Distribution and vulnerability models to improve conservation efforts for fish species under climate change

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Summary

The declaration of protected areas (PAs) is generally considered one of the main tools to counteract the constant decline in global biodiversity. Despite a strong increase in global PA-coverage during the last two decades, the downwards trend in biodiversity has not yet stopped or even reversed. Freshwater ecosystems, both lotic and lentic, are especially species rich, but show stronger biodiversity declines compared to terrestrial or marine ecosystems. Unfortunately, freshwaters are often not explicitly considered in the declaration of PAs and, as one consequence, freshwater biodiversity is underrepresented in existing PA-networks. Future climate change is predicted to further impact the effectiveness of existing PAs, because of a decrease in habitat suitability within PAs for target species. Hence, there is an urgent need to anticipate the impacts of climate change and other emerging pressures to adjust existing, or declare new PAs to optimise them for the future. In addition, the growing demands of the human population for space and natural resources aggravate the complexity of nature conservation efforts.

The aim of my thesis was to close some of the related knowledge gaps to protect freshwater biodiversity under future climate change. My research showcases, with the example of the upper Danube river basin, how predictive models can be applied to river ecosystems and how model outputs can be used to identify future possible environmental pressures, their temporal dynamics, and how conservation management can be informed by this knowledge.

The thesis is divided into three parts. First, I investigated how spatial resolution affects model outcomes in river habitat suitability models (HSMs). Second, I assessed if environmental pressures for riverine fish species differ between the past 200 years and in the future until 2100, by using climate niche factor analysis. Third, I analysed if the established network of PAs within a selected study area protects native fish species under current environmental and future climate change conditions. Third, I used these findings to optimise the existing network by adding individual PAs based on a systematic conservation planning approach, aiming at sufficiently protecting native fish species and selecting PAs that will serve as environmental refugia in the future.

Based on a compiled extensive fish occurrence database, I used ensemble HSMs to relate the occurrence of 48 native fish species with environmental parameters including topography, land-use, climate and hydrology at the respective locations. HSMs were calculated on a sub-basin level as modelling unit and for ten different spatial resolutions (i.e. average sub-basin size), while keeping all other model parameters constant. With this approach, I showed that predictor importance (which is a measure of which model parameters are more or less important to predict fish habitat) and predicted suitability patterns (i.e. the distribution of areas that are predicted to be suitable as fish habitat) are highly dependent on the spatial resolution of the model. Furthermore, by correlating predicted suitability among nested sub-basins, I was able to identify a scale tipping-point at which the set of environmental parameters predicted habitat suitability patterns best (i.e. habitat suitability patterns did not improve even if a finer scale was applied).

I used the species-specific distribution patterns at the finest modelled resolution together with a unique time series of modelled and observed hydrological and climate data for 1800–2100 to analyse how environmental pressures for riverine fish species differ in type, spatial distribution or both between the past 200 years and in the near future in 2100. I used climate-niche factor analysis to calculate species-specific vulnerabilities, i.e. the magnitude of a species to be impacted in a specific location, and the driving environmental pressures. I showed that historical and future environmental pressures resulted in similar vulnerability estimates for native fish species which were, however, caused by different environmental pressures in 1800 compared to 2100. Historically, fish species were mainly impacted by a change in hydrology (more specifically by a decrease in the variance of monthly discharge), while in the future temperature will be the main pressure (i.e. the predicted increase in mean annual temperature). This change in main environmental pressures was accompanied by a spatial shift of areas that were predicted to be especially impacted.

To investigate whether native fish species are sufficiently protected within the existing network of PAs, currently and in the future, I grouped all native fish species according to their threat status based on the IUCN Red List categories. Then, I analysed the coverage of each group within the PAs and their changes in vulnerabilities under future climate change scenarios within the existing PA-network. I found that the existing PA-network currently insufficiently protects the distribution range of native fish species when applying the 20-60% guidelines (i.e. protect 20 -60% of a species distribution range depending on the species ecology, distribution, and population trends) suggested by the European Commission. Consequently, the conservation planning analysis revealed that an additional c. 6000 sub-basins need to be added to the c. 2000 current sub-basins to reach sufficient protection for native fish species. In addition, I showed that the existing PA-network is located in areas in which fish species will be especially exposed to future pressures from climate change. To spatially optimise the PA-network under future climate change conditions, I used the magnitude of predicted climate change-induced habitat alterations in each sub-basin as a cost factor in the systematic conservation planning analysis. Therefore, the proposed PA-network is located in areas that experience the lowest habitat alterations in the future. For all planned networks (current and future) I found a high spatial overlap, indicating that a currently optimised network can also safeguard native fish species under future environmental conditions.

With this thesis I demonstrated the feasibility of predictive models to identify habitat suitability patterns of native fish species in river ecosystems. In addition, I showed how model results can be used to identify areas that are predicted to especially suffer climate change impacts and how such predictions can inform conservation planning analysis. The results of the conservation planning analysis can directly inform the revision of the existing PA-network in the Upper Danube River basin to effectively protect native fish species into the future.

Zusammenfassung

Das Ausweisen von Naturschutzgebieten wird als ein entscheidender Eckpfeiler für den Biodiversitätsschutz weltweit betrachtet und entsprechend, angesichts einer anhaltenden Biodiversitätskrise, hat in den letzten zwei Jahrzehnten die Bedeckung der Erdoberfläche mit Naturschutzgebieten stark zugenommen. Nichtsdestotrotz konnte bisher der globale Verlust an Biodiversität nicht gestoppt werden. Süßgewässer sind außergewöhnlich artenreiche Ökosysteme mit einer entsprechend großen Bedeutung für die Biodiversität weltweit. Allerdings weisen Süßgewässer einen stärkeren Verlust an Biodiversität auf als terrestrische oder marine Ökosysteme. Gleichzeitig finden Süßgewässer nur selten explizit Berücksichtigung bei der Planung von Naturschutzgebieten. Als Folge sind Süßgewässerarten oft nur unzureichend in bestehenden Naturschutzgebietsnetzwerken repräsentiert. In Zukunft könnte der Klimawandel die Effektivität von existierenden Naturschutzgebieten weiter verringern, da er zu einer Verschlechterung der Habitat-Eigenschaften für Zielarten innerhalb der Naturschutzgebiete führen kann. Als Konsequenz ist es notwendig mögliche Folgen des Klimawandels, und daraus resultierende neue oder verstärkte Umweltbelastungen, zu antizipieren um so die räumliche Verteilung von neuen Naturschutzgebieten möglichst effektiv gestalten zu können. Zusätzlich zu diesen Herausforderungen bringt der stetige Zuwachs der Weltbevölkerung und der damit einhergehende steigende Flächen- und Ressourcenbedarf, eine zusätzliche Ebene der Komplexität für effektiven Naturschutz mit sich.

Das Ziel der vorliegenden Arbeit ist es, einige der assoziierten Wissenslücken am Beispiel des oberen Donaueinzugsgebietes und 48 heimischen Fischarten zu schließen, um den Schutz von Süßwasser-Biodiversität in Zeiten des Klimawandels zu verbessern. In dieser Arbeite zeige ich beispielhaft, wie statistische Artverteilungsmodelle in Flussökosystemen angewendet werden können und wie die Modellergebnisse dazu genutzt werden können, um zukünftige Umweltbelastungen für Süßwasserarten zu identifizieren und deren zeitliche und räumliche Dynamiken zu bestimmen. Darüber hinaus zeige ich, wie das gewonnene Wissen genutzt werden kann, um eine Naturschutzplanungsanalyse so durchzuführen, dass das entstehende Naturschutznetzwerk besser an die Herausforderungen des Klimawandels angepasst ist. Die Arbeit umfasst drei Kapitel. Im ersten Kapitel habe ich untersucht, wie sich die räumliche Auflösung eines Artverteilungsmodels auf die Modelergebnisse auswirkt. Im zweiten Kapitel habe ich analysiert, ob sich die Umweltbelastungen, die heimische Fischarten im oberen Donaueinzugsgebiet bedrohen, zwischen den vergangenen 200 Jahren und einem nahen Zukunftsszenario im Jahr 2100, in ihrer Art und/oder in ihrer räumlichen Verteilung unterscheiden. Im dritten Kapitel habe ich die Ergebnisse aus den ersten beiden Kapiteln genutzt, um zu prüfen, ob das existierende Schutzgebietsnetzwerk unter heutigen und zukünftigen Umweltbedingungen die heimischen Fischarten im Untersuchungsgebiet effektiv schützt. Ergänzt wurde das dritte Kapitel durch eine Naturschutzplanungsanalyse. In dieser Analyse habe ich die Ergebnisse aus den vorigen Analysen genutzt, um ein Naturschutznetzwerk zu planen, das zum einen den effektiven Schutz von heimischen

Fischarten gewährleistet und zum anderen in solchen Regionen im Untersuchungsgebiet verortet ist, die möglichst geringe Veränderungen durch den Klimawandel erfahren werden.

Auf Grundlage einer umfangreichen, für das Untersuchungsgebiet zusammengestellten, Fischvorkommensdatenbank, habe ich Artverteilungsmodelle kalibriert, die die Vorkommensdaten statistisch mit Umweltprädiktoren verknüpft haben. Die Umweltprädiktoren haben Aspekte der Topographie, der Landnutzung, des Klimas und der Hydrologie für das Untersuchungsgebiet beschrieben. Da die Modelle auf ein Flussökosystem angewendet wurden, dienten Teileinzugsgebiete als Modellierungseinheit. Insgesamt habe ich zehn verschiedenen Modelle kalibriert, wobei ich systematisch die Modelauflösung, also die mittlere Größe der modellierten Teileinzugsgebiete, geändert habe. Alle weiteren Modellparameter waren konstant. Durch diese systematische Vorgehensweise konnte ich zeigen, dass die Modellauflösung einen bedeutenden Einfluss auf die Modellergebnisse hat. Sowohl die relative Bedeutung der einzelnen Prädiktoren für die Bestimmung der potenziellen Artverbreitungsgebiete, als auch die Verbreitungsgebiete an sich, waren stark von der Modellauflösung abhängig. Durch die Korrelation von modellierten Vorkommenswahrscheinlichkeiten zwischen räumlich zusammengehörigen Teileinzugsgebieten auf unterschiedlichen Modellauflösungen, konnte ich zeigen, dass es eine Modellauflösung gibt, unter der die hier angewendeten Umweltprädiktoren nicht mehr in der Lage sind, fein aufgelöste Artverteilungsmuster zu bestimmen.

Die aus der vorigen Analyse entstandenen art-spezifischen Verbreitungsgebiete auf der höchstmöglichen Modellauflösung habe ich dann mit einer umfangreichen Zeitreihe von beobachteten und modellierten Daten, die hydrologische und klimatische Bedingungen im Untersuchungsgebiet für den Zeitraum von 1800 bis 2100 beschreiben, verknüpft. Diese Zeitreihe hat es mir ermöglicht, basierend auf einer ökologischen Nischen Faktorenanalyse, aufzuzeigen, dass zwischen dem historischen und zukünftigen Zeitraum ein Wechsel in der Art und der räumlichen Verteilung der Hauptumweltbelastungen für Fischarten stattgefunden hat. Im Detail konnte ich zeigen, dass historische hydrologische Veränderungen einen ähnlich großen Druck auf Fischarten ausgeübt haben, wie es zukünftige Klimawandel bedingte Temperaturerhöhungen tun werden. Allerdings gibt es einen räumlichen Unterschied zwischen den Gebieten, die historisch besonders starken Veränderungen ausgesetzt waren und jenen, die es Zukunft sein werden.

Um zu prüfen, ob das existierende Naturschutznetzwerk die heimischen Fischarten im Untersuchungsgebiet ausreichend schützt, habe ich zunächst alle Fische basierend auf ihrer Rote Liste Gefährdungskategorie gruppiert. Für jede der Gruppen habe ich anschließend die Abdeckung des modellierten Verbreitungsgebietes mit den aktuellen Naturschutzgebieten analysiert. Die Analysen haben gezeigt, dass das jetzige Naturschutznetzwerk nur unzureichend die Verbreitungsgebiete der heimischen Fischarten schützt. Als Maßstab für einen effektiven Schutz wurde die 20- 60% Richtlinie der Europäischen Kommission für den Schutz von Tier- und Pflanzenarten in Naturschutzgebieten anlegt. Diese Richtlinie zielt darauf ab, dass sich zwischen 20% und 60% des Verbreitungsgebiets einer

Art~~,~~ in Abhängigkeit von der Ökologie, der Verbreitung und des Populationstrends, in Naturschutzgebieten befinden sollen. Neben der unzureichenden Abdeckung der Verbreitungsgebiete konnte ich ebenfalls zeigen, dass sich das jetzige Naturschutznetzwerk in Regionen des Untersuchungsgebietes befindet, die im Jahr 2100 besonders stark von projizierten Umweltbelastungen betroffen sein werden. Aufbauend auf diesen Ergebnissen habe ich im Anschluss eine Naturschutzplanungsanalyse durchgeführt, um die Effektivität des bestehenden Naturschutznetzwerks zu erhöhen und es räumlich so anzuordnen, dass es in Gebieten liegt, die möglichst geringen Umweltbelastungen in der Zukunft ausgesetzt sind. Diese Analyse hat gezeigt, dass zusätzlich zu den aktuell geschützten knapp 2000 Teileinzugsgebieten ungefähr 6000 zusätzliche Teileinzugsgebiete geschützt werden müssten. Außerdem zeigte sich, dass ein für die heutigen Umweltbedingungen optimiertes Netzwerk, das heimische Fischarten effektiv schützt, auch in der Zukunft einen bestmöglichen Schutz gewährleisten kann.

Mit der vorliegenden Arbeit habe ich gezeigt, wie Artverteilungsmodelle in Flussökosystemen angewendet werden können, um flächendeckende Verteilungsmuster von Zielarten möglichst genau zu bestimmen. Zusätzlich habe ich gezeigt, wie diese Ergebnisse genutzt werden können, um Gebiete zu identifizieren, die besonders von zukünftigen Umweltbelastungen durch den Klimawandel betroffen sein werden. Diese Modellergebnisse habe ich dann in eine Naturschutzplanungsanalyse einfließen lassen, um ein Naturschutznetzwerk zu entwerfen, welches Zielarten effektiv schützt und gleichzeitig in Gebieten verortet ist, die in möglichst geringem Umfang durch den Klimawandel betroffen sind. Die Ergebnisse der Naturschutzplanungsanalyse können direkt genutzt werden, um als Grundlage für eine Erweiterung des jetzigen Naturschutzgebietsnetzwerkes im oberen Donaueinzugsgebiet zu dienen und so Fischarten möglichst effektiv in der Zukunft schützen zu können.

General introduction

The declaration of protected areas (PAs) is generally considered one of the main tools to protect biodiversity (Le Saout et al., 2013; Watson et al., 2014; Acreman et al., 2019) to counteract the constant decline in global biodiversity (Butchart et al., 2010). Due to a strong increase in number and area covered over the past decades (Watson et al., 2014), today between 15% (Maxwell et al., 2020) and 17% (UNEP-WCMC, 2018) of terrestrial and freshwater area globally are covered. Aichi target 11, aiming at protecting 17% of the worlds terrestrial and inland water area to stop the loss of biodiversity, set by the Convention on Biological Diversity (CBD), is nearly fulfilled or fulfilled (CBD, 2021a). However, so far, the loss of biodiversity has not stopped or even reversed (Leclere et al., 2020; Tickner et al., 2020; WWF, 2020) and, consequently, strong efforts are made to further increase the global coverage with PAs (Pringle, 2017; Woodley et al., 2019; Geldmann et al., 2021). Those efforts have only recently been streamlined into the global biodiversity framework with a stand-alone target aiming at covering at least 30% of the planet with an effective and well connected system of PAs by 2030 (CBD, 2021b).

While freshwater ecosystems cover less than 1% of the earth surface and provide only a neglectable portion of the habitable volume on earth (freshwater:terrestrial:marine = 1:7:5015; Dawson (2012)) they provide habitat for approximately 5% of all known species on earth (Grosberg et al., 2012). For some groups of species this share is even higher, e.g. 10% of all known vertebrates and more than 50% of all known fish species depend on freshwater ecosystems, at least to a certain degree to fulfil their lifecycle (Lévêque et al., 2008; Carrete Vega & Wiens, 2012). At the same time no other ecosystem is so tightly connected to human civilizations (Macklin & Lewin, 2015), due to human needs for drinking water, food, or energy which are all provided by fresh waters (Funge-Smith & Bennett, 2019; Reid et al., 2019). A dramatic increase in the demand for these freshwater-related ecosystem services during recent years (Vörösmarty et al., 2010; Steffen et al., 2015) led to freshwater species suffering now from a mix of threats, including land-use change, invasive species, river fragmentation, flow alterations, climate change (Dudgeon, 2019), and a combination of those (Craig et al., 2017). For example, only since 2009, we have lost one-third of all wetlands globally (Hu et al., 2017). Therefore, a crucial habitat type for many freshwater taxa, including macroinvertebrates, amphibians, or fish (Colvin et al., 2019), are ultimately lost. Moreover, river flow, a characteristic of rivers linked to e.g. fish species richness and distribution (Xenopoulos & Lodge, 2006), has been anthropogenically altered globally (Nilsson et al., 2005; Grill et al., 2019). Consequently, negative effects on e.g. richness, abundance, and endemism of multiple freshwater taxa are omnipresent (Rolls & Bond, 2017). In total one-quarter of the world's total river runoff is stored in reservoirs (Nilsson et al., 2005) or abstracted for human demands (Vörösmarty & Sahagian, 2000). River fragmentation is peaking with only 37% of all rivers globally remain free-flowing (Grill et al., 2019) and a further decrease is to be expected (Zarfl et al., 2014). The length of free-flowing river stretches is directly impacting the number of endemic species and the occurrence of species which migrate over long distances (Liermann et al., 2012; Rolls et al., 2018), as dams obstruct access to spawning grounds (Hall et al., 2010) and, therefore, lead to local extinctions (Zeug et al., 2011). As a consequence, freshwater biodiversity is declining globally at a dramatic rate that is much higher for fresh waters than for marine or terrestrial ecosystems (WWF, 2020). For example, more than 6000 freshwater fish species have been listed as threatened by extinction (IUCN, 2021) and more than two-thirds (71%) of all freshwater megafauna species with known population trends (partly including fish) are declining (He et al., 2018). Overall, to date roughly one third of all known freshwater species face the threat of extinction (WWF, 2020).

Especially for river ecosystems and the species therein, existing PA-networks often fall short of expectations (Hermoso et al., 2015; Leal et al., 2020; WWF, 2020). The underlying reasons are manifold (Hermoso et al., 2016); for example many PAs have been implemented and are managed for terrestrial purposes (Abell & Harrison, 2020) and, even to date, conservation actions often fail to target river species and habitats explicitly (WWF, 2020). This is especially problematic as rivers and their integrity are tightly connected to the surrounding landscape (Hynes, 1975; Vannote et al., 1980). As early as in 1975, Hynes (1975) proposed that rivers have to been seen as "*parts of the valleys that they drain*", emphasising the strong influence of basin properties on the abundance and distribution of river species. Shortly afterwards, Vannote et al. (1980) introduced the "*continuous gradient of physical conditions*" from the source to the mouth along a river ecosystem, i.e. the River Continuum Concept. Consequently, rivers need special, spatial consideration, i.e. basin-wide management planning (Abell et al., 2007; Leal et al., 2018) to identify conservation actions which effectively protect freshwater species (Acreman et al., 2019).

Future climate change is further challenging the effectiveness of PAs for river ecosystems (Hannah, 2008; Thomas & Gillingham, 2015; Reid et al., 2019). Rising temperatures and changes in the amount and distribution of precipitation caused a constant decline of surface water runoff within PAs during the past 40 years (Bastin et al., 2019). Moreover, due to projected changes in habitat conditions many species will be forced to migrate out of established PAs (Araújo et al., 2011; Bonebrake et al., 2018). Traditional pressures on river ecosystems, such as the ones mentioned above, are complemented by direct impacts from climate change and the human responses to it (Pittock et al., 2008; Döll & Zhang, 2010), which can be even more severe than the traditional ones (Döll & Zhang, 2010). A change in the combination of prevalent pressures is likely accompanied by a shift in their spatial distribution. Consequently, it remains largely questionable if a current PA-network, which was primarily established to mitigate traditional pressures, can offer refuge for species under a changing climate (Bruno et al., 2018; Bates et al., 2019; Elsen et al., 2020).

Systematic conservation planning (Margules & Pressey, 2000) offers a strong tool to systematically design effective PA-networks by e.g. considering multilateral connectivity for river ecosystems (Hermoso et al., 2012). Additionally, systematic conservation planning can give guidance on the planning and design of PA-networks to meet the challenges of future climate change (Reside et al., 2017). However, conservation efforts are almost always linked to the occurrence and distribution of species (Guisan et al., 2013; Turak et al., 2017) and consequently conservation efforts often rely on predictive models to get range wide estimates of the potential distributions of the targeted species (Nel et al., 2009). Therefore, predictive models have become an essential tool to facilitate conservation purposes (Wood et al., 2018; Travers et al., 2019) and guide conservation actions (Lawler et al., 2011). One class of predictive models, habitat suitability models (HSMs, also referred to as species distribution models or environmental niche models) has gained special attention in conservation science (Lawler et al., 2011; Guisan et al., 2013; McShea, 2014; Sofaer et al., 2019; Muscatello et al., 2021). HSMs statistically combine species occurrence data with environmental predictors and create range-wide predictions of the distribution of suitable habitats for the targeted species, given the predictors used (Elith & Leathwick, 2009). Therefore, HSMs offer a statistical solution to e.g. the Wallacean-Shortfall (Hortal et al., 2015). Moreover, the relative importance of HSM-respective predictors allows inferring the importance of distribution and niche-defining variables (Smith & Santos, 2020), which is invaluable information to assess the effects of potential threats on species and their distributions (Herrera et al., 2020). Despite their wide application, the interpretation of HSM outputs needs careful consideration (Araújo & Peterson, 2012; Yates et al., 2018; Sofaer et al., 2019). This is due to the fact that heterogeneity in the quality and resolution of input data, as well as model-development decisions (e.g. model resolution, choice of predictor variables), can significantly influence model outcomes (Guisan et al., 2007; Manzoor et al., 2018). For example, Connor et al. (2018) showed that a decrease in model resolution from 50 to 1600 m causes a four-times overprediction of inhabited area for a generalist species, and a thirteen-times overprediction for a specialist species. As range contraction is closely linked to the extinction risk of a species (Wolf & Ripple, 2017), and range contraction and expansion are used to inform biodiversity indicators such as the IUCN Red List of threatened species (IUCN, 2021), uncertainties in the predictions of occupied area can greatly influence conservation decisions. In addition, because HSMs were initially developed for terrestrial applications, available scientific and model development knowledge is strongly biased towards terrestrial ecosystems (Booth et al., 2014). Only recently HSMs have been applied in fresh waters, specifically in river ecosystems (Domisch et al., 2015b). However, the highly complex structure, i.e. longitudinal and lateral connectivity and a lack of river-specific predictors, e.g. missing hydrological data (Irving et al., 2018), challenge the application of HSMs in river basins (Domisch et al., 2015b). Moreover, due to the long ranging lateral and longitudinal connectivity of rivers, it can be expected that the variability in model outputs is even larger than in terrestrial systems. Hence, careful assessments of the drivers and the magnitude of model output variability are needed to make HSMs a useful and reliable tool to support spatial conservation planning in river ecosystems (Schuwirth et al., 2019).

Research gaps

Rivers and the species therein are in peril with population sizes constantly and dramatically declining for the majority of taxa (WWF, 2020). Climate change is predicted to further increase the pressures on the integrity of river ecosystems (Reid et al., 2019). Conservation efforts are almost always linked to the occurrence and distribution of species (Guisan et al., 2013; Turak et al., 2017). Therefore, range wide information of a species' distribution are needed to guide effective protection of biodiversity in rivers. HSMs offer an effective tool to gain such information. However, to date HSMs have only occasionally been applied to river ecosystems (Domisch et al., 2015b). Hence, the **first prominent research gap** can be identified as a knowledge gap regarding if and how model resolution is influencing model outcomes, especially predicted distributions but also predictor importance in river ecosystems. Based on terrestrial studies, I anticipate that resolution has an effect on model outcomes (Connor et al., 2018) and that this effect can be even larger in river ecosystems than in terrestrial counterparts based on the long ranging lateral and longitudinal connectivity of rivers with the surrounding landscape (Hynes, 1975; Vannote et al., 1980). The first gap is accompanied by the challenge to identify the finest possible model resolution at which available environmental predictors can deliver meaningful predictions.

The **second research gap** for effective river conservation is a lack of understanding whether future climate change and the resulting environmental pressures - such as changes in the amount and distribution of precipitation – will, in terms of magnitude and spatial distribution, pose similar threats to river biodiversity as traditional pressures did. Rivers have been subjected to human alteration since the beginning of civilization (Macklin & Lewin, 2015). However, especially, since the industrialization, the magnitude and severity of human interventions into river ecosystems have increased dramatically (Macklin & Lewin, 2015; Haidvogl et al., 2019). At the same time the direct and indirect pressures resulting from climate change are increasing at an accelerating rate (IPCC, 2021). For effective river conservation, we need (i) to understand the severity of climate change impacts in relation to traditional pressures to anticipate possible effects on species; and (ii) we need to identify regions that will be especially impacted by climate change to inform conservation management.

The third research gap for river conservation addresses the PA-network itself. As outlined above, river ecosystems and the species therein are only rarely explicitly considered when PAs are established (WWF, 2020). Consequently, current, static PA-networks, established to mitigate traditional pressures (Pittock et al., 2008; Pimm et al., 2018), have failed so far and many river taxa are at the brink of extinction (WWF, 2020). Therefore, at first, we need to understand if an established PA-network is currently effectively protecting river biodiversity. In addition, we need to assess if an existing PA-network will also protect river biodiversity in the future. For many rivers globally, it is expected that the main pressures on species will change in the nearer future or have already changed (Pittock et al., 2008; Döll & Zhang, 2010). Therefore, it is likely that the effectiveness of existing PAs will further decrease (Pittock et al., 2008; Alagador et al., 2014; Bruno et al., 2018). This is because species that have been protected from traditional pressure in the past could be exposed to the negative effects of climate change in the future (Bates et al., 2019). As a consequence, we need to identify the regions of high conservation value under future climate conditions, i.e. regions with high species numbers and low pressures, which can amend the current network of PAs to protect freshwater biodiversity in the long run.

Aims

My thesis aims to add new knowledge to protect freshwater biodiversity under climate change. My research showcases how an essential tool for biodiversity conservation, i.e. HSMs, can be applied to river ecosystems. It also elucidates how model outputs, i.e. predicted distributions and predictor importance, can be used to identify potential sources of environmental pressures, their temporal dynamics, and how conservation management can be informed by this knowledge. My research focuses on the upper Danube river basin. The Danube river basin has a long history of anthropogenic alterations (Haidvogl et al., 2019) and is predicted to be severely impacted by future climate change (van Vliet et al., 2013). Furthermore, my research focuses on fish species, a group which is divers in freshwaters (McDermott, 2021) and especially threatened by traditional pressures and future climate change (WWF, 2020).

The thesis is divided into three main components, each addressing a research question:

In **chapter 1,** I investigate how model resolution is affecting model outcomes in river HSMs. I compiled a database of fish occurrence in the Upper Danube river basin based on information from federal ministries and scientific or community-driven projects. I used ensemble HSMs to statistically combine the fish occurrence-data with environmental predictors describing topographical, land-use, climatic and hydrological aspects of the study area. HSMs were calculated for ten different model resolutions, i.e. the average size of a sub-basin, while keeping all other model parameters constant. With this approach, I demonstrated the effects of model resolution on model performance, predictor importance, and predicted suitability patterns. Based on studies in terrestrial systems (Connor et al., 2018), I expected model performance not to be affected by modelled resolution. However, I hypothesized to find a change in predictor importance with changing model resolution, with large scale environmental predictors, such as climate and topography driving predictions on coarse resolutions, while hydrology would mainly explain distribution patterns on finer resolutions. Moreover, I expected to find a sub-basin predicted as suitable on a coarse resolution at least partly to be predicted suitable on a finer resolution.

