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Combining expert-based and computational approaches to design protected river networks under climate change

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Abstract

Aim: Estimate the current and future distribution of brown trout and identify priority areas for conservation of the species.

Location: Rhône River basin and Mediterranean streams.

Methods: We first developed a spatially explicit species distribution model to estimate the current and future distribution of brown trout for three time horizons (2030, 2055 and 2080) and two climate change scenarios (RCP 4.5 and RCP 8.5). We then performed a prioritization analysis to identify priority areas for brown trout conservation, accounting for: (a) spatial dependencies along the riverine system, (b) several sources of uncertainty arising from climate-related forecasts and (c) different protected area scenarios by comparing hypothetical, optimal protected networks to an actual protected network designed by regional fish experts.

Results: Future projections of brown trout densities exhibited a general trend towards a gradual range contraction, with a significant risk of extirpation across mountainous regions of low to mid-elevation. Overall, the projected current and future distributions were well-covered by the existing protected network. In addition, up to 70% of the river reaches included in this expert-based protection network were also priorities in the optimal priority set (e.g. the best set of areas to maximize biodiversity protection). Finally, a large proportion of these reaches were invariably identified regardless of climate change scenarios and uncertainties or spatial dependencies.

Main conclusions: Our analytical approach highlighted priority areas for brown trout conservation which were robust to a set of climate and connectivity assumptions. This core priority network could be further refined by taking into account key fine-scale processes like thermal refugia. Therefore, we advocate for combining computational and expert-based approaches in conservation planning of riverine ecosystems to achieve a relevant consensus between regional-scale management and fine-grain ecological knowledge.

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KEYWORDS

Brown trout, climate change uncertainty, conservation planning, directed longitudinal connectivity, protected river networks, riverine systems, *Salmo trutta*, spatial stream network model, species distribution model, species range shifts

1 | INTRODUCTION

Freshwater ecosystems are among the most threatened by global change (Strayer & Dudgeon, 2010; Vörösmarty et al., 2010; Woodward et al., 2010). Changes in temperature and streamflow conditions have and continue to have strong effects on the distribution of many riverine fishes (Clavero et al., 2017; Comte et al., 2013; Darwall & Freyhof, 2016). Observed responses to recent climate change involve expansion or contraction of suitable riverine habitats and/or shifts in species ranges poleward, and towards higher elevations and upstream reaches (Comte & Grenouillet, 2013; Maire et al., 2019), consistently with those observed across terrestrial ecosystems (Chen et al., 2011). In contrast to terrestrial biomes, nonetheless, the linear nature of dendritic riverine systems makes them even more vulnerable to climate change due to a high level of fragmentation and isolation which makes fish migration more difficult and sometimes impossible (Olden et al., 2011; Woodward et al., 2010). Freshwater fishes have indeed limited dispersal opportunities owing to the constraints imposed by riverine system structures (Abell et al., 2008; Grant et al., 2007), further exacerbated by the introduction of climate-induced thermal or artificial barriers (Ficke et al., 2007; Letcher et al., 2007; Radinger & Wolter, 2015). Yet, they have to disperse through suitable corridors connecting favourable isolated habitats to track their climate niche at the same pace as isotherm shifts (Crimmins et al., 2011; Isaak & Rieman, 2013). As a result, many fish species are unable to keep pace with climate change velocity (Comte & Grenouillet, 2013, 2015; Radinger et al., 2017).

Given the climate risks posed to freshwater systems and the additional dispersal constraints on these species, it is critical to consider potential range shifts when designing protected area networks. Well-funded and well-managed reserves are the forefront of the actions needed to build more resilient ecosystems and to make a successful transition to sustainability (Ripple et al., 2017). Surprisingly, while designing protected areas is the flagship tool for terrestrial and marine biodiversity conservation (Margules & Pressey, 2000), it has received much less attention for streams and rivers (Abell et al., 2017; Cooper et al., 2019; Williams et al., 2011). As a result, while the protection of target areas can meet biodiversity conservation objectives (Geldmann et al., 2013; Pollock et al., 2017), up to 70% of river reaches worldwide still have no protection (Abell et al., 2017). Accounting for the directionality and connectivity of riverine systems, as well as the various and complex life cycles of species living therein, is crucial for conservation planning of freshwaters (Domisch et al., 2019; Hermoso et al., 2011). While the implementation of effective conservation actions is always challenging (Beatty et al., 2014; Collier, 2011; Esselman & Allan, 2011; Hermoso et al., 2018), the design of protected river networks can

now benefit from insights and tools provided by a long experience in conservation planning of terrestrial and marine systems (Margules & Pressey, 2000; Watson et al., 2014). Likewise, more recent advances and developments of conservation prioritization methods have been dedicated to running waters (Alexander et al., 2018; Hermoso et al., 2012, 2016; Moilanen et al., 2008).

In order to achieve effective conservation and management of high-priority species, relevant projections of current and future distribution with respect to environmental changes are critical (Olden et al., 2010). In this context, species distribution models (SDM; Guisan & Thuiller, 2005) are a useful tool to provide an assessment of range shifts and a spatially explicit quantification of losses and gains of suitable areas, especially regarding climate change (e.g. Thuiller et al., 2011). Moreover, the relevance of SDM for streams and rivers in particular can be further improved by accounting for the directionality and connectivity of those dendritic systems (Esselman & Allan, 2011; Isaak et al., 2017; Ver Hoef & Peterson, 2010). In addition to the challenges of projecting distributions into the future, these modelled projections and their inherent uncertainties must be then incorporated into the conservation planning process. The long-term persistence of biodiversity is likely dependent on successfully making this transition from models to spatial prioritization (Jones et al., 2016; Kujala et al., 2013).

