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

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27

29 **Abstract**

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

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

**54 Introduction**

55 Despite their small spatial extent, freshwater ecosystems, and running waters in  
56 particular, maintain a disproportionately high amount of global biodiversity (Strayer and  
57 Dudgeon 2010). Freshwater biodiversity is also declining at an alarming rate that is far greater  
58 than those in the most affected terrestrial systems (Dudgeon et al. 2006). To effectively  
59 protect freshwater ecosystems, careful selection of conservation areas is urgently needed in a  
60 number of the world's biogeographic areas and ecoregions. Although conservation planning  
61 for freshwater habitats still lags far behind that of terrestrial and marine ecosystems (Abell et  
62 al. 2007; Strecker et al. 2011), significant progress has been made. To date, the majority of  
63 conservation planning examples for fresh waters have been dominated by measures of  
64 richness, rarity and conservation value of charismatic freshwater groups (e.g. Filipe et al.  
65 2004; Bergerot et al. 2008) or have used landscape level surrogates (i.e. habitat types, Higgins  
66 et al. 2005; Nel et al. 2007) to suggest areas for protection. Nevertheless, the key principles of  
67 systematic conservation planning (Margules and Pressey 2000), the most common approach  
68 used in the identification of conservation priorities worldwide, have also started to be  
69 increasingly applied in the selection of freshwater conservation areas (e.g. Esselman and Alan  
70 2011; Hermoso et al. 2011).

71 Briefly, systematic conservation planning (hereafter SCP) approaches optimise the  
72 selection of planning units (the basic units of the conservation selection procedure, e.g.  
73 subcatchments in freshwater systems) by minimising area and maximizing biodiversity  
74 representation (Pressey and Nicholls 1989). To achieve conservation targets at the minimum  
75 cost, complementarity based algorithms are used, which maximise the representativeness of  
76 biodiversity when a new site is added to an existing set of sites. Recent applications of SCP to  
77 riverine systems give special attention to connectivity among river segments, subcatchments  
78 or catchments to select priority areas for conservation (Moilainen et al. 2008; Hermoso et al.  
79 2011; Linke et al. 2012). Due to the longitudinal connectedness of rivers, the long-term  
80 persistence of freshwater biodiversity within a protected area strongly relies on the system's  
81 capacity to maintain some key ecological process (e.g. migrations) and the propagation of  
82 threats along the river network. Failing to adequately account for key ecological processes -  
83 essential for maintaining freshwater biodiversity over time - could therefore limit the success  
84 of conservation efforts in freshwater ecosystems (Saunders et al. 2002; Abell et al. 2007).  
85 The majority of existing protected areas were not established with consideration to freshwater

86 biodiversity or processes and subsequently fail to adequately protect these ecosystems and  
87 dependent species (Nel et al. 2007, 2009).

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

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

113

## 114 **Materials and methods**

### 115 *Study area*

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

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

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

133

#### 134 *Planning units and biodiversity data*

135 Our planning area was Hungary. We used Geographic Information Systems (GIS) to  
136 generate planning units (PUs) within Hungary, which consisted of 952 subcatchments  
137 (hereafter catchments) of streams and rivers and of Lake Balaton. The mean area ( $\pm$ SD) of  
138 individual catchments was 97.7 ( $\pm$ 117.6) km<sup>2</sup>.

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

146

#### 147 *Species distribution models*

148 Ideally, the distribution of all species across a study region would be known. However,  
149 data collection is expensive and time-consuming (Balmford and Gaston 1999), resulting in  
150 incomplete coverages for many species (Balmford and Gaston, 1999; Pressey 2004). To  
151 overcome the limited coverage of biological data, various methods have been proposed and  
152 used in conservation planning exercises across the globe (Pressey 2004). Here, we used a

153 predictive modelling framework, Multivariate Adaptive Regression Splines (MARS) to  
154 supplement observed sampling data by predicting the occurrence of species for each  
155 catchment. MARS is a flexible nonparametric regression method that is often used for  
156 modelling complex non-linear relationships between species occurrences and environmental  
157 data (Leathwick et al. 2005; Elith et al. 2006; Ferrier & Guisan 2006; Leathwick et al. 2006).  
158 MARS has been shown to be robust for predicting distributions for data-poor species, because  
159 data-rich species can help to inform models for these species (Ferrier & Guisan, 2006).