In **chapter 2,** I ask the question if environmental pressures for riverine fish species differ between the past 200 years and the nearer future in 2100. I used a unique data set of observed and modelled climate and hydrological data ranging from 1800 to 2100, including two Representative Concentration Pathways (RCPs) to calculate species-specific vulnerabilities, i.e. the possibility to be negatively affected, and the drivers of such for historical and future environmental conditions. Species-specific vulnerabilities were calculated using the climate niche factor analyses (Rinnan & Lawler, 2019). Climate niche factor analyses recently evolved from environmental niche factor analyses (Hirzel et al., 2002) and calculates vulnerability as a combination of a species' specialisation and the environmental departure, given the predictors used. I expected the drivers of species-specific vulnerabilities to change over the analysed time period. Moreover, I hypothesized that a change in the main environmental pressures on fish species is accompanied by a change of their spatial distribution, i.e. a change in areas especially affected by the respective environmental pressures.

In **chapter 3,** I ask the question if the current network of PAs is protecting native fish species in the upper Danube river basin sufficiently today and under future climate change conditions. In this chapter I grouped all native fish species in the upper Danube river basin according to their threat status based on the IUCN Red List categories and used the current network of PAs to analyse the coverage of each group by PAs. Because freshwaters and the species therein are only rarely explicitly considered in conservation effort, I expected to find the current PA-network to be insufficient in protecting the distribution range of threatened fish species. In addition, I hypothesized that under future climate change conditions, given an expected change in the distribution of environmental pressures (Döll & Zhang, 2010), the current static network will further lose its ability to protect freshwater fish species in the upper Danube river basin. Finally, I used the conservation planning software Gurobi to demonstrate how the current PA-network has to be expanded to protect all species sufficiently and to be located in areas which can serve as environmental refugia in the future.

Chapter 1

From topography to hydrology - the modifiable area unit problem impacts freshwater species distribution models

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Abstract

Species distribution models (SDMs) are statistical tools to identify potentially suitable habitats for species. For SDMs in river ecosystems, species occurrences and predictor data are often aggregated across sub-catchments that serve as modelling units. The level of aggregation (i.e. model resolution) influences the statistical relationships between species occurrences and environmental predictors - a phenomenon known as the modifiable area unit problem (MAUP), making model outputs directly contingent on the model resolution. Here we test how model performance, predictor importance, and the spatial congruence of species predictions depend on the model resolution (i.e., average sub-catchment size) of SDMs. We modelled the potential habitat suitability of 50 native fish species in the upper Danube catchment at ten different model resolutions. Model resolutions were derived using a 90 m digital elevation model by using the GRASS-GIS module r.watershed. Here, we decreased the average sub-catchment size gradually from 632 km² to 2 km². We then ran ensemble SDMs based on five algorithms using topographical, climatic, hydrological and land-use predictors for each species and resolution. Model evaluation scores were consistently high, as sensitivity and True Skill Statistic values ranged from 86.1-93.2 and 0.61-0.73, respectively. The most contributing predictor changed from topography at coarse, to hydrology at fine resolutions. Climate predictors played an intermediate role for all resolutions, while land-use was of little importance. Regarding the predicted habitat suitability, we identified a spatial filtering from coarse to intermediate resolutions. The predicted habitat suitability within a coarse-resolution was not ported to all smaller, nested sub-catchments, but only to a fraction that held the suitable environmental conditions. Across finer resolutions the mapped predictions were

spatially congruent without such filter effect. We show that freshwater SDM predictions can have consistently high evaluation scores while mapped predictions differ significantly and are highly contingent on the underlying sub-catchment size. We encourage building freshwater SDMs across multiple catchment sizes, to assess model variability and uncertainties in model outcomes emerging from the MAUP.

Introduction

We face a global knowledge gap regarding the actual distribution and the distribution of suitable habitats for the majority of species (Pimm et al., 2014; Pelayo-Villamil et al., 2015), a challenge also coined as the "Wallacian shortfall" (Bini et al., 2006). Combined with the lack of resources for comprehensive species monitoring over large spatial scales (Collen et al., 2008), species distribution models (SDMs) have become an often applied tool in the field of spatial ecology and conservation biology (Seo et al., 2009; Carvalho et al., 2011; Elith & Franklin, 2013; Markovic et al., 2014; Ochoa-Ochoa et al., 2016; Domisch et al., 2019). SDMs provide range-wide estimates of the actual and potential habitat suitability given the species data and environmental predictors at hand. SDMs can also be used in exploratory analyses by assessing environmental tolerances given the modelled predictor importance, for better understanding species abiotic requirements towards the protection and potential restoration of suitable habitats for target species (Lomolino, 2004; Porfirio et al., 2014).

In SDMs, species occurrences and predictors are statistically combined (Elith & Leathwick, 2009) to create range wide habitat suitability predictions. Traditionally, as SDMs have been developed in terrestrial systems (Booth et al., 2014) species occurrence data and environmental predictors are aggregated on gridded or hexagonal, i.e., regular, modelling units (Domisch et al., 2019). The size of the modelling units (e.g. 1km²) defines the model resolution and is often only limited by the availability of predictors at that given spatial resolution (Araújo et al., 2005; Manzoor et al., 2018).

In contrast to the artificial and regular modelling units used in terrestrial systems, topography-dependent and nested modelling units are the basis for freshwater SDMs, especially for river ecosystems. To effectively include results from river SDMs into conservation management and planning, they have to be developed for catchments and sub-catchments as modelling units (Nel et al., 2009; Domisch et al., 2015b). Sub-catchments are irregular and non-randomly distributed units that are contingent on topography and geomorphometry (Amatulli et al., 2018). Hence, the spatial resolution of a model is the average area of sub-catchments, opposed to a fixed value of e.g. 1 km² as used for regular modelling units (see also the Pfafstetter ’levels’ in freshwater ecosystems; Stein et al. (2014)). Due to the dependency of sub-catchments on landscape properties, sub-catchments represent a hierarchically nested system across different resolutions (Fig. 1.1A).

The modifiable area unit problem (MAUP, Jelinski & Wu, 1996) is a common source of statistical uncertainty in spatial analyses. The MAUP occurs when statistics are performed over continuous or point data, which is aggregated on artificial spatial units. Changes in size ("scale problem") or configuration ("zoning problem"), sensu (Jelinski & Wu, 1996) of the spatial units are likely to change statistical relationships. Spurious or even misleading predictions can be the result. Especially in the field of conservation biology such spurious predictions can have dramatic consequences for the effectiveness of species protection and conservation measures (Moat et al., 2018).

According to the MAUP, any output of SDMs is contingent on the spatial scale and resolution, which the model is built on (Lobo et al., 2008; Connor et al., 2018), and estimated habitat suitability and predictor importance can vary considerably according to the spatial resolution (Seo et al., 2009; Connor et al., 2018). For instance, Seo et al. (2009) assessed range predictions for narrow, intermediate, and widely distributed plant species. They found that the predicted range sizes increased by a factor of almost three with a decrease in resolution from 1 km² to 64 km². Similarly, Connor et al. (2018) showed for virtual species with narrow or wide habitat niches that the range predictions for coarse resolutions (~2.5 km²) were up to 14 times higher compared to finer resolutions (~0.06 km²). Additionally, they showed that relative predictor importance for modelled, suitable habitat estimates changed from elevation to aspect (i.e. the compass direction that a slope faces) with increasing resolution. In the study from Connor et al. (2018) general model performance decreased from finer to coarser resolution. However, according to Thuiller (2003) and Swets (1988) the models from Connor et al. (2018) performed in more than 90% well, even at the coarsest resolution. In contrast, Guisan et al. (2007) found that model performance only slightly decreased when resolution decreased by a factor of 10 (100 m to 1 km, and 1 km to 10 km).

Current research tries to assess the dependency of predictions on modelled spatial resolution and an assessment of uncertainty (Hui et al., 2010). Hui et al. (2010) suggested to systematically change the orientation of the modelling unit or increase/decrease their size to assess how contingent identified statistical relationships are on the modelled resolution. However, despite their large importance for biodiversity conservation (McRae et al., 2017), fresh waters and especially rivers have experienced little attention in the SDM literature (Booth et al., 2014). Despite the potentially far-reaching implications, there are almost no studies (but see Kärcher et al. (2019) for an example of resolution dependency) assessing how the MAUP is reflected in ecologically nested systems like river systems, where the modelling units are strongly dependent on topography and, consequently, their orientation and size cannot be manipulated arbitrarily.

The objectives of this study were threefold: To assess the consequences of the MAUP for SDMs on (i) general model performance, (ii) predictor importance, and on (iii) predicted suitable habitats and their dependencies among resolutions (i.e., hierarchically nested sub-catchments) using riverine species. We hypothesized that, despite the same set of predictors and species occurrence data used, a) general model performance will not be influenced by the model resolution (sensu Domisch et al. (2013)), b) predictor importance will change from a high contribution of coarse-resolution predictors at a coarsely modelled resolution towards an increased contribution of small resolution predictors with increasing model resolution (i.e. with smaller, nested sub-catchments), and that c) the predicted habitat suitability patterns will be highly dependent on the spatial resolution. In terms of hierarchically nested sub-catchments, we expect that a high habitat suitability for a species is present in at least one of the next-smaller, nested sub-catchments (Fig. 1.1B I; see Fig. 1.1B II - IV for other theoretical possibilities).

To test our hypotheses, we modelled habitat suitability for 50 native fish species in the Upper Danube Catchment at ten different spatial resolutions ranging from an average area of ~633 km² to ~2 km², representing a wide range of resolutions that are often used for SDMs (Record et al., 2018). To assess the changes in predictor importance with changing spatial resolutions, we used a set of environmental predictors which are regularly applied in SDMs (climate, topography, land use). Additionally, we also used a hydrological time-series as a predictor, since hydrology is known to affect the distribution of fish species (Xenopoulos & Lodge, 2006).

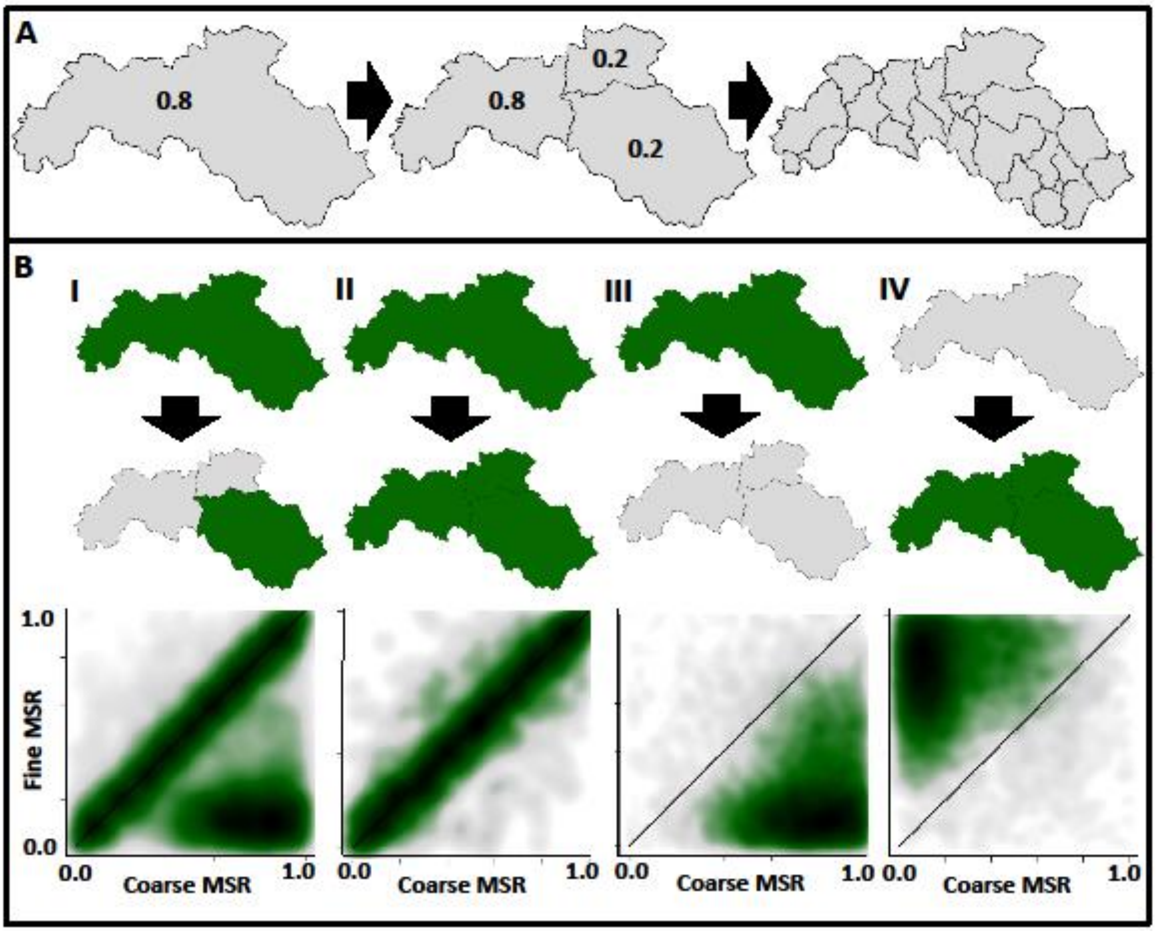

Figure 1.1: Nestedness of sub-basins and conceptual overview. (A) Nestedness of sub-catchments between different spatial resolutions. The modelled resolution increases from left to right. Additionally, the left and mid panel show a theoretical example of predicted habitat suitability values. To analyse the spatial dependency, we correlated the theoretical value of 0.8 at the coarse resolution with all the predicted values (i.e. 0.8, 0.2 and 0.2) at the next finer resolution. (B) A conceptual overview of the possible outcomes of the hierarchical spatial dependency. The x-axis represents the coarser modelled spatial resolution (MSR), while the y-axis shows the finer resolution. Darker shading indicates a higher density of the probability values. Panel I shows a hypothetical "filter" effect. A high predicted habitat suitability at a coarse resolution results in partly high predicted suitability at a finer resolution. Panel II shows a perfect match scenario without any environmental filtering. A high suitability at a coarser

resolution resulted in a high suitability in all spatially related sub-catchments at a finer resolution. Panel III shows the theoretical case were a sub-catchment at coarse resolution is predicted to have a high predicted habitat suitability and all the spatially related sub-catchments at a finer resolution have a low predicted suitability. Panel IV shows the opposite case.

Methods

Study area

Our study was conducted in the Upper Danube Catchment from the source in the very Southwest of Germany up to the gauging station close to Vienna (Austria, Fig. 1.2A). The upper Danube catchment mainly covers parts of Germany and Austria (more than 90%), as well as small parts in Switzerland, Italy, and the Czech Republic. We used the Shuttle Radar Topography Mission (SRTM) 90 m Digital Elevation Database (http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1) as our base Digital Elevation Model (DEM) to extract sub-catchments, e.g. modelling units. To force the hydrological routing to follow the observed streams, we carved the vectorized European river network provided by GEOFABRIK (https://www.geofabrik.de/de/index.html, Frederik et al. (2014)) into the DEM, by a depth of 20 m. This improves the spatial representation of the observed river network, especially in topographically flat areas.

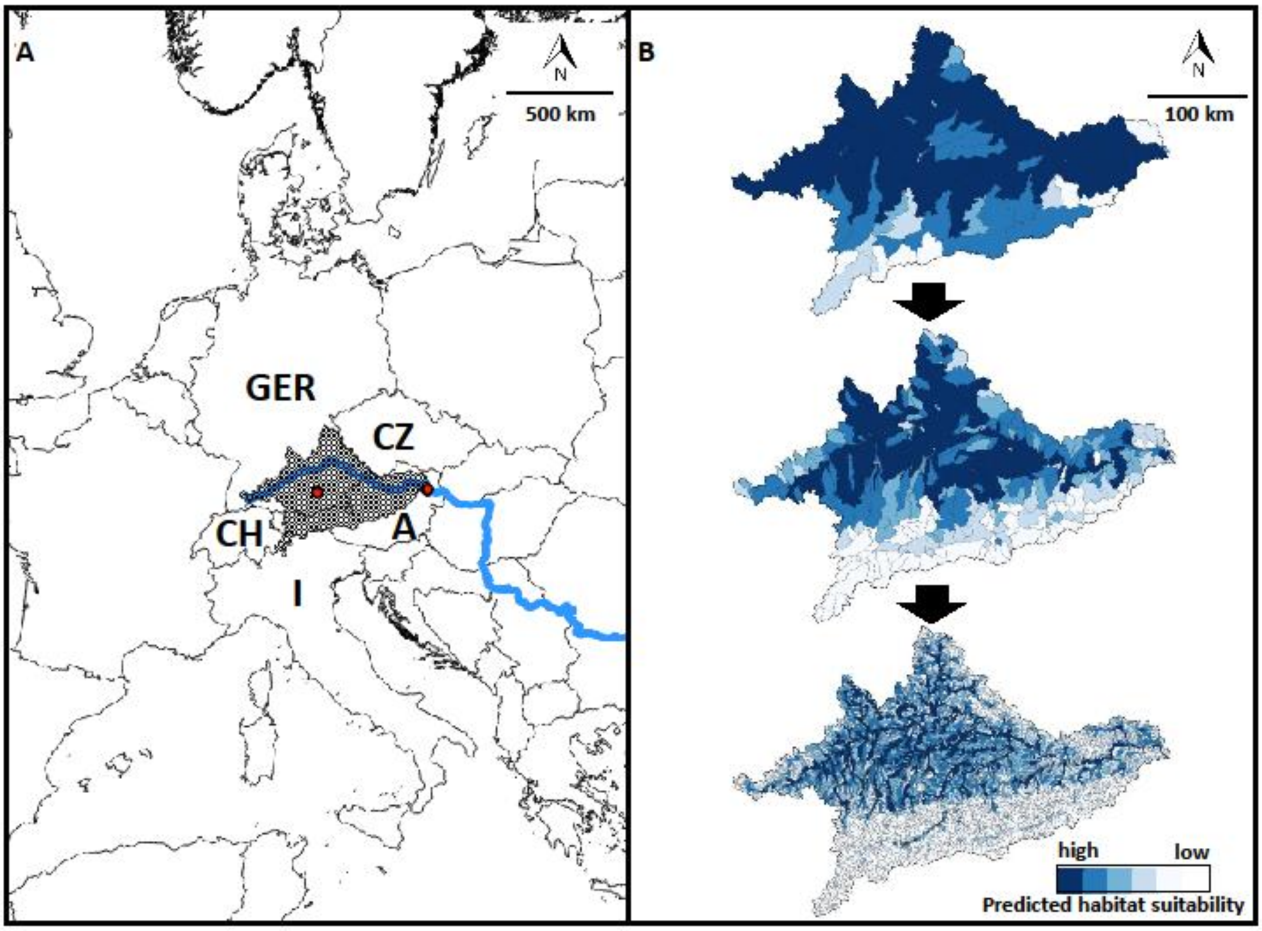

Figure 1.2: (A) Location of Upper Danube catchment within Europe. Countries which have a share of the catchment are named, GER= Germany, A= Austria, I=Italy, CH= Switzerland, CZ= Czech Republic.

Blue line indicates the Danube river. Red dots in Germany and Austria represent Munich and Vienna, respectively. (B) Example of Abramis brama probability of habitat suitability within the study area at three different modelled spatial resolutions (average size of sub-catchments: upper panel 632 km², mid panel 89 km², lower panel 15 km²). The darker the blue the more suitable is the habitat predicted.

Defining model resolutions

We defined ten different resolutions given the flow accumulation within the study area, i.e. the number of upstream grid cells contributing to a river reach. We first applied the GRASS-GIS function 'r.watershed' (Ehlschlaeger, 1989) on the DEM, which yielded flow accumulation, drainage direction, the stream network, and the catchment delineation. We then used the "threshold" flag to define the minimum number of upstream contributing grid cells to initiate a river, and thus to create sub-catchments based on the flow accumulation. The lower the threshold is set, the smaller the sub-catchments become. We used ten different thresholds starting from 102,400 and ranging down to 200 grid cells, where the next smaller threshold was half the size of the previous threshold (i.e., 102400, 51200, 25600, etc.; see Fig. 1.2B for sub-catchments created with thresholds of 102400, 12800, and 1600 upstream grid cells). The spatial resolution based on the smallest threshold (200) contained the highest number of sub-catchments (i.e., 162153) and, therefore, offers the finest resolution (for details regarding the number and the average area of sub-catchments see Table 1.1). To cover a wider environmental gradient for each species and to avoid truncated response curves in the models (Thuiller et al., 2004), we performed all calculations and models on a ~4 times larger modelling domain than the final study area (Table 1.1). To obtain the final predictions and results, we extracted the study region from the modelling domain. Throughout this paper, the size and number of modelling units is always given for the entire modelling domain.

Fish species data

We compiled a fish occurrence database for the upper Danube catchment combining occurrence data from five different sources. For the German part of the upper Danube catchment, we obtained fish occurrence data from the Federal Ministries of Bavaria and Baden-Württemberg. These databases contain point occurrence data from official monitoring programs, e.g. for the EU Water Framework Directive. For Austria, we used occurrence data collected within the "Improvement and Spatial extension of the European Fish Index" Project (EFI+, Pont et al., 2009). We supplemented the database with occurrence data from the Global Biodiversity Information Facility (GBIF, GBIF, 2018). From GBIF, we (i) used only data collected by acknowledged sources, such as universities or federal ministries, and (ii) added only occurrence records for those species that were already listed in the datasets from Bavaria, Baden-Württemberg, or EFI+ (i.e., range filling). Similarly, to how we utilized GBIF information, we used fish occurrence data from the "Digitaler Fischartenatlas von Deutschland und Österreich" (Brunken et al., 2008), i.e., digitized fish occurrence data collected by universities. From all data sources, we only used records spanning from 1970 to 2016. In total, we collected data for 136 fish species and removed all duplicate records per species and sub-catchment at each resolution. We used occurrence information at the species level in each sub-catchment per model resolution as response variable. To use an identical set of fish species across all spatial scales and to resolve a trade-off between number of species and data availability per species, we selected those that occur in the coarsest resolution (Threshold 102400) with at least five unique records (van Proosdij et al., 2016). We followed Jungwirth et al. (2014) and Schiemer and Waidbacher (1998) to define the native fish species for the upper Danube catchment and further excluded all invasive and artificially introduced species from our analyses, resulting in a total of 50 fish species (for details see Supplementary Table S1.1).

Environmental data

Climate predictors

Climate predictors were obtained from the WorldClim Version 2 - Global Climate Database (http:// worldclim.org/bioclim, Fick and Hijmans (2017)). WorldClim provides free climate data for ecological modelling on a 1 km² resolution for the time period from 1970 to 2000. We initially used nine predictors describing various temperature metrics within our study region (see Supplementary Table S1.2 for details). We calculated the average value of each predictor across each sub-catchment at each spatial resolution. We aimed to use a similar time frame for all environmental predictors, and since WorldClim was the most restricted, we used the time frame from 1970 to 2000 for all environmental predictors. Note that the longer period of fish data was chosen due to data availability (an addition of almost 60% of fish records compared to 1970-2000) as well as due to the longevity of several fish species (e.g. Esox lucius 30 years, Abramis brama 23 years, Squalius cephalus 22 years; maximum reported age, www.fishbase.de, Froese and Pauly (2010)).

Land-use predictors

Land-use predictors were obtained from the HIstoric Land Dynamics Assessment project (HILDA, Fuchs et al. (2013)). HILDA provides global land-use data from 1900 to 2010 on a decadal basis in five categories (forest, grassland, settlement, water, other land) in percentage cover per grid cell. The spatial resolution of the data is 1 km². We only used data that covered the time frame from 1970 to 2000, and calculated the mean percent coverage of each land-use category for each sub-catchment across all spatial resolutions.

Topographical predictors

Global topographical variables were obtained from the EarthEnv project (Amatulli et al. (2018), https://www.earthenv.org/topography). We used roughness, eastness, northness, and slope at 1 km² resolution. This data is not expected to change over the time period from 1970 to 2000. We calculated the average and range of each variable resulting in eight topographical variables (e.g. average roughness and the range of roughness across a sub-catchment, Supplementary Table S1.2).

Hydrological predictors

Discharge data for the study region were obtained for 16 gauging stations from the German Federal Institute of Hydrology (BFG, Kling et al., 2012a; Kling et al., 2012b). The BFG provided a time-series of monthly observed discharge data across 1970 to 2000. Discharge data from each gauging station was extrapolated to each sub-catchment at each resolution using a linear relationship between observed discharge and flow accumulation. The average R^2 values for these relationships were 0.96 with a range from 0.85 to 0.99. Based on this extrapolation, we calculated the average annual discharge and the coefficient of variance of monthly discharge. Those two were included as predictors for the modelling procedure (Supplementary Table S1.2).

Predictor pre-processing

To reduce collinearity and a potential model over-fit (Dormann et al., 2013), we assessed the pairwise collinearity among all predictors. From an original set of 25 variables, we excluded one of the pair-wise correlated variables from the analyses that had a correlation coefficient higher than |0.7|. From the remaining 14 variables, we selected two for each category (climate, land-use, topography, and discharge), totalling in eight predictors for the SDMs (Supplementary Table S1.2). All predictors were centred (so all predictors have a mean of 0) and scaled by dividing by their standard deviations. All geographical data processing was performed using the GRASS-GIS 7.4 software (Neteler et al., 2012). Unless specified otherwise, we used the ’r.univar’ function to calculate average and range values, and ’r.mapcalc’ to perform calculations on the gridded maps.

Habitat suitability modelling

We built all models using the biomod2 package in R (Thuiller et al., 2009; Thuiller et al., 2016) that offers the possibility to run up to 10 state-of-the-art algorithms, whose predictions can be combined into a weighted ensemble model (Marmion et al., 2009). The weights allow to focus on the best algorithms in the ensemble prediction, while not completely discarding results from other algorithms (Araújo & New, 2007). Furthermore, biomod2 allows setting a variety of model parameters and extracting model evaluation scores and predictor importance for every single model and the ensemble. We ran biomod2 with five algorithms, which are widely applied in the SDM literature (Merow et al., 2014): two machine learning algorithms (Artificial Neural Networks, ANN; Maximum Entropy, MaxEnt) and three regression techniques (Generalized Linear Model, GLM; Generalized Additive Model, GAM; Multivariate Adaptive Regression Splines, MARS). As our fish occurrence data was presence-only data, we had to create pseudo-absences (Elith & Leathwick, 2009). To enable a cross-scale comparison, we kept the ratio of pseudo-absences relative to the number of sub-catchments fixed at one third (e.g., in case of 3000 sub-catchments we used a maximum of 1000 pseudo-absences). This amount was chosen to balance the need for a high amount of pseudo-absences required for linear models, while a lower amount is required by machine learning techniques (Barbet-Massin et al., 2012). For each species, we selected pseudo-absences once, randomly. Models were evaluated by ten separate model runs, where 70% of the data was used to calibrate the model, and 30% was used for model validation, resulting in 5,000 models (50 species x 10 repetitions x 10 spatial resolutions). For each species, model runs were combined to a weighted ensemble model, specific to each spatial resolution. Proportional weights were assigned to all single models according to the True Skill Statistic (TSS) of a given model prior to creating the ensemble. The TSS values range from -1 to 1, where values close to 1 indicate a good to very good fit and values of 0 and lower indicate model performance not better than random. The assignment of weights to the models allows to automatically select the models with the best data fit for the ensemble, without completely discarding results from all other algorithms (Norberg et al., 2019). The ensemble model was then used to predict the final probabilistic habitat suitability for each species across all sub-catchments at a given spatial resolution.

Model evaluation

We used the model sensitivity and TSS to evaluate the performance of the ensemble models. As we were using presence-only data for the modelling approach, we chose model sensitivity as an evaluation metric, because sensitivity is the proportion of observed positives that were predicted to be positive. Sensitivity is therefore not influenced by the amount of pseudo-absences. As a second evaluation metric, we used TSS, because it is a widely applied measure of model performance in SDM studies. However, we are aware that TSS is affected by the amount of pseudo-absences (Allouche et al., 2006).

Predictor importance

To analyse, which environmental predictors were mainly driving the predictions based on the ten different spatial resolutions, we used the by default calculated predictor importance values for the ensemble model within the biomod2 package for each species at each spatial resolution. Those values range between 0 and 1 and give an estimate of how well a certain predictor correlates with the predicted habitat suitability for a species. We calculated the median value for each predictor across all 50 species at each spatial resolution.

Spatial congruence of predictions

We analysed the spatial congruence between predictions at different spatial resolutions using the species- specific suitability maps at each resolution. This was achieved by relating the predicted habitat suitability values of a species within a sub-catchment at a coarser resolution to all the nested probabilistic habitat suitability values of the same species at the next finer resolution using linear models and by extracting the goodness of fit (Fig. 1.1A and B). We did not translate continuous predicted probabilities into binaries (presence-absence response), because there is still discussion regarding an appropriate threshold selection (Guillera-Arroita et al., 2015). Data preparation (except for geographical processing), analyses and the species distribution modelling were done using the open source software R version 3.5.2. (R-Core-Team, 2018).