Here, we provide one of the first conservation planning studies to account for both spatial dependencies and climate-related sources of uncertainty on riverine systems. We focused on an existing protected river network in south-eastern France targeting brown trout (*Salmo trutta*), which is acknowledged as an indicator species of cold water ecosystems due to its inherent sensitivity to warming temperatures at all stages of its life cycle (Clavero et al., 2017; Kovach et al., 2016; Muhlfeld et al., 2019; Tisseuil et al., 2012). Significant range shifts have already been observed or are forecasted for this species (Kovach et al., 2016), especially at the warm edge of its current distribution (Almodóvar et al., 2012; Filipe et al., 2013; Segurado et al., 2016), including the South of France (Comte et al., 2013; Lassalle & Rochard, 2009). Our overall objective was to identify spatial priority areas for brown trout and determine how well an expert-designed protected area network represents those priorities. To do this, we first developed a spatially explicit SDM to (a) estimate the current (i.e. for the recent decade 2004–2013) and future (i.e. at the horizons 2030, 2055 and 2080) distribution of brown trout in south-eastern France under two future climate change scenarios (RCP4.5 and RCP8.5) and (b) assess the potential species range shifts under these future scenarios. Based on the current and future projections of brown trout density (i.e. conservation features), we then performed a spatial prioritization analysis using different methods of incorporating spatial dependencies and climate forecast uncertainty.

Finally, we compared the brown trout range protected under a set of optimal scenarios to that protected based on an existing protected network designed by regional fish experts.

2 | METHODS

2.1 | Study area and data

The study focused on the south-eastern quarter of France that includes the whole Rhône River drainage basin as well as streams and rivers directly flowing into the Mediterranean Sea (c. 122,000 km²; Figure 1a). The corresponding hydrographic system (c. 65,500 km) was represented by c. 22,000 reaches (median length = c. 1.7 km) among which 34.3% belong to a protected river network designed by regional fish experts in 2010 (hereafter referred to as the expert network; Figure 1a) and included in the management schemes of the Water Framework Directive (SDAGE: "Schéma Directeur d'Aménagement et de Gestion des Eaux"). This network is targeted for brown trout (*S. trutta*) and aims at protecting key areas for the species regarding reproduction (spawning habitats, nurseries), dispersal (recruitment, migration), feeding and/or refugia. More specifically, while reaches belonging to the protected network are not necessarily entirely preserved from anthropogenic impacts, any new development projects must preserve the functionality of these key areas and their influence on connected reaches within catchments. In particular, 95% of the total length of the network benefits from a regulatory ban on any new physical, thermal or chemical barriers impeding the movements of biological organisms and sediments.

Trout data were compiled at 640 sites across the study region from the French Biodiversity Office (the national organization in charge of the protection and conservation of biodiversity in France) database (www.naiades.eaufrance.fr; Figure 1b). Trout densities (ind/ha; minimum length of individuals = c. 40 mm) were collected at each site over the 2004–2013 decade (4 ± 2 sampling years per site) using a standard electrofishing protocol conducted during low-flow periods (i.e. fish were mostly captured by wading using

a two-pass removal; Poulet et al., 2011). Following the findings of Veloz et al. (2015) on protection networks representing <50% of the total area, we used densities (rather than occurrence) for more accurately identifying the highest priority areas. Moreover, the time window was selected assuming that possible positive effects of the expert network implementation on trout densities were not yet detectable.

Altitude (m) and distance from the headwater source (km) were derived at each sampling site from the BD TOPO® GIS layer. They were used as correlates of the upstream–downstream gradient along which fish populations, especially salmonids, are distributed (Matthews, 1998). In addition, daily data for air temperature and precipitation were extracted at a resolution of 8 km × 8 km (i.e. from the cells encompassing the sampling sites) from the French weather service model SAFRAN (Météo France; Vidal et al., 2010) and used to derive four climatic variables: mean temperature of the warmest quarter (°C), monthly temperature seasonality (standard deviation × 100), cumulated precipitation of the wettest month (mm) and monthly precipitation seasonality (coefficient of variation). Owing to the sensitivity of fish to extreme conditions and climatic seasonality (Matthews, 1998), these variables are commonly acknowledged as relevant with regard to their influence on fish distribution (Buisson et al., 2010; Comte & Grenouillet, 2015; Myers et al., 2017). Air temperature was used as a substitute for water temperature according to their strong correlation at regional scales (e.g. Orr et al., 2014). Climatic variables were calculated for each year and averaged over the 2004–2013 decade.

In order to estimate and project the current distribution of brown trout over the entire drainage basin, the six geographic and climatic variables were also defined at the mid-length points of the 22,000 reaches. For future conditions, we extracted temperature and precipitation forecasts from EURO-CORDEX simulations (Jacob et al., 2014) available on the Drias portal (www.drias-climat.fr; Lémond et al., 2011) at the same resolution of 8 km × 8 km as current climate (i.e. from the cells encompassing the mid-length points). Future climate data were used to derive the four climatic variables at the 22,000 reaches for the decades 2029–2038, 2054–2063 and

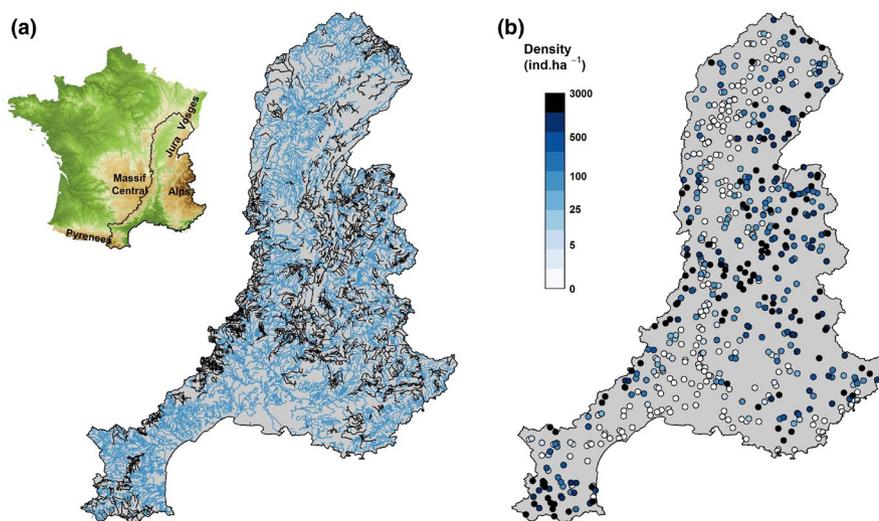


FIGURE 1 (a) Distribution of the regional protected river network (black reaches) within the study area. The main surrounding topographic relief are shown on the top-left hill-shade map. (b) Average brown trout density over the 2004–2013 decade at the 640 sampling sites

