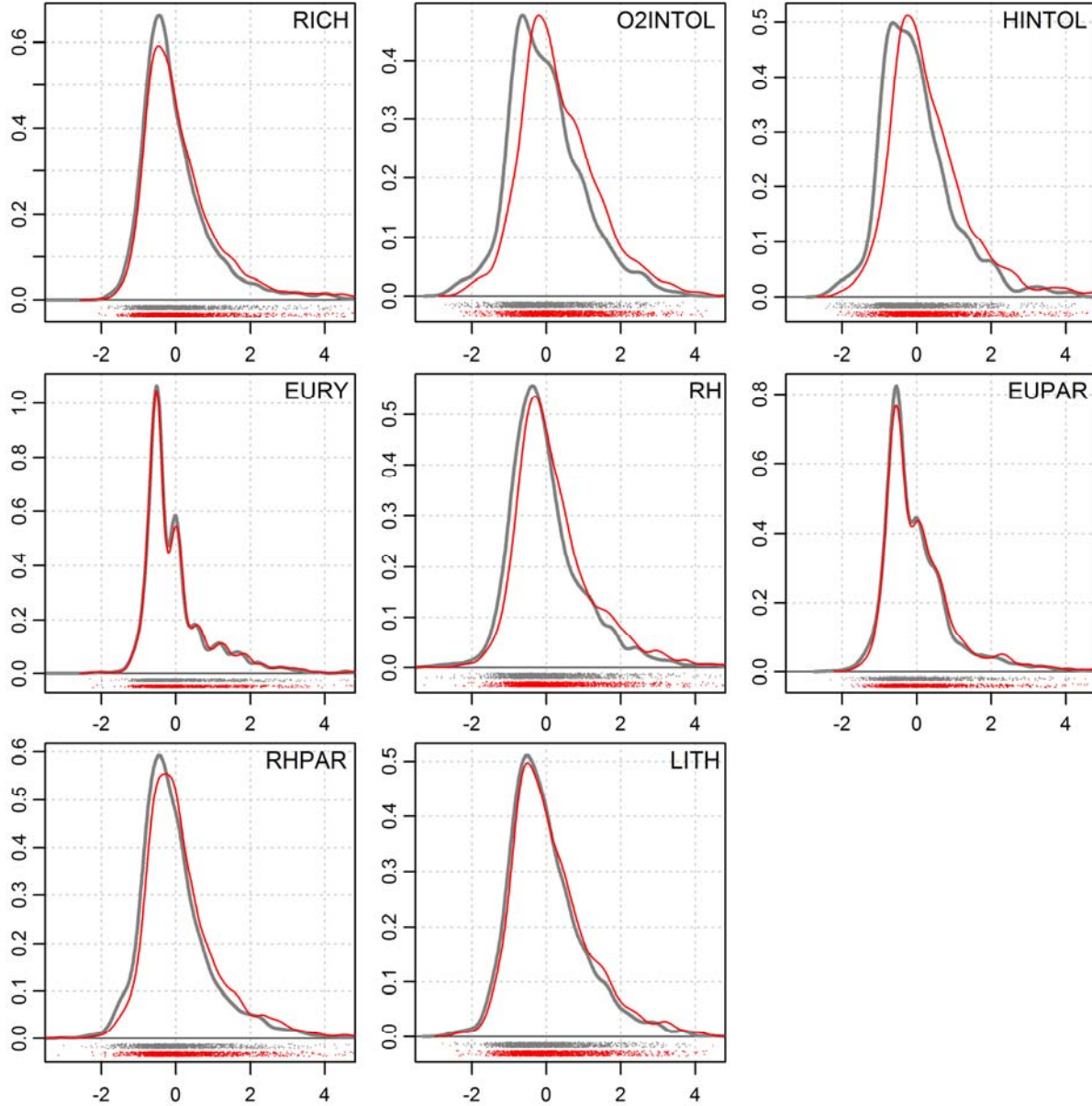


Predicted distributions of grayling for current environmental conditions (Potential) and for four global change scenarios: a1, a2, b1 and b2. The blue dots represent new presence of this species at a site (compared to current situation), red dots represent disappearance of this species at a site and black dots represent unchanged predicted presence at a site.