Table 1.1: Overview of modelled resolutions, mean SD area of sub-catchments in km² and number of sub-catchments for each modelled scale (modelling domain and study area). Note: The size and

amount of sub-catchments within the study area is defined by the threshold value we used in r.watershed function to extract the sub-catchment from the digital elevation model.

Modelled resolution	Average size modelling domain	Number modelling domain	Average size study area	Number study area	Classification
Threshold 102400	632 ±781	595	714 ±917	173	coarse
Threshold 51200	333 ±400	1130	367 ±435	278	coarse
Threshold 25600	183 ±227	2052	201 ±244	508	coarse
Threshold 12800	89 ±102	4207	105 ±108	977	intermediate
Threshold 6400	53 ±54	7138	57 ±55	1807	intermediate
Threshold 3200	28 ±29	13292	30 ±29	3441	intermediate
Threshold 1600	15 ±15	24806	16 ±14	6608	intermediate
Threshold 800	8 ±8	46594	8 ±7	12697	fine
Threshold 400	4 ±5	87935	4 ±4	23983	fine
Threshold 200	2 ±3	162153	2 ±2	44860	fine

Results

General model performance

The median sensitivity for all ensemble models ranged between 93.2 for the coarsest resolution (Threshold 102400) to 86.1 for intermediate resolutions (Threshold 6400), and sensitivity values for the models built at other spatial resolutions fell in between (Fig. 1.3A). The median TSS values ranged from 0.73 for both the coarsest and finest resolutions, to 0.61 for an intermediate resolution (Threshold 6400). All other models ranged between those values (Fig. 1.3B).

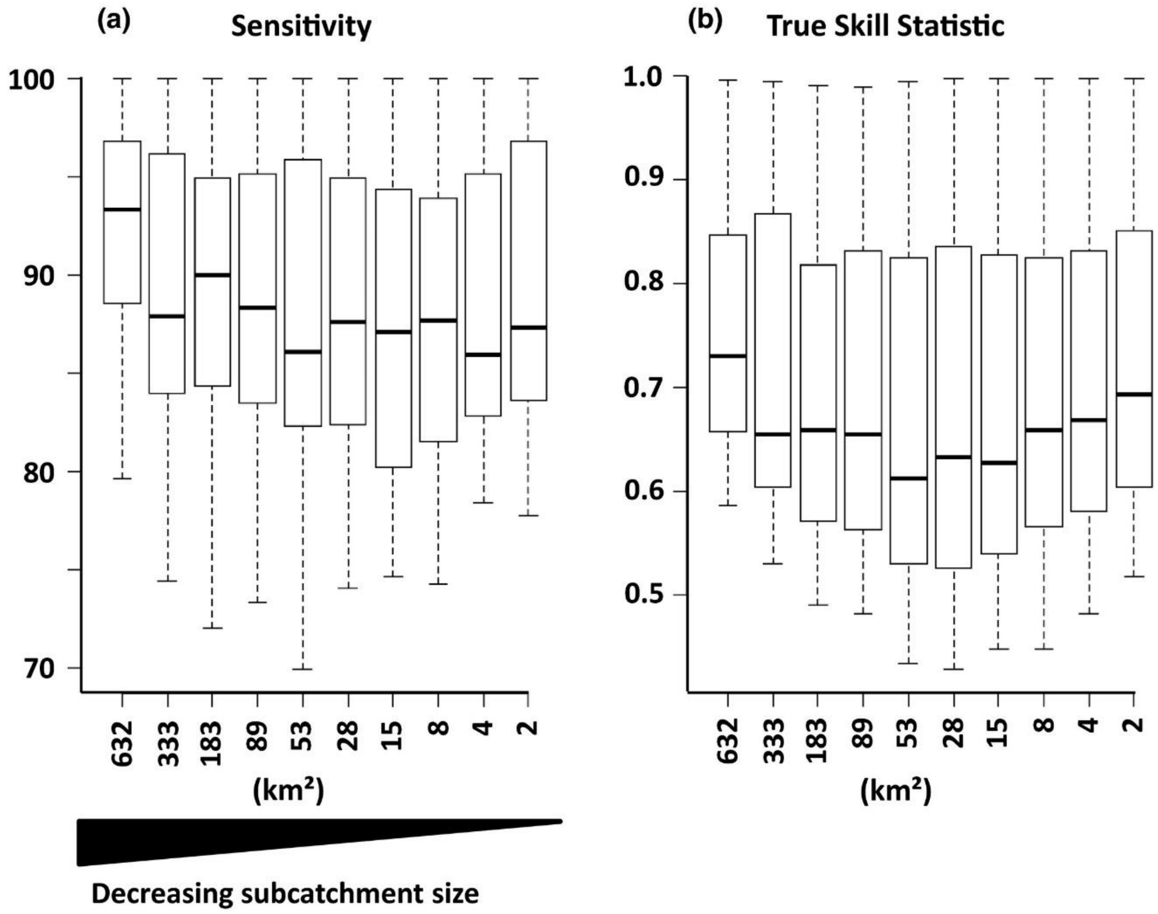

Figure 1.3: Median sensitivity (A) and median True Skill Statistic (B) values for the 50 modelled fish species in the upper Danube catchment at different modelled spatial resolutions. On the x-axis, the average area of sub-catchments/modelled units in square kilometres are given. Boxes indicate 1st and 3rd quantile, and whiskers indicate minimum and maximum values.

Predictor importance

We found that the median predictor importance was contingent on the spatial resolution (Fig. 1.4). For the predictions at the coarsest resolution, topography and climate contributed most to species habitat suitability predictions (grey and yellow box-plots, Fig. 1.4A). With a decreasing average area of sub-catchments between 333 and 15 km², the relative importance of climate related predictors further increased (yellow box-plots, Fig. 1.4B-G). At fine spatial resolutions, the relative importance of hydrological predictors (blue box-plots, Fig. 1.4G-J), especially the coefficient of variance of monthly discharge contributed most to the predictions. Land use predictors (green box-plots) were not of high importance in any of the final ensemble models.

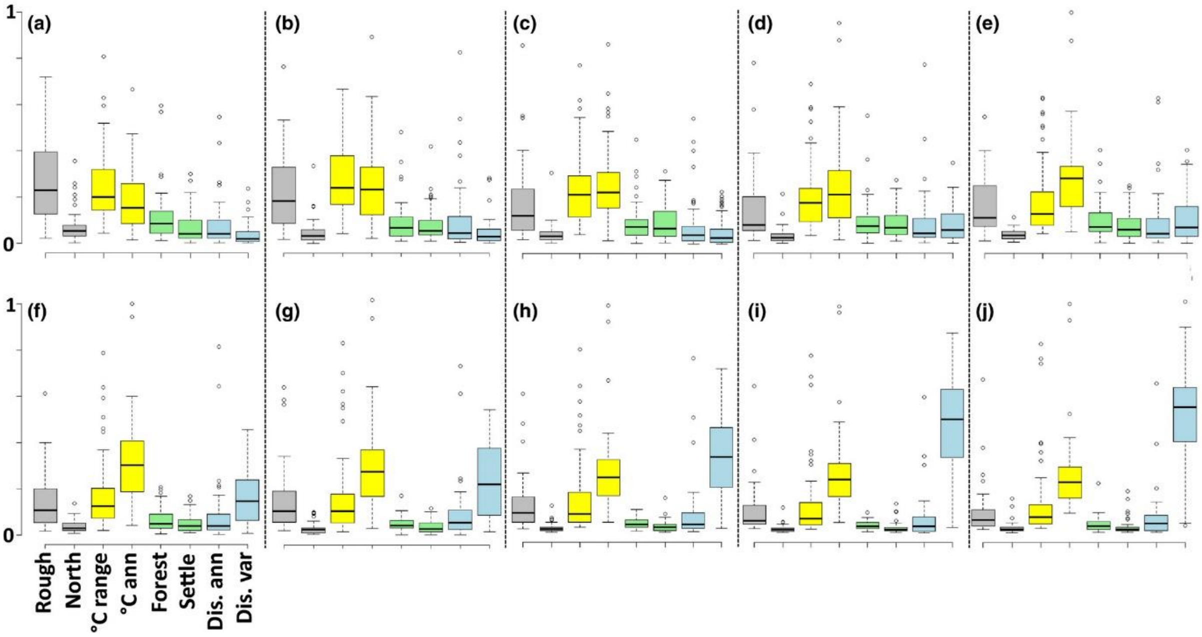

Figure 1.4: Variable importance for ensemble model predictions for 50 species in the upper Danube catchment at 10 different, modelled spatial resolutions (panels A-J are ordered from coarse spatial resolution [A = average size of the modelled sub-catchment 633 km²] to fine spatial resolution [J = average size of the modelled sub-catchment 2 km²]). For details see Table 1.1). Colours indicate the group of predictors; from left to right: grey = topography (roughness range and average northness), yellow = climate (temperature range and average annual temperature), green = land use (average area covered by forests and mean area covered by settlements), blue = hydrology (average annual discharge and coefficient of variance of annual discharge).

Spatial dependency across spatial resolutions

For all combinations of a coarse vs. the next-finer spatial resolution (Fig. 1.5), linear models revealed a significant positive relationship between the predicted habitat suitability of a coarser resolution and that of the next finer resolution. Although, all the identified relationships were positive, we found an increase in R² values the higher the modelled resolution gets (Fig. 1.5). Especially for coarse resolutions (Fig. 1.5A-C), we found lower R² values when comparing predicted habitat suitability between related modelled resolutions. Almost all non-matching probabilities (i.e. pronounced difference between predicted probability at coarser resolution with predicted probability at next finer resolution,) were below the regression line indicating a pronounced "filter effect", meaning that only a fraction of coarse-resolution sub-catchments were suitable in the nested (i.e., next finer resolution) sub-catchments (Fig. 1.5A-F, dark green area in the lower right corner). For fine resolutions the R² values increased, indicating that this "filtering effect" was less pronounced, e.g. habitat suitability predictions did not differ between a sub-catchment at a coarser resolution and those that are nested within the next finer resolution (Fig. 1.5G-I).

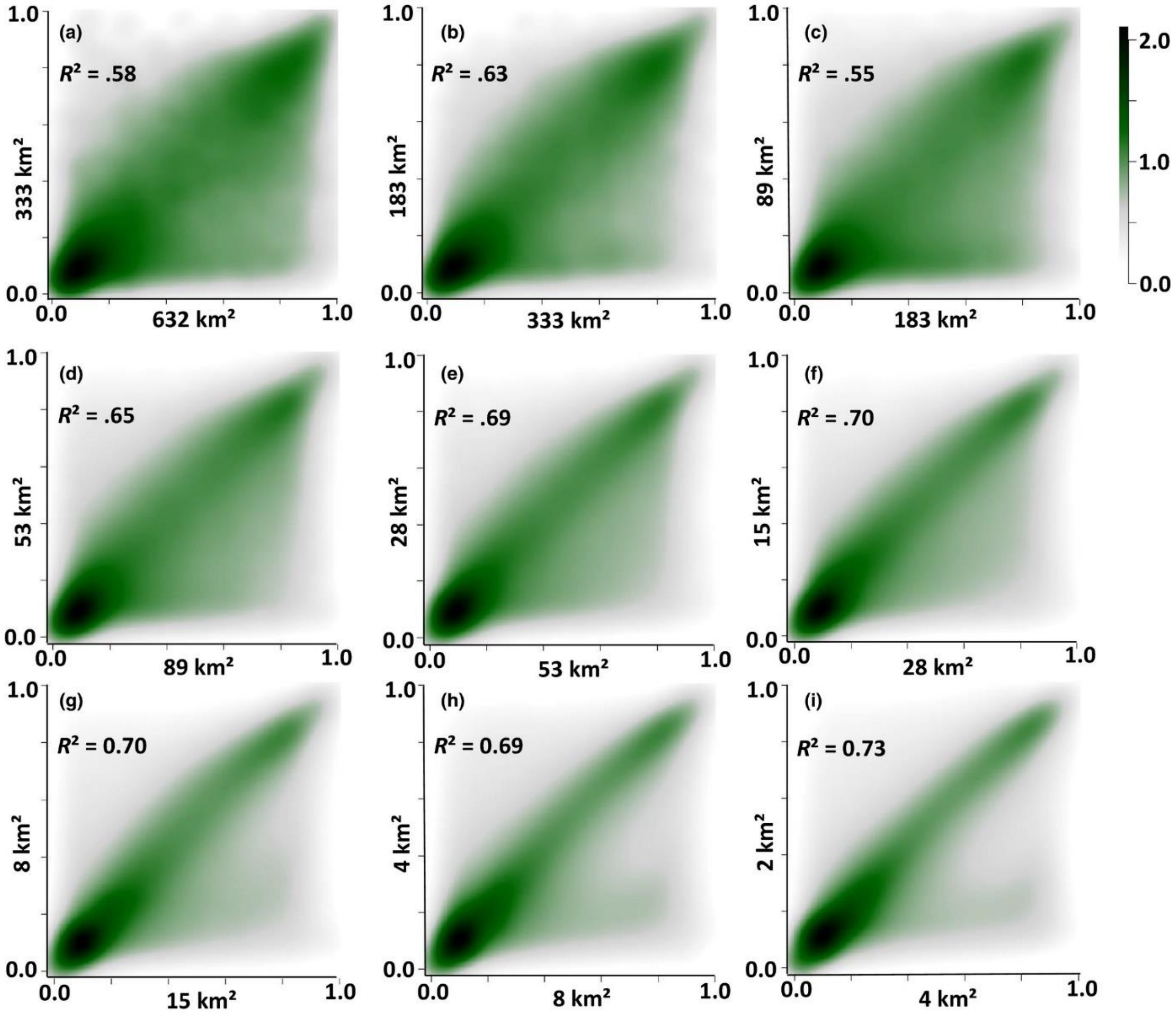

Figure 1.5: Relationship between predicted summed probabilities for each sub-catchment at a lower modelled spatial resolution (x-axis) and the highest predicted probability for the spatially related sub-catchment at the next finer modelled spatial resolution (y-axis). Axis labels indicate the average size of modelled sub-catchments. Panels are ordered from coarse to fine resolutions.

Discussion

Using a weighted ensemble SDM approach, we analysed the effects of ten different spatial resolutions on the general model performance, predictor importance, and the contingency on modelled resolution of predicted habitat suitability for 50 native fish species in the Upper Danube Catchment. The general model performance remained high across all spatial resolutions, whereas predictor importance was contingent on the spatial resolution (i.e., average sub-catchment size). Additionally, we identified strong spatial dependencies in the mapped habitat suitability patterns across spatial resolutions.

General model performance

For all spatial resolutions, model performance measures - sensitivity as well as TSS - were high to very high (Fig. 1.3), indicating the validity and applicability of the respective model (Swets, 1988; Thuiller, 2003). This finding confirms our first hypothesis and is of special interest when considering that models at coarse, intermediate, and fine resolutions were mainly driven by topography, climate, or hydrology, respectively (Fig. 1.4). The constantly high model performance over all modelled resolutions with changing predictor importance suggests that, at a given spatial resolution, the model uses the most informative environmental predictors that increase the proportion of explained variance regarding the distribution of suitable habitats. As we let the model "decide" which predictors are most useful (opposed to a pre-selection of predictors), it remains to be assessed how a strictly defined set of predictors at each spatial resolution would impact model outcomes (Synes & Osborne, 2011). We hypothesize that a further increase in model resolution would call for a new set of e.g. hydraulic predictors at even finer spatial resolutions, since our hydrological predictors would not be able to reflect such patterns.

Predictor importance

The importance of topographical, climatic and hydrological predictors on model outputs were dependent on the given spatial resolution. Models at coarse resolutions were mainly driven by topography, climate was dominating the intermediate resolutions, and hydrology was found to mainly affect predictions at fine spatial resolutions. This finding confirms our second hypothesis. However, we argue that this finding is directly linked to the MAUP and is not a species or organism specific result. Most likely the aggregation of predictor values (1 km² grid cell values) across modelled sub-catchments at each spatial resolution is causing the observed change in predictor importance. For 30 of the 50 studied fish species most suitable habitats were located in lowland regions. In lowland regions, we find only small gradients of topography and climate across large areas. Consequently, the spatial aggregation of topography and climate predictors within each sub-catchment yield only minor changes compared to the original values. Hydrology (i.e. the coefficient of variation of annual discharge), however, can be highly variable across "flat" regions if measured across multiple stream orders. During the spatial aggregation process this variability in hydrology flattened and resulted in an overall weak contribution in model predictions.

Land use related predictors, which are often identified as one of the main factors driving habitat suitability predictions of fish, besides climate (Radinger et al., 2016), did not play an important role in any of the modelled resolutions. We argue that the strong gradients within the other predictors (e.g. topography and climate from alpine to lowland, and hydrology from very small streams to the main channel) may mask the effects of the rather broad land use categories used in our analysis (Feld et al., 2016; Manzoor et al., 2018).

By using a variety of model resolutions, we were able to show a very general problem for freshwater SDM studies with far reaching implications: the modelled spatial resolution affects predictor importance. In most SDMs, the choice of predictors is, besides being ecologically meaningful, driven by their availability (Booth et al., 2014), while the model resolution is often chosen according to the resolution of the predictor and species occurrence data (Manzoor et al., 2018). Our results highlight that conclusions drawn from SDM-outputs built at a specific spatial resolution may be seen as a "spatial snap shot" and are only valid for the specific resolution used. Hence, such results need to be interpreted carefully, even when the SDM performs well in terms of evaluation scores.

Predicted habitat suitability correlated between resolutions

Spatially related sub-catchments and their predicted species-specific suitability values across different resolutions were strongly correlated. Interestingly, this pure statistical finding reveals strong parallels to the landscape filter hypothesis (Poff, 1997). According to the landscape filter hypothesis, an organism has to pass several environmental filters to thrive at the location where it is observed. In line with the landscape filter hypothesis, we found that a sub-catchment with a high predicted habitat suitability at a coarse resolution was at least partly suitable at the next finer resolution (i.e. only when a species is able to pass a filter at a coarse resolution it can occur in parts of this area at finer resolutions). The statistical possible, but ecological impossible opposite case was only rarely observed. This "filter effect" (Fig. 1.5, green area in the lower right corner of each panel) was less pronounced at finer spatial resolutions, indicating a tipping point of the spatial resolution beyond which the filter effect did not apply anymore given the chosen predictors. It remains to be tested whether using even smaller sub-catchments (and e.g. hydrologic variables over shorter time periods) would lead to a continuation of this pattern. Given the predictors set, we could not identify the opposite case of such a filter effect, i.e. where a low habitat suitability at a coarse resolution would turn into a high suitability in the nested sub-catchments.

Implications for spatial conservation planning

Despite that statistical SDMs and the evaluation scores only assess the mathematical correctness of the model and do not provide any information on the ecological meaningfulness (Mouton et al., 2010; Domisch et al., 2013), SDMs are regularly used for conservation purposes (Record et al., 2018). Our finding that predictor importance - a measure often used to inform conservation management (Lomolino, 2004; Porfirio et al., 2014) - and predictions itself are contingent on the modelled spatial resolution is important, e.g. when SDM outputs inform decisions regarding the delineation of protected areas (Loiselle et al., 2003) or the assessment of species' environmental habitat preferences (e.g. Markovic et al., 2014; Radinger et al., 2016; Pringle, 2017). Any output derived from an SDM should be evaluated in context of the chosen predictors and the spatial resolution at which the model is built. According to the MAUP, and in the absence of the possibility to change orientation and/or configuration of modelling units (Hui et al., 2010), our study highlights the necessity of performing catchment-based river SDMs at multiple spatial resolutions to assess uncertainties and/or range in predictor importance and predictions made. This is of special interest considering that model performance measures are not affected by the MAUP and, consequently, do not reflect those uncertainties. Without considering the MAUP, any generalization about habitat suitability and predictor importance beyond a specific spatial resolution, at which the model has been built, have to be formulated and/or used carefully.

Our results in a practical context

Hydrology was the main driver of habitat suitability predictions for fish species at fine resolutions in our study. Hence, fine scale predictions are required when SDM outputs should support conservation management in freshwater ecosystems (Groves et al., 2002). The increasing availability of high-resolution predictors at global scale (e.g. Domisch, Amatuilli et al. 2015, and especially hydrology; Barbarossa et al. 2018) is promising to improve the accuracy needed to use SDMs for the on-ground implementation of conservation measures. By only using the results from our fine resolution model, protecting morphological intact stream stretches and restoring a natural flow regime may seem to be appropriate measures to create suitable habitats for the majority of fish species in this area. However, as expected by the MAUP, this strong statistical relationship is contingent on the modelled spatial resolution. As a consequence, only applying the fine resolution model, climate would not be important for habitat suitability estimates in our study region. In contrast, with similar performance, our models on intermediate spatial resolutions identified climate as the main driver for habitat suitability predictions. Hence, the spatial allocation of conservation measures and protected areas should take the advantage of this "filter effect", focusing on climatically suitable areas, although climate has not been identified as important for the fine resolution models. If the potentially protected or restored sites would be located in climatically unsuitable areas, either today or in the near future, it is likely that they would not be successful in supporting a healthy fish fauna.

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Chapter 2

300 years of change for native fish species in the upper Danube river basin – historical flow alterations versus future climate change

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Abstract

River ecosystems belong to the most threatened ecosystems on Earth. Historical anthropogenic alterations have, and future climate change will further affect river ecosystems and the species therein. While many studies assess the potential effects of expected future changes on species, little is known about the severity of these changes compared to historical alterations. Here, we used a unique 300-year time series of hydrological and climate data to assess the vulnerability of 48 native fish species in the upper Danube river basin. We calculated species-specific vulnerability estimates relative to the reference period (1970-2000) for the periods 1800-1830, 1900-1930, and 2070-2100, including two Representative Concentration Pathways (RCP 4.5 and 8.5) and identified the environmental drivers of vulnerability estimates. Models showed that future changes under RCP 4.5 would result in moderate species vulnerability compared to historical conditions, while under RCP 8.5, the vulnerability for all species increased substantially. In addition, species vulnerability was mainly driven by hydrology in the past and is likely to be driven by temperature in the future. Our results show that future climate change would alter environmental conditions for riverine fish species at a similar magnitude as historical anthropogenic hydrological river alterations have. Shedding light on such long-term historical and

possible future anthropogenic alterations provides valuable insights for prioritising conservation actions for riverine fish species.

Introduction

Freshwaters belong to the most threatened ecosystems on Earth (Dudgeon, 2019; Reid et al., 2019), with almost one-third of all freshwater species facing the threat of extinction (Collen et al., 2014) and a global freshwater vertebrate population decline of 84% on average in the past 50 years (WWF, 2016). Among all known freshwater fish species, one quarter faces extinction (Su et al., 2021). Fish species in river ecosystems react sensitively to alterations in discharge (Xenopoulos & Lodge, 2006; Beatty et al., 2014; Rolls & Arthington, 2014; Ward et al., 2015) and in temperature (Buisson et al., 2008; Buisson & Grenouillet, 2009; Lyons et al., 2010; Comte et al., 2013; Kriaučiūnienė et al., 2019). Globally riverine fish species suffered in the past mainly from anthropogenic discharge alterations (Hohensinner et al., 2004; Böhm & Wetzel, 2010; Haidvogl et al., 2014; Grill et al., 2019), while pronounced long-term temperature increases were only relatively recently observed (IPCC, 2017). In contrast, for the future, studies suggest that the significant rise in air temperatures and changes in precipitation patterns (with consequential but probably less pronounced changes in discharge) will be the main driver of vulnerability, i.e. susceptibility to being negatively affected by climate change (Pacifici et al., 2015), for riverine species (Jaric et al., 2019; Kriaučiūnienė et al., 2019; Reid et al., 2019).

The majority of large rivers globally have been modified by humans over decades to meet social demands such as transportation, energy production, flood and disease control, or drinking and agricultural water supply (Jungwirth et al., 2014; Grizzetti et al., 2017; Grill et al., 2019), resulting in a severe loss of natural characteristics of rivers (Cazzolla Gatti, 2016; Wohl, 2019). Climate change scenarios predict a further, significant increase in pressures for river ecosystems within the near future (Rodell et al., 2018; Dudgeon, 2019; Grill et al., 2019; Jaric et al., 2019). For example, climate change will result in increased water temperatures (IPCC, 2017), which often results in a reduction of suitable habitats for native species (Markovic et al., 2014) or an increase in thermal stress as species will be subjected to their upper thermal boundaries (Till et al., 2019; Crear et al.). In addition, expected increases in water use and changes in the amount and the spatial distribution of precipitation (Rodell et al., 2018) will result in enhanced hydrologic pressures for biotic communities in rivers (Kakouei et al., 2018; Rolls et al., 2017; Yoshikawa et al., 2014). One of the many rivers with a long history of human alteration and expected severe climate change effects in the future is the Danube river, one of the largest and most fish species divers rivers in Europe (Jungwirth et al., 2014). For the Danube river basin the 19th century was dedicated to flood prevention and channelization, especially for the upper part (Jungwirth et al., 2014). However, severe impacts on the fish fauna started at the end of the 19th century, when channelization reached its maximum and soon after the first hydroelectric power stations were built (Zauner & Schiemer, 1994; Jungwirth et al., 2014). In 1956 the first hydroelectric power station in the main channel was completed, and to date, more than 70 hydroelectric power stations exist in the main stem of the upper Danube river (Jungwirth et al., 2014). Considering future alterations, mean annual temperature is predicted to steadily increase with an accelerating rate (IPCC, 2017) in the upper Danube river basin (Jacob et al., 2014). However, the predictions for changes in precipitation are more divers and effects on the fish fauna are difficult to anticipate (Giorgi et al., 2016). A reduction in precipitation, especially in the summer months, is expected, but some regional climate models also predict an increase with a change from rain to snow, especially in higher alpine areas (Giorgi et al., 2016).

When assessing conservation needs for freshwater biodiversity under future climate change scenarios, the majority of studies neglect the often dramatic historical environmental alterations (Wohl, 2019) and their impact on species or populations. Without quantifying historical alterations, with “historical” referring to a time period in which major anthropogenic changes started until the current point in time, and their impact on species, future predictions can only deliver relative estimates of vulnerability, i.e., relative to the current point in time. Studies focussing on future predictions of possible impacts on species or populations (Markovic et al., 2017; Radinger et al., 2017; Kakouei et al., 2018; McMahan et al., 2020), deliver certainly crucial information for effective conservation planning and management (Bonebrake et al., 2018; Domisch et al., 2019), however predictions often come with high uncertainty (Yates et al., 2018) and are likely to e.g. overestimate the importance of temperature, because the expected rapid increase in temperature will be more pronounced than a gradual change in discharge driven by precipitation changes. Such uncertainties can hinder practical implication of modelling results (McShea, 2014; Porfirio et al., 2014; Schuwirth et al., 2019). Therefore, placing predicted future changes into a historical context can deliver useful information regarding the magnitude of change that species have already been exposed to, compared to what they would expect under future climate change scenarios. Such information would significantly increase the effectiveness of current conservation management efforts (Bonebrake et al., 2010; Pont et al., 2015; Novaglio et al., 2020).

Here, we employ a unique historical time series of observed (1800-2007) and modelled (2007-2100) climate and hydrological data for a 300-year period from 1800 to 2100 for the area of the upper Danube river basin (Fig. 2.1). The extensive period allows comparing the effects of major historical alterations in discharge and temperature on the vulnerability of fish species (Zauner & Schiemer, 1994; Jungwirth et al., 2014) with predicted effects for the near future driven by expected alterations in climate conditions (Klein et al., 2011; Kling et al., 2012a; Stanzel & Kling, 2018). In addition, the time series allows quantifying the drivers of expected vulnerability for the historical alterations and comparing them to the quantification of drivers in the future scenarios.

We first used habitat suitability models (HSMs) to assess the current distribution of suitable habitats for 48 native fish species. We then used the current predicted fish habitat distributions (and species-habitat relationships) as a baseline for climate niche factor analyses (CENFA; Rinnan & Lawler, 2019) to assess species vulnerability for historical alterations and future change scenarios. We hypothesised that (i) historical vulnerability estimates will be mainly driven by discharge-related environmental factors. We further expected that under future environmental change scenarios, the importance of discharge-related factors will play a lesser role than temperature-related environmental factors. In addition, we hypothesised (ii) that historical discharge alterations caused by the damming and channelisation affected riverine fish species stronger than the combined changes in climate and climate-driven flow characteristics would do in the future. We expect that this difference is indicated by overall higher historical vulnerability estimates than for future scenarios.