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

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

180 We fit a multiresponse MARS model with a generalised linear model (GLM) using the  
181 ‘earth package’ (Milborrow et al. 2014) in R (R Core Team 2013). In this procedure, a MARS  
182 model is fitted on the raw presence/absence data first, which results in the so called basis  
183 matrix of the MARS algorithm; then GLMs are invoked and fitted on the basis matrix to yield  
184 fitted values in a form of species occurrence probabilities (for a nice and concise description  
185 on how MARS works see Leathwick et al. 2006; Ferrier & Guisan 2006). To evaluate model  
186 performance, ten 3-fold cross validations (CV) (i.e. a total of 30 CV) were carried out during

187 model fitting. We also used the generalized coefficient of determination ( $GR^2$ ) to estimate the  
188 general performance of the model (i.e. predictive applicability on data different from the  
189 training data set). In other words,  $GR^2$  is an estimation of the  $R^2$  that would be expected to get  
190 when the fitted model were used to predict data independent from the training data. For more  
191 details see the help pages of the ‘earth’ package (Milborrow et al. 2014) and references  
192 therein.

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

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

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

215

### 216 *Conservation design*

217 We identified catchments of high potential conservation value using the conservation  
218 planning software MARXAN (Ball et al. 2009). MARXAN uses an optimization algorithm to  
219 maximize the representation of predefined conservation targets while minimizing the cost of  
220 including planning units. We used catchment area and a predefined amount of each species to

221 be represented in the final solution as cost and target in our design, respectively. Preliminary  
222 analyses at different target levels showed that even a relatively high target level, where each  
223 species occur in at least 30 catchments can be a feasible conservation strategy since even such  
224 an outcome does not require more space than the current total area of conservation reserves in  
225 Hungary and would require less space than 20% of the area of the country. Our final target  
226 was to represent 30 occurrences of each species, and we determined the cost, amount of  
227 catchment area needed to achieve this target.

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

241         The importance of connectivity in the optimization process can be weighted through a  
242 Boundary Length Modifier (BLM). When the BLM is set to 0, the selection of planning units  
243 happens without any consideration of connectivity relationships among the catchments. This  
244 may yield that valuable catchments are selected further from each other, which may harden  
245 the selection of both compact conservation areas and large connected catchments. In contrast,  
246 maximizing BLM increases the spatial clumping of the planning units (i.e. decreasing  
247 boundary length of the areas), which can happen at the expense of increasing cost (area of  
248 catchments) if the neighbouring catchments do not represent enough species to reach the  
249 defined conservation target. Consequently, careful selection of the BLM is necessary for  
250 optimizing between total area of catchments to reserve, their biodiversity value (species  
251 representation), and connectivity. To calibrate the BLM for further analyses (see Hermoso et  
252 al., 2011 for details), we evaluated the relationship between the amount of area protected and  
253 connectivity (increasing the value of connectivity through BLM). ). To do this, we evaluated  
254 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



255 for a given conservation scenario (for details see Hermoso et al. 2011). Note, that above the  
256 BLM value of 1.5 all units were selected by the program to keep the defined target level, and  
257 therefore we did not apply higher BLM values in the analyses. Although total area increased,  
258 the boundary value decreased considerably with increasing BLM values, showing that the  
259 selected priority areas were more compact when connectivity was considered more  
260 intensively among the catchments (results not shown). Because the BLM was stable at 0.1,  
261 we only report priority area outcomes for this value.