Appendix 3: Shift from reference conditions

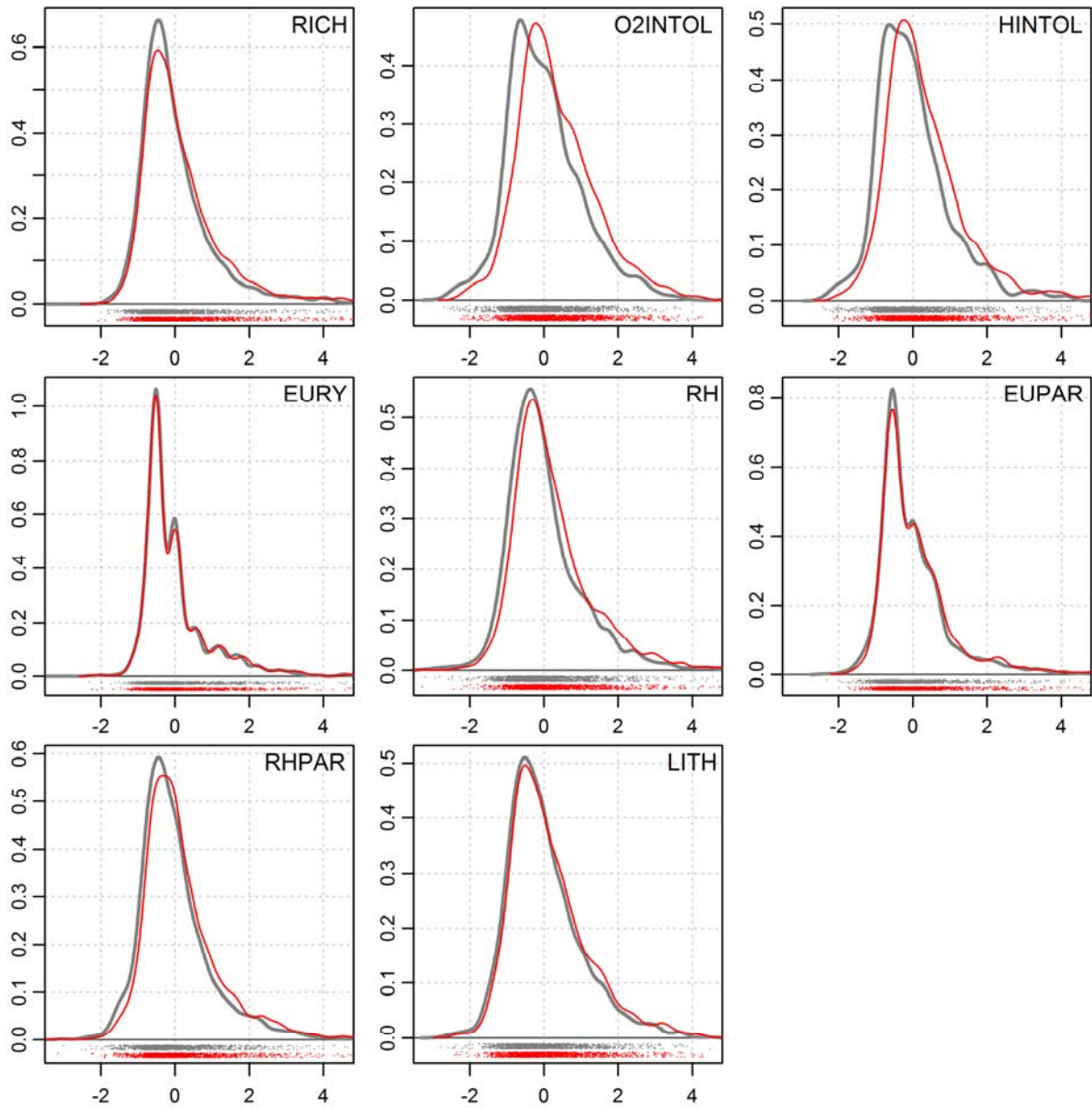
2020–2030

Scenario A1F1



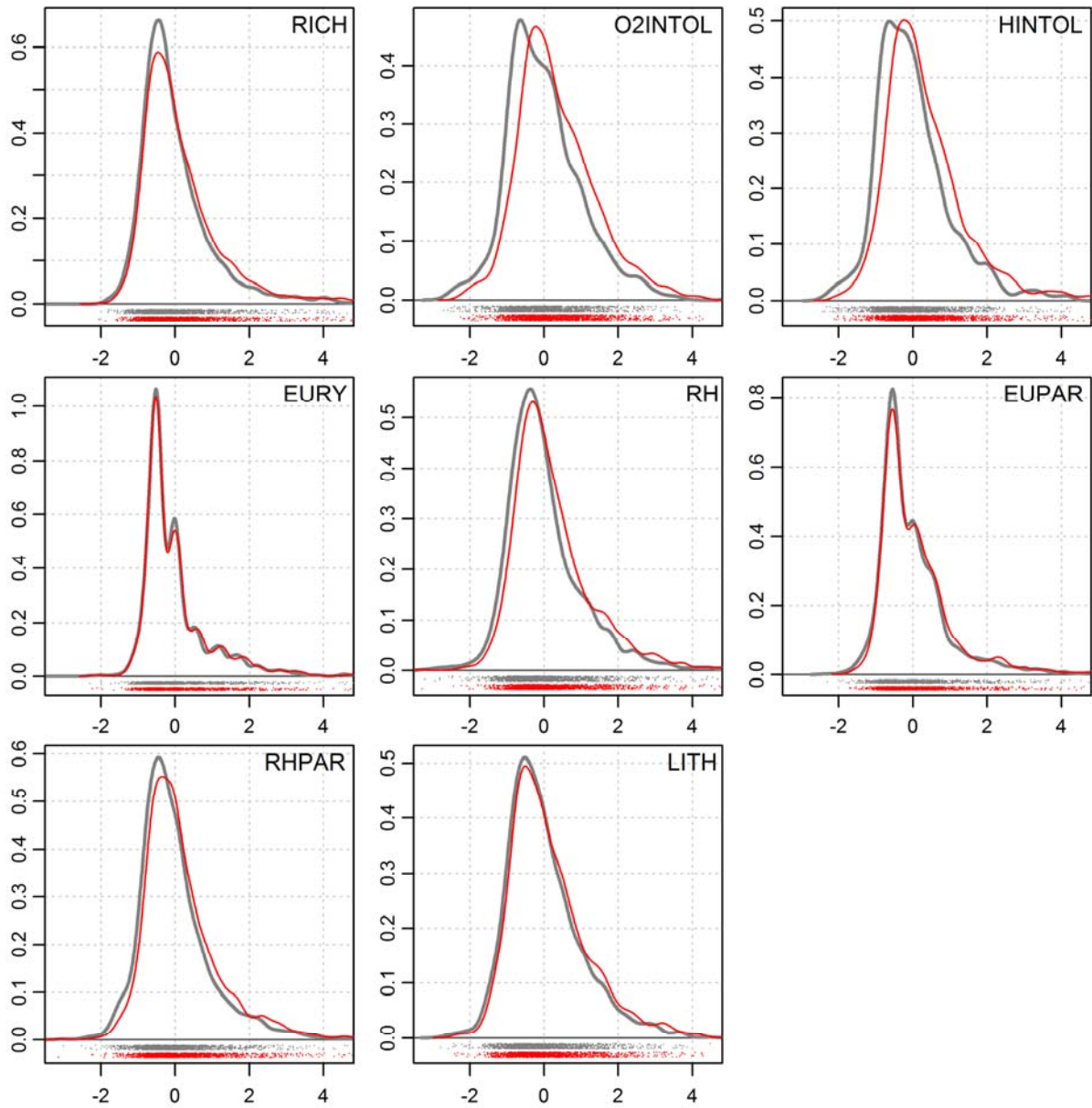
Density (kernel estimation) of the standardized metrics on the current environmental conditions (in grey) and for the scenario A1F1 (in red).