2079–2088 (hereafter referred to as horizons 2030, 2055 and 2080, respectively) under the two emission scenarios RCP4.5 and RCP8.5 (Moss et al., 2010). These two scenarios were chosen as contrasting plausible pathways, respectively, referred to as an intermediate and a “business-as-usual” scenarios. For each time horizon and RCP scenario, climatic variables were calculated for six different combinations of global and regional climate models (Table S1).

2.2 | Current and future distribution modelling

To project the current and future distribution of brown trout in south-eastern France, we used SDM statistically relating brown trout densities to the six geographic and climate variables. First, altitude and distance from the source were log-transformed to correct for deviation from normality. Because they were strongly correlated with climatic variables, each geographic variable was regressed onto the four climatic variables by fitting generalized additive models (GAMs) with up to four degrees of freedom. The residuals from these models were used as individual predictors independent of the climatic variables for the next analyses (e.g. Buisson, Thuiller, et al., 2010). After this correction, all the six variables were poorly correlated ($|r| < .55$).

Then, we built a spatially explicit species distribution model (hereafter referred to as spatial SDM) following a two-step procedure. First, we fitted a SDM to relate $\ln(x + 1)$ -transformed trout densities to geographic and climatic predictors using a GAM with up to four degrees of freedom. Second, we looked at potential spatial autocorrelation within the GAM residuals by fitting a spatial stream network (SSN) model (Ver Hoef & Peterson, 2010). This geostatistical modelling tool has been developed to account for spatial dependencies in physical and ecological processes across riverine systems by considering their specific dendritic structure (Peterson & Ver Hoef, 2010; Ver Hoef & Peterson, 2010; Ver Hoef et al., 2006). Autocorrelation between nearby sites is specified using covariance functions based on straight-line (i.e. Euclidean) and/or in-stream (i.e. hydrologic) distances (Ver Hoef & Peterson, 2010). Hydrologic distances further make the distinction between “flow-connected” sites (going from a headwater to an outlet) and “flow-unconnected” sites (going from a headwater to an outlet and then back “against the flow” to another headwater), represented by “tail-up” and “tail-down” covariance functions, respectively (Ver Hoef & Peterson, 2010).

We built a set of spatial SDM using different combinations of Euclidean (Cauchy, Spherical, Exponential or Gaussian), tail-up and/or tail-down (Linear-with-Sill, Spherical, Exponential, Mariah or Epanechnikov) covariance functions (Ver Hoef & Peterson, 2010). These spatial models, as well as the pure SDM (i.e. the one not accounting for spatial autocorrelation), were then compared using the Akaike information criterion (AIC; Akaike, 1974), penalizing for both the number of degrees of freedom in the GAM component and the number of autocovariance parameters in the SSN component, if any (Table S2). The predictive performance of the models was assessed by calculating the coefficient of determination (r^2) and root-mean-square error (RMSE) estimated through leave-one-out

cross-validation (e.g. Isaak et al., 2017). According to these three criteria, the best model retained as the final spatial SDM was a combination of the GAM component and a spatial component specified through a mixture of Euclidean and tail-up covariance functions ($r^2 = .61$, RMSE = 1.9).

Finally, projections at the 22,000 reaches were derived from this spatial SDM to estimate the current and future distribution of brown trout. For each of the thirty-six future projections (3 time horizons \times 2 RCP scenarios \times 6 climate models), we calculated a species range change (SRC) as follows (e.g. Buisson, Thuiller, et al., 2010):

$$\text{SRC} = \frac{\sum_r d_{f,r} \cdot l_r - \sum_r d_{c,r} \cdot l_r}{\sum_r d_{c,r} \cdot l_r}$$

where $d_{f,r}$ and $d_{c,r}$ are, respectively, the future and current trout densities projected at reach r and l_r is the reach length.

2.3 | Spatial conservation prioritization

We implemented a spatial prioritization analysis (Figure 2) to identify priority areas for brown trout conservation using Zonation (version 4.0; Moilanen et al., 2014). More specifically, we ranked the 22,000 different river reaches (conservation units) using current and future distributions of brown trout density derived from the spatial SDM (① in Figure 2) as conservation features. We used the Core Area Zonation algorithm to favour selection of high-value reaches for all conservation features, including reaches with high trout density occurring in otherwise density-poor reaches (Moilanen et al., 2005).

Following the framework developed by Kujala et al. (2013), we aimed at accounting for two sources of uncertainty inherent to climate change projections. First, we performed distribution discounting to account for uncertainty between distribution maps due to variation between climate models (② in Figure 2). For this purpose, we penalized future distributions by subtracting the standard deviation of forecasts across climate models from the mean forecast for each reach separately (e.g. Kujala et al., 2013). When negative, the subtraction result was fixed to zero. Distribution discounting was applied separately to the six future distributions (3 time horizons \times 2 RCP scenarios) which were defined, along with the current distribution, as the conservation features traded-off in the following prioritization procedures (③ in Figure 2). Second, we used a differential weighting procedure to account for different levels of confidence in the future projections. Denoting C the current distribution, F_1 , F_2 and F_3 the discounted future distributions at the three time horizons, and $w(D)$ the weight given to a particular distribution D , we assumed that $w(C) \geq w(F_1) \geq w(F_2) \geq w(F_3)$, using $w(C) = 1$ and varying weights in $[0-1]$ with an increment of 0.25 for the future distributions (e.g. Kujala et al., 2013). A total of 35 weighting combinations was defined following this logic (④ in Figure 2).