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

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

289

## 290 **Results**

### 291 *Species distribution modelling*

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

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

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

314 In the first scenario, all species achieved the target (i.e. all species were represented in at  
315 least 30 catchments), and the total area of selected PUs was 3683 km<sup>2</sup>. Neither Lake Balaton  
316 nor the catchments belonging strictly to the Danube were selected in the first scenario with the  
317 exception of one Danubian PU with 39 species (Fig. 3a). For Lake Balaton this was probably  
318 because the unit contained relatively common species (21 species, which occurred frequently  
319 in other catchments, too), relative to its size. Many other units contained equally high species  
320 richness to that of the Danube. Specifically, PUs belonging to the Tisza River catchment were  
321 selected as priority areas in the first scenario. Scenario 2, which excluded catchments of the  
322 Danube and Lake Balaton, did not substantially increase the total area of selected PUs to

323 achieve the same target as scenario 1. The required total area to achieve the conservation  
324 targets for all species was 3727 km<sup>2</sup>.

325         Regardless of the scenario, the total catchment area needed to achieve the conservation  
326 target increased with increased BLM values (i.e. increased catchment connectivity). For  
327 scenario 2 it was 4428 km<sup>2</sup> at a BLM value of 0.1 (Fig. 3b). Exclusion of the catchments  
328 belonging to the Tisza River (scenario 3) increased the total area up to 5693 km<sup>2</sup> at a BLM  
329 value of 0.1 (6.12 % of the territory of the country; Fig. 3c) to allow achieving the target level  
330 of minimum 30. Moreover, all species could still achieve this minimum target. The further  
331 exclusion of the Dráva and Ipoly Rivers from the SCP exercise (scenario 4) did not  
332 significantly change the required area either as it yielded a conservation area of 5225 km<sup>2</sup>  
333 (5.61 % of the territory of the country; Fig. 3d) at a BLM value of 0.1. However, the target  
334 level of 30 could not be fulfilled for all species in this scenario. For example, one species with  
335 high conservation value (*Romanogobio kessleri*) occurred only in 28 catchments after the  
336 exclusion of the Danube, Tisza, Dráva, Ipoly rivers, and therefore, this was the maximum  
337 reachable representation of this species in this SCP scenario.

338         Current protected areas (i.e. national parks and other conservation areas) cover only 9.1  
339 % of the country (8507 km<sup>2</sup>). We found a weak spatial overlap between priority areas  
340 identified across the different conservation planning scenarios and the current reserve system  
341 (Fig. 4), which ranged between 0.17 and 7.06 %. Moreover, when using SCP to extend the  
342 current reserve system, the catchment area selected remained below 20% of the country's  
343 total area, ranging between 11548 and 13709 km<sup>2</sup> (12.4 and 14.74 % of the country's total  
344 area) across the different scenarios.

345

## 346 **Discussion**

347         Here, we demonstrate the trade-offs between ease of implementation of conservation  
348 recommendations and its cost for freshwater systems shared across different jurisdictional  
349 units. We found that in order to achieve conservation targets within river systems completely  
350 within Hungary, we would require more area than if collaboration with neighbour countries  
351 for protecting very large rivers was feasible. Despite its higher cost we showed that freshwater  
352 fish species can be effectively protected in Hungary within the catchments of smaller rivers.  
353 Selection of conservation areas within catchments that belong to a single country avoids  
354 complex negotiations with other countries, which makes implementation of conservation  
355 more feasible. Our findings are particularly relevant to current conservation policy and  
356 decision making in Eastern and Central European countries that share the Danube. This is

357 because countries, responsible for different lengths of the Danube and other large rivers, have  
358 different priorities for freshwater conservation and possibly have variable budgets for  
359 conservation or international collaboration. However, we also show that transboundary  
360 collaboration with a reduced number of countries could significantly improve the  
361 effectiveness of protection. In fact, using Marxan and considering connectivity in the planning  
362 process allowed compromise, identifying solutions that both maintain fish diversity in  
363 different catchments and reduce dependence on transboundary collaboration.