Scenario A2



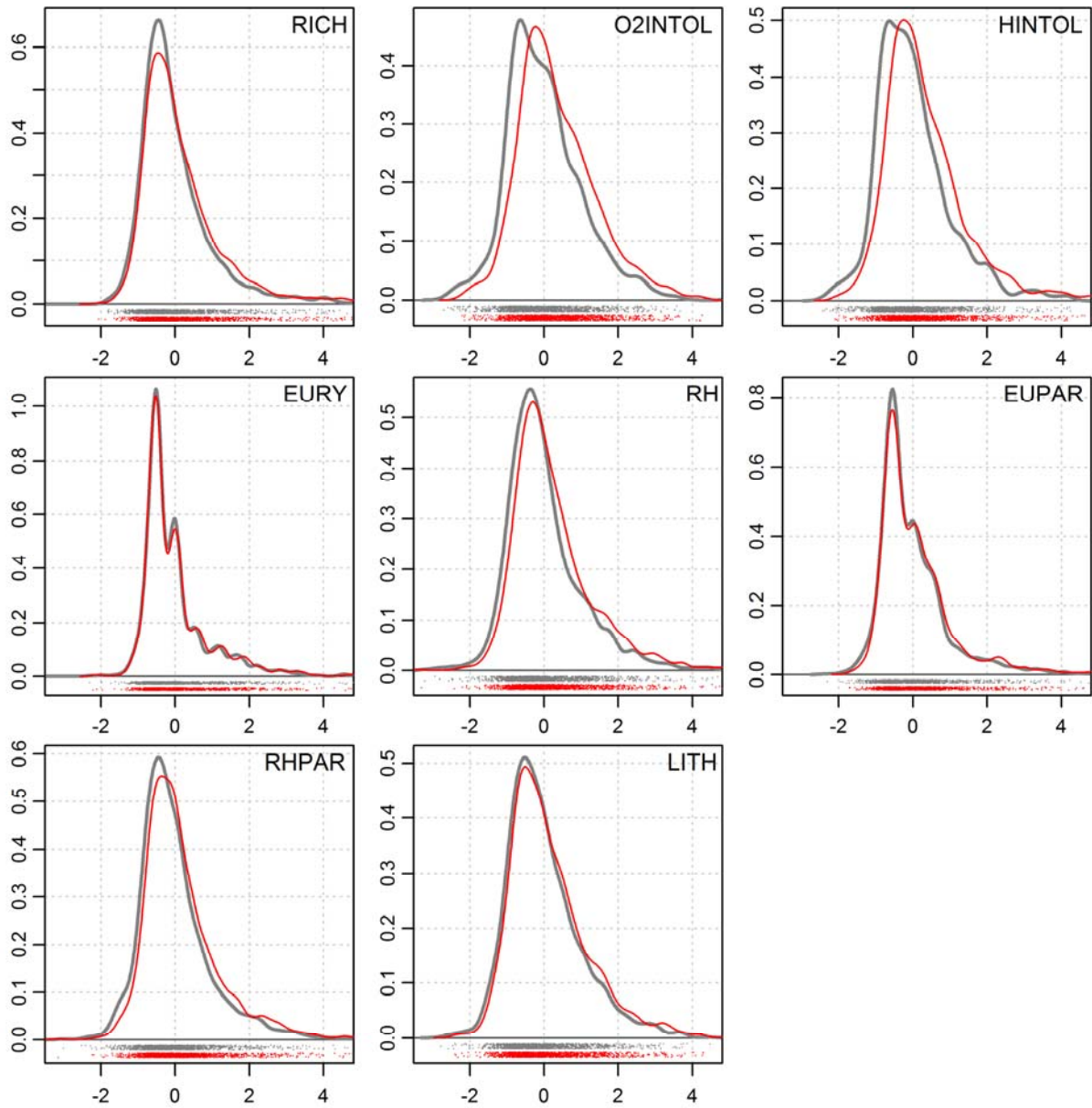
Density (kernel estimation) of the standardized metrics on the current environmental conditions (in grey) and for the scenario A2 (in red).

Scenario B1



Density (kernel estimation) of the standardized metrics on the current environmental conditions (in grey) and for the scenario B1 (in red).

