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4 **A Unified Model for Optimizing Riverscape Conservation**

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30 **Abstract**

- 31 1. Spatial prioritization tools provide a means of finding efficient trade-offs between
32 biodiversity protection and the delivery of ecosystem services. Although a large number
33 of prioritization approaches have been proposed in the literature, most are specifically
34 designed for terrestrial systems. When applied to river ecosystems, they often fail to
35 adequately account for the essential role that landscape connectivity plays in maintaining
36 both biodiversity and ecosystem services. This is particularly true of longitudinal
37 connectivity, which in many river catchments is highly altered by the presence of dams,
38 stream-road crossings, and other artificial structures.
- 39 2. We propose a novel framework for coordinating river conservation and connectivity
40 restoration. As part of this, we formulate an optimization model for deciding which
41 subcatchments to designate for ecosystem services and which to include in a river
42 protected area (RPA) network, while also deciding which existing river barriers to remove
43 in order to maximize longitudinal connectivity within the RPA network. In addition to
44 constraints on the size and makeup of the RPA network, the model also considers the
45 suitability of sites for conservation, based on a biological integrity index, and connectivity
46 to multiple habitat types. We demonstrate the usefulness of our approach using a case
47 study involving four managed river catchments located in Hungary.
- 48 3. Results show that large increases in connectivity-weighted habitat can be achieved
49 through targeted selection of barrier removals and that the benefits of barrier removal are
50 strongly depend on RPA network size. We find that (i) highly suboptimal solutions are
51 produced if habitat conservation planning and connectivity restoration are done separately
52 and (ii) RPA acquisition provides substantially greater marginal benefits than barrier
53 removal given limited resources.

54 4. *Synthesis and applications.* Finding a balance between conservation and ecosystem
55 services provision should give more consideration to connectivity restoration planning,
56 especially in multi-use riverscapes. We present the first modelling framework to directly
57 integrate and optimize river conservation and connectivity restoration planning. This
58 framework can help conservation managers to account better for connectivity, resulting in
59 more effective catchment scale maintenance of biological integrity and ecosystem services
60 delivery.

61

62 **Introduction**

63 One of the greatest challenges facing society today is the urgent need to halt the global
64 decline of biodiversity, while maintaining the capacity of ecosystem services for human well-
65 being (Bennett *et al.*, 2015). Various studies have investigated the complex relationship
66 between biodiversity and ecosystem services (Reyers *et al.*, 2012; Howe *et al.*, 2014). Ideally,
67 management actions should be designed to provide a wide range of benefits, both in terms of
68 conservation and ecosystem services (a win-win situation). Often, increased biodiversity
69 conservation can only be achieved at the loss of certain ecosystem services and vice versa (a
70 win-lose situation). This is frequently the case in heavily used, human dominated landscapes,
71 where environmental managers must make difficult choices between biodiversity and
72 ecosystem service provision (Palomo *et al.*, 2014).

73 A potential solution to this dilemma is to try to maximize the number of win-win and decrease
74 the number of win-lose situations by using spatial prioritization to find the best trade-off
75 between biodiversity protection and the delivery of ecosystem services (Cordingley *et al.*,
76 2016; Doody *et al.*, 2016). Such approaches, however, are still uncommon in practice. Most
77 spatial prioritization methods focus on the delineation of ecosystem service hotspots (i.e., by
78 selecting areas that are high in value for one or sometimes multiple services), rather than
79 explore potential conflicts and synergies between biodiversity and ecosystem services
80 (Cimon-Morin *et al.*, 2013; Schröter & Remme, 2016).

81 Looking specifically at prioritization in riverine ecosystems, a frequently neglected
82 consideration is the critical role that landscape connectivity plays in the maintenance of both
83 biodiversity and ecosystem services (Taylor *et al.*, 1993; Mitchell *et al.*, 2013). Rivers provide
84 a multitude of vital ecosystem services, such as water supply, navigation, hydropower,
85 fishing, and recreational opportunities (Vörösmarty *et al.*, 2010). Many of these services are
86 dependent on basic ecosystem processes, including species movements, genetic exchange, and

87 material and energy flows, which are all strongly regulated by longitudinal connectivity. At
88 the same time, the dendritic structure of rivers makes them particularly susceptible to
89 connectivity disruption (Grant *et al.*, 2007; Hermoso *et al.*, 2011), which, in turn, can
90 adversely impact ecosystem integrity. Indeed, river ecosystems are among the most threatened
91 worldwide, in large part because of the presence of large numbers of dams, stream-road
92 crossings, and other hydromodifications (Dynesius & Nilsson, 1994; Januchowski-Hartley *et*
93 *al.*, 2013).

94 To date, research on prioritizing river habitat protection and connectivity restoration actions
95 has progressed mostly along two separate paths. One line of enquiry concerns the
96 development of planning tools for prioritizing the repair/replacement/removal (i.e.,
97 mitigation) of artificial river barriers that impede aquatic organism passage, mainly fish, using
98 graph theory and optimization techniques (Erős *et al.*, 2011; Neeson *et al.*, 2015; King *et al.*,
99 2017). A separate strand of research has focused on applying reserve selection methods
100 (Moilanen *et al.*, 2008; Newbold & Siikamäki, 2009; Linke *et al.*, 2012, Hermoso *et al.*,
101 2017) to the design of freshwater conservation networks. Within this latter group,
102 connectivity, when it has been considered, is incorporated in a fairly simplistic manner by
103 trying to ensure that selected areas (usually subcatchments) are spatially adjacent. In neither
104 of these two research themes has the potential presence of instream barriers and their
105 associated impacts on longitudinal connectivity been addressed together with conservation
106 planning.

107 In this study, we address this shortcoming by proposing a novel approach to systematic river
108 conservation and connectivity restoration planning. More specifically, we formulate a model
109 for jointly optimizing the selection of river protected areas and barrier removals. Given a set
110 of biodiversity elements (i.e., habitat classes) in need of conservation, the aim of the model is
111 to maximize longitudinal connectivity between selected areas through targeted barrier

112 removals, subject to lower/upper limits on the amounts of protected habitat and a cap on the
113 number of barrier removals. The model adopts a limiting factors approach, in which
114 connectivity of any given river protected area is based on the minimum level of connectivity
115 to any other habitat class. We subsequently demonstrate the usefulness of our model using a
116 case study involving four river catchments located in Hungary.

117 Underpinning our optimization model is a conceptual model (Fig. 1) that provides general
118 guidelines on how to systematically plan out management actions in the context of
119 biodiversity protection and ecosystem services delivery. The conceptual model combines
120 three main steps: 1) establishment of biodiversity and ecosystem service indicators; 2)
121 definition of a suitable connectivity metric; and 3) application of a spatially explicit
122 prioritization approach to efficiently allocate land use and connectivity restoration
123 management actions.