Finally, all analyses were performed separately for the two RCP scenarios and also by accounting (or not) for (a) spatial dependencies between upstream and downstream reaches, using Zonation's

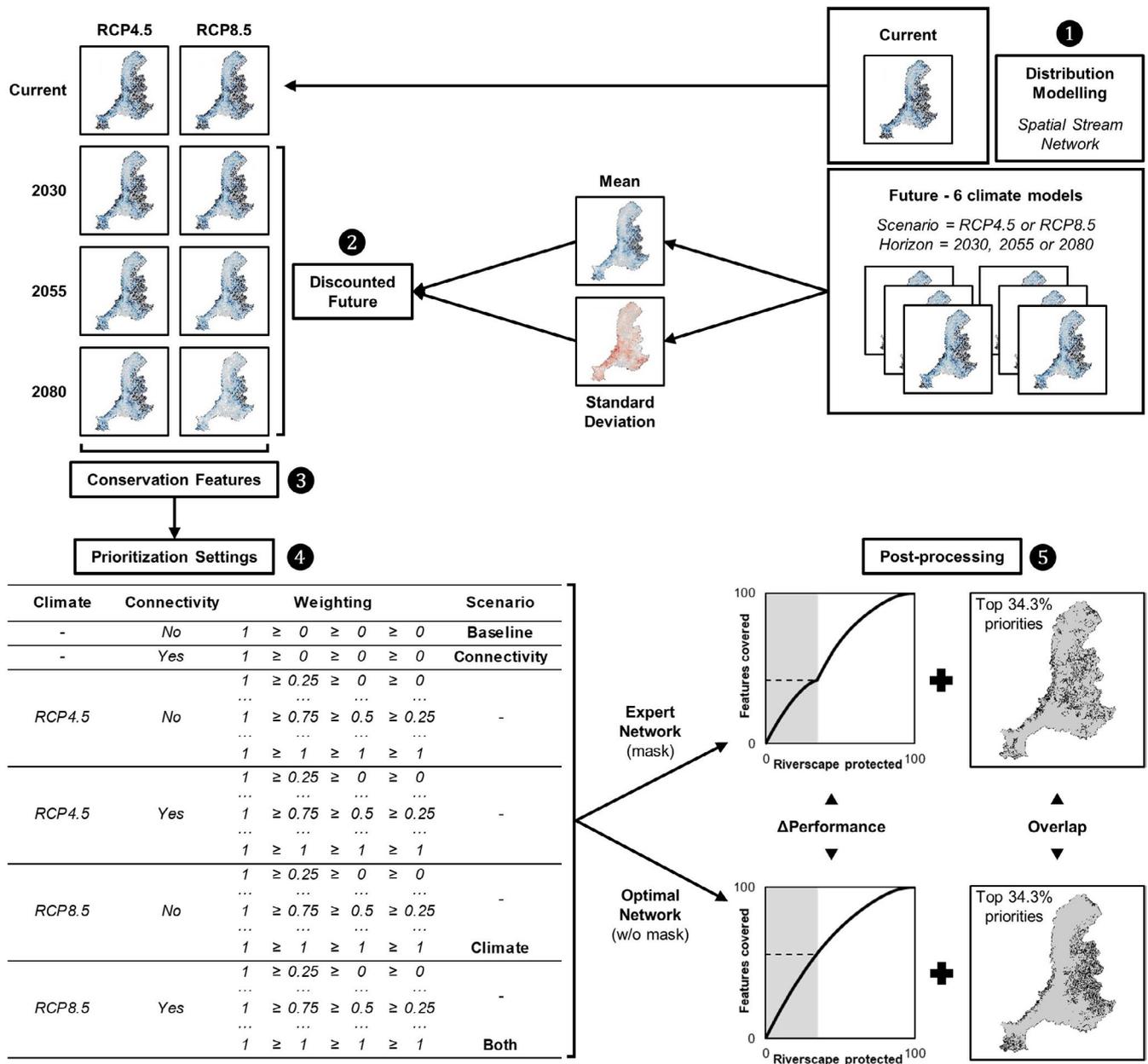


FIGURE 2 Flow chart of the spatial prioritization analysis used to identify priority areas for brown trout conservation and their overlap with the existing expert network. ① Current ($n = 1$) and future ($n = 36$) distributions are derived from a SSN model. ② A distribution discounting is applied to future distributions to account for uncertainty arising from variability across climate models. ③ Current and discounted future distributions are defined as conservation features. ④ Based on these features, spatial prioritizations are run with 140 different settings (2 RCP scenarios \times with-or-without connectivity \times 35 weighting combinations) both using a hierarchical mask of the expert network and selecting optimal priority networks (see text for further details). The “Scenario” column outlines key examples of settings illustrated in Figure 5. ⑤ In post-processing, performance variations (Figure 5) and overlaps (Figure 6) between optimal networks and the existing expert network are assessed by focusing on the top 34.3% priority areas (i.e. the spatial extent of the expert network) of each prioritization result

directed freshwater connectivity module (Moilanen et al., 2008), and (b) the protection status of reaches given by the expert network (④ in Figure 2). For this purpose, a penalization applied during the prioritization process for removing interconnected reaches was defined based on two penalty curves assuming a stronger response of brown trout to fragmentation upstream than downstream (Figure S3). Other cost measures could be implemented in such analyses, for example

costs related to land prices or human disturbances, but this issue was beyond the scope of our study. As a result, a total of 140 prioritization settings (35 weighting combinations \times 2 RCP scenarios \times with-or-without “connectivity”) was defined. First, we carried out the 140 prioritizations using a hierarchical mask of the expert network, which forces the ranking to be run first on the reaches along the surrounding riverscape (i.e. excluding the protected network) and then

on those belonging to the expert network (Moilanen et al., 2014). The same set of 140 prioritizations were then run without this mask to enable comparisons between the existing expert network and optimal priority networks.

