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thesis abstract

Potential impacts of climate change on the distribution of freshwater fishes in French streams and uncertainty of projections

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Climate change and its impact on biodiversity are receiving increasing attention from scientists and people managing natural ecosystems. Recent modifications of climate have induced diverse functional (e.g. phenology, physiology) and structural (e.g. species distribution shifts, range contraction, local extinctions) responses among organisms (Walther et al. 2002). Given the projections of future climate change, these responses are expected to continue throughout the 21st century and climate change could thus have major consequences on species and assemblages. A common approach to project the potential impacts of environmental changes on the distribution of biodiversity is the use of species distribution models (SDM) (e.g. Thuiller 2003). These correlative models first relate the present-day species distribution to a set of climate and other environmental descriptors. Then, the application of scenarios of future climate changes provides predictions of the habitats potentially suitable in the future for the species. In spite of their widespread use, a growing concern has emerged for the variability in the predicted impacts by such models due to the methodological decisions taken during the modeling process (Thuiller 2004). Improvements in the accuracy of predictions combined with an estimation of the uncertainty inherent to those predictions are thus urgently needed.

Among freshwater ecosystems, stream fish have no physiological ability to regulate their body temperature and could therefore be very sensitive to climate warming, especially cold-stenotherm fish such as salmonid species. Stream fish also have to cope with hydrological variability of streams and strong anthropogenic pressures (e.g. habitat loss, stream fragmentation). In addition, they have limited dispersal ability within hydrographic networks in which they currently live. Yet their response to current and future climate change has been poorly documented and few studies have used SDM to assess the potential consequences of the on-going climate change on freshwater fish species distribution, especially in European streams.

In that context, the aim of my PhD thesis was to assess the potential impacts of climate change on fish in French streams, mainly on species distribution and assemblages' structure. I used fish data provided by the Office National de l'Eau et des Milieux Aquatiques (ONEMA), the institution in charge of the protection and conservation of freshwater ecosystems in France. These data were combined with climate and environmental descriptors through the use of correlative statistical modeling. As my goal was to provide reliable estimates of the future impacts of climate change on stream fish, I have considered recent criticisms (e.g. choice of statistical method, pure bioclimatic models) of species distribution models by justifying each step and optimizing the use of such models. In all, five papers are derived from my PhD work. The first three papers set the bases for the building of the models by considering the uncertainty in predictions, while the latest two assess the impacts of climate change on stream fish species and assemblages.

In stream fish ecology, many studies have been conducted to identify the environmental drivers structuring fish assemblages (reviewed in Matthews 1998). It appears that fish species distribution and structure of fish assemblages are determined by a complex interplay of biotic, abiotic and spatial factors (Jackson et al. 2001). Disentangling the relative effect of climate versus the one of non-climatic factors (i.e. habitat, topography) on the distribution of fish species was thus of the utmost importance before assessing the potential consequences of changing climate. This issue was addressed in a first study (Buisson et al. 2008a) in which we modeled the spatial distribution of 28 fish species within a river network (the Adour-Garonne watershed) according to a set of climatic and non-climatic factors. Applying both statistical approaches (hierarchical partitioning and generalized additive models), we found that a combination of both thermal variables (mean temperature) and variables describing the local habitat and the position within the river network (upstream-downstream gradient) was important to explain the current distribution of fish species. This result showed that distribution models for stream fish species should combine both climate and other environmental descriptors and not be restricted to the climate envelope, especially at the regional scale (Pearson and Dawson 2003). We also found that the predictive performances of the GAM were high (on average, AUC = 0.85) indicating that the studied climate and physical factors were relevant to predict fish species distribution. However, fish species responded differently to the environmental factors highlighting the need of a species-specific modeling approach to predict species responses to environmental changes.

During the last few decades, a large number of statistical methods modeling species distributions have been developed. Recent studies have highlighted that the predictive performance and predictions of species distributions vary depending upon the method implemented. The emerging recommendation is to combine the outputs of several statistical methods in an ensemble modeling framework and to explore the range of resulting predictions with consensus approaches (Araujo and New 2007; Marmion et al. 2009). It has also been emphasized that species' ecological characteristics may influence the outputs of SDM (McPherson and Jetz 2007), but no studies have addressed the potential relationship between species ecological attributes and the results of ensemble modeling and consensus approaches.