124 The first step is to develop a set of “indicators” of biodiversity and ecosystem services,
125 namely the key biological/physical elements of a system that help to maintain biodiversity and
126 ecosystem services and the various pressures that degrade ecosystem structure and function
127 (Grizetti *et al.*, 2016; Maes *et al.*, 2016). For example, physical and chemical water quality,
128 land use type, invasive species threats, and the presence of in-stream barriers can provide
129 useful indicators of overall ecosystem health in freshwaters (Nelson *et al.*, 2009, Terrado *et*
130 *al.*, 2016; Vital-Abarca *et al.*, 2016).

131 The next step is to assess the role of connectivity in relation to biodiversity and ecosystem
132 services regulation in a particular system and to propose a metric that adequately describes
133 connectivity. An important consideration is the role of connectivity in producing trade-offs
134 between biodiversity and various ecosystem services. Although connectivity is critical for the
135 structuring and functioning of natural ecosystems, its importance to the delivery of ecosystem
136 services varies greatly. In stream ecosystems, for example, connectivity is critically important

137 for the dispersal of fish species, which are key components of ecosystem function and provide
138 various ecosystem services (e.g., recreational and commercial fishing, aesthetic value, see
139 Holmlund & Hammer, 1999). On the contrary, connectivity may be less important for the
140 provision of urban/agricultural water supply or for electricity, where, in fact, the damming of
141 rivers is the main way these are supplied (Auerbach *et al.*, 2014; Grizetti *et al.*, 2016).

142 With regard to the choice of a suitable connectivity metric, this depends on basic
143 characteristics of the system. In terrestrial applications, the adjacency/compactness of spatial
144 units makes intuitive sense (McDonnell *et al.*, 2002; Nalle *et al.*, 2002). In riverine systems,
145 however, connectivity between two different points in a river is dictated by the river's flow
146 paths, making indices like the Dendritic Connectivity Index (Cote *et al.*, 2009), which take
147 into account the passability of in-stream barriers, much more suitable (Erős *et al.*, 2012).

148 Lastly, because resources for conservation and connectivity restoration are limited, it is
149 essential for landscape management to allocate resources in the most efficient way possible.

150 The recommendation to use a spatially explicit prioritization approach leaves two reasonable
151 alternatives: graph theory models (Erős *et al.*, 2011) and optimization models (King *et al.*,
152 2017). Optimization has the distinct advantage over graph theory in being prescriptive rather
153 than descriptive (King & O'Hanley, 2016), meaning that it produces a recommended course
154 of action that aims for the best allocation of limited resources to maximize benefits (i.e.,
155 biggest bang for the buck). Moreover, optimization models are perfectly suited to balancing
156 multiple, potentially competing goals, thus making them ideal for driving negotiation among
157 decision makers and delivering more win-win scenarios that promote biodiversity protection
158 and ecosystem services provision.

159

160 **Materials and Methods**

161 *Study Area*

162 We selected four river catchments located in Hungary for our study (Fig. 2). These include
163 Lake Balaton (5775 km²), the Marcal River (3084 km²), the Sajó River (5545 km²), and the
164 Zagyva River (5677 km²). Catchments differ considerably in terms of the mix of land uses,
165 stream habitat type, and number of artificial barriers present (Tab. 1). The dominant land
166 cover type is agricultural (mainly arable land, vineyards to a smaller extent), but deciduous
167 forests, pastures, grasslands, and wetlands are also present. Urbanization is primarily confined
168 to small cities and villages. River habitat can be categorized into five broad types: lowland
169 river, lowland stream, highland river, highland stream, and submontane stream (Erős, 2007).

170 *Biodiversity and Ecosystem Services Indicators*

171 Conservation area selection methods often use simple biological diversity indicators as
172 proxies of conservation value (e.g., richness, species occurrences, endemism, species
173 composition). Rarely is attention given to the biological integrity of the ecosystem, even
174 though this may be a better indicator of a particular location's value for conservation purposes
175 (Angermeier & Karr, 1994; Karr, 1999; Peipoch *et al.*, 2015). According to Angermeier and
176 Karr (1994), "diversity is a collective property of system elements, integrity is a synthetic
177 property of the system." Diversity quantifies the variety of items in the system (e.g., species
178 richness, number of functional forms), whereas integrity refers to the number of components
179 (diversity) and the processes that contribute to the continued functioning of the system in a
180 natural state. In this sense, integrity emphasizes the degree to which a system has been altered
181 from its natural (i.e., undisturbed) state (Hawkins *et al.*, 2000; Pont *et al.*, 2006). An
182 ecosystem with high integrity indicates that natural ecological, evolutionary, and
183 biogeographic processes are intact (Angermeier & Karr 1994; Angermeier 2000; Beechie *et*
184 *al.*, 2010). Although biodiversity and biological integrity are often confused, it is important to
185 distinguish between the two, especially in the context of examining biodiversity/integrity and

186 ecosystem service relationships. For example, a reservoir created by the presence of a dam
187 may have higher biodiversity than a free-flowing stretch of river because of the occurrence of
188 both lotic and lentic species (especially waterbirds and macrophytes, which are normally less
189 abundant in undisturbed lotic areas). Stream segments impounded by a reservoir can also be
190 valuable for the provision of ecosystem services (e.g., water storage/withdrawal and
191 recreational fishing), but clearly have lower biological integrity compared to natural stream
192 segments (Beechie *et al.*, 2010; Thorp *et al.*, 2010; Auerbach *et al.*, 2014).

193 We quantified the biological integrity of stream segments and their associated subcatchments
194 using five indicators of conservation quality and naturalness. These include: 1) land use
195 intensity; 2) absolute conservation value for fish fauna; 3) relative conservation value for fish
196 fauna; 4) biological integrity of fish fauna; and 5) biological water quality. Land cover
197 categories are important indicators of ecosystem services (Grizetti *et al.*, 2016; Maes *et al.*,
198 2016). In this study, we used the land use index (LUI) of Böhmer *et al.* (2004), which
199 describes land use intensity and impact within a catchment along a gradient from natural
200 forest cover to agricultural and urban use. The index, which has been used in other studies
201 (e.g., Ligeiro *et al.*, 2013), is calculated as follows:

$$\text{LUI} = \% \text{ pasture} + 2 \times \% \text{ arable land} + 4 \times \% \text{ urban area}$$

202 Fish assemblages are frequently used for selecting conservation areas in riverine ecosystems
203 (Filipe *et al.*, 2004; Sowa *et al.*, 2007). Fish are also an important focus for river connectivity
204 restoration. The absolute (ACV) and relative (RCV) conservational value of fish fauna in each
205 stream segment was determined using the index of Antal *et al.* (2015). To calculate ACV,
206 increasing weights were assigned to fish taxa according to their extinction risk as follows:

$$\text{ACV} = 6n_{\text{EW}} + 5n_{\text{CR}} + 4n_{\text{EN}} + 3n_{\text{VU}} + 2n_{\text{NT}} + n_{\text{LC}}$$

207 Here, n_{EW} is the number of extinct species in the wild, n_{CR} is the number of critically
208 endangered species, n_{EN} is the number of endangered species, n_{VU} is the number of
209 vulnerable species, n_{NT} is the number of near threatened species, and n_{LC} is the number of
210 least concern species (see Erős *et al.*, 2011, Antal *et al.*, 2015). To calculate RCV, the
211 absolute value was divided by the total number of species. Similar approaches for other
212 taxonomic groups can be found in the literature (Fattorini, 2006).

