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Restricted by borders: trade-offs in transboundary conservation planning for large river systems

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Abstract

Effective conservation of freshwater biodiversity requires accounting for connectivity and the propagation of threats along river networks. With this in mind, the selection of areas to conserve freshwater biodiversity is challenging when rivers cross multiple jurisdictional boundaries. We used systematic conservation planning to identify priority conservation areas for freshwater fish conservation in Hungary (Central Europe). We evaluated the importance of transboundary rivers to achieve conservation goals by systematically deleting some rivers from the prioritization procedure in MARXAN and assessing the trade-offs between complexity of conservation recommendations (e.g., conservation areas located exclusively within Hungary vs. transboundary) and cost (area required). We found that including the segments of the largest transboundary rivers (i.e. Danube, Tisza) in the area selection procedure yielded smaller total area compared with the scenarios which considered only smaller national and transboundary rivers. However, analyses which did not consider these large river segments still showed that fish diversity in Hungary can be effectively protected within the country's borders in a relatively small total area (less than 20% of the country's size). Since the protection of large river segments is an unfeasible task, we suggest that transboundary cooperation should focus on the protection of highland riverine habitats and their valuable fish fauna, in addition to the protection of smaller national rivers and streams. Our approach highlights the necessity of examining different options for selecting priority areas for conservation in countries where transboundary river systems form the major part of water resources.

Keywords: freshwater conservation areas, systematic conservation planning, Marxan, rivers, fish

Introduction

Despite their small spatial extent, freshwater ecosystems, and running waters in particular, maintain a disproportionally high amount of global biodiversity (Strayer and Dudgeon 2010). Freshwater biodiversity is also declining at an alarming rate that is far greater than those in the most affected terrestrial systems (Dudgeon et al. 2006). To effectively protect freshwater ecosystems, careful selection of conservation areas is urgently needed in a number of the world's biogeographic areas and ecoregions. Although conservation planning for freshwater habitats still lags far behind that of terrestrial and marine ecosystems (Abell et al. 2007; Strecker et al. 2011), significant progress has been made. To date, the majority of conservation planning examples for fresh waters have been dominated by measures of richness, rarity and conservation value of charismatic freshwater groups (e.g. Filipe et al. 2004; Bergerot et al. 2008) or have used landscape level surrogates (i.e. habitat types, Higgins et al. 2005; Nel et al. 2007) to suggest areas for protection. Nevertheless, the key principles of systematic conservation planning (Margules and Pressey 2000), the most common approach used in the identification of conservation priorities worldwide, have also started to be increasingly applied in the selection of freshwater conservation areas (e.g. Esselman and Alan 2011; Hermoso et al. 2011).

Briefly, systematic conservation planning (hereafter SCP) approaches optimise the selection of planning units (the basic units of the conservation selection procedure, e.g subcatchments in freshwater systems) by minimising area and maximizing biodiversity representation (Pressey and Nicholls 1989). To achieve conservation targets at the minimum cost, complementarity based algorithms are used, which maximise the representativeness of biodiversity when a new site is added to an existing set of sites. Recent applications of SCP to riverine systems give special attention to connectivity among river segments, subcatchments or catchments to select priority areas for conservation (Moilainen et al. 2008; Hermoso et al. 2011; Linke et al. 2012). Due to the longitudinal connectedness of rivers, the long-term persistence of freshwater biodiversity within a protected area strongly relies on the system's capacity to maintain some key ecological process (e.g. migrations) and the propagation of threats along the river network. Failing to adequately account for key ecological processes - essential for maintaining freshwater biodiversity over time - could therefore limit the success of conservation efforts in freshwater ecosystems (Saunders et al. 2002; Abell et al. 2007). The majority of existing protected areas were not established with consideration to freshwater biodiversity or processes and subsequently fail to adequately protect these ecosystems and dependent species (Nel et al. 2007, 2009).

While a single conservation planning solution could work for large countries, where most of the rivers originate and flow within the country's border (e.g. Australia, Unites States), selection of priority areas for conservation can be problematic in countries which receive most of their rivers from outside their borders. In fact, many of the world's large rivers are transboundary (e.g. Amazon, Nile and Mekong) and experience myriad of human pressures in the countries they flow through. Additionally, rivers often form geopolitical borders between countries and, although it is evident that international cooperation is required for effective conservation strategies in transboundary ecosystems, this remains unrealistic because of political and economic reasons. In such cases, conservation planners should give consideration to alternative scenarios that require more or less cooperation among countries. For example, planners could investigate how much of the regional biodiversity (i.e. total biodiversity) can be conserved by only protecting streams and rivers situated within a country's borders.

Here, we explore the trade-offs associated with different management options for conservation of freshwater fish diversity in a country sharing a very large international river (the Danube River in Hungary). From source to mouth the Danube drains 19 countries, which makes the Danube basin the most international catchment in the world (http://www.icpdr.org/main/danube-basin). We evaluate the opportunities and risks of transboundary collaboration by simulating different conservation planning scenarios, allowing areas shared with different countries to contribute to the achievement of conservation goals, or constraining the search to areas within Hungary. We first include all rivers in the country, and then selectively remove large rivers from the process of SCP, to examine how such modifications influence the selection of priority areas. Our purpose is to reveal complementary hotspots of biodiversity in the country and to provide alternative schemes to guide freshwater conservation decision making.

Materials and methods

Study area

The Danube River is the second largest river in Europe, after the Volga River, with a catchment area of 796,250 km^2 and a total length of 2,847 km (Fig. 1). The Danube occupies two different freshwater ecoregions (Abell et al. 2008): the Upper Danube and the Dniester-

Lower Danube . The Dniester-Lower Danube, where Hungary is located, is the most species diverse ecoregion in Europe (Bănărescu 1990; Abell et al. 2008).

Surrounded by two mountain ranges, the Alps in the west and the Carpathians in the north and east, Hungary has a specific geological position in the Carpathian basin (Fig. 1). Two-thirds of the country's 93,000 km^2 falls within lowlands (i.e. plains, up to 200 m a.s.l.), and the remaining area is mainly composed of highlands (200-500 m), with only a small proportion located in submontane regions (highest mountain peak is 1014 m). Ninety five percent of the water supply (i.e. streams and rivers) originates in other countries, which requires a careful selection of waterways for conservation purposes. Most of the water is provided by the Danube and Tisza Rivers, but other smaller international rivers also flow into the country or form geopolitical borders between Hungary and other countries (Fig. 1). Consequently, Hungary represents a good case study for exploring the role of international rivers in biodiversity preservation, from the second largest river in Europe (Danube River), to other smaller transboundary and internal river systems.