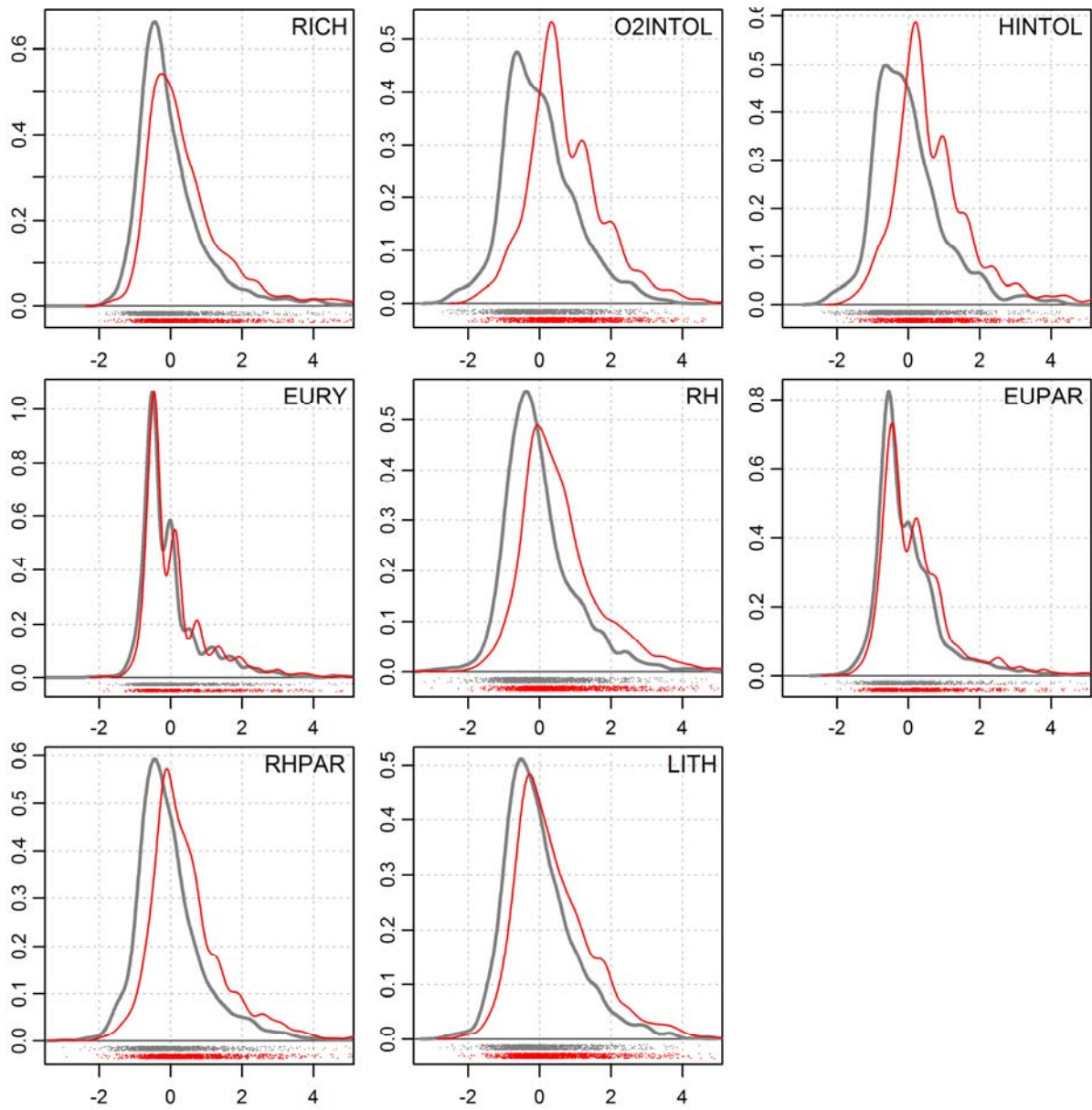
Scenario B2



Density (kernel estimation) of the standardized metrics on the current environmental conditions (in grey) and for the scenario B2 (in red).