213 Biological integrity of fish assemblages (BIF) was determined using the method of Sály and
214 Erős (2016). BIF quantifies the degree of alteration of fish assemblages compared to near-
215 natural (reference) fish assemblages based on the structural and functional properties of the
216 fish fauna and their responses to different stressors (i.e., land use, water quality, and
217 hydromorphological alteration). Conceptually, BIF is similar to many other fish based biotic
218 indices (Roset *et al.*, 2007). Additional information about how BIF was determined are
219 provided in an online appendix (see Appendix S1, Supporting Information).

220 Biological water quality (BWQ) is an integrative measure of the overall quality of the water
221 for biota. Following procedures established by the EU Water Framework Directive, biological
222 water quality was determined using the worst quality class value of five biological quality
223 indices, which measure biological water quality based on the taxonomic and functional
224 structure of benthic and water column algae, macrophytes, macroinvertebrates, and fish (Birk
225 *et al.*, 2012). Further details about BWQ are discussed in an online appendix (see Appendix
226 S1, Supporting Information).

227 All five indices (LUI, ACV, RCV, BIF, and BWQ) were measured on a 5-point scale. An
228 aggregate biological integrity index (BII) was then determined for each stream segment by
229 taking the median of the five indices (Erős *et al.*, 2018). Stream segments with high biological
230 integrity scores represent locations with higher biodiversity conservation value. They are also

231 essential for various regulatory (e.g., natural nursery areas) and cultural (e.g., recreational
232 hiking) ecosystem services (Grizetti *et al.*, 2016; Vital-Abarca *et al.*, 2016).

233 Besides the quantification of biological integrity, we also used several pressure indices to
234 identify areas within the river networks that may be better suited for alternative uses other
235 than conservation and connectivity restoration. This includes subcatchments with a high
236 urban/agricultural land use index and those where fish ponds, reservoirs, and waste water
237 treatment plants are present. Such areas are often primarily devoted to agriculture/aquaculture,
238 recreational fishing, flood control, or other ecosystem service uses and usually have low
239 biological integrity anyway (a clear win-lose situation). Based on this initial screening
240 process, all subcatchments deemed unsuitable for conservation/connectivity restoration *a*
241 *priori* were assigned a BII value of zero (Fig. 2).

242 *Barrier Survey Data*

243 Barrier locations were extracted from a geo-database developed by the National Water
244 Authority of Hungary. The database includes GPS referenced location information, structure
245 type (e.g., dam, road crossing, sluice), and binary passability values of potential artificial
246 barriers to fish movements. During field surveys, we further refined and updated this database
247 for the four catchments in our case study during the summer and autumn of 2016 (July to
248 November). We verified the exact location of barriers (Fig. 2), measured basic structural data,
249 and estimated upstream-downstream passability. A road network map was also used to
250 identify the location of bridges and estimate passability values for this type of barrier. In the
251 field, we determined for each barrier its height, length, and slope, type (e.g., sluice, weir, dam,
252 culvert, bridge), primary construction material (e.g., concrete, rock with concrete),
253 internal/overflow water velocity, and substrate percentages (rock, stone, gravel, sand, silt, and
254 concrete) both downstream and upstream of the barrier “wall.”

255 To estimate upstream barrier passabilities for adult cyprinids (the dominant fish species in our
256 study area), we used the rapid barrier assessment methodology described in King *et al.*
257 (2017). Passability represents the fraction of fish (in the range 0-1) that are able to
258 successfully negotiate a barrier in a particular direction. Each barrier assessed in the field (n =
259 703) was assigned one of four passability levels: 0 if a complete barrier to movement; 0.3 if a
260 high-impact partial barrier, passable to a small portion of fish or only for short periods of
261 time; 0.6 if a low-impact partial barrier, passable to a high portion of fish or for long periods
262 of time; and 1 if a fully passable structure (these latter structures were subsequently excluded
263 from analysis). We estimated adult cyprinid passability under both normal flow conditions
264 and bankfull width conditions. Bankfull width levels were clearly visible from the shape of
265 the channel and the location of riparian vegetation (Gordon *et al.*, 1992). For barriers that
266 could not be surveyed because of logistical difficulties (n = 101), we assigned the median
267 passability values for a given barrier type.

268 Our surveys revealed the dominant types of barriers were stepped weirs, notched weirs (for
269 flow measurement), small fishpond dams, large reservoir dams (for irrigation and water
270 supply), and sluices. Contrary to many other countries (e.g., the US) where road culverts
271 represent the main barrier type (Januchowski-Hartley *et al.*, 2013), such barriers are relatively
272 rare across Hungary (<1% of barriers surveyed). We also found that passability estimates
273 were very similar regardless of normal versus bankfull width flow conditions. Consequently,
274 we used passabilities under normal flow conditions for assessing river connectivity. Further,
275 given that 95% of surveyed bridges were fully passable, we excluded this type of barrier in
276 our analysis.

277 *River Protection and Connectivity Optimization Model*

278 To design efficiently a river protected area (RPA) network, we developed a spatial
279 optimization model to decide: 1) which subcatchments to include within the RPA network and

280 2) which barriers to mitigate (i.e., remove, repair, install with a fish pass, etc.) to maximize
281 longitudinal connectivity of the RPA network. Unlike existing optimization based methods
282 for designing RPA networks, conservation planning and connectivity restoration are made
283 simultaneously and their interactive effects were accounted for within our model. Full
284 mathematical details of the model are provided in an online appendix (see Appendix S2,
285 Supporting Information).

286 In brief, we assume that a study area is composed of one or more large, self-contained
287 catchments, with each catchment made up of potentially multiple subcatchments. Any spatial
288 resolution can be considered, from a few large subcatchments down to many small
289 subcatchments. Although a subcatchment is the main selection unit, we do not necessarily
290 assume that an entire subcatchment must be fully protected, just the river segments within a
291 selected subcatchment. The conservation value of river segments is based on a weighted
292 combination of the amount of habitat (i.e., length) and biological integrity (i.e., BII).

293 Longitudinal connectivity is quantified using a novel extension of the dendritic connectivity
294 index (DCI) proposed by Cote *et al.* (2009). More specifically, we evaluate DCI at the local,
295 segment-level scale (Mahlum *et al.* 2014) separately for each habitat type (lowland river,
296 lowland stream, highland river, highland stream, and submontane stream) and then take the
297 *minimum* value as an overall measure of segment connectivity. In this way, our model adopts
298 a “limiting factors” approach by focusing on the habitat type in shortest supply.

299 There are a number of constraints considered within the model for modifying the size and
300 makeup of the RPA network. These include:

- 301 (i) An upper limit on the size of the RPA network (i.e., the RPA network must be less
302 than or equal to some fraction of available river habitat).

303 (ii) There must be a certain mix of habitat types within the RPA network (i.e., the
304 fraction of each river habitat type must be greater than or equal to a specified
305 threshold).

306 (iii) A constraint on the number of barrier removals.