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

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

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

405         After excluding the Danube and the Tisza Rivers from the analyses (i.e. scenario 1, 2  
406 and 3) a small number of highland and lowland rivers and their smaller tributaries became the  
407 core areas for freshwater conservation. Although scenario 4 can be a solution to minimize  
408 transboundary cooperation, we believe that scenario 3 (i.e. when some transboundary  
409 highland rivers are also retained for priority conservation areas) could be the best compromise  
410 solution for conserving freshwater fish in this ecoregion. From a conservation viewpoint,  
411 highland rivers host the most diverse and valuable riverine fish fauna in this ecoregion (Erős  
412 2007) with many protected and strictly protected species by national laws and international  
413 directives (e.g. Habitat Directive of the European Union). Transboundary highland rivers,  
414 such as the Dráva (between Hungary and Croatia) and the Ipoly (between Hungary and  
415 Slovakia) contain a large proportion of the overall population size of some Danubian endemic  
416 species (e.g. *Romanogobio kessleri*, *Sabanejewia aurata*, *Zingel streber*, *Zingel zingel*). Most  
417 catchments of these rivers were selected in scenario 1, 2 and 3 for inclusion in conservation  
418 areas. Further, the Dráva River also contains relatively abundant and stable populations of  
419 those protected species (i.e. *Gobio uranoscopus*, *Cottus gobio*) which are very rare in  
420 Hungary (Harka and Sallai 2004), and had to be discarded from the models due to their rarity.  
421 Unfortunately, the extent of highland rivers is low in the country. Therefore, efforts should be  
422 made to strengthen the cooperation between Hungary and Croatia and Slovakia to design  
423 transboundary freshwater protected areas for the catchments of highland rivers.

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

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

457 species of high conservation concern do actually occur in selected catchments, our analyses is  
458 verified.

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

468

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693 Table 1: Relative frequency of occurrence (i.e. prevalence) of the fish species in the training  
 694 data; and MARS–GLM performance. R2: coefficient of determination. GR2: generalized  