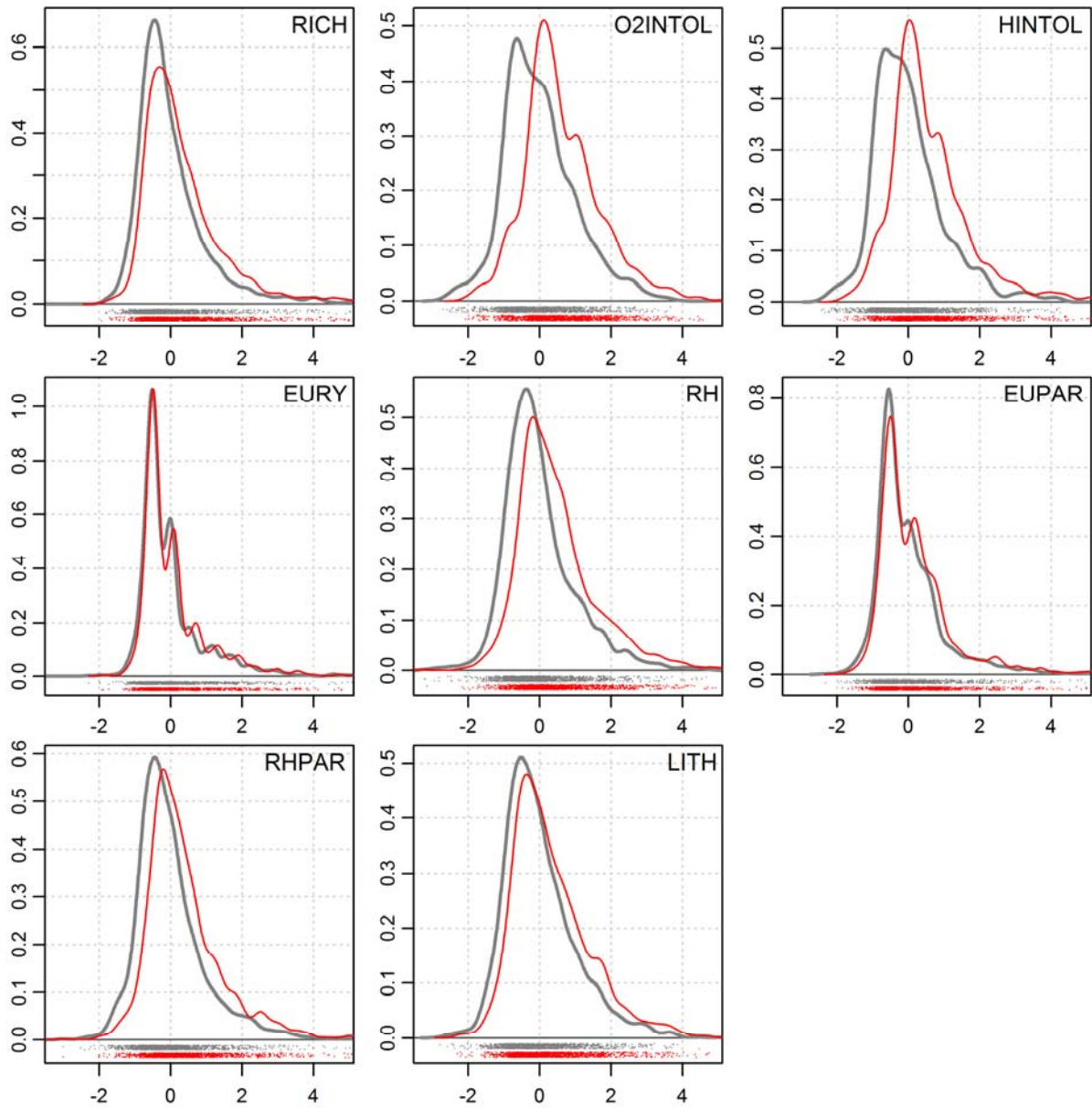
2020–2030

Scenario A1F1



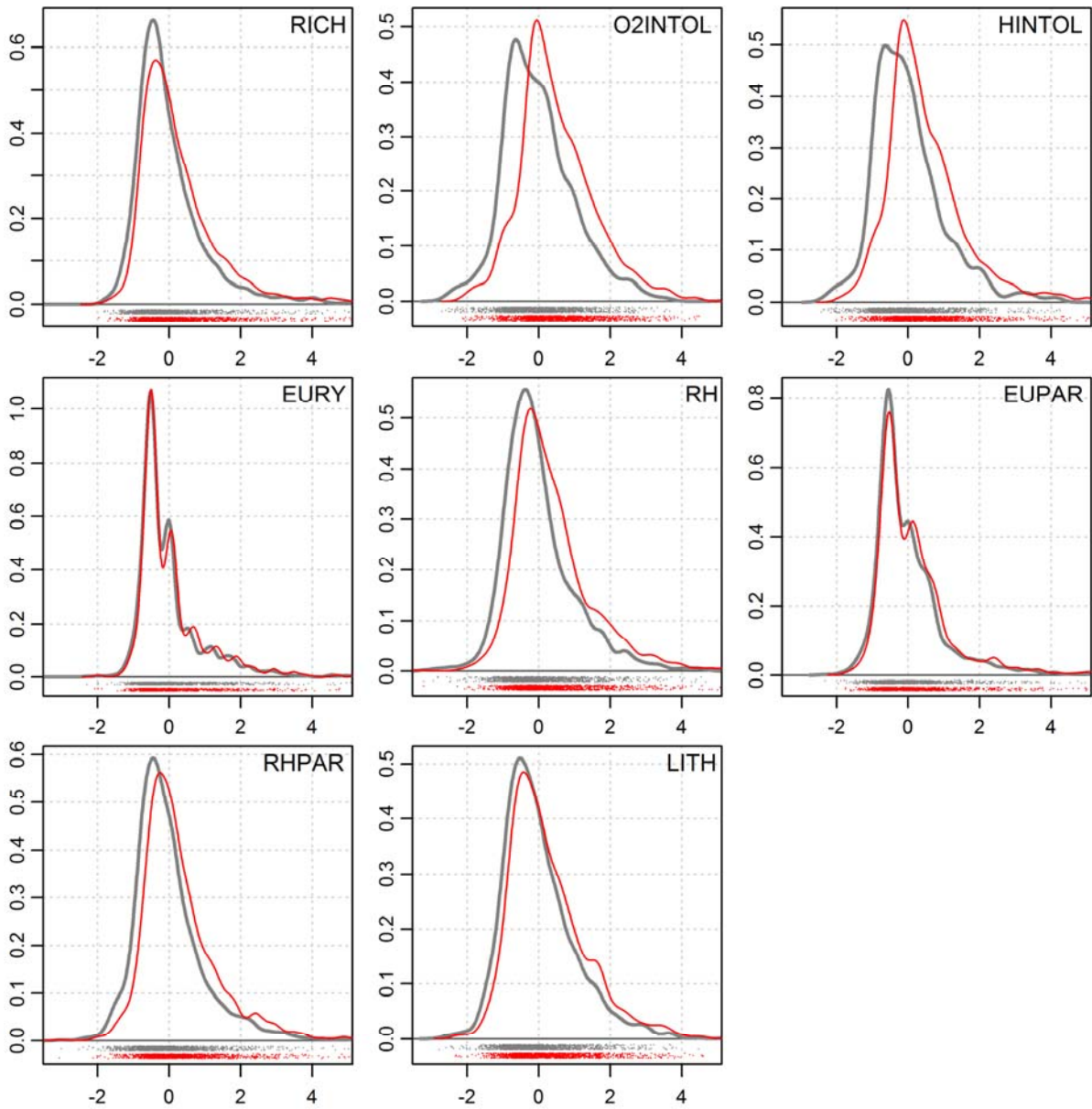
Density (kernel estimation) of the standardized metrics on the current environmental conditions (in grey) and for the scenario A1F1 (in red).