Planning units and biodiversity data

Our planning area was Hungary. We used Geographic Information Systems (GIS) to generate planning units (PUs) within Hungary, which consisted of 952 subcatchments (hereafter catchments) of streams and rivers and of Lake Balaton. The mean area (±SD) of individual catchments was 97.7 (±117.6) km^2.

We compiled presence/absence data for 75 freshwater fish species in 389 catchments (or PUs we use these terms interchangeably) drawing from both our own country wide data set and species occurrences determined through literature reviews. In the reviewed studies, fish were collected with standardized protocols following the methodology of the National Biodiversity Monitoring Program, which is fully compatible with international standards such as the FAME protocol (see e.g. Erős 2007; Sály et al. 2011). The database we used contains more than 2500 survey data and is based on the collection of more than 500,000 individual.

Species distribution models

Ideally, the distribution of all species across a study region would be known. However, data collection is expensive and time-consuming (Balmford and Gaston 1999), resulting in incomplete coverages for many species (Balmford and Gaston, 1999; Pressey 2004). To overcome the limited coverage of biological data, various methods have been proposed and used in conservation planning exercises across the globe (Pressey 2004). Here, we used a predictive modelling framework, Multivariate Adaptive Regression Splines (MARS) to supplement observed sampling data by predicting the occurrence of species for each catchment. MARS is a flexible nonparametric regression method that is often used for modelling complex non-linear relationships between species occurrences and environmental data (Leathwick et al. 2005; Elith et al. 2006; Ferrier & Guisan 2006; Leathwick et al. 2006). MARS has been shown to be robust for predicting distributions for data-poor species, because data-rich species can help to inform models for these species (Ferrier & Guisan, 2006).

Fish species with occurrence records in fewer than 10 PUs were excluded from the modelling procedure, because so few occurrences can influence model reliability. Note, that although this exclusion included some protected species (i.e. *Cottus gobio, Gobio uranoscopus, Eudontomyzon danfordi, Eudontomyzon marie*), the PUs in which these species occur were selected in the final priority area network, because they were important for representing other protected species (see discussion for more details). We excluded non-native species from our analyses, because these species do not have conservation value. We also omitted four PUs in the main stem of the Danube River, because their habitat features were different to any others represented in the model, and could affect the predictive ability of the model. For these catchments, we used a complete list of species available from previous studies. Our final presence/absence data matrix consisted of 42 fish species in 385 PUs.

Eighteen ecologically relevant landscape scale environmental variables were selected for modelling species distributions (Appendix A). The 18 variables have been successfully used in other freshwater studies (e.g. Hermoso et al. 2011; Linke et al. 2012), and characterized regional climate, land use, geology and river basin topography. We summarized the 18 environmental variables within each of the 385 PUs. To extract the values of the abiotic variables we used the following GIS data: catchments of Hungary, watercourses and lakes of Hungary, the WorldClim data base for climate and altitude (Hijmans et al. 2014), the CORINE 2006 database for land use data (Steenmans et al. 2006), and the Global Human Footprint version 2 database (Sanderson et al. 2002).

We fit a multiresponse MARS model with a generalised linear model (GLM) using the ‘earth package’ (Milborrow et al. 2014) in R (R Core Team 2013). In this procedure, a MARS model is fitted on the raw presence/absence data first, which results in the so called basis matrix of the MARS algorithm; then GLMs are invoked and fitted on the basis matrix to yield fitted values in a form of species occurrence probabilities (for a nice and concise description on how MARS works see Leathwick et al. 2006; Ferrier & Guisan 2006). To evaluate model performance, ten 3-fold cross validations (CV) (i.e. a total of 30 CV) were carried out during model fitting. We also used the generalized coefficient of determination (GR^2) to estimate the general performance of the model (i.e. predictive applicability on data different from the training data set). In other words, GR^2 is an estimation of the R^2 that would be expected to get when the fitted model were used to predict data independent from the training data. For more details see the help pages of the ‘earth’ package (Milborrow et al. 2014) and references therein.

After model fitting, the trained MARS model was applied to predict the occurrence of the 42 fish species for PUs without fish occurrence data. Predicted occurrence probabilities were converted into presence/absence data using an appropriate threshold value for each species. We chose an occurrence probability value that maximized the sum of sensitivity and specificity as a threshold (Cantor et al. 1999; Freeman and Moisen 2008), because this measure is one of the most accurate threshold criteria (Liu et al. 2005; Jiménez-Valverde and Lobo 2007).

Finally, we compiled the predicted presence/absence data for the PUs and the directly observed species occurrence data for the Danube River and Lake Balaton into a single incidence data matrix with a size of 952 PUs × 42 species. This single data matrix represented the biological features of the PUs of the initial planning region (i.e. the whole territory of Hungary) in the later SCP analyses. Because species distribution modelling only determines potential occurrence of species as a function of their abiotic habitat requirements, we deleted species from catchments where they had not been found in former biological surveys (Harka and Sallai, 2004).

Data processing described above including all phases of the species distribution modelling was conducted in QGIS (QGIS Development Team 2012) and in R environment (R Core Team 2013). We used the ‘maptools’ (Bivand and Lewin-Koh 2014), ‘sp’ (Pebesma and Bivand 2005), ‘rgeos’ (Bivand and Rundel 2014) and ‘raster’ (Hijmans 2014) R packages to characterize the catchments with the values of the predictor variables, and the ‘earth’ package (Milborrow et al. 2014) for the MARS model, and the ‘PresenceAbsence’ package (Freeman and Moisen 2008) to convert probabilities into presence/absences.