 695 coefficient of determination. AUC: area under the receiver operating curve averaged across  
 696 the results of ten 3-fold cross validations. Protected species are indicated with bold, and  
 697 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
<b>Alburnoides bipunctatus</b>	<b>albbip</b>	<b>0.23</b>	<b>0.23</b>	<b>0.16</b>	<b>0.74</b>	<b>0.05</b>
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
<b>Barbatula barbatula</b>	<b>ortbar</b>	<b>0.45</b>	<b>0.43</b>	<b>0.38</b>	<b>0.86</b>	<b>0.03</b>
Barbus barbus	barbar	0.17	0.29	0.22	0.8	0.05
<b>Barbus charpaticus*</b>	<b>barpel</b>	<b>0.09</b>	<b>0.36</b>	<b>0.31</b>	<b>0.84</b>	<b>0.06</b>
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
<b>Cobitis elongatoides</b>	<b>cobelo</b>	<b>0.58</b>	<b>0.16</b>	<b>0.09</b>	<b>0.67</b>	<b>0.05</b>
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
<b>Gobio gobio</b>	<b>gobgob</b>	<b>0.55</b>	<b>0.25</b>	<b>0.19</b>	<b>0.76</b>	<b>0.04</b>
<b>Gymnocephalus baloni</b>	<b>gymbal</b>	<b>0.08</b>	<b>0.22</b>	<b>0.15</b>	<b>0.82</b>	<b>0.06</b>
Gymnocephalus cernua	gymcer	0.17	0.09	0.01	0.68	0.06
<b>Gymnocephalus schraetser</b>	<b>gymsch</b>	<b>0.05</b>	<b>0.31</b>	<b>0.25</b>	<b>0.88</b>	<b>0.09</b>
<b>Leucaspius delineatus</b>	<b>leudel</b>	<b>0.17</b>	<b>0.04</b>	<b>-0.04</b>	<b>0.56</b>	<b>0.06</b>
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
<b>Leuciscus leuciscus</b>	<b>leuleu</b>	<b>0.24</b>	<b>0.18</b>	<b>0.11</b>	<b>0.72</b>	<b>0.05</b>
Lota lota	lotlot	0.12	0.34	0.29	0.83	0.05
<b>Misgurnus fossilis</b>	<b>misfos</b>	<b>0.29</b>	<b>0.12</b>	<b>0.05</b>	<b>0.68</b>	<b>0.05</b>
Perca fluviatilis	perflu	0.53	0.17	0.10	0.67	0.05
<b>Phoxinus phoxinus</b>	<b>phopho</b>	<b>0.11</b>	<b>0.11</b>	<b>0.03</b>	<b>0.76</b>	<b>0.05</b>
<b>Rhodeus sericeus</b>	<b>rhoser</b>	<b>0.62</b>	<b>0.16</b>	<b>0.08</b>	<b>0.67</b>	<b>0.03</b>
<b>Romanogobio kessleri*</b>	<b>romkes</b>	<b>0.03</b>	<b>0.13</b>	<b>0.05</b>	<b>0.84</b>	<b>0.10</b>
<b>Romanogobio vladykovi</b>	<b>romvla</b>	<b>0.27</b>	<b>0.21</b>	<b>0.14</b>	<b>0.72</b>	<b>0.04</b>
<b>Rutilus pigus virgo</b>	<b>rutpig</b>	<b>0.03</b>	<b>0.25</b>	<b>0.19</b>	<b>0.89</b>	<b>0.09</b>
Rutilus rutilus	rutrut	0.71	0.22	0.15	0.73	0.04
<b>Sabanejewia aurata</b>	<b>sabaur</b>	<b>0.10</b>	<b>0.20</b>	<b>0.13</b>	<b>0.79</b>	<b>0.05</b>
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
<b>Umbra krameri*</b>	<b>umbkra</b>	<b>0.07</b>	<b>0.08</b>	<b>0.00</b>	<b>0.78</b>	<b>0.06</b>
Vimba vimba	vimvim	0.12	0.14	0.06	0.74	0.06
<b>Zingel streber*</b>	<b>zinstr</b>	<b>0.04</b>	<b>0.21</b>	<b>0.14</b>	<b>0.87</b>	<b>0.11</b>