2.4 | Post-processing analyses and priority network comparison

For each prioritization setting, we compared the “optimal” priorities (current protection not considered) to those of the existing priority network for brown trout conservation and management (⑤ in Figure 2). To this end, we defined the top priorities as the highest-ranked 34.3% of areas to match the area of the expert-based priority network. First, we estimated the performance of each prioritization solution as the combined proportional spatial coverage of the weighted conservation features (i.e. current and discounted future distributions) provided by the mask-variant or optimal priority network. Then, we assessed variations in the spatial patterns of priority networks by calculating the spatial overlap between the expert network and the top-34.3% priority areas of optimal networks. Finally, we used paired *t* tests (a) to compare the coverage levels between mask-variant and optimal priority networks and (b) to evaluate how prioritization settings (i.e. weightings, RCP scenarios and connectivity) can affect the outcomes for both coverage levels and overlaps.

All analyses were conducted with ArcGIS and R, using the STARS toolbox (Peterson & Ver Hoef, 2014) and the *MGCv* (Wood, 2006) and *SSN* (Ver Hoef et al., 2014) packages.

3 | RESULTS

The highest values of brown trout density predicted by the selected spatial SDM for the current period were more frequent within the protected network than in the rest of the drainage basin (Figure 3a). These high-density river reaches were mainly located across the high and mid-elevation mountain regions, including the

central Alps for the former and the Pre-Alps (western border of the Alps), the eastern end of the Pyrenees, the eastern border of the Massif Central, the Jura and the southern Vosges for the latter (Figures 1a and 3b).

On average, future projections for the RCP4.5 scenario derived from the spatial SDM highlighted a moderate expansion of the brown trout range at the horizon 2030 in comparison to the current distribution (SRC = $4.3 \pm 7.1\%$; Figure 4). While forecasted changes in species range remained slightly positive at the horizon 2055 (SRC = $1.2\% \pm 8.2$; Figure 4), they exhibited moderate losses at the horizon 2080 (SRC = $-4.5 \pm 13.2\%$; Figure 4). Regarding the RCP8.5 scenario, projections were similar to the RCP4.5 scenario at the horizon 2030 (SRC = $4.3 \pm 8.8\%$; Figure 4) but then highlighted a gradual contraction of the species range with strong losses at the horizon 2080 (SRC = $-33.0 \pm 11.9\%$; Figure 4). Variation (i.e. standard deviation) among projections related to the six different climate models was increasingly important with time, and only projections at the horizon 2080 for the RCP8.5 scenario showed SRC values of the same sign for all models (Figure 4, Figures S4 and S5).

Outputs from spatial prioritization analyses showed that the expert network covers brown trout range close to or better than a 1:1 relationship, including when accounting for spatial dependencies between reaches and/or future climate changes (Figure 5a). Limited albeit significant differences in coverage levels were observed when comparing prioritization results for the different RCP scenarios (paired *t* test, mean of the differences = 0.2%, $p < .001$) and weighting combinations (paired *t* tests, 0%–1.2%). Greater differences were observed between the two connectivity options (paired *t* test, 12.4%, $p < .001$). These patterns remained similar with optimally selected reaches (Figure 5b), although differences between connectivity options were lower (paired *t* test, 5.9%, $p < .001$). In addition, the existing expert network covers on average a weighted mean of $34.9 \pm 6.2\%$ of current and future projected distribution regardless of prioritization settings (Figure 5a,c), while this coverage could reach $48.2 \pm 3.3\%$ for optimal priority networks (Figure 4b,c). This difference was also significant according to pairwise comparisons (paired *t* test, 13.2%, $p < .001$; Figure 5c).

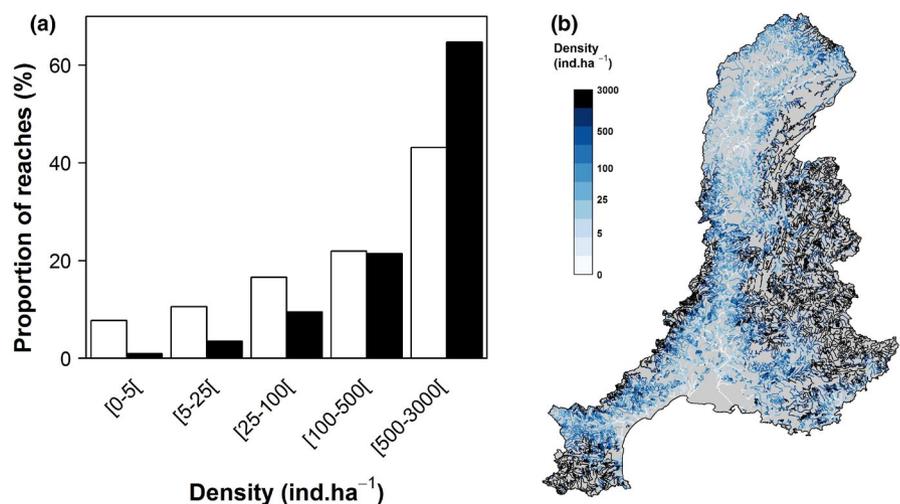


FIGURE 3 Spatial patterns of brown trout density derived from the spatial SDM for the current period (2004–2013): (a) predicted densities outside (white bars) and inside (black bars) the protected river network and (b) map of predicted densities