Methods

Study region

The study region is the upper Danube river basin from its source in Germany's Southwest up to the gauging station close to Vienna, Austria, covering 102.113 km² and roughly 1000 km of the Danube river main stem. The upper Danube river basin mainly covers parts of Germany and Austria (> 90%) and minor parts of Switzerland, Italy, and the Czech Republic (Fig. 2.1B). For subsequent analyses, we divided the study area into >18.000 sub-basins (Fig. 2.2A) and considered each sub-basin with at least one occurrence of a particular species as a sub-basin with said species presence (Fig. 2.2B).

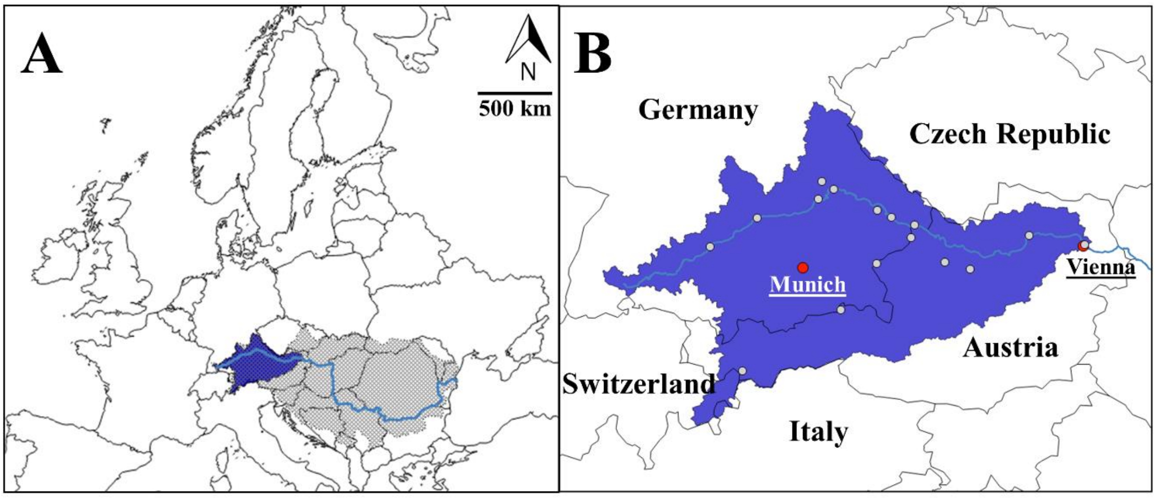


Figure 2.1: Overview of the study area. A) The location of the upper Danube river basin within Europe. The light grey area indicates the whole Danube river basin. In light blue the Danube main stem is shown. Dark blue indicates the study area. B) Study area in detail. Large red dots indicate the location of Munich and Vienna. Small grey dots show the distribution of the gauging stations we used to extrapolate discharge values across the study area (see "Hydrological data" for details).

Fish distribution data

We compiled fish species occurrence data from four different sources. For the German part of the upper Danube river basin, we used the occurrence data collected by the Federal Ministries of Bavaria and Baden-Württemberg to comply with the EU Water Framework Directive. For the Austrian part of the upper Danube river basin, we used occurrence data collected for the project "Improvement and Spatial extension of the European Fish Index" (Pont et al., 2009). In addition to this large-scale monitoring data, we used occurrence data from Brunken et al. (2008). From Brunken et al. (2008) we only used data collected by acknowledged sources, such as universities and federal ministries for species listed in the data sources from Bavaria, Baden Württemberg or EFI+. We filtered all fish occurrence data for sampling dates between 1970 and 2016. Here, we included data from 2000 to 2016 as this resulted in an addition of almost 60% of high-quality fish records compared to 1970–2000. In total we gathered data for 48 native fish species (Tab. S1).

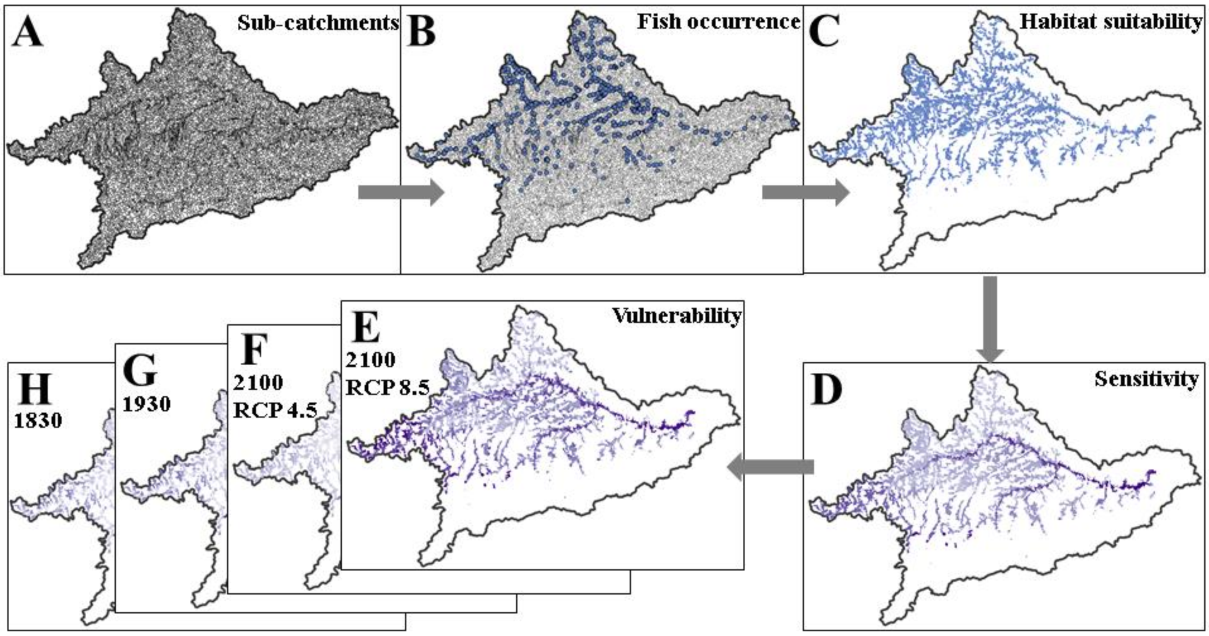


Figure 2.2: General workflow. A) The study area divided into 18.708 sub-basins with a mean area of 8 ± 8 km². B) Spatial overlay of the fish occurrence data (here the common bream, *Abramis brama*) with the sub-basins in the study area. C) For each species occurring in at least ten sub-basins, present-day habitat suitability was calculated based on the sub-basins as modelling units and six environmental predictors (i.e. mean annual temperature, temperature annual range, mean monthly discharge, coefficient of variance of monthly discharge, mean northness, and roughness range), to obtain a range-wide estimate of the habitat suitability for a target species. D) A sub-basin-specific sensitivity estimate for each species within its potential distribution was calculated based on the average sensitivity of a given species (i.e. the average environmental conditions used by that species) compared to the average environmental conditions within a given sub-basin. For instance, a low sensitivity would be assigned to a sub-basin, where the environmental conditions match the average environmental conditions used by that species across the entire study area, and vice versa. E-H) For each species, a sub-basin specific vulnerability estimate for the different time intervals and climate change scenarios was calculated (for details see Departure and vulnerability analysis).

Environmental data time-series

Hydrological and climate data were obtained from the German Federal Institute of Hydrology (BfG; Stanzel & Kling, 2018).

Hydrological data

Monthly hydrological data for 16 gauging stations within the study area (Fig. 2.1B) were obtained from the precipitation runoff model COSERO for a time interval from 1800 to 2100 (Stanzel & Kling, 2018). Historical discharge simulations from COSERO are based on gridded monthly temperature data and precipitation data available in the HISTALP data base (Auer et al., 2007; Chimani et al., 2013). Future discharge simulations are based on temperature and precipitation projections of Regional Climate

Models (RCMs) from the EUR-11 ensemble of the EURO-CORDEX initiative (Jacob et al., 2014). We used future discharge simulations based on ten different global-regional climate model (GCM/RCM) combinations (i.e. CERFACS-CNRM-CM5/CCLM4-8-17, EC-EARTH/CCLM4-8-17, HadGEM2-ES/CCLM4-8-17, M-MPI-ESM-LR/CCLM4-8-17, EC-EARTH/RACMO22E, HadGEM2-ES/RACMO22E, EC-EARTH/HIRHAM5, IPSL-CM5A-MR/WRF331F, CERFACS-CNRM-CM5/ALADIN53, M-MPI-ESM-LR r2i1p1/REMO2009) and for the two Representative Concentration Pathways (RCP; van Vuuren et al., 2011) 4.5 and 8.5 (Stanzel & Kling, 2018). For further details on COSERO and its performance see Klein et al. (2011); Kling et al. (2012a); Kling et al. (2012b). To create discharge estimates for each sub-basin, we extrapolated the modelled discharge values from the 16 gauging stations using a linear model of flow accumulation (number of grid cells contributing to a given stream grid cell) and monthly discharge (see also Kuemmerlen et al., 2014). From the entire time series of simulated monthly discharge data, we extracted two historic time intervals (1800-1830 and 1900-1930), a current time interval (1970-2000) and a future time interval (2070-2100) with two scenarios (RCP 4.5 and RCP 8.5). For each time interval and scenario, we calculated the coefficient of variance of monthly discharge and the mean annual discharge and for each sub-basin (see Tab. 1 for an overview of the raw values), which were later used as predictors for the habitat suitability modelling (HSM; only the current time interval) and CENFA.

Table 2.1: Summary statistics of predictors used for the HSM and CENFA analyses (static topography related predictors are not shown). For each time interval and scenarios, the mean value ± standard deviation, the median value with the first and third quartile, and the highest and the lowest value are shown. CoV = coefficient of variance, sd = standard deviation.

Time interval	Predictor	Mean (± sd)	Median (1st and 3rd quartile)	Highest value	Lowest value
1800 - 1830	CoV of monthly discharge	2.23 (0.93)	2.70 (1.62; 2.98)	3.06	0.25
	Mean annual discharge (m³/s)	322.31 (747.03)	67.7 (61.60; 120.93)	3251.50	8.28
	Temperature annual range (°C)	25.99 (2.64)	26.57 (26.11; 27.33)	28.37	3.31
	Mean annual temperature (°C)	6.69 (2.04)	7.13 (6.72; 7.79)	8.52	-3.01
1900 - 1930	CoV of monthly discharge	2.28 (0.96)	2.75 (1.61; 3.06)	3.14	0.27
	Mean annual discharge (m³/s)	313.87 (744.37)	61.50 (55.60; 113.42)	3268.10	7.51
	Temperature annual range (°C)	24.22 (2.63)	24.80 (24.35; 25.65)	26.51	3.10
	Mean annual temperature (°C)	6.36 (2.02)	6.83 (6.33; 7.49)	8.07	-3.28
1970 - 2000	CoV of monthly discharge	1.45 (0.55)	1.74 (1.13; 1.87)	1.91	0.21
	Mean annual discharge (m³/s)	337.35 (741.17)	85.40 (79.50; 137.73)	3276.10	10.50
	Temperature annual range (°C)	24.73 (2.63)	25.30 (24.89; 26.13)	27.10	3.16
	Mean annual temperature (°C)	7.13 (2.03)	7.67 (7.04; 8.29)	8.78	-2.56
2070 - 2100 RCP 4.5	CoV of monthly discharge	1.29 (0.50)	1.55 (0.99; 1.68)	1.72	0.20
	Mean annual discharge (m³/s)	332.30 (741.58)	80.40 (74.50; 132.36)	3266.20	9.88
	Temperature annual range (°C)	25.20 (2.58)	25.77 (25.27; 26.62)	27.52	3.21
	Mean annual temperature (°C)	9.03 (2.04)	9.51 (8.97; 10.20)	10.82	-0.44
2070 - 2100 RCP 8.5	CoV of monthly discharge	1.51 (0.67)	1.84 (0.98; 2.06)	2.13	0.22
	Mean annual discharge (m³/s)	314.92 (741.35)	64.30 (58.70; 113.26)	3273.40	7.87
	Temperature annual range (°C)	25.20 (2.53)	25.87 (25.22; 26.56)	27.62	3.23
	Mean annual temperature (°C)	10.58 (1.92)	11.02 (10.56; 11.65)	12.35	0.95

Temperature data

To be consistent with the discharge model COSERO, we used the same monthly temperature data (i.e. same historic data and the same regional climate models). COSERO is driven by temperature data, which was downscaled to 61 hydrological response units within the study area based on elevation (Kling et al., 2012a; Kling et al., 2012b). We used this downscaled monthly climate data to calculate mean annual temperatures and temperature annual ranges for each sub-basin and each of the aforementioned four time intervals (1800-1830, 1900-1930, 1970-2000, and 2070-2100 with RCP 4.5 and RCP 8.5; see Tab. 1).

Topographical data

Topographical data was used for the present-day HSM, because topography-related predictors were found to be important when modelling habitat suitability of fish species in the upper Danube river basin (Friedrichs-Manthey et al., 2020). Topography is not expected to change over the analysed 300 years' time period, therefore we used topography related predictors only to obtain the best possible current predictions in our HSM approach and excluded them from the CENFA analyses. Topographical data was obtained from the EarthEnv topography dataset (Amatulli et al., 2018), providing topographical data on a 1 km² resolution globally. From these, we calculated the mean northness and roughness range for each sub-basin.

Habitat suitability modelling

To further increase spatial completeness of the compiled distribution data, we used habitat suitability models (Elith & Leathwick, 2009). HSMs use a statistical relationship between species occurrence data and environmental predictors to create range-wide predictions of habitat suitability for target species. We built models using the biomod2 package in R (Thuiller et al., 2009; R-Core-Team, 2013). We used weighted ensemble models (Marmion et al., 2009) consisting of five machine learning and regression algorithms (Artificial Neural Networks, Maximum Entropy, Generalized Linear Model, Generalized Additive Model and Multivariate Adaptive Regression Splines) that are widely applied within the HSM literature (Araújo & New, 2007; Merow et al., 2014). We only used species with at least ten unique occurrences (i.e., present in sub-basins) to model the potential habitat suitability (van Proosdij et al., 2016a) and a fixed number of one third of all sub-basins as pseudo absences. As predictors we used six uncorrelated environmental variables from three different categories, which have shown to be appropriate to model habitat suitability of fish species in the upper Danube river basin (Friedrichs-Manthey et al., 2020): hydrology - average annual discharge and coefficient of variance of monthly discharge, climate - mean annual temperature and temperature annual range, and topography - average northness and roughness range. We assigned proportional weights to all single models (e.g. single algorithms) before combining them to a final ensemble model for each species. The assignment of weights allows focusing on the best algorithm without discarding results from other algorithms completely (Araújo & New, 2007). Weights were assigned according to the True Skill Statistic (TSS, Allouche et al., 2006). TSS values range between -1 and +1, with values around zero indicating that a model is not better than random and values of +1 indicating a perfect fit. The final ensemble models were evaluated using TSS by means of data splitting: we used ten separate model runs, where 70% of the data was used for calibration and 30% for model validation. Predicted habitat suitability was transformed to a binary presence/absence information (Fig. 2.1D; from here on called suitable habitats of a species) using a species-specific cut-off value, which minimises the absolute difference between sensitivity (i.e., true positive rate: how well a model depicts the true known presences of a certain species) and specificity (i.e., true negative rate: how well a model depicts the randomly created pseudo-absences). Note that the model sensitivity in the HSM validation is disconnected from a sensitivity estimate used in the CENFA analyses, described below.

Departure and vulnerability analysis

We used the CENFA package in R (Rinnan & Lawler, 2019) to calculate average environmental sensitivity estimates for all species, species-specific departures between the time intervals, and species specific vulnerability estimates for each time interval except for the current point in time. The average environmental sensitivity reflects the average degree of specialisation of a species for each environmental predictor (Rinnan & Lawler, 2019). These environmental sensitivity values are always positive and interpreted in comparison among analysed species. The higher the sensitivity of a species, the smaller the estimated environmental niche of that species given the predictors used in relation to other species. In a second step, we calculated the species-specific departure (i.e. the environmental distance) between the current time interval and the two historical time intervals and two future scenarios for each sub-basin. Departure is defined as a measure of change between baseline habitat conditions (here the present day conditions) and historic or future habitat conditions (Rinnan & Lawler, 2019). The departure estimate is always positive and has no upper limit. In total, we calculated 22 departure estimates for each species (2 historic, and 2 future * 10 RCMs). As the ten RCMs were highly variable and consequently produced a large variety in departure estimates, we used the median to create one future departure layer per species and RCP, combining all ten RCM models. All calculations are relative to the present, modelled habitat suitability of a species. Finally, vulnerability estimates are a combination of environmental sensitivity and departure. The species-specific sensitivity estimate weights the overall departure estimate of a given location. Consequently, high sensitivity values and high departure estimates result in a predicted high vulnerability. A stand-alone vulnerability estimate has no meaning but does so when compared to species or within species for different time intervals. We calculated the vulnerability for each sub-basin given the species that have a present-day predicted suitable habitat for the two historical time intervals and the two future scenarios (Fig. 2.1E-H). Again, we calculated the ten future climate models separately and then combined them to one vulnerability layer for each species and future scenario using the median. We compared the four resulting mean vulnerability layers using the 'modOverlap' function in the R package fuzzySim (Barbosa, 2015) and calculated Schoeners'D (Warren et al., 2008), which can range from 0 (no overlap) to 1 (total overlap), between each time interval and the two future scenarios.

Results

SDM performance

The TSS values for all species ranged between 0.40 for species with >400 initial occurrences (*Salmo trutta*) to 0.99 for species with <20 occurrences (i.e. *Telestes souffia*), indicating a good to very good model performance for all species (Bean et al., 2012; for details see table S1).

Departure

Relative to the suitable habitats modelled for the current point in time (1970-2000), the median departure values, i.e. the environmental distance, for the environmental predictors showed large differences between the analysed time intervals and scenarios. The environmental departure of the coefficient of annual discharge was similar between the two historic time intervals (1800-1830: 0.58, 0.49 and 0.69; 1900-1930: 0.60, 0.51 and 0.72; median, *1st and 3rd quartile, respectively*) and more than two times higher than the median departure for the RCP 4.5 scenario (0.23, 0.19 and 0.27). Compared to the RCP 4.5 scenario, the departure increased for the RCP 8.5 scenario (0.39, 0.32 and 0.47), but remained lower than the departure values for the historic time intervals (Fig. 2.3, light blue box-plots).

The median departure for the annual mean discharge constantly increased from the historic time interval 1800-1830 to the historic time interval 1900-1930 and to the future scenarios, with its highest values for the future RCP 8.5 scenario (0.13, 0.13 and 0.14: Fig. 2.3, dark blue box-plots). We found the same pattern for the median departure for the annual mean temperature: the highest departure was calculated for the future RCP 8.5 scenario with a median value of 0.94 (0.94 and 0.94, Fig. 2.3, orange box-plots). We found the opposite pattern for the median departure for the annual temperature range. The median departure was highest in the historic time interval 1800-1830 (0.1, 0.1 and 0.1) and lowest for the future RCP 4.5 scenario (0.04, 0.04 and 0.04) and only slightly increased for the future RCP 8.5 scenario (0.06, 0.06 and 0.06, Fig. 2.3, red box-plots).

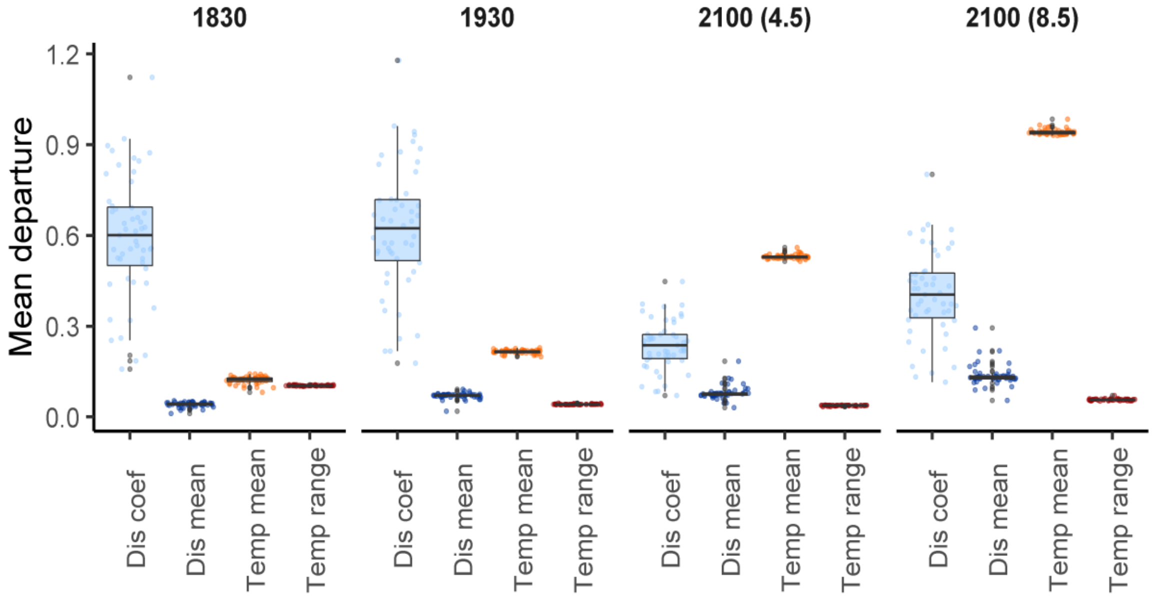


Figure 2.3: Mean departure values for the four environmental predictors used in the CENFA for 48 native fish species in the upper Danube river basin. Departure is always measured as the distance between the current point in time (1970-2000) and the respective time interval or scenario. Dis coef = Coefficient of variance of annual discharge, Dis mean = Mean annual discharge, Temp mean = Mean annual temperature, Temp range = Range of mean monthly temperatures.

Vulnerability

Median vulnerability for all 48 native fish species was lowest for the RCP 4.5 scenario (0.55, 0.51 and 0.66; median, 1st and 3rd quartile, respectively) and almost doubled for the RCP 8.5 scenario (1.02, 0.91 and 1.16; Fig. 2.4). The two historic time intervals ranged in between the future scenarios (distant historic: 0.60, 0.47 and 0.74; near historic: 0.65, 0.52 and 0.79; Fig. 2.4).

The comparison of similarity (Schoeners'D; Warren et al., 2008) between predicted mean vulnerability estimates showed that similarity between scenarios was highest for the historical time intervals (0.99; Fig. 2.5B). The two future scenarios showed a high similarity as well (0.96). Similarity was lowest when comparing any historical time interval with any future scenario (0.88 for both historical scenarios against future RCP 4.5; Fig. 2.5B).

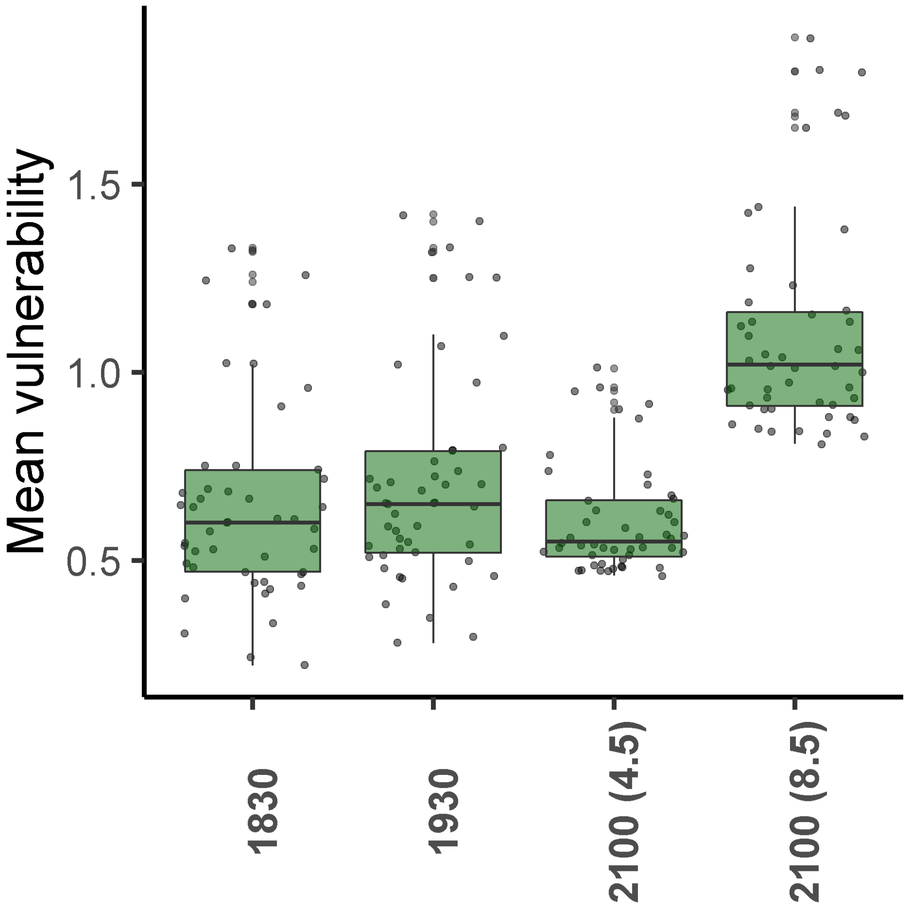
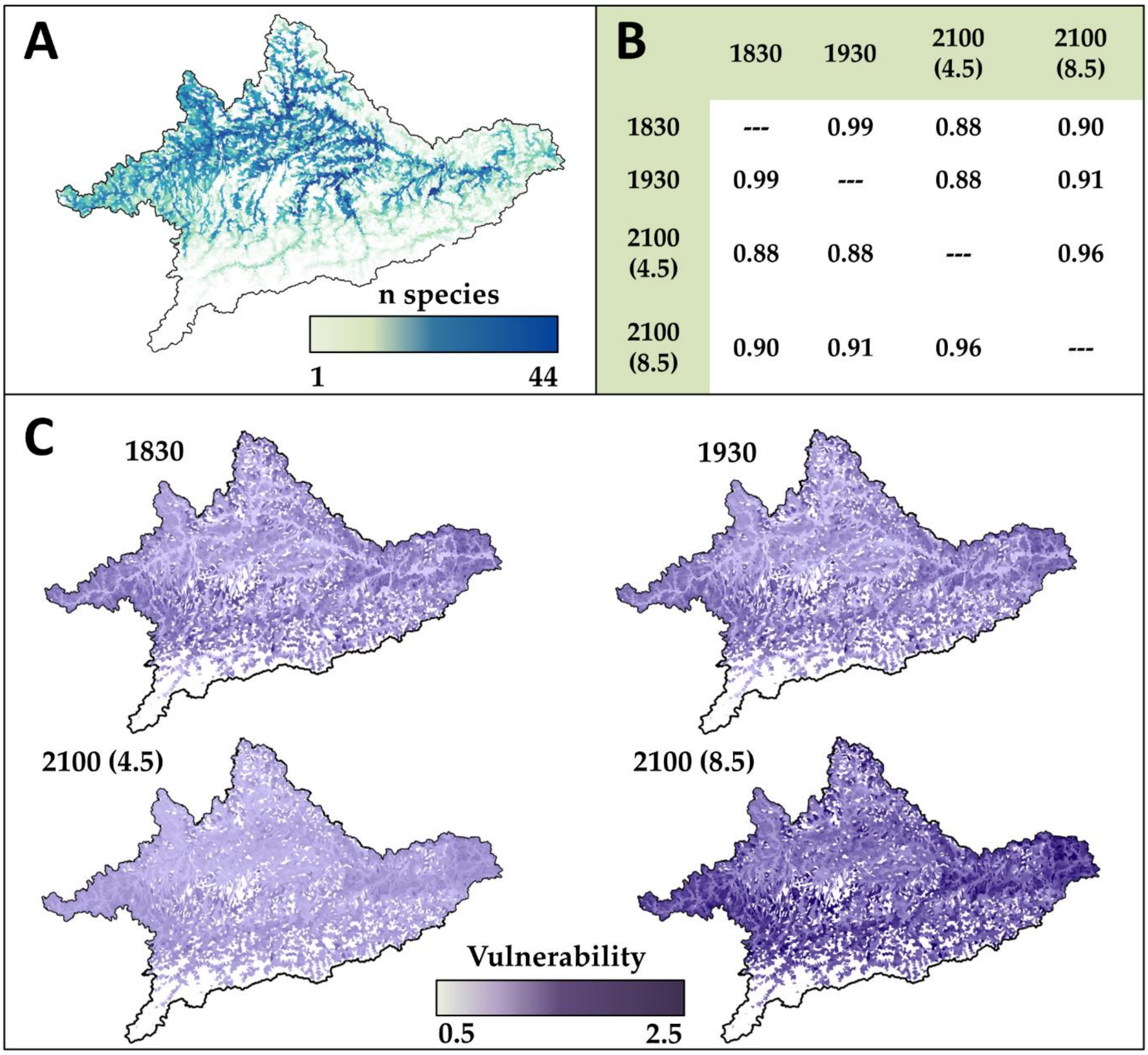


Figure 2.4: Mean vulnerability estimates for 48 native fish species in the upper Danube river basin. Note: The y-axis shows species mean vulnerability which is calculated as the mean value across all sub-basins in the predicted distribution range for each of the 48 species.