Conservation design

We identified catchments of high potential conservation value using the conservation planning software MARXAN (Ball et al. 2009). MARXAN uses an optimization algorithm to maximize the representation of predefined conservation targets while minimizing the cost of including planning units. We used catchment area and a predefined amount of each species to be represented in the final solution as cost and target in our design, respectively. Preliminary analyses at different target levels showed that even a relatively high target level, where each species occur in at least 30 catchments can be a feasible conservation strategy since even such an outcome does not require more space than the current total area of conservation reserves in Hungary and would require less space than 20% of the area of the country. Our final target was to represent 30 occurrences of each species, and we determined the cost, amount of catchment area needed to achieve this target.

Considering connectivity relationships among catchments is especially important for fish and other aquatic taxa, because dispersion can happen only by instream movement. It is also critically important, because only well connected and protected series of catchments can maintain diversity and ecosystem processes in stream networks (Abell et al. 2007). For this reason we also used a connectivity penalty following the approach proposed by Hermoso et al. (2011) to address longitudinal connectivity in our solutions. This approach forces the selection of longitudinally connected catchments along the river network by penalizing missing connections, weighted by the distance between each pair of subcatchments (the further they are the lower the penalty applied for missing the connection). We characterized connectivity between catchments by coding neighbouring catchments with one, two, and so on up to seven connections. We truncated the distance matrix so that catchments with more than seven connections were not included in our analyses, because a greater distance would not influence actual ecological connectivity between fish populations.

The importance of connectivity in the optimization process can be weighted through a Boundary Length Modifier (BLM). When the BLM is set to 0, the selection of planning units happens without any consideration of connectivity relationships among the catchments. This may yield that valuable catchments are selected further from each other, which may harden the selection of both compact conservation areas and large connected catchments. In contrast, maximizing BLM increases the spatial clumping of the planning units (i.e. decreasing boundary length of the areas), which can happen at the expense of increasing cost (area of catchments) if the neighbouring catchments do not represent enough species to reach the defined conservation target. Consequently, careful selection of the BLM is necessary for optimizing between total area of catchments to reserve, their biodiversity value (species representation), and connectivity. To calibrate the BLM for further analyses (see Hermoso et al., 2011 for details), we evaluated the relationship between the amount of area protected and connectivity (increasing the value of connectivity through BLM).). To do this, we evaluated nine BLM values (0, 0.001, 0.005, 0.01, 0.05, 0.1, 0.5, 1.0 and 1.5) and total catchment area for a given conservation scenario (for details see Hermoso et al. 2011). Note, that above the BLM value of 1.5 all units were selected by the program to keep the defined target level, and therefore we did not apply higher BLM values in the analyses. Although total area increased, the boundary value decreased considerably with increasing BLM values, showing that the selected priority areas were more compact when connectivity was considered more intensively among the catchments (results not shown). Because the BLM was stable at 0.1, we only report priority area outcomes for this value.

There are big differences among the rivers in their feasibility of successful cross-border protection. For example, effective protection of segments of very large rivers, such as the main stem of the Danube cannot be assumed because of upstream and downstream catchments intersecting neighbouring countries. Similarly, effective protection of Lake Balaton is also complicated by the large size of the lake and multipurpose utilization by society. However, both the main stem of the Danube and Lake Balaton support species of conservation concern. With this in mind, we evaluated how the exclusion of large international rivers and Lake Balaton might compromise the achievement of conservation targets. We compared reserve selection outcomes between four hierarchical levels (i.e. scenarios), 1) when all catchments are considered in the SCP procedure, 2) when catchments belonging purely to segments of the Danube and Lake Balaton are excluded from the analyses, since these are the biggest catchments, which clearly could not be protected effectively, 3) when catchments belonging purely to the Tisza River, the second longest river of the Danube River catchment are excluded from the analyses, and 4) when two smaller but international rivers, the Dráva and Ipoly Rivers are also excluded from the analyses, because both rivers would require intensive international cooperation to be protected effectively. The Dráva and the Ipoly Rivers form geopolitical borders between Hungary and Croatia and Hungary and Slovakia, respectively. Yet, examining their role is critically important at the national level, because they are still relatively natural and provide large habitat area for a diverse and valuable aquatic fauna. Note, that for the first, basic scenario we did not include connectivity penalty in the SCP procedure, because we were just interested to see the importance of Danubian segments or Lake Balaton in area selection.

Finally, we examined how the priority areas identified in this study in the four scenarios overlap with the current protected area network in Hungary (i.e. national parks and other conservation areas). We overlaid the two types of GIS layers (i.e. maps of the suggested freshwater and the currently protected area) and calculated the common and complementary areas for both types (Fig. 4).

Results

Species distribution modelling

The MARS algorithm selected seven of the 18 abiotic variables (shape index, altitude, isothermality, WFD rank mean, precipitation seasonality, total number of lakes and ponds in PU, WFD rank minimum) as the best predictors of fish species distributions in Hungary (see appendix A for explanation).

The overall fit of the MARS model on the training data was $R^2 = 0.21 \pm 0.09$ SD (mean and standard deviation across the 42 species), which is comparable with other studies (Hermoso et al. 2011). According to the cross validation procedure, the overall predictive power of the MARS model was $GR^2 = 0.14 \pm 0.09$ SD (mean and standard deviation across the 42 species). The averaged value of the area under the receiver operating curve (AUC) across the 42 species and the corresponding standard deviation was 0.76 ± 0.07 (Table 1). Most species which had relatively low AUC values are in fact rather common, generalist species which occur rather evenly among the lowland catchments (e.g. *Cyprinus carpio, Leucaspius delineatus, Perca fluviatils, Rhodeus sericeus,* Harka and Sallai 2004). Protected and endemic species with specific habitat requirements received high AUC values (e.g. *Barbus charpaticus, Gymnocephalus schraetser, Rutilus pigus, Zingel spp*).

Species showed different responses to environmental heterogeneity from predicted species distributions restricted to submontane and highland areas (Fig. 2a) to species occupying only lowland areas (Fig. 2b). Some important species of high conservation value had a distribution restricted only to medium or large rivers with hard substrate (Fig. 2c, 2d). The number of predicted species per catchment varied between 1 and 39, with a mean value of 13.64. Species richness varied between 37 and 39 species for all catchments (i.e. segments) of the Danube.