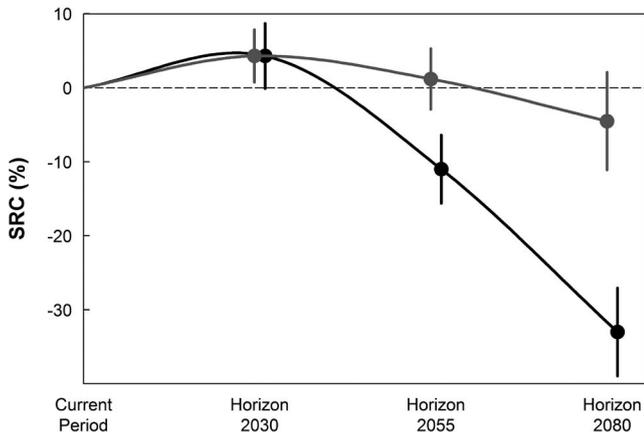


FIGURE 4 Species range change (SRC) projected for the three future horizons under the RCP4.5 (grey line) and RCP8.5 (black line) scenarios. Dots and error bars display means and standard deviations across the projections based on the six different climate models, respectively

On average, $50.3 \pm 0.6\%$ of the expert network overlapped with the top-34.3% priority areas of optimal networks. Despite the hundreds of prioritizations performed, we found little difference in the spatial overlap derived from these runs, ranging from 49.5% to 51.2%. Consistently, the prioritization settings, decisions whether to include spatial dependencies or not and how to weight the future distributions, had a weak albeit sometimes statistically significant influence on overlap values (paired *t* tests, mean of the differences = 0.9% and 0%–0.4% for connectivity options and weighting combinations, respectively). Additionally, we found very little difference in priorities for the two RCP scenarios (paired *t* tests, mean of the differences = 0.3%).

Moreover, up to 68.3% of the expert network was overlapped by reaches selected at least once among the 140 optimal networks (Figure 6a). This overall overlap was still of 57.6% when considering reaches selected in half of the 140 optimal networks and of 28.9% for those selected in all the optimal networks (Figure 6a). This core of optimally selected reaches represented the very large majority of those overlapping the expert network (red lines in Figure 6b)

FIGURE 5 Examples of performance curves from prioritizations using (a) the protected area mask or (b) optimal ranking. The grey area represents the spatial extent of the expert network (i.e. 34.3% of the entire river network). “Baseline” denotes a prioritization setting not accounting for connectivity nor climate (i.e. null weights given to forecasted future distribution), “Connectivity” a setting accounting for only connectivity; “Climate” a setting accounting for only climate (equal weights of 1 given to current and future distribution based on the RCP8.5 scenario) and “Both” a setting accounting for both connectivity and climate (see also Figure 2). (c) Box plots of the coverage levels extracted from performance curves for both mask-variant (expert) and optimal ranking. Coverage levels corresponding to the examples given above (see a and b) are also displayed

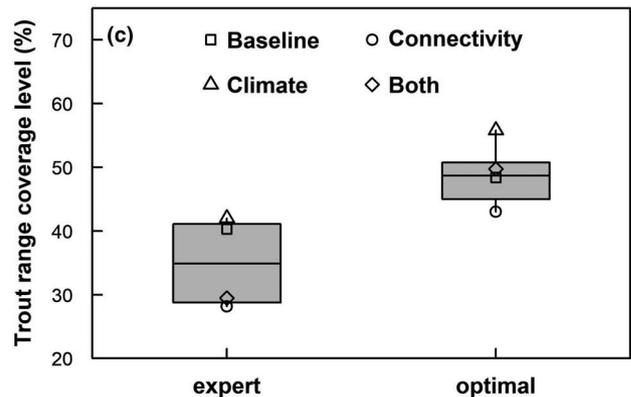
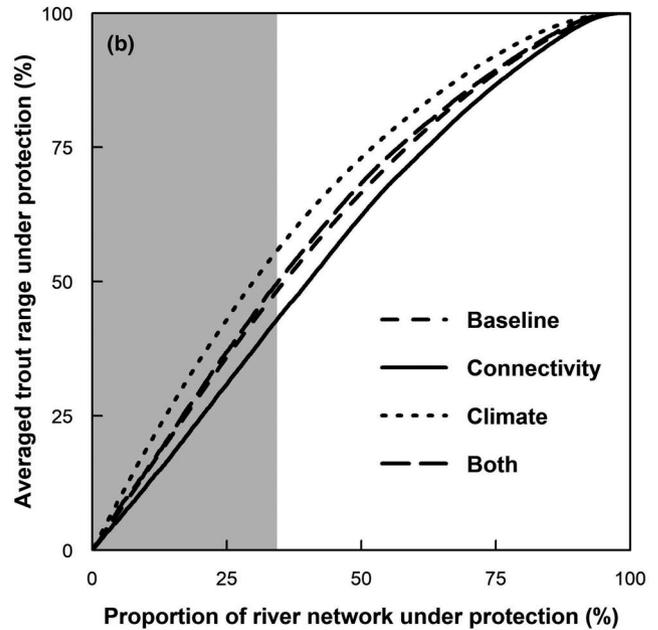
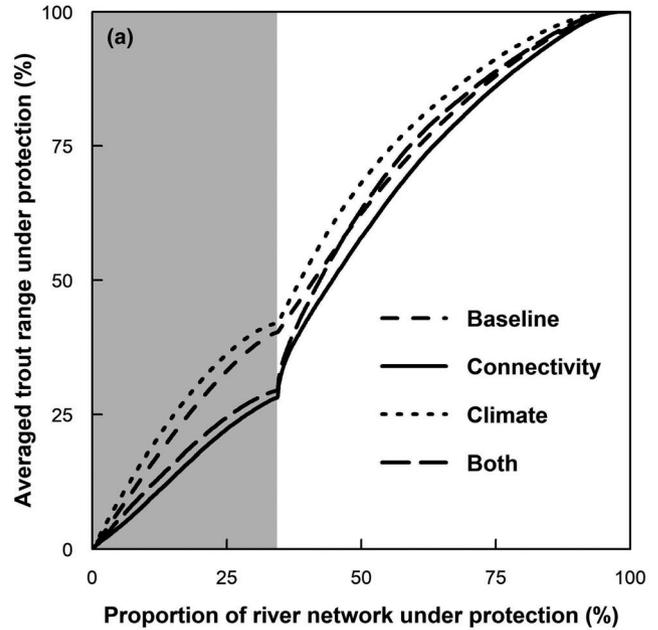
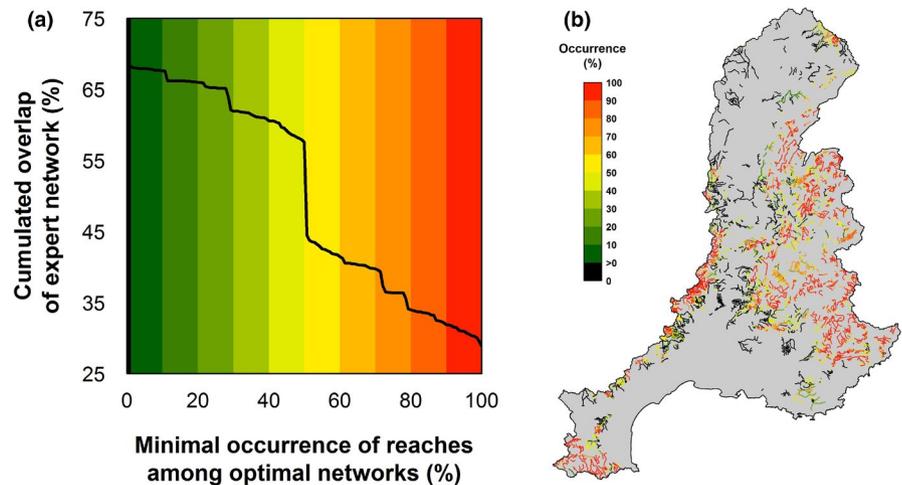