307 For our case study, we considered two barrier mitigation options: 1) full barrier removal, with
308 passability restored to 1 and 2) partial barrier removal, with passability restored to 0.5 if
309 passability currently less (Noonan *et al.*, 2012). We assumed full removal was possible only if
310 a barrier was located in the RPA network. For a barrier outside the RPA network, only partial
311 removal was available under the presumption that the barrier was essential in providing other
312 ecosystem services (e.g., irrigation and water supply).

313 Our basic model includes separate constraints for RPA size and number of barrier removals
314 (constraints (i) and (iii) above). Given cost estimates for barrier removal and RPA land
315 acquisition, these can be easily replaced by a single budget constraint on overall cost. To
316 explore this option, a figure of €5000 per ha was used for RPA purchase (based on the cost of
317 prime agriculture land), €400k for full barrier removal, and €200k for partial barrier removal.
318 As the cost of acquiring an entire subcatchment is prohibitively expensive, we assumed that
319 only riparian areas within a 30 m distance of selected river segments had to be purchased.
320 Studies have indicated that ≥ 30 m buffer strips are generally sufficient to protect most aquatic
321 species (Lee *et al.*, 2004).

322

323 **Results**

324 BII values varied widely both within and among the catchments (Fig. 2). In general, the
325 Balaton Catchment contained a high number of subcatchments with low or zero BII values,
326 indicating that a large part of this catchment is not ideally suited for conservation but other

327 land use functions instead. The Sajó Catchment, on the other hand, contained the highest
328 number of subcatchments with high BII values.

329 Maximum connectivity-weighted habitat for different sized RPA networks varied as a
330 function of the number of full/partial barrier removals (Fig. 3). Even with a small number of
331 barrier removals, impressive gains in connectivity-weighted habitat could be achieved. For
332 example, with a moderate sized RPA network comprising 40% of selectable river length
333 ($\theta = 0.4$), connectivity-weighted habitat increased by more than 100% (from a baseline value
334 of 1355.46 to 2813.28) when just 6 barriers were removed. In fact, strong diminishing returns
335 were observed as the number of barrier removals increased, as indicated by the concaved
336 shapes of the connectivity-weighted habitat versus barrier removal curves. Further, the
337 benefits of barrier removal were proportional to the size of the RPA network. For example,
338 for the smallest sized network encompassing 10% of selectable river length ($\theta = 0.1$), the
339 removal of 4 barriers resulted in a 26% increase in connectivity-weighted habitat. In contrast,
340 for a much larger sized network incorporating 60% of selectable river length ($\theta = 0.6$), the
341 removal of 4 barriers resulted in a 132% increase in connectivity-weighted habitat.

342 To investigate how equitably protection resources are allocated among the different river
343 catchments (Balaton, Marcal, Sajó, and Zagyva), we determined the fraction of the RPA
344 network contained in each catchment for selected values of θ given no barrier removal versus
345 an unrestricted number of barrier removals (Figs. 4 and 5). We found that both network size
346 and barrier removals strongly influenced the spatial pattern of selected subcatchments. For the
347 smallest sized reserve network ($\theta = 0.1$), protection resources are concentrated almost
348 entirely in the Balaton (95%) regardless of whether barriers can be removed or not (Figs. 4a,
349 4b, and 5a). At the other extreme, the possibility of removing barriers also does not appear to
350 dramatically alter the spatial distribution of the largest sized network ($\theta = 0.9$), with a much
351 more even spread among catchments appearing with and without barrier removal. For the

352 intermediated sized networks ($\theta = 0.3, 0.5, 0.7$), the pattern is more complex. Without barrier
353 removals (Fig. 4a), the distribution of protected habitat among catchments becomes
354 progressively more balanced with increasing RPA network size. With barrier removals (Fig.
355 4b), conservation resources are directed out of the Zagyva and Balaton and into the Marcal
356 ($\theta = 0.3$) and then the Sajó ($\theta = 0.5, 0.7$; see also Fig. 5b).

357 The clear preference for concentrating conservation resources in the Balaton for the smallest
358 sized RPA network is somewhat surprising given that it is one of the most well-developed
359 areas in Hungary in terms of urbanization, aquaculture, and tourism and has a barrier density
360 (number of barriers per length of river) more than double that of any other catchment (Tab. 1).
361 Nevertheless, the Balaton is an ideal location for constructing an RPA network given very
362 limited conservation resources; it contains a significant proportion of three out of five habitats
363 types (i.e., highland stream, lowland stream, and lowland river) and a particularly favorable
364 arrangement of mostly well-connected river segments. The only way for the allocation of
365 conservation resources to dramatically shift is by modifying the basic design of the RPA
366 network (i.e., by adjusting the minimum percentage of each habitat type). Overall, the two
367 least common habitats in the four catchments are submontane stream (5.6%) and lowland
368 river (6.6%). Doubling the minimum fraction of these habitats from 80% to 160% (i.e., setting
369 $\alpha = 1.6$ for these two habitat types and leaving the others at 0.8), the Balaton would account
370 for a greatly reduced, albeit still high, share (59-64%) of the $\theta = 0.1$ sized RPA network (see
371 Appendix S3, Supporting Information). Putting very high α weights on submontane streams
372 and highland rivers, the two least common habitat types in the Balaton, would similarly
373 reduce the amount of resources allocated to the Balaton (results not shown). These examples
374 demonstrate the flexibility of the model with regard to finding alternative solutions that meet
375 management needs. They also show that when optimizing limited conservation/restoration
376 resources, rather counterintuitive results can sometimes be obtained. For example, each

377 catchment contains roughly similar amounts of river length eligible for conservation (Tab. 1),
378 with the Balaton, Marcal, Sajó, and Zagyva contributing 22%, 19%, 33%, and 26% of the
379 total, respectively. Yet the fraction of river habitat conserved in each catchment can be very
380 far from equal depending on the size of the RPA network and the barrier removal budget.

381 We also wanted to ascertain the importance of coordinating river protection and barrier
382 removal decisions. There is considerable variability in relative connectivity-weighted habitat
383 gain when river protection decisions are made first and barrier removal decisions second (Fig.
384 6). Note that solutions for $b = 0$ and $\theta = 1$ are not considered, as these will always be
385 optimal using a two-stage approach. Results showed that river protection and restoration
386 decisions are strongly interdependent (Fig. 6). By optimizing barrier removal decisions
387 separately from river protection decisions, far less connectivity-weighted habitat is obtained,
388 with the effect exacerbated as the size of the reserve network increases. For smaller sized
389 networks ($0.1 \leq \theta \leq 0.3$), 68-91% of maximum connectivity-weighted habitat can be
390 achieved (interquartile range) across all barrier removal scenarios. For moderate and large
391 sized networks ($0.4 \leq \theta \leq 0.9$), however, the opportunity cost of sequential decision making
392 are much higher, with only 57-76% of the maximum being achieved (interquartile range). In
393 the worst case, just 52% of the maximum is achieved, demonstrating that highly suboptimal
394 solutions may be obtained if river protection and connectivity restoration decisions are not
395 properly coordinated.