**Zingel zingel \***

<b>zinzin</b>	<b>0.06</b>	<b>0.31</b>	<b>0.25</b>	<b>0.86</b>	<b>0.06</b>
Mean ± SD	0.25 ±	0.21 ±	0.14 ±	0.76 ±	0.05 ±
	0.20	0.09	0.10	0.07	0.02

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## 701 APPENDIX A

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

Variable	Description	Min	Max	Mean $\pm$ 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. (dimensionless)	1.096	16.861	1.844 $\pm$ 1.101
[2,]"tot_riv_length"	Total length of the rivers within the PU. (km)	0.952	163.814	20.958 $\pm$ 18.980
[3,]"drainage_density"	Total length of the rivers within the PU divided by the area of the PU. (km/km <sup>2</sup> )	0.030	43.109	0.495 $\pm$ 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 $\pm$ 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 $\pm$ 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 $\pm$ 80.6
[7,]"ruggedness"	Average of the ruggedness index within the PU.	1.360	312.295	48.373 $\pm$

	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 <sup>2</sup> )	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 <sup>2</sup> )	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 <sup>2</sup> )	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

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720 Captions to figures

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

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

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

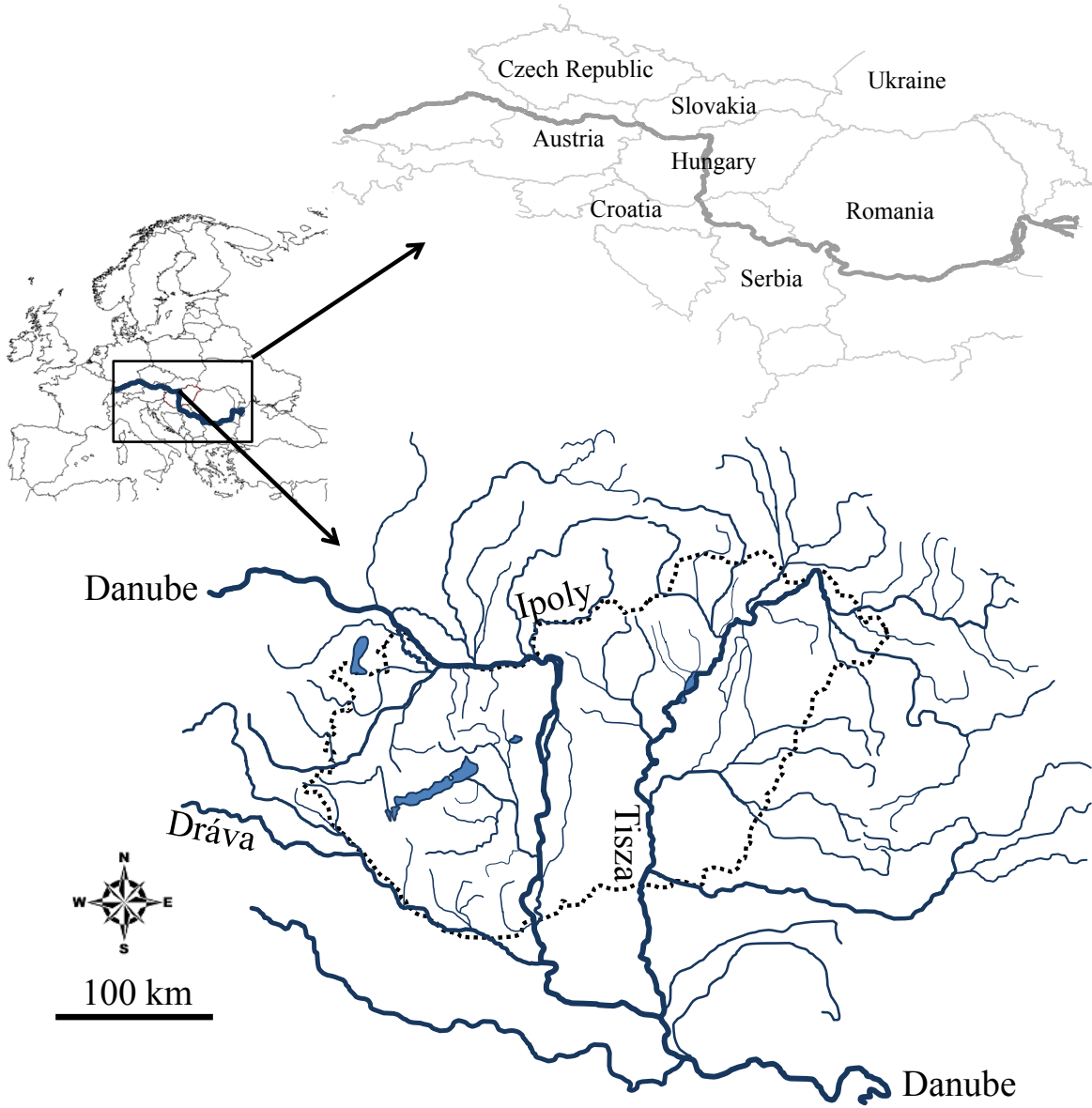
734 Fig. 4. A comparison between the selected freshwater and the current conservation areas in  
735 case of four scenarios (a) all catchments are included in the analyses including the Danube  
736 and Lake Balaton, (b) catchments belonging purely to segments of the Danube and Lake  
737 Balaton are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

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Fig. 1

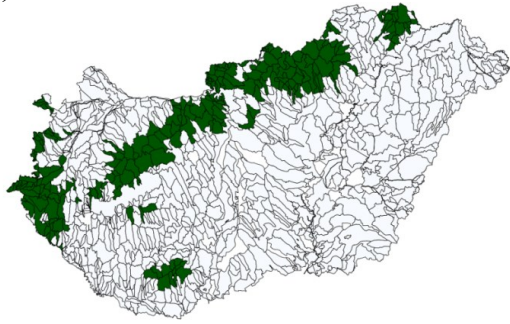


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Fig. 2

(a)