Scenario A2



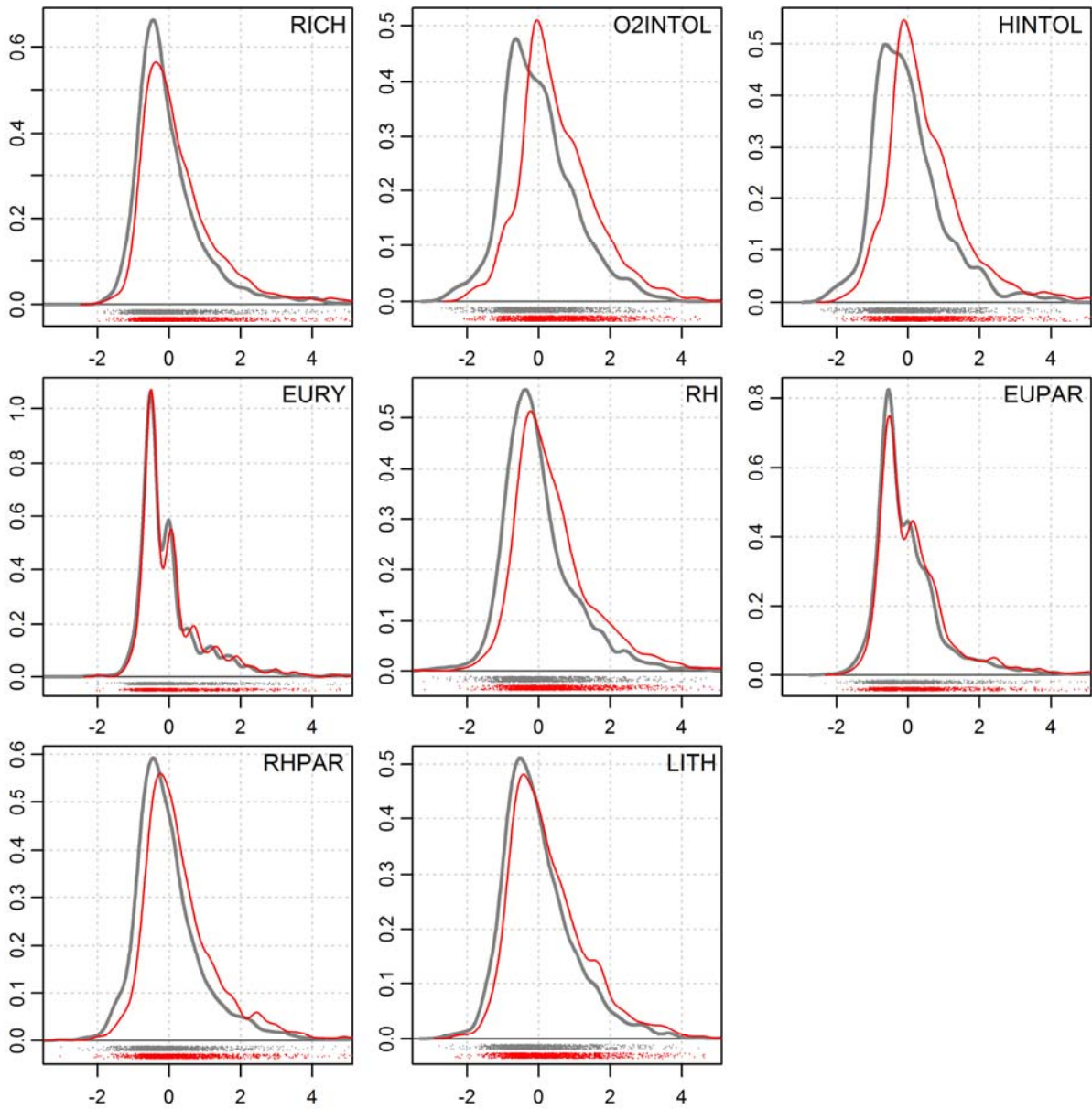
Density (kernel estimation) of the standardized metrics on the current environmental conditions (in grey) and for the scenario A2 (in red).

Scenario B1



Density (kernel estimation) of the standardized metrics on the current environmental conditions (in grey) and for the scenario B1 (in red).

Scenario B2



Density (kernel estimation) of the standardized metrics on the current environmental conditions (in grey) and for the scenario B2 (in red).

Appendix 4: Effect of human pressures and climate change

Alburnoides bipunctatus

Comparison between observed spiralin presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	294	163	288	169	286	171	289	168	290	167
Pres	27	42	30	39	30	39	30	39	30	39

Comparison between observed spiralin presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	294	163	321	136	295	162	279	178	281	176
Pres	27	42	49	20	39	30	33	36	33	36

Alburnus alburnus

Comparison between observed bleak presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	592	412	466	538	471	533	469	535	471	533
Pres	35	279	16	298	16	298	16	298	16	298

Comparison between observed bleak presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	592	412	331	673	368	636	393	611	391	613
Pres	35	279	10	304	12	302	13	301	12	302

Anguilla anguilla

Comparison between observed eel presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	535	386	521	400	513	408	511	410	508	413
Pres	67	401	51	417	50	418	50	418	48	420

Comparison between observed eel presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	535	386	643	278	626	295	607	314	606	315
Pres	67	401	118	350	94	374	81	387	77	391

Barbatula barbatula

Comparison between observed stone loach presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	281	395	304	372	301	375	302	374	303	373
Pres	97	330	133	294	124	303	129	298	127	300

Comparison between observed stone loach presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	281	395	354	322	337	339	322	354	325	351
Pres	97	330	197	230	163	264	145	282	145	282

Barbus barbus

Comparison between observed barbel presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	477	304	377	404	376	405	376	405	374	407
Pres	21	189	22	188	19	191	20	190	19	191

Comparison between observed barbel presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	477	304	384	397	372	409	373	408	369	412
Pres	21	189	69	141	38	172	27	183	29	181

Chondrostoma nasus

Comparison between observed nase presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	191	251	130	312	131	311	132	310	135	307
Pres	3	65	13	55	14	54	14	54	16	52

Comparison between observed nase presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	191	251	231	211	180	262	149	293	154	288
Pres	3	65	50	18	38	30	30	38	30	38

Cottus gobio

Comparison between observed bullhead presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	377	472	622	227	617	232	618	231	623	226
Pres	68	204	162	110	157	115	156	116	161	111

Comparison between observed bullhead presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	377	472	792	57	746	103	669	180	699	150
Pres	68	204	250	22	233	39	200	72	204	68

Esox lucius

Comparison between observed northern pike presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	604	403	643	364	640	367	645	362	645	362
Pres	83	303	65	321	66	320	67	319	67	319