B	1830	1930	2100 (4.5)	2100 (8.5)
1830	---	0.99	0.88	0.90
1930	0.99	---	0.88	0.91
2100 (4.5)	0.88	0.88	---	0.96
2100 (8.5)	0.90	0.91	0.96	---

Figure 2.5: A) Number of species predicted to find suitable habitats within a sub-basin. B) Similarity (Schoeners'D; Warren et al., 2008) between predicted vulnerability estimates for the two historic time intervals and the two future scenarios. C) Mean vulnerability for each sub-basin for the two historic time intervals and the two future scenarios, all relative to the present distribution range.

Discussion

In our study we showed that the drivers of species-specific vulnerability shifted in their importance from hydrological predictors in the past to climatic predictors in the future. Resulting vulnerability estimates were in terms of magnitude similar between the historical time intervals and the moderate RCP 4.5 scenario. However, for the more severe RCP 8.5 scenario we identified an almost two-fold increase in vulnerability estimates compared to the RCP 4.5 scenario.

Fish species vulnerability in a historical context

Humans started to regulate the upper Danube river basin as early as at the end of the 16th century (Jungwirth et al., 2014). Flood control measures and improvement of inland navigation, especially for the Austrian Danube river basin, were the main force driving river alteration. By the end of the 19th century, flood control and channelization resulted in a loss of 15% of river length for the German and

Austrian Danube main stem (Jungwirth et al., 2014). Main stem embankment reached its maximum at the beginning of the 20th century. To date, more than 90% of all floodplains have been disconnected along the German part of the Danube (Brunotte et al., 2009), while the shoreline of the upper Danube mainstem is to more than 90% embanked (Jungwirth et al., 2014). Those anthropogenic changes have influenced the seasonal patterns of the discharge regime in the upper Danube river basin with an increase of mean monthly flows in winter months and a decrease in the summer months, whereas the overall mean annual flow remained constant over the last 100 years (Klein et al., 2011). We found that these historically documented habitat alterations did not result in pronounced differences of vulnerability estimates for the analysed fish species for the two historical time intervals (1800-1830 and 1900-1930; Fig. 2.4, Fig. 2.5C). This finding seems contradictory, since the more pristine upper Danube river basin around 1800-1830 was environmentally more distant to the current point in time than the more regulated Danube river basin around 1900-1930. However, flood regulation and river channelization measures during the 19th century were mainly made of wood and, therefore, were not durable against annual ice floods and had to be renewed almost every year (Hohensinner et al., 2013). Therefore, their effect on river discharge regimes was likely low as supported by our results. Those measures did neither affect annual variability in discharge nor monthly discharge, or not in a way that would have been captured by our hydrological predictors with a temporal resolution of a month. Discharge data on a daily resolution could potentially capture a higher variability than our monthly predictors, however, those predictors are currently not available and we can only conclude that the flood regulation and river channelization measures applied in the beginning of the 19th century had a relatively low effect on our vulnerability estimates.

In contrast, we found a pronounced change in hydrological conditions from the current point in time to 1900-1930 mainly caused by a change in the variability of discharge (Fig. 2.3). Interestingly, after channelization was mostly completed at the beginning of the 20th century (at least for the main stem), damming started in many tributaries and in the Danube main stem in the upper Danube river basin (Bettzieche, 2010; Jungwirth et al., 2014; Habersack et al., 2016). To date, countless, mainly small (< 1MW) hydropower plants exist in the upper Danube river basin (Habersack et al., 2016). In the Danube main stem in Germany and Austria more than 70% of the river length is dammed (Jungwirth et al., 2014) and free-flowing river stretches disappeared (Schiemer & Spindler, 1989; Brinker et al., 2018; Duarte et al., 2020). Our predictors and, consequently, our models picked up on those range-wide hydrological changes, resulting in a dramatic decrease in variability of monthly discharge from 1900-1930 to the current point in time. However, model results showed similar average vulnerability estimates for fish species for both historical time intervals and the climate change scenario under RCP 4.5 (Fig. 2.4). This finding leads to the assumption that historical discharge alterations induced by dams have resulted in comparable pressures for native species as future changes under RCP 4.5 will do. Since we found a change in the main driver of vulnerability estimates between 1900-1930 and 2070-2100, i.e. from variability in discharge to mean annual temperature, respectively, we can assume that, ecologically, future climate change will impose a different threat to native fish species than the historical discharge-driven alterations, at least for the moderate RCP 4.5 scenario. Regarding the more extreme RCP 8.5 scenario, which tracks current CO2-emissions best (Schwalm et al., 2020), we observed a pronounced increase in overall vulnerability estimates compared to the two historical time intervals and the RCP 4.5 scenario (Fig. 2.4). This increase was mainly driven by an overall +4 °C increase in mean annual temperature (compared to the current status and a +2 °C mean increase compared to the RCP 4.5; Tab. 1). Interestingly, the variability of monthly discharge returned as an essential driver of vulnerability estimates for RCP 8.5. Hence, our results indicate that future climate change would cause temperature-driven flow alterations comparable to historical anthropogenic alterations. Considering that COSERO does not account for new dams planned to be built, the cause for these discharge alternations are a result of changes in climate and precipitation only. Consequences for the native fish species in the upper Danube river basin under RCP 8.5 would be a significant temperature increase and additional hydrological pressures, similar in magnitude to what they have already experienced historically.

Practical implications

For some organism groups, such as benthic invertebrates (Durance & Ormerod, 2009) or marine fish (Roberts et al., 2017), a reduction of environmental pressures can promote the resilience towards anticipated climate pressures. For instance, Durance and Ormerod (2009) showed that for benthic invertebrate communities in small streams, expected changes in species community due to warming waters over an 18 year period were buffered by a steadily increasing water quality over the same time period. Hence in simple terms, a decrease in one pressure balanced an increase in another pressure. Our results indicate an analogy for the upper Danube river basin and its fish community. The overall environmental distance caused by the reduction of monthly discharge variability is similar to the overall environmental distance that would be expected under future climate change scenarios, which is induced by increased mean annual temperatures.

For the upper Danube river basin only a few species, mainly anadromous sturgeons, went regionally extinct when comparing the current fish community with the community around 1800 (Hensel & Holcík, 1997; Friedrich, 2018). For the sturgeons, this regional extinction is mainly caused by large dams which act as migration barriers and poaching in the lower Danube regions (Jungwirth et al., 2014). For other fish species "only" a pronounced change in relative abundance after damming was observed (Schmutz et al., 2013; Galik et al., 2015). This observation indicates that the historical fish community itself is still present in the upper Danube river basin, an important precondition for effective fish species conservation in river ecosystems (Stoll et al., 2014). To relieve the environmental pressure induced through hydrological alterations, conservation measures such as floodplain rehabilitation have shown to be very effective for fish communities (Roni et al., 2008; Ramler & Keckeis, 2019). In the upper Danube river basin, roughly 25% of the historically available and nowadays unconnected floodplain area has a good potential for rehabilitation measures (Hein et al., 2016). Additionally, in view of the increasing temperature pressure, the upper Danube river basin with its many headwater regions might offer a suitable temperature refuge for sensitive fish species (Isaak et al., 2016).

While our study provides a generally promising outlook, we acknowledge that it is also a result of the "survivorship bias" (Budd & Mann, 2018). Using monitoring data from 1970 to 2016, we excluded species that went already regionally extinct before 1970 from our analyses. Additionally, using only species with more than ten occurrence points, we excluded range-restricted species that are either hard to detect or less abundant (Cruickshank et al., 2016). Furthermore, the species-environment relationship that we have used to model habitat suitability might be incomplete, since species might not reach all suitable habitats due to, i.e. migration barriers. Extinction and low abundance can both be a result of historic discharge alterations. By excluding those species, and the possibility that some species-environment relationships are incomplete, we likely underestimated the effect of historic discharge alterations in the upper Danube river basin.

A conservative approach to reduce uncertainty

In this study, we modelled how native fish species in the upper Danube river basin were affected by historic environmental alterations and how they would be affected by future climate change within their current distribution ranges. We used HSMs to fill monitoring gaps of the current distribution of species, but we did not use them to assess potential changes in their spatial distribution neither historically nor in the future, as it is usually done (Ehrlén & Morris, 2015; Radinger et al., 2017; McMahan et al., 2020). In contrast, we analysed the environmental conditions that drive the habitat suitability of the species at different points in time. We decided to use this more conservative approach, because it is well understood that any prediction based on HSMs comes at the cost of uncertainty, especially when a model is transferred to new environments or time frames (Werkowska et al., 2017; Yates et al., 2018). In this sense, our approach has the advantage that we can be more certain about the expected changes in the future within the current distribution range of a species, at least regarding the predictors we used. Therefore, our results have the potential to provide guidance towards future conservation actions and conservation management (Schuwirth et al., 2019).

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Chapter 3

Systematic conservation planning for native fish species in the upper Danube river basin – Making an existing network fit for climate change

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Abstract

Protected areas (PAs) are considered a cornerstone to protect biodiversity from anthropogenic pressures and, therefore, PAs are considered an important tool to stop the loss of biodiversity. Fresh waters are an especially threatened ecosystem with a more pronounced decline in biodiversity than terrestrial or marine counterparts. Despite this high demand for biodiversity protection, fresh waters are currently often underrepresented in existing PA-networks. Future climate change is predicted to shift current pressures on freshwater biodiversity spatially or cause a general shift in the type of main pressure. However, it remains largely unclear if an existing PA-network can offer effective protection from main environmental pressures for freshwater species. In this study, we used a unique 300 years-time series of modelled and observed river discharge and temperature data, ranging from 1800 to 2100 and including two future climate scenarios (RCP 4.5 and RCP 8.5), to identify spatial or general shifts in main pressures for 48 native fish species in the upper Danube river basin. To identify general patterns according to a species threat status, we grouped species into their IUCN Red List categories. On a sub-basin level with an average size of 8 km^2, we combined habitat suitability models and a climate-niche factor analysis to evaluate the existing PA-network towards its effectiveness to protect native fish species. We amended those analyses by a systematic conservation planning analysis to optimise the existing PA-network towards its ability to protect fish species under future climate conditions. To do so, we adopted existing targets suggested by the European Commission for the worlds' largest network of PAs, Natura 2000. In addition, we used the predicted magnitude of environmental change in each sub-basin as a cost factor. We found that, despite the PA-network covering areas of the Danube river basin that were less impacted by human alterations during the past 200 years compared to non-protected areas, it insufficiently protects fish biodiversity. Our spatial conservation planning revealed that approximately 6000 sub-basins would need to be added to the existing PA-network (approximately 2000 sub-basins) to protect 60% of the distribution range of all threatened fish species and 20% of the distribution range of all non-threatened fish species. For the year 2100, with an expected shift in main pressures from anthropogenic flow alterations to direct climate pressures, we found that the existing network of PAs is exposing species especially to the predicted pressures from climate change. However, our conservation planning exercise for future environmental conditions revealed a high spatial overlap between all planned networks (current and future), indicating that a currently optimised network can also safeguard native fish species under future environmental conditions. Our study showcases, how information derived from a coupling of predictive models, i.e. habitat suitability models and climate niche factor analyses can inform the spatial design of PA-networks to ensure long-term protection of target species under future climate change.

Introduction

Biodiversity is declining globally with one of the most species-rich ecosystems - fresh waters - being especially threatened (Reid et al., 2019; Arthington, 2021). Over the past 50 years, for example, freshwater vertebrates faced an average population decline of 84% (WWF, 2016). Today, roughly one third of all known freshwater species face the threat of extinction, including one third of all known freshwater fish species (Tickner et al., 2020). Under future climate change the pressures on freshwater ecosystems and the species therein are predicted to further increase (Markovic et al., 2017; Reid et al., 2019).

An indispensable cornerstone of biodiversity protection, also for freshwater species, is the designation of protected areas (PA) (Hermoso et al., 2016). However, despite approximately 15% of the world's surface area currently covered by PAs (Maxwell et al., 2020), they have failed so far to stop or even reduce the loss of biodiversity (Pimm et al., 2018) and strong efforts are made to further increase the coverage of PAs globally (Pringle, 2017; Woodley et al., 2019), targeting at least 30% of the planet with an effective and well connected system of PAs by 2030 (CBD, 2021b).

The question when a species is sufficiently protected within a PA-network is an ongoing debate (Noss, 1996; Stoms, 2000; Tear et al., 2005; Di Marco et al., 2016). However, it is well accepted that species with a small population sizes and narrow distribution ranges need to be covered to a higher degree in PA-networks than those with large population sizes and wide distribution ranges and that e.g. International Union for the Conservation of Nature (IUCN) Red List categories can guide such allocations (Rodrigues et al., 2006). For the worlds' largest PA-network, Natura 2000 (Evans, 2012), the European Commission recommended conservation targets for species between 20 and 60% of their distribution range depending on the species ecology, distribution, and population trends (EC, 1997; Evans, 2012), i.e. Red List threat status (IUCN, 2021). For freshwater ecosystems, even Natura 2000 was shown to be ineffective in covering the distribution ranges of target species (Hermoso et al., 2015). This ineffectiveness can largely be attributed to the designation process of PAs in which fresh waters rarely play a central role (Acreman et al., 2019; Abell & Harrison, 2020; WWF, 2020) and, in addition, is often opportunity-driven and biased towards remote areas with low economic value (Joppa & Pfaff, 2009). This combination results in a pronounced underrepresentation of freshwater species within PAs (Abell & Harrison, 2020; Leal et al., 2020).

Future climate change further challenges the effectiveness of PAs globally (Araújo et al., 2011; Alagador et al., 2014; Duffield et al., 2021). PAs might even turn into an environmental trap for species (Bruno et al., 2018). This happens when a species is protected from a specific pressure within a PA, but becomes exposed to a new pressure to which it is especially vulnerable - this has been coined by Bates et al. (2019) as the "conservation paradox". Considering longer time-scales the conservation paradox can occur when main pressures on target species change over time and a static network of PAs, declared to mitigate traditional pressures, turns into an environmental trap. One of the rare examples of the conservation paradox over time has been predicted for marine PAs globally where, currently, the PA network provides good protection for target species but will likely suffer pronounced climate change effects by 2050 (Bruno et al., 2018).

River ecosystems have been altered by humans through history (Schmid, 2014; Macklin & Lewin, 2015; Gregory, 2019), especially in the 19th century (Schmid, 2014), when rivers played a key role for industrial progress (Tvedt, 2010). Water abstraction, damming, canalisation, and river embankment (from here on referred to as traditional pressures) have caused e.g. severe changes in natural flow globally (Nilsson et al., 2005; Döll et al., 2009), a key feature of rivers which is closely linked to the distribution, abundance, and species richness of diverse taxa (Rolls & Bond, 2017; Jumani et al., 2018; Kakouei et al., 2018). However, in recent years direct impacts from climate change (e.g. changes in the amount of precipitation) and the human response to it (e.g. intensified water abstraction for irrigation), have become an additional source of pressures, which are expected to further increase in relevance in the future (Pittock et al., 2008). As an example, Döll & Zhang (2010) showed that more pronounced global flow alterations are expected under future climate change compared to the ones caused in the past by traditional pressures. More specifically they predicted that climate change will lead to an increase in annual average river flows on 50%, and to a decrease on 25% of the global land area, respectively. In contrast, historical flow alterations caused a decrease in annual average river flows on approx. 17% of the global land area only and no increase anywhere. Given a predicted change in spatial distribution and type of environmental pressure, it can be assumed that an existing, static PA-networks may become ineffective, or even more ineffective, in protecting freshwater species in the future.

The main objective of this study was to test this assumption with the example of the upper Danube river basin by assessing the efficiency of the existing PA-network in protecting the native fish fauna (according to their IUCN Red List categories) now and in the future. Specifically, we asked:

1. Does the existing network of PAs within the study area sufficiently protect the distribution range of target fish species?
2. Does the current network of PAs cover areas that will serve as a climate refuge for native fish species under future climate conditions?

We hypothesized (1) that the existing PA-network does not sufficiently protect native fish, because their populations are still declining in the upper Danube river basin (Schletterer et al., 2017; Liška et al., 2021); and (2) that the current PA-network will not be effective in protecting native fish species under future climate change conditions, based on the assumption that the spatial distribution and type of main environmental pressures under future climate change differs from traditional ones (Döll & Zhang, 2010).

Material and Methods

Study region

The study region was the upper Danube river basin from its source in Germany's southwest up to the gauging station close to Vienna, Austria, covering 102,113 km². More than 90% of the upper Danube river basin falls within the borders of Germany and Austria (Fig. 3.1B). Minor parts are located within Switzerland, Italy, and the Czech Republic (Fig. 3.1B). For all analyses the study area was divided into 15.489 sub-basins each of them covering an area of 8 ± 7 km².

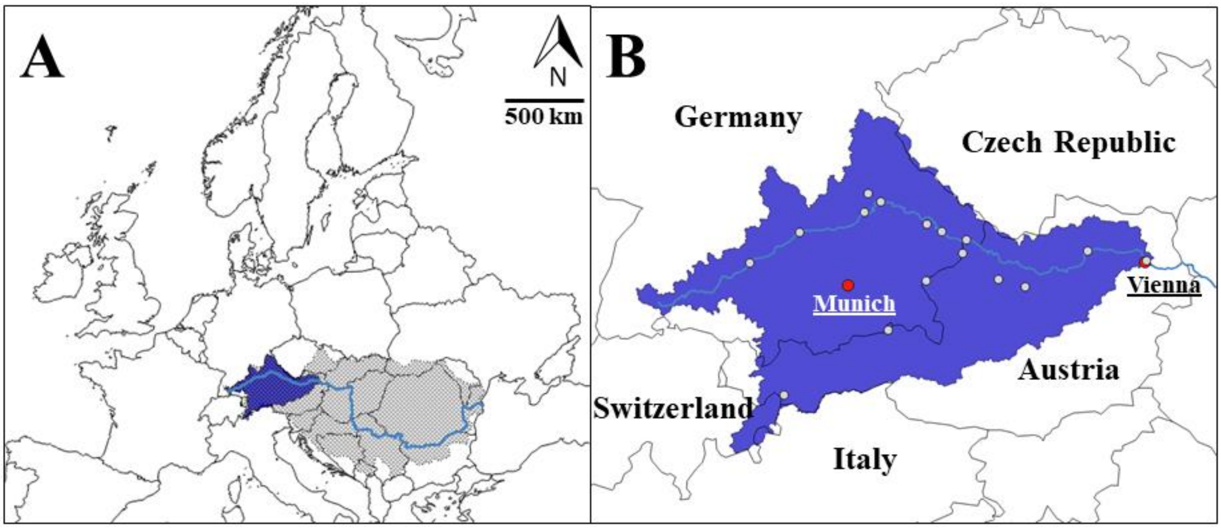

Figure 3.1: Overview of the study area. A) The location of the upper Danube river basin within Europe. The light grey area indicates the whole Danube river basin. In light blue the Danube main stem is shown. Dark blue indicates the study area. B) Study area in detail. Small grey dots show the distribution of the gauging stations we used to extrapolate discharge values for the whole study area (see “Hydrological data” for details).

Fish distribution data

Fish species occurrence data was compiled from four different sources: We compiled data from the two federal states that have a share on the upper Danube river basin, i.e. Baden-Württemberg and Bavaria, who collected the information to conform with the EU Water Framework Directive. For the Austrian part of the upper Danube river basin, we used occurrence data collected during the project “Improvement and Spatial extension of the European Fish Index” (EFI+, Pont et al., 2009). We completed our database with data from the “Fischartenatlas für Deutschland und Österreich” (Brunken et al., 2008), which we filtered for acknowledged sources (e.g. universities, federal ministries etc.) and for species which were already present in the sources from Baden-Württemberg, Bavaria, or EFI+. Regardless of the data source, we only used fish occurrence data collected between 1970 and 2016. We considered each sub-basin with at least one occurrence of a particular species as a sub-basin with said species presence.

Environmental data time-series

Hydrological data

Hydrological and climate data was obtained from the German Federal Institute of Hydrology (BFN) (Kling et al., 2012a). The study area contains 16 gauging stations for which we obtained monthly hydrological data from the precipitation runoff model COSERO for a time interval from 1800 to 2100 (Stanzel & Kling, 2018). COSERO is a well-established and calibrated precipitation runoff model, especially for the upper Danube river basin (for further details and its general performance see Kling et al. (2006); Kling et al. (2015)). Historical discharge simulations from COSERO are based on gridded monthly temperature data and precipitation data available in the HISTALP data base (Auer et al., 2007; Chimani et al., 2013). For future discharge simulations, COSERO uses temperature and precipitation projections based on Regional Climate Models (RCMs) from the EUR-11 ensemble of the EURO-

CORDEX initiative (Jacob et al., 2014). In total we used future discharge simulations based on ten different global-regional climate model (GCM/RCM) combinations (i.e. CERFACS-CNRM-CM5/CCLM4-8-17, EC-EARTH/CCLM4-8-17, HadGEM2-ES/CCLM4-8-17, M-MPI-ESM-LR/CCLM4-8-17, EC-EARTH/RACMO22E, HadGEM2-ES/RACMO22E, EC-EARTH/HIRHAM5, IPSL-CM5A-MR/WRF331F, CERFACS-CNRM-CM5/ALADIN53, M-MPI-ESM-LR r2i1p1/REMO2009) and for the two Representative Concentration Pathways (RCP) (van Vuuren et al., 2011) 4.5 and 8.5 (Stanzel & Kling, 2018). We used a linear model of flow accumulation (number of grid cells contributing to a given stream grid cell based on topography) and the monthly discharge at a given stream grid cell to extrapolate discharge estimates for each sub-basin (see also (Kuemmerlen et al., 2014)). We extracted three 30-year time intervals: (i) ranging from 1800 to 1830 (henceforth called "baseline"), (ii) from 1970 to 2000 (henceforth called "current scenario"), and (iii) ranging from 2070 to 2100. For (iii) we calculated two scenarios based on the RCP 4.5 and 8.5 (henceforth called "future scenario 4.5" and "future scenario 8.5", respectively). For the baseline and each scenario, we calculated the coefficient of variance of monthly discharge and the mean annual discharge for each sub-basin (see Supplementary Table S3.1 for an overview of the raw values). Those variables were later used as predictors for the habitat suitability modelling (HSM; only for the current scenario) (see section on "Habitat suitability modelling") and to calculate sub-basin specific estimates of environmental departures (see section on "Environmental departure") as well as species-specific vulnerabilities (see section on "Species specific vulnerability").

Temperature data

To ensure consistency with the hydrological data, we used the same monthly temperature data that was used for the discharge simulations (i.e. the same historic data and the same RCMs) for our analyses. For the discharge simulations in COSERO, temperature data is downscaled to 61 hydrological response units (HRUs) (Korres & Schneider, 2018) within the study area based on elevation (Kling et al., 2006; Kling et al., 2012a). HRUs are defined as areas with homogeneous soil, land-use, and topographical features (Korres & Schneider, 2018). We used the HRUs to calculate the means and ranges of annual temperatures for each sub-basin for the baseline and the scenarios. As for the hydrological data, those variables were later used for the HSM and to calculate the environmental departure and species-specific vulnerabilities.

Topographical data

We obtained topographical data from the EarthEnv topography dataset (Amatulli et al., 2018), which provides data on a 1 km² resolution, to calculate mean northness and the range of roughness for each sub-basin. We used this data for the habitat suitability modelling (HSM), but excluded it from the departure and vulnerability analyses, since topography is not expected to change over the analysed 300 years' time period.

Habitat suitability modelling

We used a HSM approach to further increase the compiled distribution data's spatial completeness, because or compiled point occurrences cannot depict the full potential distribution of a species on the modelled resolution (Elith & Leathwick, 2009). HSMs are based on the statistical relationship between a species' occurrence and the environmental conditions at the respective location. We built the habitat suitability models with the biomod2 package in R (Thuiller et al., 2009; Core-Team, 2013). We decided to use weighted ensemble models (Marmion et al., 2009) consisting of five algorithms (Artificial Neural Networks, Maximum Entropy, Generalized Linear Model, Generalized Additive Model and Multivariate Adaptive Regression Splines), which are widely applied within the HSM literature (Merow et al., 2014). We only included species which were present in at least ten different sub-basins (van Proosdij et al., 2016b). For all species a fixed value of one-third of all sub-basins was assigned as pseudo-absences. We used the six uncorrelated predictors from three thematic groups, which (Friedrichs-Manthey et al., 2020) found to be suitable for fish distribution modelling in the upper Danube river basin: hydrology - average annual discharge and the coefficient of variance of monthly discharge; climate – mean annual temperature and the annual range of temperature; and topography - average northness and the range of roughness. Before combing all single models (e.g. single algorithms) to the final ensemble models for each species, proportional weights were assigned to each single model. Weights were created using the True Skill Statistic (TSS) (Allouche et al., 2006), ranging from -1 to +1, where zero indicates a model not better than random and +1 a model with perfect fit. Final model evaluation was also done using TSS and additional data splitting. For the data splitting we calculated ten separate model runs, where 70% of the data was used for calibration and 30% for model validation. Finally, we transformed the predicted habitat suitability into presence/absence information (henceforth called predicted distribution rage of a species) using a species-specific cut-off value that minimises the absolute difference between sensitivity (e.g. true positive rate: how well a model depicts the true known presences of a certain species) and specificity (e.g. true negative rate: how well a model depicts the randomly created pseudo-absences). The derived species-specific distribution maps were later used as input for the climate-niche factor analyses and the spatial conservation plans.

Climate-niche factor analyses

We used the CENFA-package in R (Rinnan & Lawler, 2019) to calculate sub basin-specific environmental departures and species-specific vulnerabilities, respectively.

Environmental departures

Environmental departure is a measure of change between historical and future habitat condition within species current distribution ranges (Rinnan & Lawler, 2019). The sub basin-specific values for each predictor, i.e. coefficient of variance of monthly discharge, mean annual discharge, mean annual temperature, and temperature annual range, indicate the degree of environmental change a certain sub-basin has experienced in the past or will experience in the future, with larger values indicating greater environmental departure. The departure estimate is always positive and has no upper limits. In our case, the sub basin-specific environmental departure for the scenarios was calculated as the difference between baseline environmental conditions and the respective scenario. In total, we calculated 21 departure estimates for each species (one for the current scenario plus two future scenarios * 10 global-regional climate model combinations) for each sub-basin in which a species is predicted to find suitable habitat. We used the 21 departure estimates as a direct input for the species-specific vulnerability analyses (see below). For the spatial conservation planning, we used the median of the ten different departure estimates for each predictor for each future scenario, because predictions where highly variable between the ten global-regional climate models (see "Conservation planning exercise").

Species-specific vulnerabilities

Species-specific vulnerability is a measure of how severely a species might become affected by changing environmental conditions within its current distribution range, given the predictors used (Rinnan & Lawler, 2019). To calculate the species-specific vulnerability for each sub-basin in which a species is predicted to occur, the sub basin-specific departure estimates are weighted by species-specific sensitivities. The species-specific sensitivity assumes that a species which tolerates only very specific environmental conditions (i.e. inhabiting a small environmental niche) is more likely to be negatively affected by changing habitat conditions (Rinnan & Lawler, 2019). Following Rinnan and Lawler (2019), sensitivity is calculated as the range of environmental conditions a species tolerates (a corrected specialization vector adapted from the ENFA framework (Hirzel et al., 2002)) with respect to a given environmental predictor. Therefore, the species-specific sensitivity reflects the habitat specialisation of a species, with higher values indicating a smaller environmental niche inhabited by a species. Similar to the departure, the sensitivity estimates are always positive with no upper limits and they have no meaning as a standalone indicator, but can be used to compare species in the same study area. In total we calculated 21 vulnerability estimates combining sensitivity and departure. We used the median of the 10 species-specific vulnerability estimates calculated for the global-regional climate model combinations for each future scenario in each sub-basin. A high species-specific sensitivity (i.e. narrow occupied niche) and a high sub-basin specific departure estimate (i.e. pronounced environmental changes) result in a high vulnerability estimate for a certain species in a sub-basin in which the species is predicted to occur. As with departure and sensitivity, the interpretation of vulnerability estimates is done by comparing vulnerabilities between species, group of species or within species or groups of species for different scenarios within the same study area.