396 Lastly, we wanted to examine the relative effectiveness of barrier mitigation against RPA land
397 purchases. To do this, we modified our basic model by first including estimates for barrier
398 removal and land purchase costs and then used a single budget for overall cost (in place of
399 separate budgets for land acquisition and barrier removal). Connectivity-weighted habitat
400 increased in a roughly linear fashion with budget (Fig. 7a). This differed from the strong
401 diminishing returns observed for our basic model with fixed RPA size and an increasing

402 number of barrier removals (Fig. 3). RPA land purchases made up the majority of total spend
403 regardless of budget (Fig. 7b). At lower budgets (€5-30M), RPA land purchases accounted for
404 up to 93% of total cost. As budget increased, this percentage decreased but never below 73%
405 of total cost (at €100M). These results suggest that RPA acquisition provide substantially
406 greater marginal benefits than barrier removal, especially if resources are limited.

407 **Discussion**

408 In this study, we demonstrate the benefits of combining river protection and connectivity
409 restoration planning in multi-use riverscapes. As with other related work (Doody *et al.*, 2016;
410 Zheng *et al.*, 2016), our framework recognizes the need for a spatially informed and strategic
411 approach to the selection of different land uses for the catchment level delivery of biodiversity
412 protection and ecosystem services. Our framework is noteworthy in being the first to directly
413 incorporate connectivity restoration planning into the prioritization process using an
414 optimization based approach. Our methodology attempts to unify systematic reserve selection
415 planning with connectivity restoration planning, thus providing a powerful tool to help guide
416 protection of river ecosystems. Optimization approaches, such as ours, are specifically
417 designed to find the best allocation of limited resources to achieve one or more planning
418 goals. They are also useful for generating Pareto optimal trade-off curves, which can reveal
419 how conservation and other objectives vary with different levels of investment (Neeson *et al.*,
420 2015).

421 Unlike some other connectivity optimization models (O’Hanley, 2011; Neeson *et al.* 2015),
422 our model considers the importance of maintaining access to multiple types of habitat.
423 Different riverine habitat types usually maintain different communities (Higgins *et al.*, 2004;
424 Erős, 2007). Diversification of habitat types within an RPA network can help to ensure the
425 maximization of biodiversity (including community types). At regional scales, the common-
426 sense approach (as we have done here) is to select habitats in proportion to their natural

427 proportions within the landscape. This ensures that habitat complexity within the protected
428 area network mirrors that of the wider landscape and that a natural pattern of biodiversity is
429 maintained (Beechie *et al.*, 2010; Thorp *et al.*, 2010; Peipoch *et al.*, 2015). Nevertheless, our
430 model provides decision makers with full flexibility in terms of specifying the composition of
431 an RPA network. For example, from the viewpoint of connectivity restoration for potamal fish
432 species, there is usually a preference for protecting mid- to high-order streams (King *et al.*,
433 2017). Conversely, with future climate change likely to exert the strongest influence on
434 headwater streams (Isaak *et al.*, 2010), it is conceivable that one would prefer to protect
435 climatically threatened low order streams. Either of these scenarios could be easily
436 accommodated for by our model (i.e., by adjusting the habitat fractions α_h and or the segment
437 weights w_s).

438 Results from our case study of four Hungarian river catchments show that impressive
439 increases in connectivity-weighted habitat can be achieved through targeted selection of
440 barrier removals, corroborating the findings of other studies (Cote *et al.*, 2009; Branco *et al.*,
441 2014; Neeson *et al.*, 2015). We also observed that the benefits of barrier removal strongly
442 depend on RPA network size – for the same number of barrier removals, significantly larger
443 gains in connectivity-weighted habitat are produced as the size of the RPA network increases.
444 This is because with larger RPA networks, a much larger number of subcatchments can
445 potentially be selected, thus providing greater leeway as to which subcatchments to protect
446 and how to connect them up through barrier removal. Our results show that outcomes are
447 markedly poorer if habitat conservation and connectivity restoration decisions are made
448 separately. In the worst case, only 52% of maximum connectivity-weighted habitat is
449 achieved using a two-stage approach where conservation decisions are made first, followed by
450 barrier removal decisions. We also found that RPA land purchases provide substantially

451 greater benefits compared to barrier removals. Using a single budget for RPA acquisition and
452 barrier removals, RPA purchase always made up the bulk of spend, ranging from 73 to 93%.

453 We found that the allocation of conservation resources were sometimes very unevenly
454 distributed among different catchments. For example, for the smallest sized RPA network
455 comprising 10% of selectable river length, 95% is concentrated in Lake Balaton. Although
456 focusing on one or few target areas may make sense from a resource efficiency standpoint, it
457 can be cause for concern from a social equitability viewpoint (Halpern *et al.*, 2013). To
458 address this, additional constraints could easily be added to our model to ensure each
459 catchments receives a certain minimum level of protection. Added justification for adopting a
460 more balanced allocation of resources might be provided if further analysis showed that
461 overall connectivity-weighted habitat only marginally decreased as a result of including these
462 supplemental constraints.

463 Our case study was framed at the multi-catchment scale, as opposed to an individual
464 catchment (Milt *et al.*, 2017). Previous studies have shown that great efficiency is attained
465 from planning at large spatial scales (Neeson *et al.*, 2015). From a practical standpoint,
466 however, it may be necessary to carry out planning on a catchment by catchment basis. For
467 example, our results suggest that conservation and close-to-nature forest management might
468 be the best land use functions in large parts of the Sajó Catchment, whereas agricultural land
469 use might be better suited in most part of the Zagyva and Marcal Catchments and in the
470 southern part of the Balaton Catchment. In the Sajó Catchment, forestry is already the main
471 land use function in several subcatchments and consequently, outdoor tourism (e.g., hiking,
472 recreational fishing) could be developed further in this region, while still conserving
473 biodiversity (a win-win solution). In the other catchments, where agriculture is the main land
474 use, managers should be able to easily identify those subcatchments that are the most valuable
475 for conservation, and then subsequently use our framework in the land use selection process.

476 Our modelling approach provides a set of solutions for prioritizing river conservation and
477 connectivity restoration actions based on pre-specified resources and design criteria.
478 However, in a real-world planning situation, modelling and evaluation should be done in an
479 iterative fashion, with active involvement of decision makers (Jax *et al.*, 2013; Grizetti *et al.*,
480 2016; McKay *et al.*, 2017, Moody *et al.*, 2017) in setting model parameters and performing
481 what-if analyses. For example, as our case study showed, which subcatchments are selected
482 can depend largely on the size of the RPA network and barrier removal budget. This suggests
483 that land use planners and stakeholder groups (e.g., water authorities, national park
484 authorities, fisheries groups) should ideally be involved in specifying the spatial extent of the
485 analysis, determining realistic conservation targets / barrier removal budgets, and in
486 evaluating how well conservation and ecosystem service needs are met. Their involvement
487 would be particularly useful if more reliable data could be provided on land acquisition and
488 barrier removal cost to help refine the analysis. Also, because outcomes will strongly depend
489 on the set of ecosystem services (and indicators) used in the analyses (Nelson *et al.*, 2009),
490 involvement of planners and stakeholders groups in the earliest phases of the planning
491 procedure is essential (Jax *et al.*, 2013).