Comparison between observed northern pike presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	604	403	734	273	713	294	693	314	694	313
Pres	83	303	96	290	80	306	72	314	71	315

Gasterosteus aculeatus

Comparison between observed three-spine stickleback presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	602	262	675	189	670	194	674	190	677	187
Pres	77	119	121	75	121	75	122	74	127	69

Comparison between observed three-spine stickleback presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	602	262	789	75	752	112	705	159	717	147
Pres	77	119	165	31	156	40	144	52	146	50

Gobio gobio

Comparison between observed gudgeon presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for the period 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	432	275	419	288	418	289	420	287	420	287
Pres	135	413	131	417	127	421	131	417	131	417

Comparison between observed gudgeon presence (Pres) or absence (Abs) in impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	432	275	438	269	422	285	417	290	417	290
Pres	135	413	180	368	157	391	139	409	141	407

Lampetra planeri

Comparison between observed brook lamprey presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	792	467	888	371	888	371	895	364	898	361
Pres	26	45	40	31	37	34	38	33	38	33

Comparison between observed brook lamprey presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	792	467	1034	225	985	274	948	311	957	302
Pres	26	45	55	16	48	23	44	27	45	26

Leuciscus cephalus

Comparison between observed chub presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	317	325	216	426	215	427	218	424	215	427
Pres	115	392	56	451	58	449	58	449	60	447

Comparison between observed chub presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	317	325	241	401	233	409	230	412	224	418
Pres	115	392	94	413	70	437	60	447	61	446

Leuciscus leuciscus

Comparison between observed dace presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	404	346	355	395	351	399	350	400	349	401
Pres	66	242	58	250	57	251	55	253	55	253

Comparison between observed dace presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	404	346	436	314	417	333	403	347	401	349
Pres	66	242	110	198	93	215	80	228	81	227

Lota lota

Comparison between observed burbot presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	263	355	274	344	271	347	278	340	275	343
Pres	13	75	15	73	15	73	15	73	15	73

Comparison between observed burbot presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	263	355	235	383	236	382	245	373	246	372
Pres	13	75	13	75	13	75	13	75	13	75

Perca fluviatilis

Comparison between observed perch presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	269	348	244	373	241	376	245	372	244	373
Pres	65	409	48	426	47	427	48	426	49	425

Comparison between observed perch presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	269	348	339	278	301	316	272	345	272	345
Pres	65	409	103	371	84	390	65	409	67	407

Phoxinus phoxinus

Comparison between observed minnow presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	370	490	428	432	425	435	428	432	431	429
Pres	76	222	136	162	132	166	134	164	134	164

Comparison between observed minnow presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	370	490	557	303	504	356	468	392	473	387
Pres	76	222	184	114	172	126	163	135	165	133

Pungitius pungitius

Comparison between observed nine-spine stickleback presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	737	154	701	190	700	191	698	193	702	189
Pres	19	24	26	17	24	19	24	19	25	18

Comparison between observed ninespine stickleback presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	737	154	819	72	779	112	729	162	742	149
Pres	19	24	36	7	33	10	28	15	28	15

Rhodeus amarus

Comparison between observed bitterling presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	293	397	107	583	111	579	111	579	111	579
Pres	12	84	3	93	3	93	3	93	3	93

Comparison between observed bitterling presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	293	397	69	621	70	620	84	606	80	610
Pres	12	84	0	96	1	95	2	94	2	94

Rutilus rutilus

Comparison between observed roach presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	267	246	221	292	220	293	221	292	220	293
Pres	80	530	54	556	54	556	53	557	55	555

Comparison between observed roach presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	267	246	276	237	258	255	236	277	233	280
Pres	80	530	119	491	76	534	65	545	66	544

Salmo salar

Comparison between observed Atlantic salmon presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	533	447	730	250	722	258	718	262	721	259
Pres	7	68	20	55	19	56	19	56	19	56

Comparison between observed Atlantic salmon presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	533	447	908	72	870	110	831	149	842	138
Pres	7	68	51	24	45	30	38	37	41	34

Salmo trutta

Comparison between observed brown trout presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	619	175	686	108	680	114	677	117	678	116
Pres	218	379	331	266	325	272	323	274	325	272

Comparison between observed brown trout presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	619	175	751	43	739	55	717	77	720	74
Pres	218	379	451	146	409	188	382	215	387	210

Telestes souffia

Comparison between observed soufie presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	242	55	147	150	146	151	144	153	144	153
Pres	7	22	12	17	11	18	10	19	10	19

Comparison between observed soufie presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	242	55	183	114	164	133	157	140	156	141
Pres	7	22	24	5	20	9	20	9	19	10

Thymallus thymallus

Comparison between observed grayling presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2020–2030.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	674	230	840	64	840	64	839	65	842	62
Pres	36	83	92	27	90	29	92	27	94	25

Comparison between observed grayling presence (Pres) or absence (Abs) at impacted sites and projections for the current environmental conditions (Current) and the four scenarios, for 2050–2060.

	Current		A1F1		A2		B1		B2	
	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres
Abs	674	230	882	22	872	32	861	43	864	40
Pres	36	83	112	7	106	13	103	16	104	15

Appendix 5: Uncertainty about species distribution projections

2020–2030

Table 14: Number of sites with expected new presence and new absence (compared to the current environmental conditions) computed from the CIs limits (low for lower and up for upper) for 2020–2030 and the four scenarios.