FIGURE 6 Degree of overlap between the existing expert network and the 140 optimal networks. (a) Relationship between the minimal number of times priority reaches were selected in common among the 140 optimal networks (i.e. occurrence) and the cumulated proportion of the expert network represented by these reaches. (b) Mapping of the expert network reaches according to their occurrence among the 140 optimal networks using the same colour-scale as in (a)



and few others were found at intermediate occurrences (green-to-orange lines in Figure 6b).

4 | DISCUSSION

Consistently with previous studies in Western Europe (Buisson et al., 2010; Filipe et al., 2013) and beyond (Beer & Anderson, 2013; Wenger et al., 2011), future brown trout densities were projected to gradually shrink across south-eastern France, mainly under the business-as-usual scenario (RCP8.5). Specifically, projections stressed a substantial risk of contraction at the edge of the regional distribution across the different mountain ranges (Alps, eastern Pyrenees, eastern Massif Central, Jura and southern Vosges). As a result, suitable river reaches should become progressively restricted to high elevations in the Alps at the end of the 21st century. This pattern was in agreement with the assumption that mountain streams and small tributaries would become refugia for many cold water species in response to temperature warming (Isaak et al., 2016). However, given that it is highly unlikely that a large majority of the south-eastern trout populations would be able to migrate up to the Alpine rivers—owing to the instream distance to disperse through, to the large proportion of stream length being unsuitable and to the additional physical barriers—some of them could be entirely extirpated, possibly including some native lineages (Conti et al., 2015; Jackson & Sax, 2009; Muhlfeld et al., 2019). Nevertheless, the forecasted decline in brown trout range varied across the emission scenario and the climate model, supporting the need to be cognisant of climate-related sources of heterogeneity and cautious when applying spatial prioritization to distribution projections (Kujala et al., 2013).

Overall, the projected current and future brown trout distributions were well-covered by the protected expert network, with a mean coverage level of about 35% regardless of prioritization settings. For the sake of comparison, a similar value was found in Kukkala et al. (2016) who assessed the effectiveness of the Natura 2000 areas for representing vertebrate species ranges across Europe. More importantly, the gain of performance which could

be attained by optimally selecting the river reaches to place under protection would be twice as weak in our study (c. 13% vs. 26% in Kukkala et al., 2016), suggesting that the expert network is not so far from an optimal priority network on average. Besides, the expert network exhibited individual matches around 50% with each analytical priority network, even though the overlap varied spatially. Howard et al. (2018), for example, found a close overlap value (i.e. around 50%) between the existing protected areas already managed for biodiversity conservation in California and an optimized network resulting from analytically prioritizing watersheds for freshwater biodiversity.

Moreover, since it was impossible to determine the most realistic configuration of climate change scenarios, future projection uncertainty and spatial dependencies, we built an ensemble of parametrization settings to encompass this range of possible situations and trends. While these ensembles represent a range of scenarios, it is possible that they do not well-represent some local areas due to non-stationarity of climate-related forecasts and associated uncertainties (Jones et al., 2016; Kujala et al., 2013) as well as the spatial heterogeneity of connectivity limitations (e.g. Radinger & Wolter, 2015). For instance, projections related to a climate scenario may be relevant for a given area but not necessarily for another where the uncertainties would be too great. Similarly, accounting for spatial dependencies is more relevant for free-flowing reaches than for those impaired by impassable barriers. As a result, different scenarios could happen simultaneously at the sub-catchment scale. A key finding of this study is that up to 70% of the river reaches included in the expert network were also considered as priority for at least one of the optimal networks derived from these configurations. Further, of this 70%, most river reaches were found in a majority of analytical networks, forming a core priority network. This core network supported the relevance of the protected expert network, because the expert network well-matched the RCP scenarios (in both coverage and overlap), even when considering this range of assumptions on climate change, connectivity and weighting schemes. Thus, neither the protection performance nor the spatial priority ranking of reaches from the expert network was substantially influenced

by the climate-related assumptions. This finding can be explained by the nested nature of the expected range contraction for brown trout, which has already been highlighted elsewhere (Almodóvar et al., 2012; Clavero et al., 2017; Filipe et al., 2013). Accordingly, river reaches which are poised to become more and more important relatively to the whole basin in the future—that is reaches which will mostly need protection—are nested within the currently most suitable reaches for the species—that is reaches which already mostly need protection.