In the first scenario, all species achieved the target (i.e. all species were represented in at least 30 catchments), and the total area of selected PUs was 3683 km^2. Neither Lake Balaton nor the catchments belonging strictly to the Danube were selected in the first scenario with the exception of one Danubian PU with 39 species (Fig. 3a). For Lake Balaton this was probably because the unit contained relatively common species (21 species, which occurred frequently in other catchments, too), relative to its size. Many other units contained equally high species richness to that of the Danube. Specifically, PUs belonging to the Tisza River catchment were selected as priority areas in the first scenario. Scenario 2, which excluded catchments of the Danube and Lake Balaton, did not substantially increase the total area of selected PUs to achieve the same target as scenario 1. The required total area to achieve the conservation targets for all species was 3727 km^2.

Regardless of the scenario, the total catchment area needed to achieve the conservation target increased with increased BLM values (i.e. increased catchment connectivity). For scenario 2 it was 4428 km^2 at a BLM value of 0.1 (Fig. 3b). Exclusion of the catchments belonging to the Tisza River (scenario 3) increased the total area up to 5693 km^2 at a BLM value of 0.1 (6.12 % of the territory of the country; Fig. 3c) to allow achieving the target level of minimum 30. Moreover, all species could still achieve this minimum target. The further exclusion of the Dráva and Ipoly Rivers from the SCP exercise (scenario 4) did not significantly change the required area either as it yielded a conservation area of 5225 km2 (5.61 % of the territory of the country; Fig. 3d) at a BLM value of 0.1. However, the target level of 30 could not be fulfilled for all species in this scenario. For example, one species with high conservation value (*Romanogobio kessleri*) occurred only in 28 catchments after the exclusion of the Danube, Tisza, Dráva, Ipoly rivers, and therefore, this was the maximum reachable representation of this species in this SCP scenario.

Current protected areas (i.e. national parks and other conservation areas) cover only 9.1 % of the country (8507 km^2). We found a weak spatial overlap between priority areas identified across the different conservation planning scenarios and the current reserve system (Fig. 4), which ranged between 0.17 and 7.06 %. Moreover, when using SCP to extend the current reserve system, the catchment area selected remained below 20% of the country's total area, ranging between 11548 and 13709 km^2 (12.4 and 14.74 % of the country's total area) across the different scenarios.

Discussion

Here, we demonstrate the trade-offs between ease of implementation of conservation recommendations and its cost for freshwater systems shared across different jurisdictional units. We found that in order to achieve conservation targets within river systems completely within Hungary, we would require more area than if collaboration with neighbour countries for protecting very large rivers was feasible. Despite its higher cost we showed that freshwater fish species can be effectively protected in Hungary within the catchments of smaller rivers. Selection of conservation areas within catchments that belong to a single country avoids complex negotiations with other countries, which makes implementation of conservation more feasible. Our findings are particularly relevant to current conservation policy and decision making in Eastern and Central European countries that share the Danube. This is because countries, responsible for different lengths of the Danube and other large rivers, have different priorities for freshwater conservation and possibly have variable budgets for conservation or international collaboration. However, we also show that transboundary collaboration with a reduced number of countries could significantly improve the effectiveness of protection. In fact, using Marxan and considering connectivity in the planning process allowed compromise, identifying solutions that both maintain fish diversity in different catchments and reduce dependence on transboundary collaboration.

Consideration of catchment or river segment connectivity has only recently started to be applied to freshwater conservation planning (Moilanen et al., 2008; Hermoso et al. 2011). Our results demonstrate the benefit of accounting for connectivity in planning. Regardless of the scenario, when considering connectivity among PUs s in the selection process, the selected catchments occupied less than 20% of the country's entire area. This finding demonstrates that fish species in Hungary can be conserved within a relatively small catchment area. Although the selected catchments are distributed throughout the country most of them are compartmentalized and large enough to maintain large populations. Further spatial aggregation (forcing more connectivity) would have required the addition of large areas and it would have compromised the implementation of conservation for its high cost. The spatial distance between selected catchments ensures that a relatively high genetic diversity can be preserved for the species. Further, most of the selected catchments are in the vicinity of existing protected areas (e.g. national parks). With this in mind, we suggest consideration be given to redesigning the existing conservation area network in Hungary to embrace the catchments identified in our analyses, while maintaining the preservation of terrestrial biodiversity.

The effective protection of very large river systems is one of the greatest challenges in conservation biology (Saunders et al. 2002; Abell et al. 2007). This task is especially difficult for international rivers, because conservation requires effective transboundary cooperation. Although river segments could be protected by law in each individual country, their effective protection maybe unfeasible, because the segments, as well as their catchments, are vulnerable to upstream or downstream perturbations from abroad (Nel et al. 2007; 2009). The most characteristic examples of upstream threats are pollution and chemical spills. Such a chemical disaster happened for example on the Tisza and Szamos Rivers in 2000, when a globally financed gold mine in Romania spilled thousands of tons of cyanide and heavy metals into these rivers (Lucas 2001; Harper 2005), killing tens of thousands of fish and other forms of wildlife and poisoning drinking water supplies in downstream countries, including

Hungary (Cunningham 2005; Antal et al. 2013). Additionally, the main stem of very large rivers are used for a variety of human purposes (e.g. shipping or fisheries), which makes the effective protection of target segments especially problematic. We have demonstrated that larger conservation areas are required when catchments of the Danube and the Tisza are not considered. Restricting conservation areas away from the Danube and Tisza can be considered a strongly supervised and potentially more effective conservation solution, because the remaining smaller rivers that were selected in our scenarios 2 and 3 are less exposed to unpredictable out of border disturbance effects and less exposed to heavy human use. Similar to findings in other regions (Pracheil et al. 2013), we suggest that strict conservation management actions are focused in smaller tributary rivers and streams, and that additional policies are leveraged to maintain the ecological potential of very large rivers as much as possible. Ensuring ecological connectivity among the protected rivers and streams within these very large catchments should be an especially important task of conservation management actions.