492 Finding a balance between conservation and ecosystem services provision is a complex and
493 difficult task. There is no a single holy-grail solution that can be used to meet this need
494 (Prager *et al.*, 2012; Terrado *et al.*, 2016). The modelling framework presented in this paper
495 will invariably help conservation management to better account for connectivity restoration in
496 conservation planning, resulting in more effective catchment scale maintenance of biological
497 integrity and ecosystem services of riverscapes.

498

499 **Authors' Contributions**

500 TE, JO'H, and IC conceived and designed the study. IC and TE collected and analyzed
501 primary research data; JO'H developed the optimization model and performed analyses of
502 model results. TE and JO'H led writing of the manuscript. All authors contributed to editing
503 manuscript drafts and gave final approval for publication.

504

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511 helpful comments made on an earlier draft of this paper.

512

513 **Data Accessibility**

514 Data available from the Dryad Digital Repository. DOI: doi:10.5061/dryad.41pj936

515

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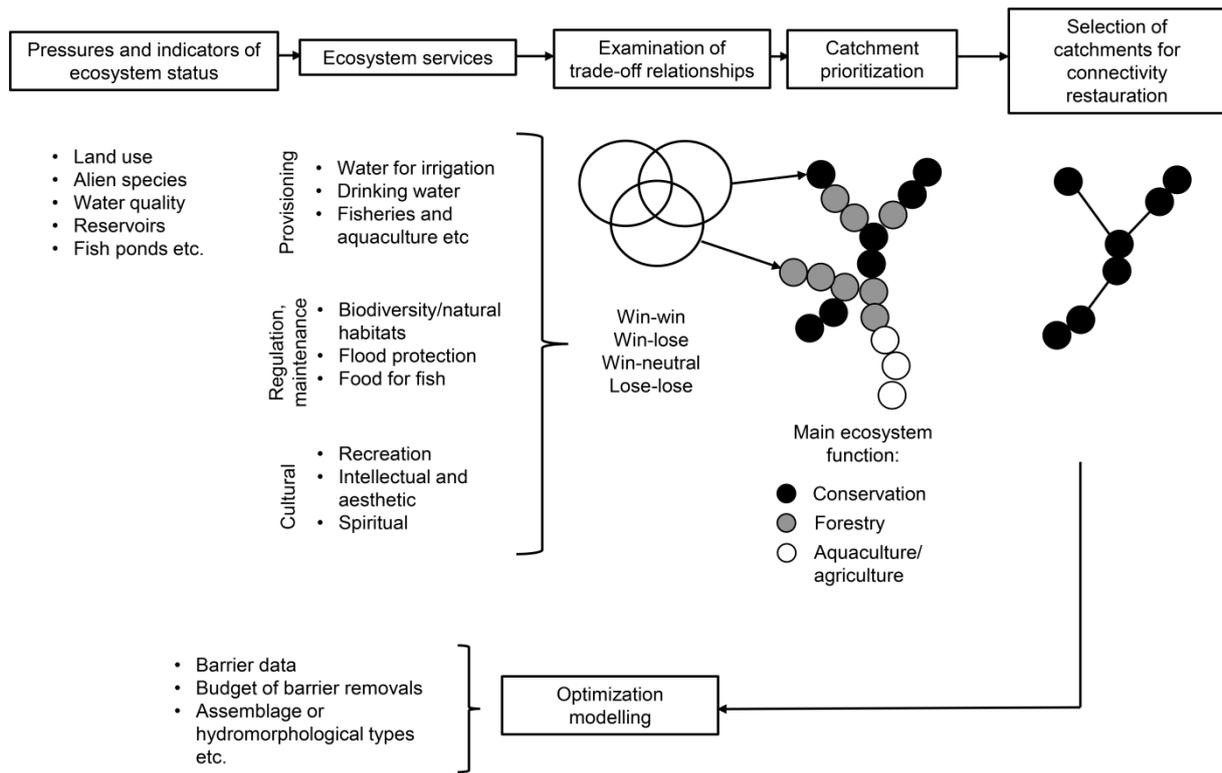
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699 **Tables**

700 **Tab. 1.** River habitat amounts, land use percentages, and number of artificial barriers in each river catchment. For river habitat, labels SMS,
 701 HLS, HLR, LLS, and LLR correspond, respectively, to submontane stream, highland stream, highland river, lowland stream, and lowland river.
 702 For land use, labels ART, AG, FOR, NFOR, WET, and WB correspond, respectively, to artificial surfaces, agriculture, forest, non-forest,
 703 wetland, and water bodies.

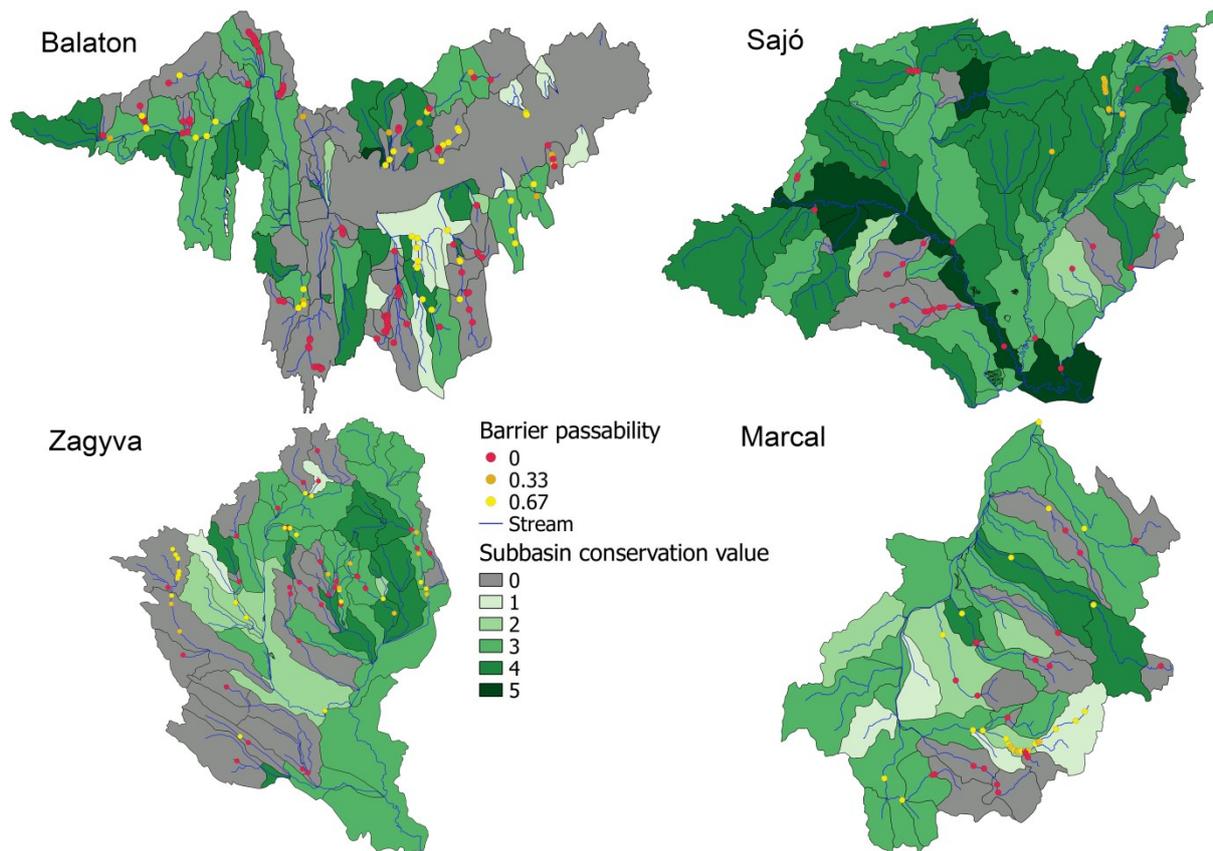
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Catchment	Habitat Amount (km)						Land Use (%)						No. of Barriers
	SMS	HLS	HLR	LLS	LLR	Total	ART	AG	FOR	NFOR	WET	WB	
Balaton	0.0	321.1	49.3	189.0	37.8	597.2	6.1	44.6	27.0	5.6	2.7	13.9	138
Marcal	20.9	157.9	0.0	252.6	70.4	501.8	5.5	64.9	24.2	5.2	0.1	0.1	50
Sajó	103.7	424.8	294.0	63.0	0.0	885.5	7.2	53.4	31.3	7.7	0.3	0.1	52
Zagyva	25.7	267.4	0.0	322.8	67.3	683.3	6.6	66.2	21.1	5.5	0.3	0.3	75
All	150.3	1171.1	343.3	827.4	175.6	2667.7	6.4	56.4	25.8	6.0	1.0	4.4	315