Conversely, accounting for spatial dependencies seemed to be decisive in the priority decision process. Performance of the expert network in regard to the average trout range under protection was significantly lower (c. 12% on average) when including species-specific responses to potential loss of connectivity with upstream and downstream reaches. Basically, this result was methodologically related to the constraints imposed by Zonation's connectivity module which, by favouring aggregated solutions of longitudinally contiguous river basins rather than patchy solutions of isolated catchments with high conservation value (Moilanen et al., 2008), is intended to reflect the importance of within catchment connectivity for conservation planning in riverine systems (Leathwick et al., 2010). For instance, in a similar exercise of catchment-based prioritizations focusing on freshwater fish species in New Zealand, Moilanen et al. (2008) showed comparable performance gaps of about 10%–20% depending on whether or not spatial dependencies were quantitatively accounted for in the identification of high-priority conservation areas. Beyond such an absolute value of performance, nonetheless, including spatial dependencies into conservation planning has the potential to increase the quality of protected areas (without increasing the quantity needed) by yielding fundamentally different spatial arrangement of conservation plans (Domisch et al., 2019). From a conservation perspective, accounting for connectivity might therefore be the best option for long-term persistence of brown trout by favouring connections among populations rather than an overall coverage of the species range. Indeed, the maintenance of important ecological and evolutionary processes, such as migration to spawning sites and gene flow between populations, is mandatory for an effective conservation of the species and its genetic diversity (Hermoso et al., 2018). Also, no significant differences were found for overlaps (whether or not spatial dependencies were accounted for) indicating that, based on empirical knowledges, the expert network did locally assume a strong influence of connectivity in the identification of reaches to place under protection. Complementarily to the core priority network discussed above, these reaches were selected as high priority under particular parameterization settings, indicating that they could be of crucial importance as suitable corridor connecting isolated favourable reaches (Abell et al., 2008; Grant et al., 2007).

In spite of these promising results, there are several limitations related to the estimation of current and future distributions of brown trout. First, other factors that we did not consider here, such as hydrological, hydromorphological and hydraulic variables (e.g. discharge, velocity, depth, bottom substrates), natural and

man-made barriers (e.g. waterfalls, dams, roads), or spatial variations and potential future changes in land use (Mantyka-Pringle et al., 2014; Radinger et al., 2017), could influence the suitability of riverine habitats. Second, we chose not to distinguish juveniles from adults, which can have different environmental requirements, especially regarding their temperature sensitivity (Elliott & Elliott, 2010; Lahnsteiner, 2012). Third, brown trout stocking practices could potentially influence local population distributions and densities (Clavero et al., 2017), but this information was not available at the regional scale. Fourth, both consumptive (Pletterbauer et al., 2016) and competitive (Van Zuiden et al., 2016) interactions may also be important to consider when predicting species responses to climate change. Finally, accounting for dispersal limitations could have important implications for conservation and management at the catchment scale (Conti et al., 2015; Engler et al., 2012).

Notwithstanding these caveats, we were able to provide confident distribution estimates highlighting relevant regional patterns and trends and exhibiting significant congruence with the existing protected network based on experts. These elements constitute a critical step in defining management strategies for riverine ecosystems threatened by climate change (Myers et al., 2017). Therefore, we assumed that the above-mentioned limitations were slightly beyond the scope of our study and that they mainly suggested that further developments could be envisaged to increase model complexity and provide more accurate estimations of brown trout distribution in south-eastern France. It is likely that the addition of such biotic and abiotic drivers acting at finer scale would in turn result in a refinement of optimal networks derived from spatial prioritization and, hence, to greater matches with the expert network which was itself established based on a local knowledge of such fine-scale processes. As an example, thermal regimes of stream reaches can exhibit substantial fine-scale variations which are poorly captured by model developed at coarser spatial resolutions (Snyder et al., 2015). In particular, groundwater inputs have a strong influence on the thermal regimes of streams and rivers and, thus, can have important ecological implications in a changing climate by offering thermal refugia for cold water species (Carlson et al., 2019; Santiago et al., 2017). Arguably, however, the ecological importance of accounting for stream thermal heterogeneity and the potential consequences for trout conservation is well-acknowledged by local biodiversity experts and managers and has prevailed to the design of the existing protected river network (e.g. Fryirs et al., 2019).

Our findings therefore advocate for using a combination of computational and expert-based approaches in conservation planning of riverine ecosystems to achieve a relevant consensus between regional-scale management and fine-grain knowledge. While a large majority of riverine systems worldwide still suffers from the absence of protected areas (Abell et al., 2017), an analytical framework like the one proposed in this study may help to target conservation priorities by (a) providing suitable regional estimates of riverine species distribution, (b) accounting for possible future impacts of climate change and their uncertainties and (c) potentially considering several facets of biodiversity such as taxonomic, functional and

phylogenetic diversity (e.g. Pollock et al., 2015; Strecker et al., 2011). Local experts can then focus their efforts on the delineated priority river reaches and/or catchments to validate the proposed selection and determine whether they could be managed for conservation purposes (Grantham et al., 2017). Such combined approaches are essential to guide local conservation and restoration actions, like increasing riparian shading to limit water warming or restoring connectivity among suitable habitats (Myers et al., 2017), with maximized benefits to broader scales (Merovich et al., 2013). Ultimately, by offering an efficient protection for target species, they can also be crucial for other species or organisms which could benefit from an umbrella effect (e.g. Howard et al., 2018; Nieto et al., 2017).

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at www.naiades.eaufrance.fr and www.drias-climat.fr (see text for details).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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