Red List grouping, protection status, and conservation planning

Red List categories

For any analyses of the current protection status and for the spatial conservation planning, we used the IUCN Red List categories, i.e. *regionally extinct*, *critically endangered*, *endangered*, *vulnerable*, *near threatened*, and *least concern* of a species to identify patterns in protection status and vulnerabilities between Red List categories. We used in total three Red Lists, the national Red List from Austria and the two federal Red Lists from Baden-Württemberg and Bavaria, respectively, since one single Red List does not exist for this region. Because of this regionality of those lists, 33 species where assigned to different categories between the specific lists. We combined those lists by using a worst-case approach, meaning that the worst Red List category of a species in any of the three lists was used as the final status for the respective species. As an exception, species that were considered *regionally extinct* in one of the lists were assigned to the *critically endangered* group, because for those species we had knowledge of their occurrence somewhere within the entire study area. In addition, we did not categorise the common carp (*Cyprinus carpio*), because the natural form of this species is probably extinct in the whole study area and the occurrence data we had is rather reflecting the intensity of stocking programs with a strongly domesticated form of this species. Figure 3.2 shows the predicted stacked distribution maps for each Red List category after the HSM.

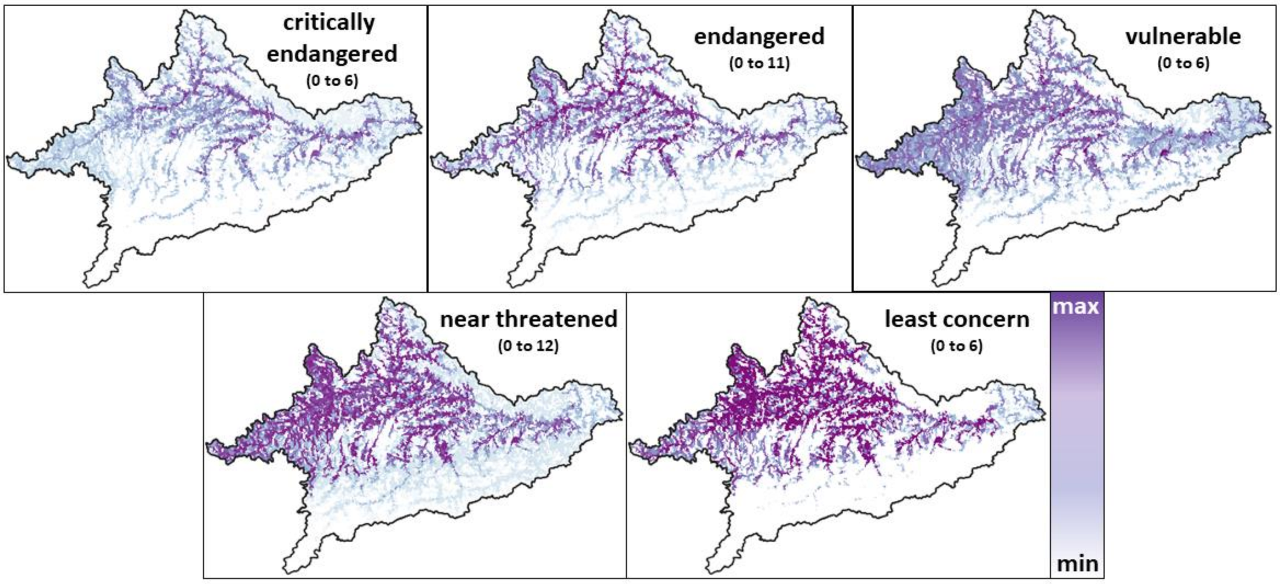

Figure 3.2: Predicted distribution range of species according to the five Red List groups derived from stacked HSMs. Numbers in brackets indicate the minimum and maximum number of species predicted to occur in a sub-basin for a specific IUCN Red List group. The darker the purple colour, the more species of a specific Red List category are predicted to occur in a sub-basin.

Protection status

All data related to PAs were extracted from the World Database on Protected Areas (UNEP-WCMC, 2018). Within the study region a total of 3092 PAs covered a total area of 30,921.7 km² (without overlapping PAs), i.e. 30.2 % of the total study area (see Fig. 3.3A for the existing network of PAs). The data did not allow to distinguish between the target ecosystems (i.e. freshwater or terrestrial). The majority of PAs have been declared around 1990 (mean ± SD: 1989 ± 19 years). The first PA, within a Swiss national Park, was declared in 1914 while the most recent PA was declared in 2019 under the Habitats Directive (Habitats Directive, 1992) in Austria. The median area of a PA was 1 km² (2nd and 3rd quartile: 0.77 and 5.83 km², respectively) with the smallest PA - protecting a pear tree in Austria - covering an area of 3 m² and the largest PA - the countryside conservation area “Bayerischer Wald” in

Germany - covering an area of 2306,5 km². Because the borders of sub-basins do not necessarily overlap with the borders of PAs, we calculated four different protection settings (Fig. 3.3B). In the first setting, each sub-basin covered by any PA, no matter to which extent, was considered as protected, i.e. the least restrictive setting (henceforth called “any PA setting”). In the second setting, only sub-basins covered by more than 50% of their area by PAs were considered as protected (henceforth called “50%-setting”). In the third and fourth protection settings sub-basins with more than 75% and 95% PA-coverage, respectively, were considered as protected (Fig. 3.3C). To answer our fist research question, i.e. how much of a distribution range of a target species is covered by PAs, between Red List categories, we calculated the number of sub-basins considered as protected for each species in a certain Red List category and compared it to the overall number of sub-basins in which this species is predicted to occur. To identify differences in vulnerabilities in the protection settings, we calculated for each species within a Red List group the overall vulnerability, i.e. the mean vulnerability for all sub-basins in which the certain species is predicted to occur, and compared it to mean vulnerabilities when only considering those sub-basins which are considered as protected in the respective protection setting. To answer our second research question, we compared differences in vulnerabilities for each Red List categories for the different protection settings for each scenario. To identify differences in vulnerabilities between the existing PA-network and all planned networks for the different scenarios, we calculated the mean vulnerability for each species within a Red List category only considering those sub-basins in which the species is predicted to occur and which are considered as protected.

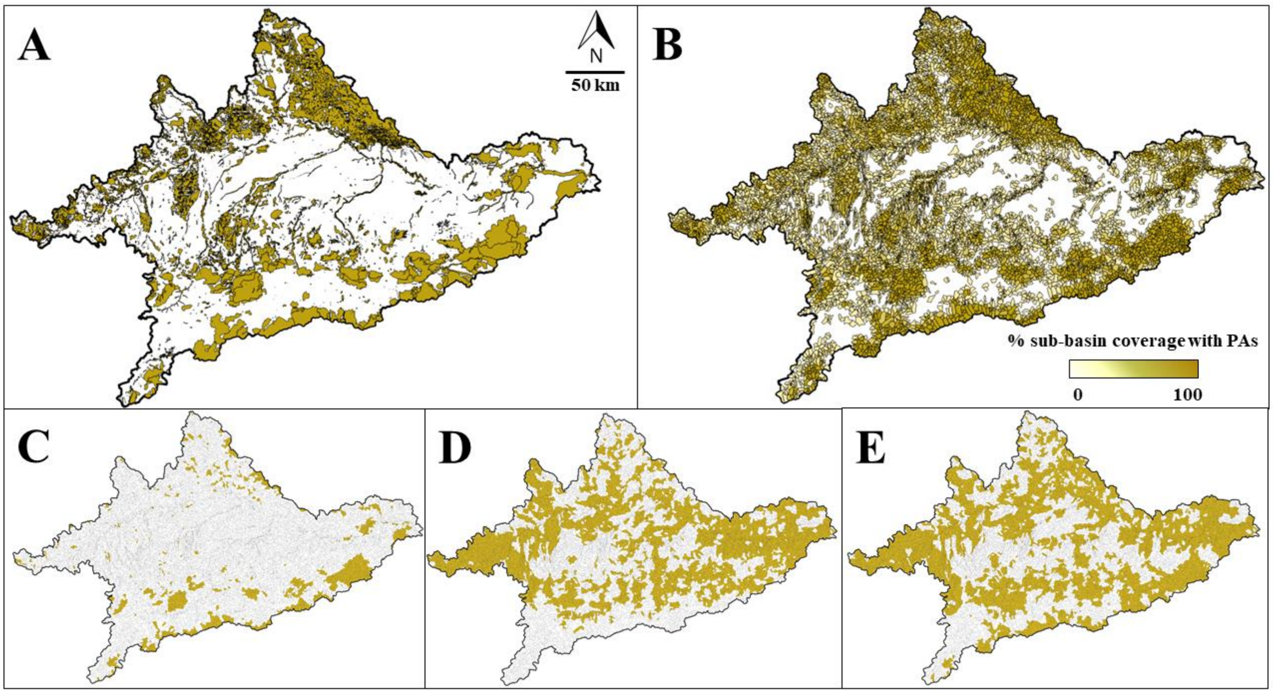

Figure 3.3: Distribution of protected areas (PAs), PA-coverage of sub-basins and spatially optimised PA-networks. A) Distribution of protected areas (PAs) within the study region. B) Coverage of sub-basins with PAs. The darker the yellow, the more area of a single sub-basin is covered with PAs. C) The

distribution of sub-basins covered by more than 95% with PAs, i.e. locked-in sub-basins for the conservation planning analyses. D) Spatially optimised PA-network for the current scenario with no existing PAs locked-in. E) Spatially optimised PA-network for the current scenario with existing PAs locked-in. Note: Due to the high spatial similarity of optimised PA-networks for the three scenarios (Supplementary Table S3.4), only the spatially optimised PA-networks for the current scenario are shown.

Conservation planning analyses

The conservation planning analyses were performed with the Gurobi optimizer 9.1 software (Gurobi-Optimization, 2021) within the R-package “prioritizR” (Hanson et al., 2017). Gurobi employs integer linear programming to find optimal combinations of planning units (i.e. sub-basins in our case) which together meet pre-defined species targets. For our analyses species-specific targets were assigned following the “20-60% guideline”. To do so, we separated the species in two groups, i.e. threatened and non-threatened. The threatened group contains all species that where assigned as critically endangered, endangered, vulnerable, or near threatened in the IUCN Red List (see Supplementary Table S3.2 for species specific groupings). The non-threatened group contained all species that were assigned least concern in the red list grouping. For the threatened group, we set the number of sub-basins that should be included in the planned PA-network for a certain species to 60% of the total number of predicted suitable sub-basins. For the non-threatened group, this target was set to 20%. All needed inputs files were created in base R and followed the structure developed for Marxan (Serra et al., 2020), a widely used conservation planning program (Watts et al., 2017). For further details on the data structure see Supplementary Table S3.5).

We compared the spatial overlap between the existing network and all spatially optimised PA-networks using the ‘modOverlap’ function in the R package fuzzySim (Barbosa, 2015) and calculated Schoeners’D (Warren et al., 2008), which can range from 0 (no overlap) to 1 (total overlap) between each time interval and the two future scenarios.

Results

Habitat suitability modelling

The TSS values for all species ranged between 0.40 for species with >400 initial occurrences (*Salmo trutta*) to 0.99 for species with <20 occurrences (i.e. *Telestes souffia*), indicating a good to very good model performance for all species (Bean et al., 2012) (for species specific values see Supplementary Table S3.2).

Overall vulnerability

We found a general trend of increasing vulnerability for all Red List categories under future climate conditions (Table 3.1). However, this increase was more pronounced for critically endangered species (0.30, 0.86, 1.35 for the current scenario, future scenario 4.5 and future scenario 8.5, respectively) than e.g. for species of least concern (0.44, 0.90, 1.35).

Table 3.1: Median vulnerabilities (first and third quartile) for the groups with different protection status. CR = critically endangered, EN = Endangered, VU = vulnerable, NT = near threatened, LC = least concern.

Group	Current scenario					Future scenario 4.5					Future scenario 8.5				
	all sub-basins	any PA	> 50%	> 75%	> 95%	all sub-basins	any PA	> 50%	> 75%	> 95%	all sub-basins	any PA	> 50%	> 75%	> 95%
CR	0.30 (0.24; 0.48)	0.28 (0.22; 0.47)	0.27 (0.22; 0.46)	0.26 (0.22; 0.46)	0.26 (0.23; 0.44)	0.86 (0.64; 1.01)	0.86 (0.64; 1.02)	0.88 (0.66; 1.02)	0.90 (0.68; 1.05)	0.92 (0.72; 1.11)	1.35 (1.01; 1.53)	1.36 (1.02; 1.53)	1.40 (1.04; 1.57)	1.43 (1.07; 1.62)	1.48 (1.14; 1.68)
EN	0.30 (0.29; 0.38)	0.29 (0.29; 0.37)	0.31 (0.28; 0.36)	0.3 (0.28; 0.35)	0.3 (0.28; 0.33)	0.76 (0.74; 0.86)	0.76 (0.74; 0.88)	0.84 (0.75; 0.92)	0.87 (0.76; 0.94)	0.91 (0.80; 0.98)	1.21 (1.15; 1.33)	1.23 (1.15; 1.35)	1.32 (1.17; 1.44)	1.37 (1.21; 1.48)	1.48 (1.29; 1.56)
VU	0.46 (0.33; 0.8)	0.45 (0.32; 0.78)	0.44 (0.32; 0.78)	0.44 (0.32; 0.78)	0.42 (0.32; 0.79)	0.95 (0.84; 1.42)	0.96 (0.84; 1.46)	1.00 (0.84; 1.48)	1.02 (0.87; 1.51)	1.04 (0.91; 1.53)	1.42 (1.25; 2.07)	1.46 (1.26; 2.14)	1.51 (1.29; 2.16)	1.55 (1.33; 2.18)	1.65 (1.39; 2.24)
NT	0.44 (0.40; 0.68)	0.44 (0.39; 0.68)	0.42 (0.38; 0.70)	0.42 (0.37; 0.70)	0.39 (0.35; 0.74)	0.91 (0.86; 1.17)	0.92 (0.86; 1.17)	0.93 (0.87; 1.16)	0.96 (0.9; 1.17)	1.03 (0.96; 1.22)	1.36 (1.29; 1.68)	1.38 (1.31; 1.7)	1.41 (1.33; 1.67)	1.46 (1.37; 1.68)	1.61 (1.50; 1.78)
LC	0.44 (0.40; 0.47)	0.42 (0.39; 0.46)	0.42 (0.38; 0.45)	0.41 (0.37; 0.45)	0.39 (0.35; 0.43)	0.90 (0.86; 0.96)	0.92 (0.87; 0.97)	0.95 (0.88; 0.98)	0.97 (0.91; 1.02)	1.02 (0.98; 1.1)	1.35 (1.29; 1.42)	1.38 (1.31; 1.44)	1.44 (1.33; 1.48)	1.48 (1.38; 1.53)	1.60 (1.53; 1.71)

The existing PA network

Protection status

In the least strict protection setting ("any PA", where any sub-basin was considered as protected as soon as a PA was present within this sub-basin), 10.083 sub-basins were considered as protected. For the 95%-setting, i.e. sub-basin covered by more than 95% with PAs, 1947 sub-basins were considered as protected. The 50%-setting and the 75%-setting ranged with 4432 and 3118 PAs considered as protected, respectively, in between the two.

We found that the coverage of the predicted species distribution ranges in the "any PA"-setting was above 70% of the total distribution range for all Red List categories (Table 3.1). Coverages decreased drastically with stricter settings to lowest percentages in the 95%-setting ranging from 11.04 ± 5.00 % for critically endangered to 6.94 ± 1.03 % for least concerned species, respectively.

Vulnerabilities within Protected Areas

In all Red List categories, vulnerabilities within the existing network for the current scenario slightly decreased with stricter conservation settings (Table 3.1). For the two future scenarios this effect was reversed, especially for endangered species (e.g. 1.23, 1.48, "any PA" and "95% protection setting" for future scenario 8.5, respectively) but also for near threatened (1.38, 1.61) and least concern (1.38, 1.60) species, we found an increase in vulnerabilities with stricter protection settings. For critically endangered species (1.36, 1.48) the increase was least pronounced.

Table 3.2: Protection status of the IUCN Red List categories. "Category" = Red List category, "all sub-basins" = mean number (± SD) of sub-basins predicted to be suitable for all species within a category, "any PA" = mean number of predicted suitable sub-basins covered by any PA, "> 50%"; "> 75%"; "> 95%" = mean number of sub-basins covered by > 50%, > 75%, and > 95% by PAs, respectively. The "%" column indicates the share of sub-basins predicted to provide habitat for the five Red List categories (CR, EN, VU, NT, LC) and four protection settings (any PA, > 50%, > 75%, and > 95%). CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, LC = least concern.

Category	all sub-basins	any PA	%	> 50%	%	> 75%	%	> 95%	%
CR	2468.4 ± 1264.6	1942.2 ± 916.7	73.06 ± 4.66	786.2 ± 357.4	28.67 ± 5.80	496.6 ± 221.8	18.73 ± 5.04	285.6 ± 139.8	11.04 ± 5.00
EN	3633.8 ± 1321.9	2723.6 ± 903.8	75.66 ± 5.74	1088.5 ± 351.3	29.06 ± 3.53	664.2 ± 209.3	17.55 ± 3.17	366.8 ± 128.9	9.07 ± 3.04
VU	2966.4 ± 2226.4	2173.5 ± 1686.0	70.25 ± 9.00	825.5 ± 627.7	25.78 ± 4.05	499.6 ± 367.2	15.79 ± 3.12	261.5 ± 186.0	8.97 ± 3.50
NT	4766.7 ± 1140.1	3533.3 ± 796.4	73.65 ± 2.45	1372.3 ± 294.4	27.75 ± 1.71	822.5 ± 174.2	16.46 ± 2.48	408.4 ± 88.8	7.76 ± 2.73
LC	4768.3 ± 476.3	3564.3 ± 341.1	73.92 ± 1.48	1384.2 ± 103.1	27.28 ± 1.14	816.0 ± 59.0	15.61 ± 1.03	411.2 ± 35.0	6.94 ± 1.03

Spatial conservation planning

Spatial overlap between PA-networks

The systematically planned PA-networks fulfilled the targets set for all the Red List categories (see Supplementary Table S3.3). In addition, the planned networks fulfilled even a 60% target for species of least concern (i.e. non-threatened species), for which the target was set to 20%. The new networks for the current scenario consisted of 7003 sub-basins, and for the future scenarios 4.5 and 8.5 of 6706 and 6665 sub-basins, respectively (Fig. 3.3D). The amended networks for the current scenario contained 7942 sub-basins, and for the future scenarios 4.5 and 8.5 7767 and 7627 sub-basins, respectively (Fig. 3.3E). The spatial overlap between all new networks in the different scenarios was high with Schoeners' D values of 0.94 or above (Supplementary Table S3.4). We found the same for all amended networks for all scenarios (Table 3). The spatial overlap between the new network and the amended network was 0.72 for the future scenarios 4.5 and 8.5, and 0.74 for the current scenario (Supplementary Table S3.4). In contrast, the spatial overlap between the new networks and the existing network (considering the strict 95% conservation setting) was low with a value of 0.09 for all three scenarios (Supplementary Table S3.4).

Vulnerabilities of Red List categories within spatially optimised PA-networks

Considering the current scenario, vulnerabilities were lowest in the existing PA-network when compared to the new and amended PA-networks, while vulnerabilities between the new PA network, the amended PA network were similar for each Red List category (Fig. 3.2). In both future scenarios the existing PA-network showed the highest vulnerabilities for all Red List categories, which was especially pronounced for the least concern and endangered species, followed by the amended PA-network (Fig. 3.4). New PA-networks consistently led to lowest vulnerabilities for the future scenarios, although the difference to the amended networks was negligible.

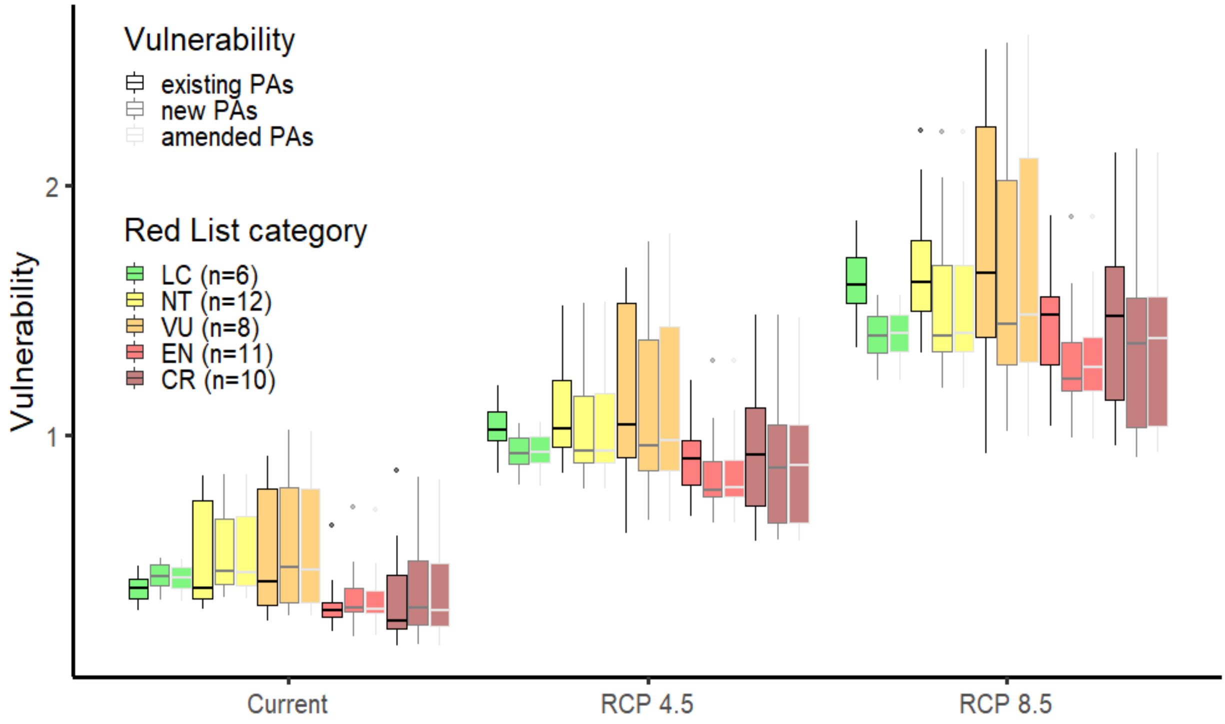

Figure 3.4: Vulnerabilities of Red List categories for the three different PA-networks. Numbers in brackets indicate the number of species for each Red List category. LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered.

Discussion

For all protection settings except the least restrictive one, we showed that the existing PA-network in the upper Danube river basin is insufficiently protecting the distribution range of native fish species. In addition, we found that the existing PA-network is located in areas that, due to climate change, will become subject to impacts on current temperature and precipitation patterns which will increase the vulnerability of all Red List categories. Spatially optimisation of the current PA-network showed that approx. 6000 sub-basins need to be added to the existing approx. 2000 PAs (95% protection setting) to sufficiently protect native fish species in the future.

The existing PA-network

Fish species conservation in river ecosystems needs to be done at the basin or sub-basin scale (Collares-Pereira & Cowx, 2004; Ramler & Keckeis, 2019), because even small disturbances within a sub-basin can lead to a pronounced decline in native fish species richness at the basin level (Weijters et al., 2009; He et al., 2021). In the four protection settings considered, we found that the area of only a small number of sub-basins (< 2000 out of almost 15.000 sub-basins), was covered by > 95% of their area with PAs. We set our conservation targets following the “20-60% guidelines” of Natura 2000 (EC, 1997). The question when a species is sufficiently protected within a PA-network is an ongoing debate (Noss, 1996; Stoms, 2000; Tear et al., 2005; Di Marco et al., 2016). Commonly used protection targets for freshwater fish range from 20% of the distribution range (Convention on Biological Diversity AICHI target 11

(CBD, 2021a)) to 100% for extremely rare or endemic species (Reis et al., 2019). However, even our relatively low targets of 60% of the predicted distribution range of threatened species (please note that we considered all species as threatened except for species categorised as *least concern* according to the IUCN Red List) were only met in our most relaxed conservation setting ("any PA"). Considering that this protection setting includes sub-basins whose area is probably only covered by a very small amount with PAs, and that we included all existing PAs (i.e. also PAs that do not target fresh waters explicitly) in our analyses, this result likely overestimates the protection status of fish species in the upper Danube river basin. Considering the 50% protection setting, the coverage for all Red List categories already decreased to <30% and the 95% protection setting only covered 11% of the distribution range of critically endangered species and less than 10% of the distribution range of all other Red List categories. Based on these results, backed-up by the fact that native fish populations within the upper Danube river basin are still declining (Schletterer et al., 2017; Liška et al., 2021), we conclude that the current network of PAs is not sufficiently protecting native fish species. However, our vulnerability analyses revealed that vulnerabilities for all Red List categories slightly decreased with increasing strictness of the protection setting. This pattern is not unexpected, because the distribution of highly protected sub-basins is biased towards the alpine areas (Fig. 3.3 C). Therefore, those sub-basins can be expected to be less impacted by human alterations due to a lower economic potential of such regions (Joppa & Pfaff, 2009; Pimm et al., 2018).

In contrast, both future scenarios led to an increase in vulnerabilities for all Red List categories with increasing strictness of protection settings. This indicates that the environmental pressures within the current PA-network will change due to the current pressures increasing in severity, shifting spatially or both, or due to a shift in the type of pressure. This change comes with a further decrease in effectiveness of existing PAs. This finding is well in line with recent studies on terrestrial (Elsen et al., 2020; Chacón-Prieto et al., 2021; Duffield et al., 2021) and marine (Bruno et al., 2018; Bates et al., 2019) PAs, which showed that some species will be especially exposed to negative effects from climate change within existing PAs.

We found the strongest increase in vulnerability with increasing strictness of the protection setting under the future scenarios for fish species which are currently considered to be of least concern. This finding is especially noteworthy, because an ongoing analyses of water framework directive fish abundance data for Germany has shown that many species, i.e. roach (*Rutilus rutilus*) or common bream (*Abramis brama*), which were previously assessed as "least concern", showed significant negative population trends over the past 15 years (Friedrichs-Manthey et al., in prep.) Therefore, they likely need special consideration in the nearer future. The expression "Keeping common species common", has only recently gained attention in the field of conservation biology (Walls, 2018; Sterrett et al., 2019), mainly because of pronounced population size declines in common species of other taxa such as macroinvertebrates (Herbst et al., 2019), butterflies (Warren et al., 2021), and birds (Rosenberg et al.,

2019) in recent years. However, a decline in common species seems to be harder to estimate for example by experts, because these species are still common and present in monitoring programs.

Spatial optimisation of current PA-network

Systematic conservation planning as a tool to develop and design networks of PAs that can support species persistence under current and future environmental conditions, has gained attention in freshwater ecosystems in the past decade (Linke et al., 2011) and is nowadays widely applied to inform conservation management (Hermoso et al., 2012; Domisch et al., 2019; Reis et al., 2019). Our conservation planning exercise revealed that in addition to the approx. 2000 highly protected sub-basin, 5600 to 6000 sub-basins (depending on the scenario, but there was a high spatial overlap between all scenarios) need to be protected to ensure a conservation target of 60% of the total distribution range of native threatened fish species, i.e. the Red List categories categorised as threatened, in the upper Danube river basin. Given the “20-60% guidelines”, our amended networks would fulfil the recommendations set by European Commission for the Natura 2000 network (EC, 1997). Although the number of 5600 to 6000 additional sub-basins suggest that further tremendous efforts are needed to protect fish species sufficiently, it is important to consider that we included only the already highly protected sub-basins in our conservation planning exercise. When considering the complete existing network of PAs as a baseline from which further efforts can be taken, approximately 50% of all sub-basins that need to be protected in our amended network for the future scenario 8.5 are already covered by some kind of PA.