We explored the usefulness of ensemble modeling approaches and tested whether the outputs of consensus models were influenced by the range of species along four environmental gradients (Grenouillet et al. 2009). Eight single statistical methods were computed to predict the current distribution of 35 stream fish species in France and then, we combined the whole predictions ensemble using the average value. Overall, we found that the predictions from single statistical methods were roughly consistent (proportion of consensus between 69.7 and 94.1% depending on species) with the exception of predictions at the edge of the recorded species distributions. However, single methods had consistently lower predictive performances than the average model, which was in accordance with some other recent studies (e.g. Marmion et al. 2009). The improvements in the accuracy of single methods by the average model were higher for species with smaller ranges along the four environmental gradients. In addition, more consensual and accurate predictions of current distribution were achieved for species with small thermal or elevation ranges validating the common hypothesis that specialist species yield models with higher accuracy than generalist ones (e.g. Luoto et al. 2005). Thus, these results strengthen the usefulness of ensemble modeling and consensus approaches and caution against the use of single modeling techniques, especially for species with large environmental ranges.

In the study described above, it has been confirmed that the statistical method may greatly influence the predictive performances and the predictions of the current distribution of species. Other studies have shown predictions to be sensitive to other methodological decisions such as model parameterization, model selection or data characteristics as well (Heikkinen et al. 2006). When projecting the potential distribution of species under future climate change, additional sources of variability arise with the use of climate change scenarios projected by a variety of General Circulation Models (GCM). Measuring the uncertainty in the projections of future distribution and quantifying the relative contribution of different uncertainty factors thus appear to be crucial issues to enhance the confidence placed in those projections.

In Buisson et al. (2009), we focused on the variability in future projections of climate change impacts on stream fish species and assemblages arising from four uncertainty factors: initial dataset, statistical method, GCM and greenhouse gas emission scenario. Several modalities of these four uncertainty sources were combined in an ensemble forecasting framework resulting in 8400 different projections. We found that the projected future impacts of climate change on fish species and assemblages were highly variable. The choice of the statistical method was the main source of uncertainty, resulting in more variability in projections than the GCM and emission scenarios, especially for short-term projections, and thus corroborating the results of recent studies (e.g. Thuiller 2004). Moreover, the variability in projections was spatially structured, indicating that the projected impacts of climate change in some particular geographical areas should be considered with great caution. Like in Grenouillet et al. (2009), these results emphasize that combining the outputs from several sources of uncertainty, especially different statistical methods, in ensemble approaches would help to enhance the reliability of projected future impacts. This would allow management and conservation decisions to be taken with awareness of the inherent uncertainty in projections.

Based on the results of the aforementioned studies, we lastly estimated the potential impacts of future climate change on fish species in French steams. The potential consequences of climate change were projected to the end of the 21st century at the levels of fish species distribution (Buisson et al. 2008b) and fish assemblages' diversity, composition and similarity by overlapping individual predictions obtained from multiple species distribution models (Ferrier and Guisan 2006: 'predict first, assemble later' strategy) (Buisson and Grenouillet 2009).