After excluding the Danube and the Tisza Rivers from the analyses (i.e. scenario 1, 2 and 3) a small number of highland and lowland rivers and their smaller tributaries became the core areas for freshwater conservation. Although scenario 4 can be a solution to minimize transboundary cooperation, we believe that scenario 3 (i.e. when some transboundary highland rivers are also retained for priority conservation areas) could be the best compromise solution for conserving freshwater fish in this ecoregion. From a conservation viewpoint, highland rivers host the most diverse and valuable riverine fish fauna in this ecoregion (Erős 2007) with many protected and strictly protected species by national laws and international directives (e.g. Habitat Directive of the European Union). Transboundary highland rivers, such as the Dráva (between Hungary and Croatia) and the Ipoly (between Hungary and Slovakia) contain a large proportion of the overall population size of some Danubian endemic species (e.g. *Romanogobio kessleri, Sabanejewia aurata, Zingel streber, Zingel zingel*). Most catchments of these rivers were selected in scenario 1, 2 and 3 for inclusion in conservation areas. Further, the Dráva River also contains relatively abundant and stable populations of those protected species (i.e. *Gobio uranoscopus, Cottus gobio*) which are very rare in Hungary (Harka and Sallai 2004), and had to be discarded form the models due to their rarity. Unfortunately, the extent of highland rivers is low in the country. Therefore, efforts should be made to strengthen the cooperation between Hungary and Croatia and Slovakia to design transboundary freshwater protected areas for the catchments of highland rivers.

Transboundary, multi-country cooperation for effective river conservation management is particularly important in Europe. Through multi-country cooperation, there is great potential to target key ecological processes operating at larger spatial (landscape) scales (e.g. migration/dispersal) which is critical for the persistence of freshwater biodiversity over time (Abell et al. 2007; Januchowski-Hartley et al. 2013). For example, the persistence of populations of endangered species in one country could be dependent annual upstream-downstream migration of individuals that originate from parts of the stream network located in another country. It is also important that some medium sized rivers are protected from source to mouth (e.g. the Ipoly River) as it will maximize the protection of both biodiversity and key ecological processes (such as species migration) of these rivers. However, cooperation between countries is not an easy task, especially given differences in the environmental policy and development between countries. For example, Croatia planned to build a hydroelectric power plant on the Dráva River on a section which belongs exclusively to its own territory at Novo Virje (Závoczky 2005). Installation of the dam in Croatia would have affected hundreds of protected and dozens of strictly protected animal species that occupy the Dráva River in Hungary, including species which are listed in international nature conservation agreements ratified by Hungary and in the Habitat and Birds Directives of the European Union (Závoczky 2005). Without cooperation between Croatia and Hungary, there is the potential both for ineffective conservation efforts and species loss, and potentially meaning that conservation efforts would be better directed towards other areas where freshwater diversity in Hungary are less sensitive to threats coming from abroad, as suggested through our scenario 4.

A limitation of our study is that we used species distribution models to aid the selection of priority areas for conservation. Although such models have started to be routinely used in SCP (e.g. Leathwick et al., 2005; Guisan et al., 2013), it should be emphasized that these data provide information on the potential distribution of species only. Predictions are subject to commission and omission errors, and the effects of these errors on conservation planning outcomes should be evaluated (Hermoso et al., 2014a; b). Therefore, the real occurrence of (at least) the species of greatest conservation concern should be validated with field data in conservation implementations. With this in mind, efforts to survey ecological assemblages should be directed to areas supporting species of conservation concern. In our study, conservation priority areas had the highest percentages of occurrence records for model verification (69-76% depending on the scenario). Consequently, given the high assurance that species of high conservation concern do actually occur in selected catchments, our analyses is verified.

In conclusion, we believe that a hierarchical design of alternative conservation plans as applied in this study can be particularly useful for informing nature conservationists, environmental managers and stakeholders about the trade-offs associated with transboundary conservation of rivers. Our results demonstrate that fish diversity can be effectively protected within a relatively small area in Hungary if alternative solutions cannot be considered. However, we still believe that transboundary cooperation with some neighbouring countries (Croatia and Slovakia) could be beneficial for the protection of highland riverine habitats and their valuable fish fauna. We suggest the application of our approach in other regions where the majority of river systems are transboundary.

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Table 1: Relative frequency of occurrence (i.e. prevalence) of the fish species in the training data; and MARS–GLM performance. R2: coefficient of determination. GR2: generalized coefficient of determination. AUC: area under the receiver operating curve averaged across the results of ten 3-fold cross validations. Protected species are indicated with bold, and strictly protected species with bold and a star symbol.