The amended networks of highly protected sub-basins cover approximately 52.000 km², slightly more than 50% of the whole study area (102.000 km²). Despite that being much, such networks would follow previously suggested and highly debated conservation goals such as the one set by the Half Earth initiative (Wilson, 2016; Büscher et al., 2017). In contrast to the existing network, an amended PA-network would offer environmental refuge (vulnerabilities within PAs are similar to the overall vulnerability of a certain Red List category) for native fish species in the upper Danube river basin under future climate conditions. In addition, it would even sufficiently protect currently non-threatened species by covering > 60% of their predicted distribution range. This is an especially interesting result considering the observed negative population trends for common fish species in the upper Danube river basin (Liška et al., 2021; Friedrichs-Manthey et.al., in prep.).

Integrated systematic conservation planning

In our study, we showed that an optimised network to protect native fish species under future climate change conditions sufficiently, needs to protect an additional approximately 6000 sub-basins. However, we also show that from these 6000 sub-basins almost 50% are sub-basins, which are covered at least to some part by existing smaller PAs. No matter if those smaller PAs have been declared for freshwater purposes, they built a strong basis for future conservation efforts (Leal et al., 2020). Only recently, Leal et al. (2020) showed that only considering e.g. connectivity (as needed for fresh waters (Hermoso et al., 2012)) in optimised PA-networks for terrestrial taxa, has pronounced benefits for freshwater taxa, without focussing on such explicitly. When freshwater and terrestrial taxa are fully integrated into the optimised PA-network, the gain for freshwater taxa is even higher (600% compared to PA-network only focussing on terrestrial taxa), while the loss for terrestrial taxa is negligible (Leal et al., 2020). Especially in the light of climate change, a growing demand for arable land of a growing human population (Crist et al., 2017), and an increasing limitation in available funds for nature conservation actions (Wilson et al., 2006), integrated systematic conservation planning offers a strong tool to balance those needs and protect biodiversity effectively (Margules & Pressey, 2000).

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General discussion

One of the main cornerstones of biodiversity protection besides legislatives (Kearney et al., 2020), is the declaration of PAs (Acreman et al., 2019). Despite a pronounced increase in global surface area covered by PAs (Maxwell et al., 2020), the loss of global biodiversity has not been reversed or even stopped so far (WWF, 2020). Future climate change is predicted to further increase the pressures on biodiversity, concurrently reducing the effectiveness of terrestrial (Elsen et al., 2020) and marine (Bruno et al., 2018) PAs. What will happen to freshwater PAs is less clear (Floury et al., 2021). This is because conservation actions have so far failed to target fresh waters explicitly (WWF, 2020), e.g. considering the special spatial connectivity with the surrounding landscape for effective conservation (Reis et al., 2019), despite fresh waters are one of the species richest ecosystems (Grosberg et al., 2012), which show a biodiversity decline at a much faster rate compared to terrestrial and marine counterparts (WWF, 2020). To increase the effectiveness of PAs for freshwater ecosystems, there is a need (i) for range-wide information on the distribution of target species on conservation-relevant spatial resolutions (Groves et al., 2002; Nel et al., 2009), because they better inform practical conservation actions (Botts et al., 2019), (ii) to anticipate emerging pressures from climate change on existing PAs (Reid et al., 2019) and (iii) to identify areas of high conservation value, i.e. low pressures and high biodiversity, under future climate conditions (Reid et al., 2019).

The main aim of this thesis was to address the aforementioned needs by means of habitat suitability models and climate niche factor analysis to assess and improve currently existing PAs for 48 native freshwater fish species in the upper Danube river basin. More specifically, I aimed at improving the HSM method, a tool to derive range-wide estimates of target species' potential distributions (Elith & Leathwick, 2009) for river ecosystems by assessing the uncertainties arising from model spatial resolution (**Chapter 1**). Furthermore, based on the results from **Chapter 1** and by using a climate-niche factor analyses (Rinnan & Lawler, 2019), I asked if pronounced changes in main environmental pressures for native fish species within the study area between the past 200 years and the nearer future in 2100 could be identified (**Chapter 2**). Finally, I used the results from **Chapter 1** and **Chapter 2** to assess, (i) if this existing PA-network within the study area is sufficiently protecting native fish species and (ii) if the PA-network will be effective in protecting native fish species in the future to predicted impacts from climate change (**Chapter 3**). Based on this information, I finally ran a spatial conservation planning analysis to identify additional areas of high conservation value to protect native fish species under future climate conditions (**Chapter 3**).

In summary, the application of HSM for native fish species in the upper Danube river basin – using ten different modelled spatial resolutions with otherwise constant model parameters – revealed that model resolution has a pronounced influence on the relative importance of environmental predictors. Parameters related to topography drove predictions at coarse resolutions, climate-related predictors dominated at intermediate resolutions, and at fine resolutions hydrology-related parameters were most important (Fig. 1.4). Thus, I confirmed my first hypothesis (see General Introduction). Predictor importance is a model outcome which is regularly used to inform conservation management (Porfirio et al., 2014) and thus this finding adds valuable knowledge to improve the interpretation of HSM-model outputs in freshwater ecosystems. Furthermore, by correlating species predicted suitability among nested sub-basins at different resolutions, I identified a strong “filter effect" between coarse (average sub-basin size between 201 km² and 714 km²) and intermediate (16 km² to 105 km²) resolutions: a sub-basin which was predicted to be suitable as habitat for a species was at least partly suitable as a habitat for that species at the next finer resolution (Fig. 1.5). At finer model resolutions (below 8 km²) this filter effect disappeared, indicating a tipping point at which the applied set of environmental predictors was not able to further depict the potential distribution of target species. However, although model performance parameters indicated a good model performance at fine resolutions (4 km² and 2 km², Fig. 1.3), predictions based on these resolutions have to be taken with care, because despite having high evaluation scores, the environmental predictors are probably not able to depict fine scaled distribution patterns (Domisch et al., 2013). Consequently, they would have led to biased analyses in Chapters 2 and 3.

Based on the predicted distributions at the finest possible resolution, I identified a shift in environmental pressures on native fish species in the upper Danube river basin between 1800, and 2100 (Fig. 2.3). Based on model parameterization, in the past 200 years fish species were mainly impacted by flow alterations, i.e. a decrease in variance of monthly discharge. These results are corroborated by numerous studies focusing on anthropogenic impacts on the upper Danube river basin (Jungwirth et al., 2014; Haidvogl et al., 2015; Schletterer et al., 2017; Friedrich, 2018; Haidvogl et al., 2019). For example, for the Danube mainstem, Jungwirth et al. (2014) described in detail how anthropogenic impacts on natural flow regimes, such as canalisation and damming, have increased in the 19th century and have gained intensity over the course of the industrialisation in Germany and Austria. For smaller tributaries, severe impacts such as damming, have started later at the end of the 19th century, mainly because the amount of harvestable energy was much lower compared to the Danube river main stem (Winiwarter et al., 2013). Under future climate-change scenarios, the mean annual temperature within the study area was predicted to increase by an average of approximately 2°C to 4°C (RCP 4.5 and 8.5, respectively) and native fish species were predicted to be mainly impacted by this increase in mean annual temperature. Although future climate change is also predicted to cause flow alterations due to e.g. changes in the distribution and amount of precipitation, the impacts of such changes are predicted to be less pronounced in the upper Danube river basin compared to middle or lower river reaches (Stagl & Hattermann, 2016). However, an increase in relevance of direct impacts from climate change, i.e. rising temperatures (Pittock et al., 2008) are widely acknowledged being one of the main threats to global freshwater biodiversity (Reid et al., 2019). Especially freshwater fish will be negatively affected, facing a predicted extinction risk of almost 50% during the coming decades (Manjarrés-Hernández et al., 2021). For

Europe, climate change is predicted to cause a loss of over 40% of suitable habitat for common fish species and a total loss of suitable habitat for some rare fish species (Markovic et al., 2014). In addition to the finding that the main pressures on native fish species within the study area will change in the 80 years, I also showed that sub-basins, which have been especially exposed to hydrological alterations in the past, are not necessarily the same that will be exposed to the most severe impacts in the future (Fig. 2.5) confirming my second hypothesis (see General Introduction). Such a shift in the spatial distribution of areas exposed to environmental pressures over time has not been shown before for freshwater ecosystems. However, such knowledge is of utmost importance for assessing the effectiveness of existing PA-networks under future climate change scenarios (**Chapter 3**).

The question at what point a target species is sufficiently protected within a PA-network, is an ongoing debate (Noss, 1996; Stoms, 2000; Tear et al., 2005; Di Marco et al., 2016). However, it is well accepted that species with a higher threat status, i.e. species populations with small sizes and narrow distribution ranges, need to be covered to a higher degree by PAs than those with a lower threat status, i.e. that have large population sizes and wide distribution ranges (Rodrigues et al., 2006). During the implementation of the worlds' largest PA-network, i.e. Natura 2000 (Evans, 2012), the "20-60% guideline" was proposed (EC, 1997). This guideline states that, depending on a target species' ecology, distribution, and population trend, 20% to 60% of its total distribution range should be covered with PAs (Evans, 2012). Using this guideline as a target, I found that the existing PA-network within the study area is far from being sufficient to protect distribution ranges of native fish species. This was due to the fact that even for species with high conservation priorities, i.e. categorised as *critically endangered* by IUCN (IUCN, 2021), on average only 11% of their distribution range was covered by PAs (only considering sub-basins whose areas were covered by more than 95% with PAs) (Tab. 3.2). For all other species, this coverage was below 10%. In addition to the insufficient protection status, I showed that within the existing PA-network, native fish species will be especially exposed to predicted pressures under future climate change scenarios. Therefore, I confirmed my third hypothesis (see General Introduction). I found this effect for all analysed species, but especially pronounced, i.e. low variability between species, for the six fish species categorised as *least concern*. Those are common species with large distribution ranges. This is noteworthy, because an ongoing analysis of fish abundance data for German rivers over the past 15 years showed a significant population decline for common species, such as bream (*Abramis brama*) and roach (*Rutilus rutilus*) (Friedrichs-Manthey et al., in prep.). These findings go hand in hand with studies for other taxa, such as macroinvertebrates (Herbst et al., 2019), butterflies (Warren et al., 2021), and birds (Rosenberg et al., 2019), which found common species to suffer the most dramatic declines in recent years compared to rarer species. Those pronounced declines indicate that common species need special attention in conservation actions in the coming decades to "keep common species common" (Sterrett et al., 2019; Walls, 2018). These findings are supported by my results, which showed that the existing PA-network is inappropriate to protect native fish species, especially common fish species, from impacts predicted for future climate change.

The systematic conservation planning analyses revealed that to increase the effectiveness of the existing PA-network according to the 20-60%-guideline, approximately 6000 sub-basins need to be protected in addition to the currently protected sub-basins (approximately 2000 out of 15.000 in total; for the scenario in which I only considered sub basins as protected which were covered >95% by PAs). Such an amended PA-network will guarantee a sufficient protection of distribution range of all threatened fish species, i.e. *critically endangered*, *endangered*, *vulnerable*, and *near threatened* IUCN Red List categories. In addition, it will also protect 60% of the distribution range of non-threatened, i.e. least concern, fish species (Supplementary Table S3.3). Moreover, because I used the magnitude of predicted climate change-induced habitat alterations (**Chapter 2**) in each sub-basin as a cost factor, the amended PA-network will be located in areas that experience the lowest habitat alterations in the future (Fig. 3.4). Consequently, such an amended PA-network will support species persistence into the future. Despite these encouraging results, their implementation into practical implementation is challenging (Adams et al., 2019), which is sometimes referred to as the “implementation crisis” (Knight et al., 2006). Only recently strategic frameworks have been proposed to bridge theory and practice (Adams et al., 2019). However, the few cases which incorporated systematic conservation planning into a practical conservation process showed positive outcomes for the acceptance of conservation measures by local stakeholders and biodiversity protection (Margules & Pressey, 2000; McIntosh et al., 2018).

Outlook

Nature conservation efforts compete with the growing demands of a growing human population (Crist et al., 2017), consequently becoming increasingly resource-limited (Wilson et al., 2006). Systematic conservation planning offers an effective tool to achieve conservation goals under circumstances of limited resources, e.g. space or funds (Margules & Pressey, 2000). Systematic conservation planning has been applied in terrestrial (Lessmann et al., 2014), marine (Álvarez-Romero et al., 2018), and freshwater (Reis et al., 2019) ecosystems and to a wide range of species (Hermoso et al., 2012; Lin et al., 2020; Combes et al., 2021). However, the full potential of systematic conservation planning as a tool to stop or even reverse the decline in biodiversity has yet to be unlocked (McIntosh et al., 2018). I see two future avenues to do so:

1) Foster the use of predictive models:

In my thesis I showed that predictive models are a promising tool to inform systematic conservation planning analyses aiming at increasing the effectiveness of existing PA-networks under future climate change scenarios. However, several challenges remain to make predictive models a widely used tool for systematic conservation planning (Schuwirth et al., 2019). One of the most prominent challenges is the quantification of uncertainties in model outputs (Nel et al., 2009; Schuwirth et al., 2019). In addition to the natural stochasticity in biological systems, all models are prone to uncertainties (Muscatello et al., 2021). In **Chapter 1**, I demonstrated the strong effects of spatial resolutions on the outputs of HSM. Similar uncertainties can arise from e.g. threshold selection to transform predicted probabilities into presence/absence information (Cao et al., 2013; Muscatello et al., 2021), bias correction (Muscatello et al., 2021), or the choice of environmental predictors (Pliscoff et al., 2014; Fourcade et al., 2018; Muscatello et al., 2021). For example, Pliscoff et al. (2014) showed that the choice of environmental predictors has a direct impact on predicted extinction risk of modelled species. Uncertainties in predicted species characteristics which are relevant for conservation planning, e.g. extinction risk, need careful quantification (Schuwirth et al., 2019), because they can influence conservation actions (Rodrigues et al., 2006). Of course, uncertainties could be quantified using systematic approaches, e.g. changing model resolution systematically (Chapter 1) (Connor et al., 2018) or systematically testing the effects of different predictor combinations (Pliscoff et al., 2014; Fourcade et al., 2018), but they are often time-consuming and not feasible. This is especially true for more complex settings with large number of predictors and species. In addition, other modelling frameworks, such as Bayesian frameworks (Gelman & Shalizi, 2013), offer a promising avenue for practical applications (Domisch et al., 2019). Bayesian statistics have gained importance in ecological research in the past decade (Touchon & McCoy, 2016) due to some important differences to frequentist statistics. For example, with a Bayesian framework it is possible to assign intermediate probabilities to hypotheses (Anderson, 1998), an important feature when quantifying uncertainties. Furthermore, they 2can be informed by “prior beliefs”, i.e. a quantitative statement of prior knowledge (Anderson, 1998). “Prior beliefs” can be derived from any source of information, e.g. from previous scientific studies, grey literature, or from expert knowledge. Such “prior beliefs” have been shown to significantly increase the precision of predicted distribution ranges of e.g. birds (Niamir et al., 2011) or freshwater mussels (Feng et al., 2019) Consequently, using species distribution ranges predicted based on prior beliefs leads to reduced (spatial) uncertainties in a subsequent systematic conservation planning analysis.

2) Foster integrated approaches:

Firstly, an integration of species and ecosystems is needed. More than 1 Million species globally are threatened with extinction and all types of natural ecosystems are heavily pressurized by humans (WWF, 2020). Consequently, systematic conservation planning has to happen across taxa and ecosystems to optimise how available resources are spent for biodiversity protection in general. For example, a recent study by Leal et al. (2020) showed that a conservation planning analysis focussing only on terrestrial species and their demands had little effect on freshwater biodiversity protection. In contrast, the benefits for freshwater species were doubled, only by including connectivity which is a pivotal parameter in freshwater PA-networks (Hermoso et al., 2012). An integrated approach, i.e. one that accounts for terrestrial and freshwater species simultaneously, yielded an increase in benefits for freshwater species by 600% while benefits for terrestrial species were only reduced by 1%.

Second, systematic conservation planning needs to be integrated into practical conservation planning processes (Botts et al., 2019). Such an integration starts with the replacement of artificial planning units (e.g. sub-basins) by planning units that are relevant for administrative purposes (e.g. property boundaries). In addition, systematic conservation planning needs to move away from being a mainly academic exercise to a much greater involvement of implementing agencies and stakeholders that will be affected by, or need to support, conservation plans and actions (Botts et al., 2019; Keeley et al., 2019). „Buy-in“ from the community and transparent planning processes are crucial for a practical implementation of designed PA-networks (Keeley et al., 2019).

In conclusion, the results of my thesis significantly contribute to the endeavour to protect freshwater biodiversity under future climate change scenarios. I demonstrated the feasibility of combining habitat suitability models with a climate niche factor analysis to identify areas that will be especially suffer from predicted impacts of climate change and I showed how such predictions can inform a conservation planning analysis. The results of the conservation planning analysis can directly inform the amendment of the existing PA-network in the upper Danube river basin to effectively protect native fish species from future climate change impacts.

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Appendices

Appendix A: Supporting information for Chapter 1

Supplementary Table S1.1: All 50 native species modeled and the number of occurrences and proportion of sub-catchments with known occurrences (in brackets) for eachspatial resolution. T. = Threshold

Species	**T. 102400**	**T. 51200**	**T. 25600**	**T. 12800**	**T. 6400**	**T. 3200**	**T. 1600**	**T. 800**	**T. 400**	**T. 200**
Abramis brama	135 (0.23)	215 (0.19)	283 (0.14)	385 (0.09)	477 (0.07)	566 (0.04)	648 (0.03)	704 (0.02)	758 (0.01)	800 (<0.01)
Alburnoides bipunctatus	135 (0.23)	220 (0.19)	296 (0.14)	373 (0.09)	460 (0.06)	532 (0.04)	618 (0.02)	698 (0.01)	756 (0.01)	814 (0.01)
Alburnus alburnus	147 (0.24)	245 (0.22)	327 (0.16)	428 (0.10)	536 (0.08)	641 (0.05)	755 (0.03)	839 (0.02)	915 (0.01)	965 (0.01)
Aspius aspius	85 (0.14)	118 (0.10)	139 (0.07)	171 (0.04)	192 (0.03)	207 (0.02)	218 (0.01)	225 (<0.01)	235 (<0.01)	240 (<0.01)
Ballerus sapa	31 (0.05)	36 (0.03)	39 (0.02)	44 (0.01)	48 (0.01)	50 (<0.01)	51 (<0.01)	52 (<0.01)	55 (<0.01)	56 (<0.01)
Barbatula barbatula	165 (0.27)	308 (0.27)	471 (0.23)	691 (0.16)	951 (0.13)	1239 (0.09)	1477 (0.06)	1693 (0.04)	1846 (0.02)	1988 (0.02)
Barbus balcanicus	20 (0.03)	31 (0.03)	37 (0.02)	42 (0.01)	51 (0.01)	59 (<0.01)	74 (<0.01)	79 (<0.01)	80 (<0.01)	85 (<0.01)
Barbus barbus	161 (0.27)	277 (0.25)	377 (0.18)	509 (0.12)	619 (0.09)	721 (0.05)	836 (0.03)	939 (0.02)	1029 (0.01)	1110 (0.01)
Blicca bjoerkna	85 (0.14)	119 (0.11)	146 (0.07)	191 (0.05)	222 (0.03)	254 (0.02)	289 (0.01)	303 (0.01)	319 (<0.01)	328 (<0.01)
Carassius auratus	62 (0.10)	75 (0.07)	92 (0.04)	119 (0.03)	129 (0.02)	142 (0.01)	156 (0.01)	164 (<0.01)	176 (<0.01)	180 (<0.01)
Carassius carassius	114 (0.19)	163 (0.14)	197 (0.10)	247 (0.06)	287 (0.04)	328 (0.02)	363 (0.01)	386 (0.01)	405 (<0.01)	418 (<0.01)
Carassius gibelio	124 (0.21)	203 (0.18)	251 (0.12)	320 (0.08)	372 (0.05)	404 (0.03)	434 (0.02)	447 (0.01)	461 (0.01)	474 (0.01)
Chondrostoma nasus	153 (0.26)	243 (0.22)	327 (0.16)	429 (0.10)	509 (0.07)	577 (0.04)	647 (0.03)	706 (0.02)	760 (0.01)	798 (0.01)

Cobitis elongatoides	45 (0.08)	70 (0.06)	82 (0.04)	93 (0.02)	107 (0.01)	121 (0.01)	129 (0.01)	137 (<0.01)	144 (<0.01)	148 (<0.01)
Cobitis taenia	62 (0.10)	82 (0.07)	112 (0.05)	173 (0.04)	225 (0.03)	279 (0.02)	325 (0.01)	376 (0.01)	414 (<0.01)	447 (<0.01)
Cottus gobio	197 (0.33)	339 (0.30)	534 (0.26)	853 (0.20)	1201 (0.17)	1577 (0.12)	1958 (0.08)	2267 (0.05)	2558 (0.03)	2774 (0.03)
Ctenopharyngodon idella	30 (0.05)	33 (0.03)	33 (0.02)	33 (0.01)	33 (<0.01)	34 (<0.01)	34 (<0.01)	34 (<0.01)	35 (<0.01)	36 (<0.01)
Cyprinus carpio	184 (0.31)	282 (0.25)	379 (0.18)	538 (0.13)	632 (0.09)	734 (0.06)	837 (0.03)	901 (0.02)	965 (0.01)	1008 (0.01)
Esox lucius	202 (0.34)	327 (0.29)	470 (0.23)	667 (0.16)	880 (0.12)	1105 (0.08)	1305 (0.05)	1479 (0.03)	1624 (0.02)	1732 (0.02)
Eudontomyzon mariae	32 (0.05)	42 (0.04)	59 (0.03)	73 (0.02)	80 (0.01)	98 (0.01)	111 (<0.01)	117 (<0.01)	122 (<0.01)	124 (<0.01)
Gobio obtusirostris	201 (0.34)	350 (0.31)	530 (0.26)	775 (0.18)	1044 (0.15)	1339 (0.10)	1598 (0.06)	1812 (0.04)	1968 (0.02)	2126 (0.02)
Gymnocephalus baloni	21 (0.04)	23 (0.02)	27 (0.01)	36 (0.01)	37 (0.01)	40 (<0.01)	40 (<0.01)	41 (<0.01)	43 (<0.01)	43 (<0.01)
Gymnocephalus cernua	77 (0.13)	97 (0.09)	111 (0.05)	143 (0.03)	160 (0.02)	170 (0.01)	178 (0.01)	185 (<0.01)	190 (<0.01)	191 (<0.01)
Gymnocephalus schraetser	27 (0.05)	31 (0.03)	33 (0.02)	37 (0.01)	39 (0.01)	41 (<0.01)	42 (<0.01)	43 (<0.01)	45 (<0.01)	45 (<0.01)
Hucho hucho	64 (0.11)	79 (0.07)	105 (0.05)	121 (0.03)	149 (0.02)	163 (0.01)	183 (0.01)	197 (<0.01)	209 (<0.01)	219 (<0.01)
Lampetra planeri	53 (0.09)	80 (0.07)	110 (0.05)	133 (0.03)	160 (0.02)	171 (0.01)	182 (0.01)	193 (<0.01)	198 (<0.01)	203 (<0.01)
Leucaspius delineatus	42 (0.07)	61 (0.05)	70 (0.03)	91 (0.02)	106 (0.01)	118 (0.01)	122 (<0.01)	129 (<0.01)	131 (<0.01)	135 (<0.01)
Leuciscus idus	90 (0.15)	135 (0.12)	171 (0.08)	220 (0.05)	254 (0.04)	279 (0.02)	302 (0.01)	318 (0.01)	335 (<0.01)	345 (<0.01)
Leuciscus leuciscus	150 (0.25)	268 (0.24)	389 (0.19)	551 (0.13)	729 (0.10)	908 (0.07)	1054 (0.04)	1186 (0.03)	1286 (0.01)	1366 (0.01)
Lota lota	129 (0.22)	189 (0.17)	249 (0.12)	333 (0.08)	409 (0.06)	469 (0.04)	506 (0.02)	539 (0.01)	568 (0.01)	591 (0.01)
Misgurnus fossilis	33 (0.06)	41 (0.04)	47 (0.02)	52 (0.01)	55 (0.01)	63 (<0.01)	71 (<0.01)	76 (<0.01)	82 (<0.01)	89 (<0.01)
Perca fluviatilis	204	349	502	716	927	1152	1345	1489	1603	1692

	(0.34)	(0.31)	(0.24)	(0.17)	(0.13)	(0.09)	(0.05)	(0.03)	(0.02)	(0.02)
Phoxinus phoxinus	156 (0.26)	265 (0.23)	374 (0.18)	539 (0.13)	670 (0.09)	810 (0.06)	946 (0.04)	1078 (0.02)	1194 (0.01)	1293 (0.01)
Rhodeus amarus	112 (0.19)	182 (0.16)	237 (0.12)	308 (0.07)	365 (0.05)	418 (0.03)	464 (0.02)	501 (0.01)	528 (0.01)	555 (0.01)
Romanogobio kesslerii	16 (0.03)	22 (0.02)	24 (0.01)	24 (0.01)	27 (<0.01)	29 (<0.01)	32 (<0.01)	33 (<0.01)	36 (<0.01)	38 (<0.01)
Romanogobio vladykovi	63 (0.11)	82 (0.07)	95 (0.05)	110 (0.03)	123 (0.02)	133 (0.01)	140 (0.01)	147 (<0.01)	155 (<0.01)	156 (<0.01)
Rutilus meidingeri	18 (0.03)	27 (0.02)	29 (0.01)	31 (0.01)	38 (0.01)	42 (<0.01)	43 (<0.01)	45 (<0.01)	49 (<0.01)	51 (<0.01)
Rutilus rutilus	180 (0.30)	318 (0.28)	481 (0.23)	726 (0.17)	955 (0.13)	1213 (0.09)	1438 (0.06)	1624 (0.03)	1776 (0.02)	1901 (0.02)
Rutilus virgo	15 (0.03)	21 (0.02)	24 (0.01)	29 (0.01)	31 (<0.01)	33 (<0.01)	40 (<0.01)	40 (<0.01)	42 (<0.01)	45 (<0.01)
Salmo trutta	186 (0.31)	359 (0.32)	614 (0.30)	1041 (0.25)	1585 (0.22)	2266 (0.17)	2963 (0.12)	3479 (0.07)	3964 (0.05)	4359 (0.05)
Sander lucioperca	99 (0.17)	149 (0.13)	189 (0.09)	242 (0.06)	274 (0.04)	304 (0.02)	338 (0.01)	353 (0.01)	372 (<0.01)	386 (<0.01)
Sander volgensis	6 (0.01)	7 (0.01)	8 (<0.01)	8 (<0.01)	9 (<0.01)	9 (<0.01)	9 (<0.01)	9 (<0.01)	9 (<0.01)	9 (<0.01)
Scardinius erythrophthalmus	184 (0.31)	280 (0.25)	375 (0.18)	526 (0.13)	653 (0.09)	771 (0.06)	890 (0.04)	974 (0.02)	1048 (0.01)	1088 (0.01)
Silurus glanis	116 (0.19)	158 (0.14)	193 (0.09)	239 (0.06)	268 (0.04)	298 (0.02)	322 (0.01)	334 (0.01)	348 (<0.01)	360 (<0.01)
Squalius cephalus	67 (0.11)	104 (0.09)	159 (0.08)	242 (0.06)	332 (0.05)	431 (0.03)	522 (0.02)	610 (0.01)	667 (0.01)	719 (0.01)
Telestes souffia	31 (0.05)	40 (0.04)	52 (0.03)	65 (0.02)	76 (0.01)	85 (0.01)	95 (<0.01)	99 (<0.01)	107 (<0.01)	116 (<0.01)
Tinca tinca	183 (0.31)	285 (0.25)	393 (0.19)	571 (0.14)	723 (0.10)	887 (0.07)	1037 (0.04)	1148 (0.02)	1245 (0.01)	1319 (0.01)
Vimba vimba	62 (0.10)	80 (0.07)	99 (0.05)	109 (0.03)	126 (0.02)	135 (0.01)	145 (0.01)	151 (<0.01)	159 (<0.01)	161 (<0.01)
Zingel streber	36 (0.06)	46 (0.04)	57 (0.03)	67 (0.02)	73 (0.01)	77 (0.01)	83 (<0.01)	87 (<0.01)	92 (<0.01)	93 (<0.01)
Zingel zingel	25 (0.04)	29 (0.03)	35 (0.02)	41 (0.01)	45 (0.01)	46 (<0.01)	48 (<0.01)	50 (<0.01)	54 (<0.01)	54 (<0.01)

Supplementary Table S1.2: Overview of variables used to model the distribution of fish species in the Upper Danube catchment. We show the full set of variables, the ones which were not correlated and the final set of variables used in the models. temp. = temperature, dis. = discharge, mtl. = monthly.