(b)



(c)



(d)

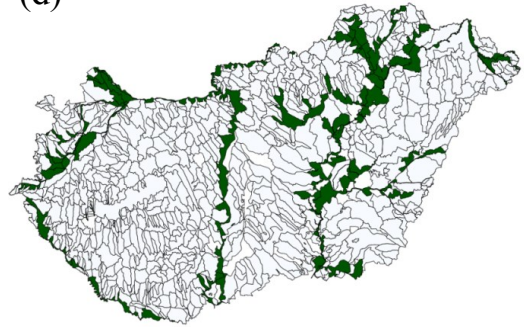


Fig. 3

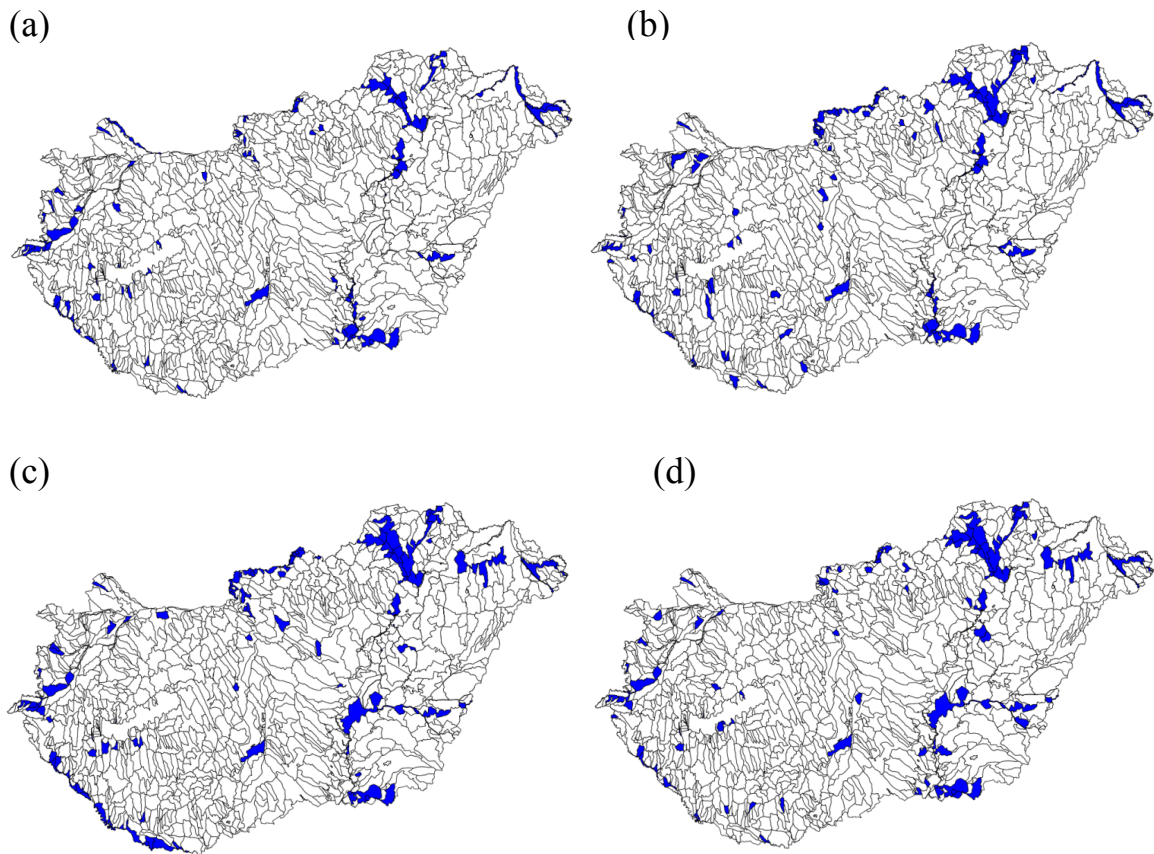


Fig. 4