Species name	Species code	Fr.occ (n=385)	R2	GR2	AUC	sd
Abramis brama	abrbra	0.34	0.25	0.18	0.75	0.05
Alburnoides bipunctatus	**albbip**	**0.23**	**0.23**	**0.16**	**0.74**	**0.05**
Alburnus alburnus	albalb	0.61	0.21	0.14	0.73	0.04
Ballerus ballerus	balbal	0.07	0.12	0.04	0.73	0.08
Ballerus sapa	balsap	0.09	0.28	0.22	0.88	0.05
Barbatula barbatula	**ortbar**	**0.45**	**0.43**	**0.38**	**0.86**	**0.03**
Barbus barbus	barbar	0.17	0.29	0.22	0.8	0.05
Barbus charpaticus*	**barpel**	**0.09**	**0.36**	**0.31**	**0.84**	**0.06**
Blicca bjoerkna	blibjo	0.39	0.27	0.21	0.76	0.04
Carassius carassius	carcar	0.14	0.10	0.02	0.68	0.07
Chondrostoma nasus	chonas	0.17	0.30	0.24	0.79	0.06
Cobitis elongatoides	**cobelo**	**0.58**	**0.16**	**0.09**	**0.67**	**0.05**
Cyprinus carpio	cypcar	0.24	0.14	0.07	0.69	0.04
Esox lucius	esoluc	0.49	0.27	0.21	0.76	0.04
Gobio gobio	**gobgob**	**0.55**	**0.25**	**0.19**	**0.76**	**0.04**
Gymnocephalus baloni	**gymbal**	**0.08**	**0.22**	**0.15**	**0.82**	**0.06**
Gymnocephalus cernua	gymcer	0.17	0.09	0.01	0.68	0.06
Gymnocephalus schraetser	**gymsch**	**0.05**	**0.31**	**0.25**	**0.88**	**0.09**
Leucaspius delineatus	**leudel**	**0.17**	**0.04**	**-0.04**	**0.56**	**0.06**
Leuciscus aspius	leuasp	0.24	0.30	0.23	0.78	0.04
Leuciscus idus	leuidu	0.23	0.23	0.16	0.75	0.05
Leuciscus leuciscus	**leuleu**	**0.24**	**0.18**	**0.11**	**0.72**	**0.05**
Lota lota	lotlot	0.12	0.34	0.29	0.83	0.05
Misgurnus fossilis	**misfos**	**0.29**	**0.12**	**0.05**	**0.68**	**0.05**
Perca fluviatilis	perflu	0.53	0.17	0.10	0.67	0.05
Phoxinus phoxinus	**phopho**	**0.11**	**0.11**	**0.03**	**0.76**	**0.05**
Rhodeus sericeus	**rhoser**	**0.62**	**0.16**	**0.08**	**0.67**	**0.03**
Romanogobio kessleri*	**romkes**	**0.03**	**0.13**	**0.05**	**0.84**	**0.10**
Romanogobio vladykovi	**romvla**	**0.27**	**0.21**	**0.14**	**0.72**	**0.04**
Rutilus pigus virgo	**rutpig**	**0.03**	**0.25**	**0.19**	**0.89**	**0.09**
Rutilus rutilus	rutrut	0.71	0.22	0.15	0.73	0.04
Sabanejewia aurata	**sabaur**	**0.10**	**0.20**	**0.13**	**0.79**	**0.05**
Sander lucioperca	sanluc	0.25	0.19	0.12	0.71	0.04
Sander volgensis	sanvol	0.11	0.12	0.04	0.75	0.06
Scardinius erythrophthalmus	scaery	0.40	0.17	0.10	0.71	0.05
Silurus glanis	silgla	0.14	0.38	0.32	0.87	0.04
Squalius cephalus	squcep	0.64	0.22	0.15	0.75	0.04
Tinca tinca	tintin	0.14	0.08	0.00	0.68	0.05
Umbra krameri*	**umbkra**	**0.07**	**0.08**	**0.00**	**0.78**	**0.06**
Vimba vimba	vimvim	0.12	0.14	0.06	0.74	0.06
Zingel streber*	**zinstr**	**0.04**	**0.21**	**0.14**	**0.87**	**0.11**

Zingel zingel *	**zinzin**	**0.06**	**0.31**	**0.25**	**0.86**	**0.06**
	Mean ± SD	0.25 ± 0.20	0.21 ± 0.09	0.14 ± 0.10	0.76 ± 0.07	0.05 ± 0.02

APPENDIX A

Description of the candidate predictor variables that were used to characterize the catchments in the species distribution modelling procedure. Minimum and maximum values show the range limit of the variables, across the 952 catchments that represented the planning units (Pus) of the initial planning region, and Mean ± SD stand for the average and the standard deviation. Note, that for variable 4, WFD rank refers to the Water Framework Directive rank of the waterflow in the Hungarian typology. The smallest the waterflow the highest its WFD rank.

Variable	Description	Min	Max	Mean ± SD
[1,]"shape_index"	This is a proportion of the perimeter of the PU to the perimeter of a circle with the area equals to the area of the PU. Shape index expresses the compactness of the PU. (dimensonless)	1.096	16.861	1.844 ± 1.101
[2,]"tot_riv_length"	Total length of the rivers within the PU. (km)	0.952	163.814	20.958 ± 18.980
[3,]"drainage_density"	Total length of the rivers within the PU divided by the area of the PU. (km/km2)	0.030	43.109	0.495 ± 1.968
[4,]"WFD_rank_mean"	Average of the WFD ranks of river segments within the PU. In case of Hungary, WFD rank means that the largest rivers (river Danube and river Tisza) have a rank value of 1, rivers that flow into them have a rank value of 2, etc.	1	10.250	4.657 ± 1.343
[5,]"WFD_rank_min"	Minimum of the WFD ranks of river segments within the PU. In contrast to Strahler rank, the smallest value of the WFD ranks refers to the size of the largest river segment within the catchment. See the description of "WFD_rank_mean".	1	5	3.737 ± 1.336
[6,]"altitude"	Average altitude above sea level of the PU. Derived from the Alt16 raster of the WorldClim database. (m)	72.0	580.7	167.4 ± 80.6
[7,]"ruggedness"	Average of the ruggedness index within the PU.	1.360	312.295	48.373 ±

	Ruggedness index summarizes the change in altitude within a grid cell, and measures terrain heterogeneity. Derived from the Alt16 raster of the WorldClim database. (m)			51.406
[8,]"m_ann_temp"	Average of the annual mean temperature within the PU. Derived from the BIO1 raster of the BioClim database. The data were in °C*10 format	7.174	11.213	10.249 ± 0.667
[9,]"isothermality"	Average of the proportion of the mean diurnal temperature range to the annual temperature range within the PU. Derived from the BIO3 raster of the BioClim database. (%)	28	32	30.30 ± 0.73
[10,]"temp_seasonality"	Derived from the BIO3 raster of the BioClim database. Standard deviation*100	7259	8064	7703 ± 167.914
[11,]"ann_prec"	Average of the annual precipitation within the PU. Derived from the BIO12 raster of the BioClim database. (mm)	513.2	821.1	606.1 ± 65.035
[12,]"prec_seasonality"	Average of the annual precipitation within the PU. Derived from the BIO15 raster of the BioClim database. (mm)	21.98	38.54	27.56 ± 3.765
[13,]"clc_1_artificial_surfaces"	Area of the artificial surfaces within the PU. Derived by unifying the area of the land cover patches coded by 111, 112, 121, 122, 123, 124, 131, 132, 133, 141, 142 in CORINE 2006 database. (km^2)	0	150.388	5.729 ± 9.040
[14,]"clc_2_agricultural_areas"	Area of the agricultural surfaces within the PU. Derived by unifying the area of the land cover patches coded by 211, 213, 221, 222, 231, 242, 243 in CORINE 2006 database. (km^2)	0	686.94	68.41 ± 84.760
[15,]"clc_3_forests"	Area of the forested vegetation surfaces within the PU. Derived by unifying the area of the land cover patches coded by 311, 312, 313 in CORINE 2006 database. (km^2)	0	175.620	19.268 ± 24.105
[16,]"pond_n_poly_tot"	Total number of lakes and ponds within the PU.	0	63	3.97 ± 5.757