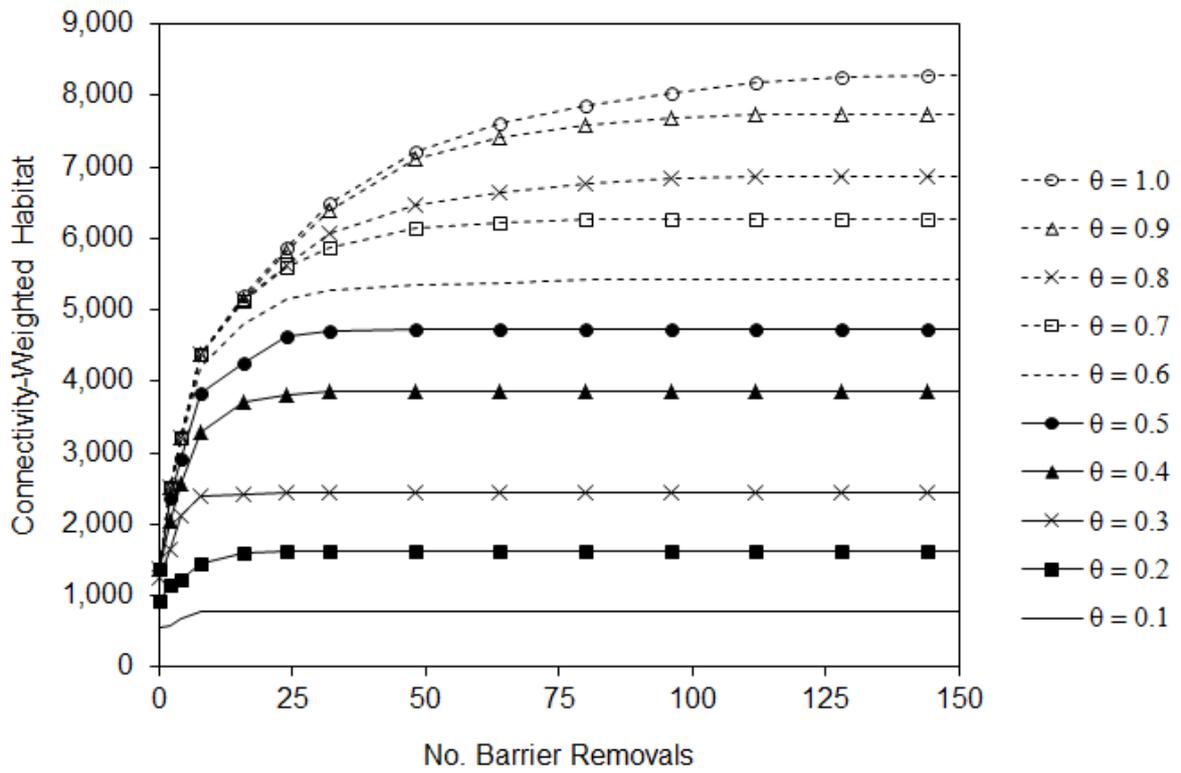
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706 **Fig. 1.** A general framework for prioritizing catchments for biodiversity conservation versus
 707 ecosystem services and targeting connectivity restoration actions.



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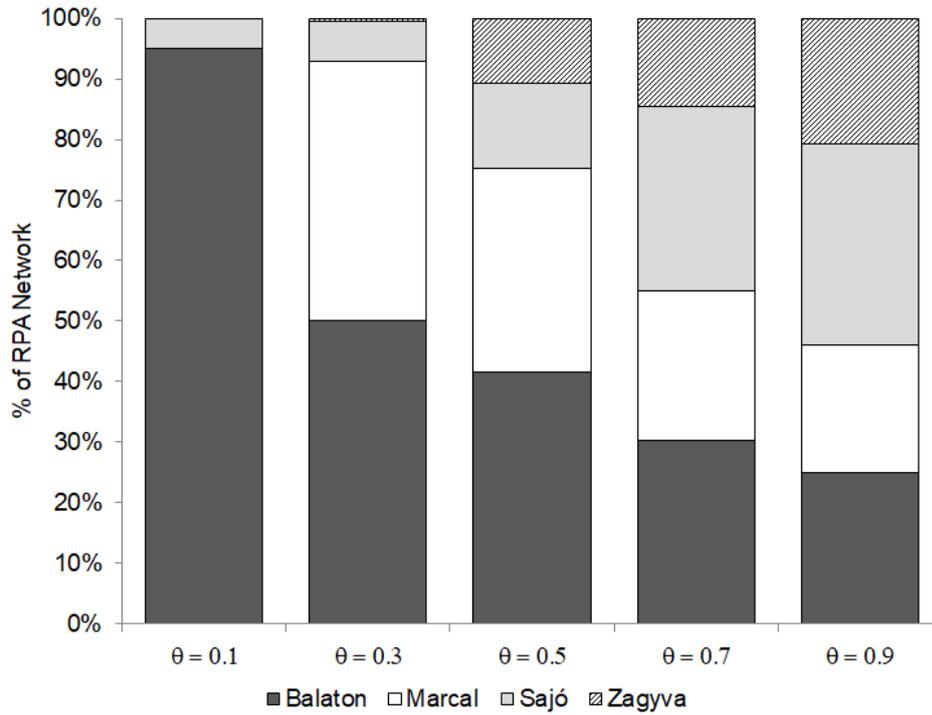
709 **Fig. 2.** Spatial pattern of biological integrity (BII) and distribution of artificial barriers in the
 710 four case study catchments: Lake Balaton, the Marcal River, the Sajó River, and the Zagyva
 711 River. BII is shown on a five-point scale, where a darker shade of green indicates higher
 712 integrity. Grey colored catchments have been assigned an integrity score of zero, indicating
 713 they were deemed better suited to land use functions other than conservation/connectivity
 714 restoration (e.g., agriculture). Note, that fully passable barriers (i.e. where barrier passability
 715 value equals 1) are not shown on the maps.