Initial Variable	**Not correlated**	**Used in the models**	**Category**	**Source**
Annual average temp.	+	+	climate	BIOCLIM
Average diurnal range			climate	BIOCLIM
Temp. seasonality			climate	BIOCLIM
Maximum temp. of warmest month			climate	BIOCLIM
Temperature annual range	+	+	climate	BIOCLIM
Average temp. of wettest quarter	+		climate	BIOCLIM
Average temp. of driest quarter	+		climate	BIOCLIM
Average temp. of warmest quarter			climate	BIOCLIM
Average temp. of coldest quarter			climate	BIOCLIM
Average area covered by forest	+	+	land use	HILDA
Average area covered by grassland	+		land use	HILDA
Average area covered by settlement	+	+	land use	HILDA
Average area covered by water	+		land use	HILDA
Average area covered by other land	+		land use	HILDA
Average roughness			topography	EarthEnv
Range roughness	+	+	topography	EarthEnv
Average eastness	+		topography	EarthEnv
Range eastness			topography	EarthEnv
Average northness	+	+	topography	EarthEnv
Range northness			topography	EarthEnv
Average slope			topography	EarthEnv
Range slope			topography	EarthEnv
Average annual dis.	+	+	hydrology	BfG
Coefficient of variance of mtl. dis.	+	+	hydrology	BfG

Appendix B: Supporting information for Chapter 2

Supplementary Table S2.1: Details on the number of initial occurrences, the number of sub-basins considered as suitable for a species after the HSM, the TSS value for the ensemble model, the mean (± standard deviation) sensitivity value, and mean (± standard deviation) vulnerability estimates for the three time intervals and two future scenarios for all 48 modelled native fish species.

Species	Occurrences	n sub-basins after HSM	TSS (ensemble)	Mean sensitivity	1830 mean vulnerability	1930 mean vulnerability	RCP 4.5 mean vulnerability	RCP 8.5 mean vulnerability
Abramis brama	526	5302	0.54	0.67 ± 0.34	0.48 ± 0.19	0.51 ± 0.19	0.47 ± 0.11	0.85 ± 0.20
Alburnoides bipunctatus	480	5411	0.53	0.65 ± 0.31	0.47 ± 0.17	0.50 ± 0.17	0.48 ± 0.11	0.84 ± 0.20
Alburnus alburnus	637	6419	0.54	0.68 ± 0.37	0.53 ± 0.20	0.56 ± 0.20	0.48 ± 0.13	0.87 ± 0.23
Alburnus mento	11	248	0.99	2.27 ± 1.12	1.26 ± 0.34	1.32 ± 0.37	0.96 ± 0.02	1.80 ± 0.41
Aspius aspius	154	3697	0.64	0.95 ± 0.48	0.33 ± 0.13	0.38 ± 0.13	0.53 ± 0.16	0.95 ± 0.24
Ballerus sapa	45	2615	0.88	0.90 ± 0.60	0.22 ± 0.11	0.28 ± 0.12	0.53 ± 0.16	0.93 ± 0.28
Barbatula barbatula	1037	6841	0.47	1.99 ± 1.20	1.18 ± 0.31	1.25 ± 0.33	0.90 ± 0.20	1.68 ± 0.38
Babus barbus	674	5286	0.54	0.65 ± 0.29	0.40 ± 0.15	0.43 ± 0.15	0.46 ± 0.10	0.81 ± 0.18
Blicca bjoerkna	251	5303	0.62	0.94 ± 0.59	0.60 ± 0.24	0.65 ± 0.24	0.56 ± 0.16	1.02 ± 0.28
Carassius carassius	129	5638	0.62	0.98 ± 0.53	0.75 ± 0.25	0.80 ± 0.26	0.60 ± 0.14	1.12 ± 0.27
Carassius gibelio	232	6338	0.56	0.85 ± 0.53	0.68 ± 0.25	0.72 ± 0.26	0.56 ± 0.16	1.03 ± 0.29
Chondrostoma nasus	479	5377	0.55	0.69 ± 0.32	0.42 ± 0.16	0.45 ± 0.16	0.47 ± 0.11	0.84 ± 0.20
Cobitis elongatoides	32	1924	0.87	1.84 ± 1.30	1.24 ± 0.38	1.33 ± 0.4	0.92 ± 0.26	1.69 ± 0.46
Cottus gobio	1401	6397	0.46	1.94 ± 0.94	1.18 ± 0.34	1.25 ± 0.35	0.88 ± 0.18	1.65 ± 0.35
Cyprinus carpio	550	5876	0.56	0.76 ± 0.41	0.61 ± 0.22	0.65 ± 0.22	0.53 ± 0.13	0.97 ± 0.24
Esox lucius	900	5540	0.52	0.68 ± 0.34	0.52 ± 0.19	0.55 ± 0.19	0.48 ± 0.11	0.88 ± 0.19
Eudontomyzon mariae	17	656	0.97	0.64 ± 0.25	0.43 ± 0.15	0.46 ± 0.14	0.48 ± 0.08	0.86 ± 0.15
Gasterosteus aculeatus	566	5379	0.57	0.78 ± 0.35	0.65 ± 0.24	0.70 ± 0.25	0.54 ± 0.11	1.01 ± 0.22
Gobio gobio	1037	5735	0.52	1.04 ± 0.63	0.75 ± 0.24	0.79 ± 0.25	0.62 ± 0.16	1.13 ± 0.30
Gymnocephalus baloni	33	2494	0.85	1.05 ± 0.75	0.58 ± 0.28	0.65 ± 0.28	0.63 ± 0.18	1.15 ± 0.31
Gymnocephalus cernua	120	6322	0.61	0.84 ± 0.54	0.66 ± 0.24	0.71 ± 0.25	0.57 ± 0.16	1.06 ± 0.29
Gymnocephalus schraetser	38	2488	0.88	1.29 ± 0.64	0.53 ± 0.28	0.59 ± 0.28	0.66 ± 0.15	1.16 ± 0.20
Hucho hucho	126	3715	0.65	0.87 ± 0.39	0.31 ± 0.13	0.35 ± 0.13	0.51 ± 0.10	0.92 ± 0.18

Lampetra planeri	68	3700	0.77	1.44 ± 0.84	1.02 ± 0.27	1.07 ± 0.28	0.78 ± 0.18	1.44 ± 0.34
Leucaspius delineatus	105	4355	0.74	1.37 ± 0.85	0.96 ± 0.28	1.02 ± 0.30	0.73 ± 0.17	1.38 ± 0.33
Leuciscus idus	252	6035	0.59	0.77 ± 0.47	0.54 ± 0.20	0.58 ± 0.20	0.52 ± 0.15	0.93 ± 0.26
Leuciscus leuciscus	866	5309	0.55	0.77 ± 0.42	0.58 ± 0.20	0.62 ± 0.20	0.53 ± 0.13	0.95 ± 0.23
Lota lota	409	6375	0.51	0.62 ± 0.36	0.49 ± 0.17	0.52 ± 0.18	0.47 ± 0.11	0.84 ± 0.20
Misgurnus fossilis	48	3108	0.80	1.16 ± 0.55	1.02 ± 0.26	1.10 ± 0.26	0.74 ± 0.12	1.42 ± 0.22
Perca fluviatilis	905	6727	0.48	0.73 ± 0.41	0.61 ± 0.19	0.65 ± 0.20	0.53 ± 0.12	0.96 ± 0.22
Phoxinus phoxinus	685	7585	0.47	2.56 ± 1.32	1.32 ± 0.39	1.40 ± 0.41	1.01 ± 0.21	1.89 ± 0.41
Proterorhinus marmoratus	40	1284	0.91	1.33 ± 0.81	0.46 ± 0.26	0.53 ± 0.27	0.63 ± 0.17	1.13 ± 0.30
Rhodeus amarus	314	5673	0.62	0.80 ± 0.49	0.60 ± 0.24	0.64 ± 0.24	0.53 ± 0.15	0.96 ± 0.27
Romanogobio vladykovi	99	5493	0.69	1.20 ± 0.67	0.74 ± 0.33	0.79 ± 0.33	0.66 ± 0.18	1.19 ± 0.32
Rutilus meidingeri	37	2575	0.79	0.72 ± 0.28	0.47 ± 0.21	0.51 ± 0.21	0.52 ± 0.10	0.91 ± 0.19
Rutilus rutilus	1131	6241	0.49	0.85 ± 0.51	0.68 ± 0.21	0.72 ± 0.22	0.56 ± 0.14	1.04 ± 0.26
Salmo trutta	2249	9168	0.40	2.23 ± 1.18	1.33 ± 0.39	1.42 ± 0.41	0.95 ± 0.20	1.80 ± 0.39
Salvelinus umbla	30	2765	0.85	1.02 ± 0.52	0.91 ± 0.26	0.97 ± 0.27	0.67 ± 0.16	1.28 ± 0.30
Sander lucioperca	242	6282	0.57	0.68 ± 0.37	0.55 ± 0.21	0.59 ± 0.22	0.49 ± 0.13	0.90 ± 0.23
Scardinius erythrophthalmus	437	5765	0.56	0.80 ± 0.43	0.66 ± 0.23	0.70 ± 0.24	0.55 ± 0.13	1.02 ± 0.25
Silurus glanis	179	6868	0.58	0.74 ± 0.37	0.64 ± 0.24	0.69 ± 0.24	0.54 ± 0.12	1.00 ± 0.24
Squalius cephalus	1463	5981	0.49	0.97 ± 0.57	0.72 ± 0.22	0.76 ± 0.23	0.60 ± 0.15	1.10 ± 0.27
Telestes souffia	18	347	0.99	0.82 ± 0.32	0.24 ± 0.13	0.30 ± 0.13	0.50 ± 0.10	0.90 ± 0.19
Thymallus thymallus	860	5718	0.58	0.78 ± 0.41	0.51 ± 0.17	0.54 ± 0.17	0.51 ± 0.11	0.91 ± 0.20
Tinca tinca	636	5042	0.52	0.87 ± 0.50	0.69 ± 0.22	0.74 ± 0.23	0.57 ± 0.13	1.05 ± 0.25
Vimba vimba	115	5067	0.64	1.01 ± 0.74	0.64 ± 0.31	0.69 ± 0.31	0.59 ± 0.18	1.06 ± 0.33
Zingel streber	56	2844	0.78	0.76 ± 0.28	0.41 ± 0.24	0.46 ± 0.24	0.49 ± 0.10	0.88 ± 0.19
Zingel zingel	30	1275	0.94	1.66 ± 0.63	0.44 ± 0.34	0.54 ± 0.35	0.70 ± 0.13	1.23 ± 0.25

Appendix C: Supporting information for Chapter 3

Supplementary Table S3.1: Summary of predictor values (mean, median, highest and lowest value) for each time-interval/scenario.

Time interval	Predictor	Mean (± sd)	Median (1st and 3rd quartile)	Highest value	Lowest value
1800 - 1830	CoV of monthly discharge	2.23 (0.93)	2.70 (1.62; 2.98)	3.06	0.25
	Mean annual discharge (m^3/s)	322.31 (747.03)	67.7 (61.60; 120.93)	3251.50	8.28
	Temperature annual range (°C)	25.99 (2.64)	26.57 (26.11; 27.33)	28.37	3.31
	Mean annual temperature (°C)	6.69 (2.04)	7.13 (6.72; 7.79)	8.52	-3.01
1970 - 2000	CoV of monthly discharge	1.45 (0.55)	1.74 (1.13; 1.87)	1.91	0.21
	Mean annual discharge (m^3/s)	337.35 (741.17)	85.40 (79.50; 137.73)	3276.10	10.50
	Temperature annual range (°C)	24.73 (2.63)	25.30 (24.89; 26.13)	27.10	3.16
	Mean annual temperature (°C)	7.13 (2.03)	7.67 (7.04; 8.29)	8.78	-2.56
2070 - 2100 RCP 4.5	CoV of monthly discharge	1.29 (0.50)	1.55 (0.99; 1.68)	1.72	0.20
	Mean annual discharge (m^3/s)	332.30 (741.58)	80.40 (74.50; 132.36)	3266.20	9.88
	Temperature annual range (°C)	25.20 (2.58)	25.77 (25.27; 26.62)	27.52	3.21
	Mean annual temperature (°C)	9.03 (2.04)	9.51 (8.97; 10.20)	10.82	-0.44
2070 - 2100 RCP 8.5	CoV of monthly discharge	1.51 (0.67)	1.84 (0.98; 2.06)	2.13	0.22
	Mean annual discharge (m^3/s)	314.92 (741.35)	64.30 (58.70; 113.26)	3273.40	7.87
	Temperature annual range (°C)	25.20 (2.53)	25.87 (25.22; 26.56)	27.62	3.23
	Mean annual temperature (°C)	10.58 (1.92)	11.02 (10.56; 11.65)	12.35	0.95

Supplementary Table S3.2: Details on the number of initial occurrences, the number of sub-basins considered as inhabited by a species after the the HSM, the TSS value for the ensemble model, the mean (± standard deviation) sensitivity value, and mean (± standard deviation) vulnerability estimates for the two future scenarios (2100; RCP 4.5 and RCP 8.5) for all 48 modelled native fish species.

Species	Occ.	n sub-basins after HSM	TSS	RCP 4.5 mean vulnerability	RCP 8.5 mean vulnerability	Red List category	Target (n sub-basins)
Abramis brama	526	5302	0.54	0.47 ± 0.11	0.85 ± 0.20	least concern	839
Alburnoides bipunctatus	480	5411	0.53	0.48 ± 0.11	0.84 ± 0.20	endangered	2557
Alburnus alburnus	637	6419	0.54	0.48 ± 0.13	0.87 ± 0.23	near threatened	3034
Alburnus mento	11	248	0.99	0.96 ± 0.02	1.80 ± 0.41	vulnerable	118
Aspius aspius	154	3697	0.64	0.53 ± 0.16	0.95 ± 0.24	critically endangered	1715
Ballerus sapa	45	2615	0.88	0.53 ± 0.16	0.93 ± 0.28	endangered	1171
Barbatula barbatula	1037	6841	0.47	0.90 ± 0.20	1.68 ± 0.38	near threatened	3249
Babus barbus	674	5286	0.54	0.46 ± 0.10	0.81 ± 0.18	vulnerable	2485
Blicca bjoerkna	251	5303	0.62	0.56 ± 0.16	1.02 ± 0.28	least concern	840
Carassius carassius	129	5638	0.62	0.60 ± 0.14	1.12 ± 0.27	critically endangered	2708
Carassius gibelio	232	6338	0.56	0.56 ± 0.16	1.03 ± 0.29	least concern	1008
Chondrostoma nasus	479	5377	0.55	0.47 ± 0.11	0.84 ± 0.20	endangered	2521
Cobitis elongatoides	32	1924	0.87	0.92 ± 0.26	1.69 ± 0.46	vulnerable	911
Cottus gobio	1401	6397	0.46	0.88 ± 0.18	1.65 ± 0.35	near threatened	3059

Cyprinus carpio	550	5876	0.56	0.53 ± 0.13	0.97 ± 0.24	NA	NA
Esox lucius	900	5540	0.52	0.48 ± 0.11	0.88 ± 0.19	near threatened	2650
Eudontomyzon mariae	17	656	0.97	0.48 ± 0.08	0.86 ± 0.15	vulnerable	302
Gasterosteus aculeatus	566	5379	0.57	0.54 ± 0.11	1.01 ± 0.22	near threatened	2590
Gobio gobio	1037	5735	0.52	0.62 ± 0.16	1.13 ± 0.30	near threatened	2756
Gymnocephalus baloni	33	2494	0.85	0.63 ± 0.18	1.15 ± 0.31	vulnerable	1161
Gymnocephalus cernua	120	6322	0.61	0.57 ± 0.16	1.06 ± 0.29	near threatened	2989
Gymnocephalus schraetser	38	2488	0.88	0.66 ± 0.15	1.16 ± 0.20	extinct	1162
Hucho hucho	126	3715	0.65	0.51 ± 0.10	0.92 ± 0.18	critically endangered	1731
Lampetra planeri	68	3700	0.77	0.78 ± 0.18	1.44 ± 0.34	critically endangered	1738
Leucaspius delineatus	105	4355	0.74	0.73 ± 0.17	1.38 ± 0.33	endangered	2084
Leuciscus idus	252	6035	0.59	0.52 ± 0.15	0.93 ± 0.26	endangered	2818
Leuciscus leuciscus	866	5309	0.55	0.53 ± 0.13	0.95 ± 0.23	near threatened	2554
Lota lota	409	6375	0.51	0.47 ± 0.11	0.84 ± 0.20	endangered	3012
Misgurnus fossilis	48	3108	0.80	0.74 ± 0.12	1.42 ± 0.22	critically endangered	1492
Perca fluviatilis	905	6727	0.48	0.53 ± 0.12	0.96 ± 0.22	least concern	1077
Phoxinus phoxinus	685	7585	0.47	1.01 ± 0.21	1.89 ± 0.41	vulnerable	3610
Proterorhinus marmoratus	40	1284	0.91	0.63 ± 0.17	1.13 ± 0.30	endangered	194
Rhodeus amarus	314	5673	0.62	0.53 ± 0.15	0.96 ± 0.27	endangered	2713

Romanogobio vladykovi	99	5493	0.69	0.66 ± 0.18	1.19 ± 0.32	endangered	2537
Rutilus meidingeri	37	2575	0.79	0.52 ± 0.10	0.91 ± 0.19	critically endangered	1169
Rutilus rutilus	1131	6241	0.49	0.56 ± 0.14	1.04 ± 0.26	least concern	1002
Salmo trutta	2249	9168	0.40	0.95 ± 0.20	1.80 ± 0.39	near threatened	4385
Salvelinus umbla	30	2765	0.85	0.67 ± 0.16	1.28 ± 0.30	near threatened	1327
Sander lucioperca	242	6282	0.57	0.49 ± 0.13	0.90 ± 0.23	near threatened	2944
Scardinius erythrophthalmus	437	5765	0.56	0.55 ± 0.13	1.02 ± 0.25	near threatened	2784
Silurus glanis	179	6868	0.58	0.54 ± 0.12	1.00 ± 0.24	vulnerable	3257
Squalius cephalus	1463	5981	0.49	0.60 ± 0.15	1.10 ± 0.27	least concern	960
Telestes souffia	18	347	0.99	0.50 ± 0.10	0.90 ± 0.19	critically endangered	146
Thymallus thymallus	860	5718	0.58	0.51 ± 0.11	0.91 ± 0.20	endangered	2644
Tinca tinca	636	5042	0.52	0.57 ± 0.13	1.05 ± 0.25	vulnerable	2395
Vimba vimba	115	5067	0.64	0.59 ± 0.18	1.06 ± 0.33	extinct	2344
Zingel streber	56	2844	0.78	0.49 ± 0.10	0.88 ± 0.19	endangered	1332
Zingel zingel	30	1275	0.94	0.70 ± 0.13	1.23 ± 0.25	extinct	605

Supplementary Table S3.3: Protection status, i.e. percentage of total distribution range covered, for the Red List groups in the existing network of PAs and the new and amended networks for the three scenarios.

Group	Existing network	New network current	Amended network current	New network RCP 4.5	Amended network RCP 4.5	New network RCP 8.5	Amended network RCP 8.5
CR	11.04 ± 4.97	67.81 ± 4.15	68.40 ± 6.14	64.05 ± 4.97	66.78 ± 4.52	63.76 ± 5.11	64.86 ± 3.95
EN	9.07 ± 3.04	64.94 ± 3.13	67.37 ± 4.96	62.15 ± 3.10	65.80 ± 4.43	62.13 ± 3.04	64.42 ± 4.10
VU	8.97 ± 3.59	69.83 ± 7.10	66.84 ± 4.57	66.79 ± 7.29	65.40 ± 3.23	66.54 ± 7.50	64.26 ± 3.34
NT	7.76 ± 2.73	63.67 ± 2.42	63.88 ± 2.65	62.28 ± 2.12	63.07 ± 2.32	62.26 ± 2.10	62.36 ± 2.15
LC	6.94 ± 1.03	62.67 ± 1.45	63.21 ± 0.97	60.92 ± 1.82	62.20 ± 1.07	60.94 ± 1.79	61.30 ± 1.33

Supplementary Table S3.4: Spatial overlap, i.e. Schoeners' D values, calculated for the current and planned networks of protected areas for all three scenarios.

	Existing Network	New network current	Amended network current	New network RCP 4.5	Amended network RCP 4.5	New network RCP 8.5	Amended network RCP 8.5
Existing Network	1	0.09	0.25	0.09	0.25	0.09	0.26
New network current	0.09	1	0.74	0.95	0.74	0.94	0.73
Amended network current	0.25	0.74	1	0.71	0.97	0.71	0.95
New network RCP 4.5	0.09	0.95	0.71	1	0.72	0.99	0.72
Amended network RCP 4.5	0.25	0.74	0.97	0.72	1	0.72	0.97
New network RCP 8.5	0.09	0.94	0.71	0.99	0.72	1	0.72
Amended network RCP 8.5	0.26	0.73	0.95	0.72	0.97	0.72	1

Supplementary Table S3.5: Description of Marxan input files

File	Description
input.dat	The input.dat-file holds the information whether a planning unit, i.e. sub-basin in our case, is protected or not protected as well as the cost for including it in a PA-network. We defined the cost for each sub-basin for each scenario as the sum of the departure values of the four environmental predictors used. We based this type of cost definition on the assumption that a higher departure in any of the environmental predictors indicates a higher degree of environmental change and, therefore, a larger effort (i.e. cost) to protect a target species within the respective sub-basin. For sub-basins in which no species was predicted to find suitable habitat and, therefore, no departure value was available, we set a 100x higher cost to discourage Gurobi from adding this sub-basin to the PA-network. We calculated two spatially optimised PA-networks for each scenario; one with no sub-basins locked-in (henceforth called "new" networks) and one with all sub-basins considered protected in the 95% protection setting locked-in to force Gurobi to include them in the spatially optimised networks (henceforth called "amended" network).
spec.dat	The spec.dat-file lists the conservation targets for each species, i.e. the number of sub-basins in which a species is present that should be included in the final network. To assign targets for each species, we separated the species in two groups, i.e. threatened and non-threatened. The threatened group contains all species that where assigned as critically endangered, endangered, vulnerable, or near threatened in the IUCN Red List (see Supplementary Table S2 for species specific groupings). The non-threatened group contained all species that were assigned least concern in the red list grouping. For the threatened group, we set the number of sub-basins that should be included in the planned PA-network for a certain species to 60% of the total number of predicted suitable sub-basins. For the non-threatened group, this target was set to 20%. These targets are recommended for species protection in the Natura 2000 network, i.e. "20-60% guidelines" (EC, 1997) (Evans, 2012).
puvspr.dat	The puvspr.dat-file lists species occurrences in each sub-basin. Input data for the puvspr.dat-file were generated from presence-absence maps for each species which were derived from HSM. Thereby, the amount of species occurring in a sub-basin was set to 1 if the HSM predicted an occurrence for the respective species in this sub-basin. As we did not model changes in species distributions, the spec.dat file was the same for all scenarios.
bound.dat	The bound.dat-file lists shared boundaries and their length between sub-basins. Connectivity has shown to be a key feature for any conservation planning exercise (Hermoso et al., 2012). We used the underlying stream network from which the sub-basins where extracted (for details on that procedure see Friedrichs-Manthey et al. (2020)) and identified, for each sub-basin, the next-upstream and the next-downstream sub-basin(s), respectively. For the identified sub-basins, we calculated the length of the shared boundaries. By doing so, we ensured that within the spatially optimised PA-network the connectivity between connected sub-basins was considered. The BLM controls the spatial compactness and, therefore, balances the spatial optimisation process between a non-connected but relatively cheap network (low BLM) and a very compact, dense, and more expensive network (high BLM). We calibrated the BLM based on the current scenario and no locked-in sub-basins (Serra et al., 2020) at 24. We kept this value constant for all planned conservation networks to ensure comparability.

Author Contributions

Chapter 1

From topography to hydrology - the modifiable area unit problem impacts freshwater species distribution models

Martin Friedrichs-Manthey, Simone D. Langhans, Thomas Hein, Florian Borgwardt, Harald Kling, Sonja C. Jähnig, Sami Domisch (2011). Ecology and Evolution 10(6)

SD, SCJ, SDL and MF-M conceived the research; MF-M and SD did the modelling; all authors drafted and commented on the manuscript. SCJ and SD contributed equally.

Chapter 2

300 years of change for native fish species in the upper Danube river basin – historical flow alterations versus future climate change

Martin Friedrichs-Manthey, Simone D. Langhans, Florian Borgwardt, Thomas Hein, Harald Kling, Philipp Stanzel, Sonja C. Jähnig, Sami Domisch. Submitted to Diversity and Distributions

SD, SCJ, SDL and MF-M conceived the research; MF-M did the analysis; all authors drafted the manuscript. SCJ and SD contributed equally.

Chapter 3

Systematic conservation planning for native fish species in the upper Danube river basin – Making an existing network fit for climate change

Martin Friedrichs-Manthey, Sonja C. Jähnig, Florian Borgwardt, Thomas Hein, Harald Kling, Philipp Stanzel, Sami Domisch, Simone D. Langhans. To be submitted

SD, SCJ, SDL and MF-M conceived the research; MF-M did the analysis; all authors drafted the manuscript. SDL and SD contributed equally.

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Statement of academic integrity

I hereby certify that the submitted thesis "*Distribution and vulnerability models to improve conservation efforts for fish species under climate change*" is my own work, and that all published or other sources of material consulted in its preparation have been indicated. All collaboration that has taken place with other researchers is indicated and I have clearly stated my own personal share in those investigations in the Author Contributions. I confirm that this work has not been submitted to any other university or examining body for a comparable academic award.

Berlin, 24th October 2021 Martin Friedrichs-Manthey

List of publications

1. Jähnig, S.C., Baranov, V., Altermatt, F., Cranston, P., **Friedrichs-Manthey, M.**, … & Domisch, S. (2021) Revisiting global trends in freshwater insect biodiversity. *WIREs Water*, 8:e1506. https://doi.org/10.1002/wat2.1506

2. **Friedrichs-Manthey, M.**, Langhans, S. D., Hein, T., Borgwardt, F., Kling, H., Jähnig, S. C.*, & Domisch, S.* (2020). From topography to hydrology—The modifiable area unit problem impacts freshwater species distribution models. *Ecology and evolution*, *10*(6), 2956-2968. https://doi.org/10.1002/ece3.6110

3. **Friedrichs-Manthey, M.**, Langhans, S.D., Hein, T., Borgwardt, F., Kling, H., Jähnig, S.C.* & Domisch, S.* (2020) Art-Areal-Modellierung für Fischarten im Einzugsgebiet der oberen Donau - Aspekte zur Interpretation der Projektionen. *WasserWirtschaft*, 110(2-3):38-40. doi: 10.1007/s35147-020-0350-x

4. Schuwirth, N., Borgwardt, F., Domisch, S., **Friedrichs, M.**, Kattwinkel, M., Kneis, D., ... & Vermeiren, P. (2019). How to make ecological models useful for environmental management. *Ecological Modelling*, *411*, 108784. https://doi.org/10.1016/j.ecolmodel.2019.108784

5. Domisch, S., **Friedrichs, M.**, Hein, T., Borgwardt, F., Wetzig, A., Jähnig, S. C., & Langhans, S. D. (2019). Spatially explicit species distribution models: A missed opportunity in conservation planning? *Diversity and Distributions*, *25*(5), 758-769. https://doi.org/10.1111/ddi.12891

6. **Friedrichs, M.**, Hermoso, V., Bremerich, V., & Langhans, S. D. (2018). Evaluation of habitat protection under the European Natura 2000 conservation network–The example for Germany. *PloS one*, *13*(12), e0208264. https://doi.org/10.1371/journal.pone.0208264

7. **Friedrichs-Manthey, M.**, Langhans, S. D., Hein, T., Borgwardt, F., Kling, H., Stanzel, P., Jähnig, S. C.*, & Domisch, S.* 300 years of change for native fish species in the upper Danube river basin – historical flow alterations versus future climate change

8. Maasri, A., Jähnig, S., Adamescu, M., Adrian, R., Baigun, C., Baird, D., ..., **Friedrichs-Manthey, M.**, … & Worischka, S. A Global Agenda for Advancing Freshwater Biodiversity Research. (submitted to *Ecology Letters*)

9. **Friedrichs-Manthey, M.**, Jähnig, S.C., Hein, T., Borgwardt, F., Kling, H., Stanzel, P., Domisch, S.*, & Langhans, S.D.* Systematic conservation planning for native fish species in the upper Danube river basin – Making an existing network fit for climate change (to be submitted)

* Authors contributed equally