[17,]"pond_area_tot"	Total area of lakes and pponds within the PU. (ha)	0	7552.82	89.22 ± 365.277
[18,]"HF"	Average of the Human Footprint score within the PU. Derived from the Global Human Footprint (Geographic) v2 (1995 – 2004) database. A value of 0 means no human influence, whereas a value of 100 means maximum human influence.	21.56	93.00	45.05 ± 9.62

Captions to figures

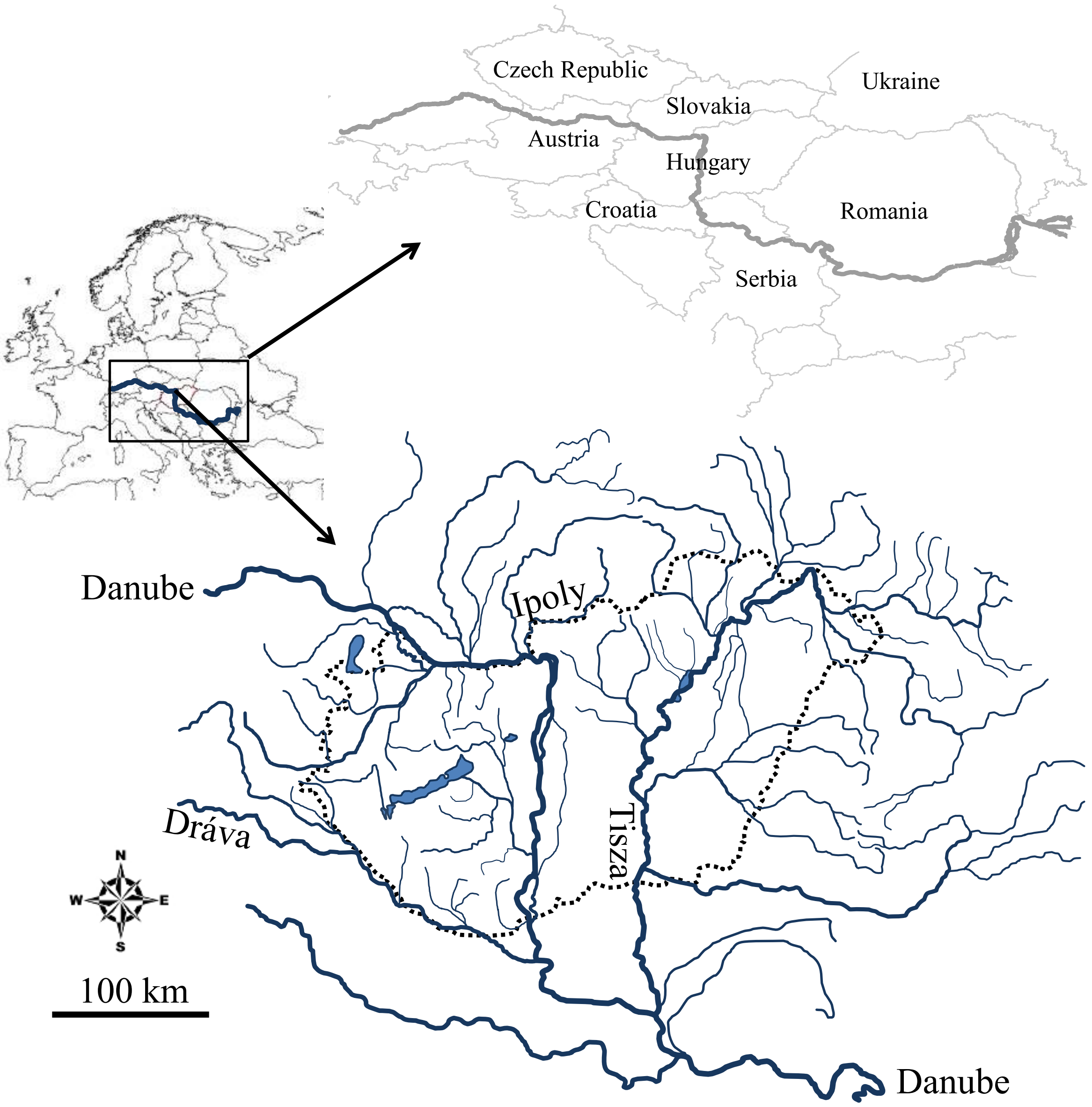
Fig. 1. Map showing the location of Hungary in the Danube River catchment in Europe, and the Central Danubian hydrosystem in the Carpathian basin (only main rivers are shown).

Fig. 2. Examples of predicted distribution maps for species with different habitat requirements: (a) the European minnow (*Phoxinus phoxinus*), the rudd (*Scardinius erythrophthalmus*), (c) the golden loach (*Sabanejewia aurata*), and (d) the zingel (*Zingel zingel*). Note, that the latter two are endemic species for the Danube basin, and their distribution is clearly restricted to medium and large rivers.

Fig. 3. The selected priority areas for conservation in case of four scenarios (a) all catchments are included in the analyses including the Danube and Lake Balaton, (b) catchments belonging purely to segments of the Danube and Lake Balaton are excluded (c) further catchments belonging purely to the segments of the Tisza River are also excluded from the analyses, (d) two smaller but international rivers, the Dráva and Ipoly rivers are also excluded from the analyses.

Fig. 4. A comparison between the selected freshwater and the current conservation areas in case of four scenarios (a) all catchments are included in the analyses including the Danube and Lake Balaton, (b) catchments belonging purely to segments of the Danube and Lake Balaton are excluded (c) further catchments belonging purely to the segments of the Tisza River are also excluded from the analyses, (d) two smaller but international rivers, the Dráva and Ipoly rivers are also excluded from the analyses. Blue and green areas represent the suggested freshwater priority areas, and the current (mostly terrestrial) reserve system, respectively.