We found that most fish species occurring in French streams could be sensitive to future climate modifications. Only a few cold-water species (i.e. brown trout, bullhead) could experience a strong reduction in the number of suitable sites, and thus restrict their distribution to the most upstream sections of river networks. For instance, the brown trout could reduce its range by 75.9%. In contrast, many cool- and warm-water fish species (e.g. barbel, European chub) could colonize newly suitable habitats and expand their range by migrating to sites located in most upstream sections of watersheds. These results were consistent with those obtained in previous studies conducted mainly in North America, which predicted a decrease in salmonids distribution but more contrasted responses for cool- and warm-water species (e.g. Mohseni et al. 2003). We also found that the projected changes in individual species distributions could lead to reshuffling of fish assemblages (i.e. change in assemblages' composition) both at the taxonomic and functional levels. For instance, at least half of the current pool of fish species could be changed in about two-thirds of the studied assemblages. The local fish species richness and trait diversity could increase (e.g. on average + 9.2 species per site in 2080) in parallel with a global fish species and trait homogenization (e.g. increase in similarity index from 0.25 to 0.51). All of those projected impacts could be remarkably different depending on the assemblages' location in France and on the position along the upstream-downstream gradient. Upstream assemblages could be more sensitive to the forecasted climate change than downstream assemblages. Most of our results corroborate the trends that have recently been observed in freshwater fish and other taxa in response to the recent climate modifications: increase in species richness (e.g. Daufresne and Boët 2007), assemblages becoming dominated by southern species having warm-temperature requirements (e.g. Daufresne et al. 2004) and biotic homogenization (e.g. Jurasinski and Kreyling 2007). Therefore, these findings indicate that the changes in the structure of fish assemblages which have already been observed would continue and could even become more pronounced with the forthcoming climate change.

However, in spite of the numerous methodological issues considered in this PhD work to project the most reliable estimates of those impacts, they may only be viewed as potential impacts. Indeed, many factors could hinder those projections to occur (Pearson and Dawson 2003) such as the natural and physical barriers to displacements (e.g. fragmentation), the limited dispersal ability of species, the interactions between species or the physiological and behavioural adjustments (e.g. phenological changes) in response to climate modifications instead of shifts in species distribution. Therefore, future research is needed to refine the projected impacts of climate change on stream fish presented here in order to provide more realistic projections to aquatic biodiversity managers.

In conclusion, my PhD thesis brings new insights for the understanding of stream fish species distribution in France and expected consequences of climate change. Overall, fish could be affected by climate modifications both at the species and assemblages levels. More fish species could expand their range than reduce it, but this finding does not mean that climate change will not have deleterious effects on fish assemblages and aquatic ecosystems functioning. This work thus provides biodiversity managers and conservationists with a basis to take efficient preservation measures, but it also raises interesting issues concerning the choice of biodiversity metrics (e.g. local vs. global diversity) and actions to prioritize (e.g. conservation of the most vulnerable species). In addition, methodological developments considered in this PhD are an important contribution to the improvements of projections by statistical models of species distribution through the use of ensemble forecasting and consensus approaches. They also allow a better understanding of the inherent uncertainty and stress the need for providing projected impacts of climate change in combination with an assessment of their uncertainty to increase the relevance of those forecasts.

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thesis abstract

Understanding the evolutionary radiation of the mega-diverse Monkey Beetle fauna (Scarabaeidae: Hopliini) of South Africa

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South Africa is the global centre of diversification for monkey beetles (Scarabaeidae: Hopliini). 69 % of the world fauna occur here, with 98% of the 1040 South African species and 80% of the South African genera being national endemics. This thesis was the first analysis of the regional distribution patterns, and the processes underlying the generation of the mega-diverse monkey beetle fauna of South Africa. Specifically, the aims of the thesis were to:

1. Identify hotspots of richness and endemism, and to explore the relationship between area and richness.
2. Compare centres of endemism of monkey beetles with those of other faunal and floral taxa, and to investigate patterns of biogeographic congruence.
3. Explore the role of local environmental factors (rainfall, temperature, habitat heterogeneity, host plant diversity) as explanatory variables of regional richness patterns of monkey beetles.
4. Model spatial turnover (beta diversity) in beetle community composition as a function of environmental (rainfall, temperature, altitude, soil fertility) and plant (host species, vegetation types, and bioregions) variables.
5. Describe and quantify patterns of sexual dimorphism and putative sexually selected traits and investigate the role of sexual selection in the generation of species richness.

Methodological procedures followed current and newly-developed analytical techniques used in the fields of biogeography, spatial ecology, and evolutionary biology. A key first methodological step was the compilation of a geo-referenced presence-only dataset from field observations, museum collections, and taxonomic revisions. This comprised 6959 unique point locality records which were analysed within a geographical information system (GIS). This allowed portraying of the spatial variation in richness and endemism across local and regional habitats.