Species	a1				a2				b1				b2			
	New absence		New presence		New absence		New presence		New absence		New presence		New absence		New presence	
	low	up	low	up	low	up	low	up	low	up	low	up	low	up	low	up
<i>Alburnoides bipunctatus</i>	380	42	14	441	380	37	14	447	390	40	11	443	392	44	13	440
<i>Alburnus alburnus</i>	56	0	70	917	70	0	60	903	80	0	61	912	77	0	67	920
<i>Anguilla anguilla</i>	179	46	94	366	159	40	111	388	139	42	113	411	139	33	120	415
<i>Barbatula barbatula</i>	537	215	104	427	511	193	101	433	525	206	98	433	528	211	110	437
<i>Barbus barbus</i>	172	71	190	582	169	69	185	580	167	67	191	590	169	71	195	591
<i>Chondrostoma nasus</i>	376	77	54	544	365	73	47	545	365	70	52	552	362	79	51	550
<i>Cottus gobio</i>	1315	829	53	221	1302	793	54	224	1316	816	54	216	1352	830	54	219
<i>Esox lucius</i>	365	115	44	439	353	111	44	441	363	117	47	440	363	118	52	445
<i>Gasterosteus aculeatus</i>	587	214	28	336	587	211	25	335	591	226	24	335	600	248	28	335
<i>Gobio gobio</i>	308	113	168	553	291	101	152	549	310	110	153	545	312	113	159	550
<i>Lampetra planeri</i>	589	209	10	216	588	187	9	222	607	196	11	215	620	204	11	213
<i>Leuciscus cephalus</i>	266	139	492	849	254	125	475	847	266	142	486	852	264	137	493	860
<i>Leuciscus leuciscus</i>	261	108	94	575	243	101	92	578	243	102	100	584	245	103	110	592
<i>Lota lota</i>	495	0	0	568	497	0	0	573	514	0	0	561	512	0	0	563
<i>Perca fluviatilis</i>	358	204	209	584	342	193	207	590	358	192	201	591	360	201	214	602
<i>Phoxinus phoxinus</i>	736	286	33	311	708	255	33	313	716	261	33	311	726	267	38	318
<i>Pungitius pungitius</i>	364	216	119	546	360	219	115	556	362	229	113	550	368	242	114	556
<i>Rhodeus amarus</i>	200	2	141	920	210	2	126	911	237	2	120	912	225	2	129	909
<i>Rutilus rutilus</i>	312	139	240	676	299	130	229	678	307	141	242	681	311	149	257	683
<i>Salmo salar</i>	666	463	0	0	631	430	0	0	626	435	0	0	652	450	0	0
<i>Salmo trutta</i>	1014	399	0	28	944	357	0	27	939	355	0	27	940	358	0	24
<i>Telestes souffia</i>	206	89	103	719	204	86	90	710	208	89	98	748	203	89	98	729
<i>Thymallus thymallus</i>	697	343	11	97	699	339	11	96	705	352	11	92	715	368	11	94

2050–2060

Table 15: Number of sites with expected new presence and new absence (compared to the current environmental conditions) computed from the CIs limits (low for lower and up for upper) for 2050–2060 and the four scenarios.

Species	a1				a2				b1				b2			
	New absence		New presence		New absence		New presence		New absence		New presence		New absence		New presence	
	low	up	low	up	low	up	low	up	low	up	low	up	low	up	low	up
<i>Alburnoides bipunctatus</i>	471	202	30	350	421	149	37	404	385	111	30	421	391	118	30	416
<i>Alburnus alburnus</i>	25	1	529	1373	24	0	380	1265	27	0	266	1147	30	0	282	1164
<i>Anguilla anguilla</i>	622	354	10	164	481	238	10	172	397	158	7	183	395	153	6	185
<i>Barbatula barbatula</i>	1038	794	190	441	881	595	176	450	741	452	168	433	747	466	172	447
<i>Barbus barbus</i>	453	289	286	622	329	189	275	607	254	128	251	581	266	141	258	585
<i>Chondrostoma nasus</i>	643	309	80	464	543	206	83	486	462	158	89	504	462	160	85	495
<i>Cottus gobio</i>	1834	1602	74	197	1740	1383	80	223	1574	1142	76	218	1633	1219	83	225
<i>Esox lucius</i>	662	441	79	373	569	331	73	402	501	241	66	414	515	250	70	410
<i>Gasterosteus aculeatus</i>	786	585	37	251	736	483	43	289	658	377	44	319	694	404	45	318
<i>Gobio gobio</i>	601	474	314	557	486	368	310	583	419	279	280	562	433	297	292	578
<i>Lampetra planeri</i>	954	649	17	153	867	505	18	182	761	404	18	196	796	433	18	194
<i>Leuciscus cephalus</i>	648	521	711	1036	503	409	673	985	420	316	620	951	438	325	636	969
<i>Leuciscus leuciscus</i>	528	388	160	486	446	260	150	504	376	191	137	514	377	191	153	522
<i>Lota lota</i>	374	0	0	614	393	0	0	617	414	0	0	596	413	0	0	603
<i>Perca fluviatilis</i>	803	613	255	578	662	458	268	621	563	333	267	616	574	350	268	621
<i>Phoxinus phoxinus</i>	1308	930	68	295	1110	735	65	301	977	563	56	309	1015	582	59	314
<i>Pungitius pungitius</i>	474	416	66	357	448	378	86	446	411	325	106	508	424	344	96	501
<i>Rhodeus amarus</i>	300	76	602	1060	204	33	511	1012	180	19	390	978	185	21	408	973
<i>Rutilus rutilus</i>	680	468	320	654	536	355	307	669	436	279	295	676	449	288	305	679
<i>Salmo salar</i>	1105	945	0	0	995	853	0	0	914	748	0	0	937	785	0	0
<i>Salmo trutta</i>	1714	1370	0	9	1553	1105	0	12	1380	811	0	12	1397	812	0	11
<i>Telestes souffia</i>	266	193	200	606	225	150	196	612	219	123	153	654	218	123	153	634
<i>Thymallus thymallus</i>	805	665	18	66	777	586	18	73	741	512	16	88	750	533	19	84