Fig. 1


Czech Republic
Ukraine
Slovakia
Austria
Hungary
Croatia
Romania
Serbia
Danube
Ipoly
Dráva
Tisza
N
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100 km
Danube

Fig. 2

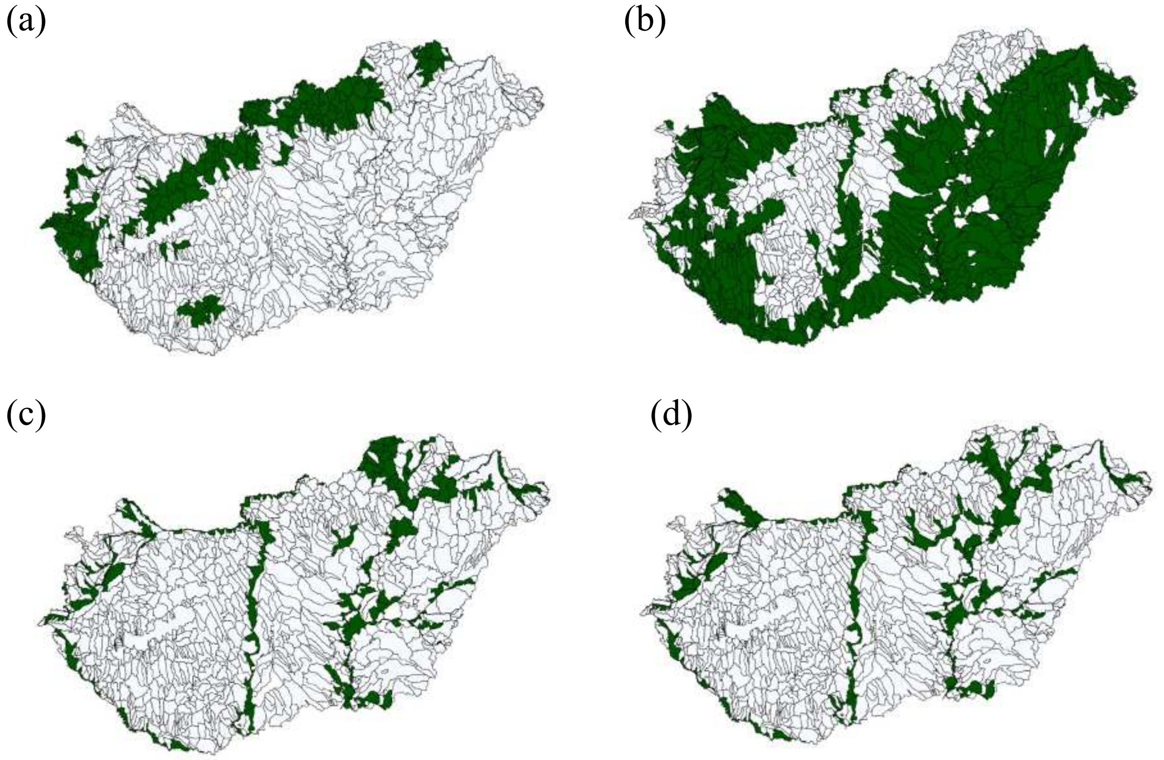

Fig. 3

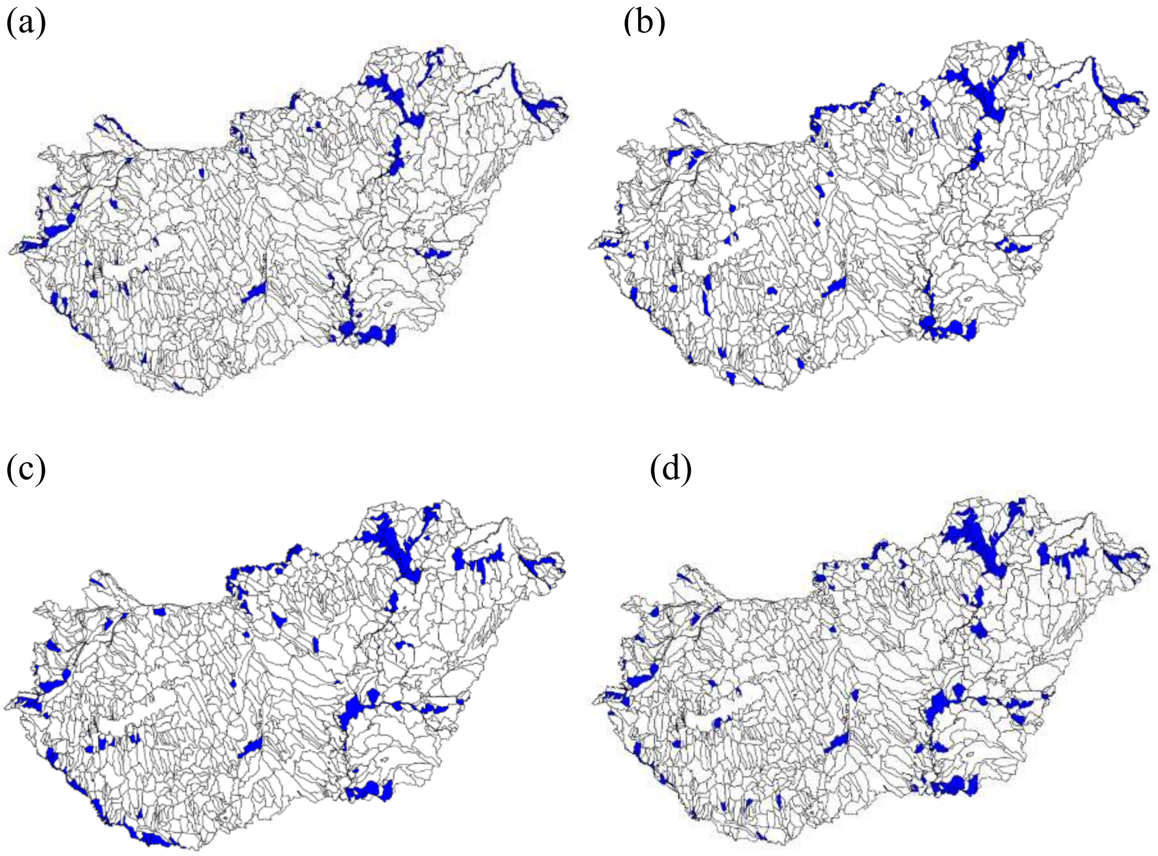

Fig. 4