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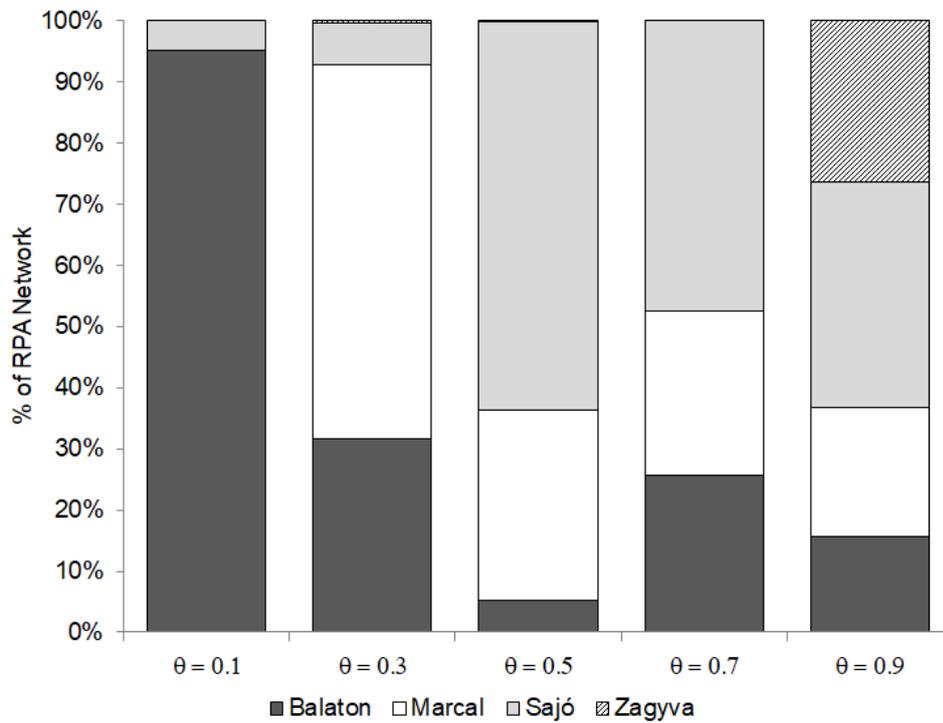
717 **Fig. 3.** Connectivity-weighted habitat versus number of barrier removals for various sized
 718 river protected area (RPA) networks.

719 (a)



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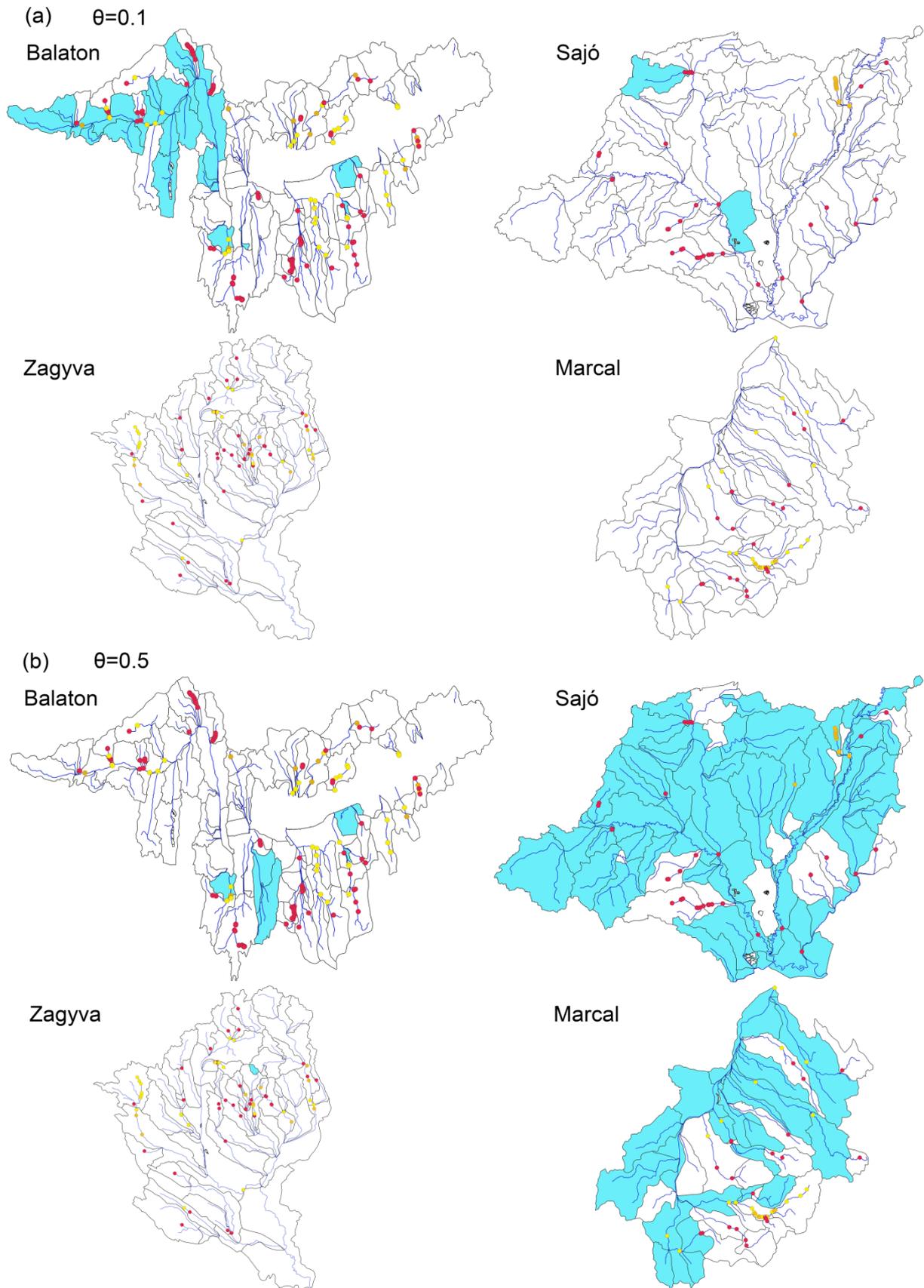
721 (b)



722

723 **Fig. 4.** Fraction of the RPA network in each river catchment given no barrier removal (a) and
724 unlimited barrier removals (b) for various RPA network sizes.

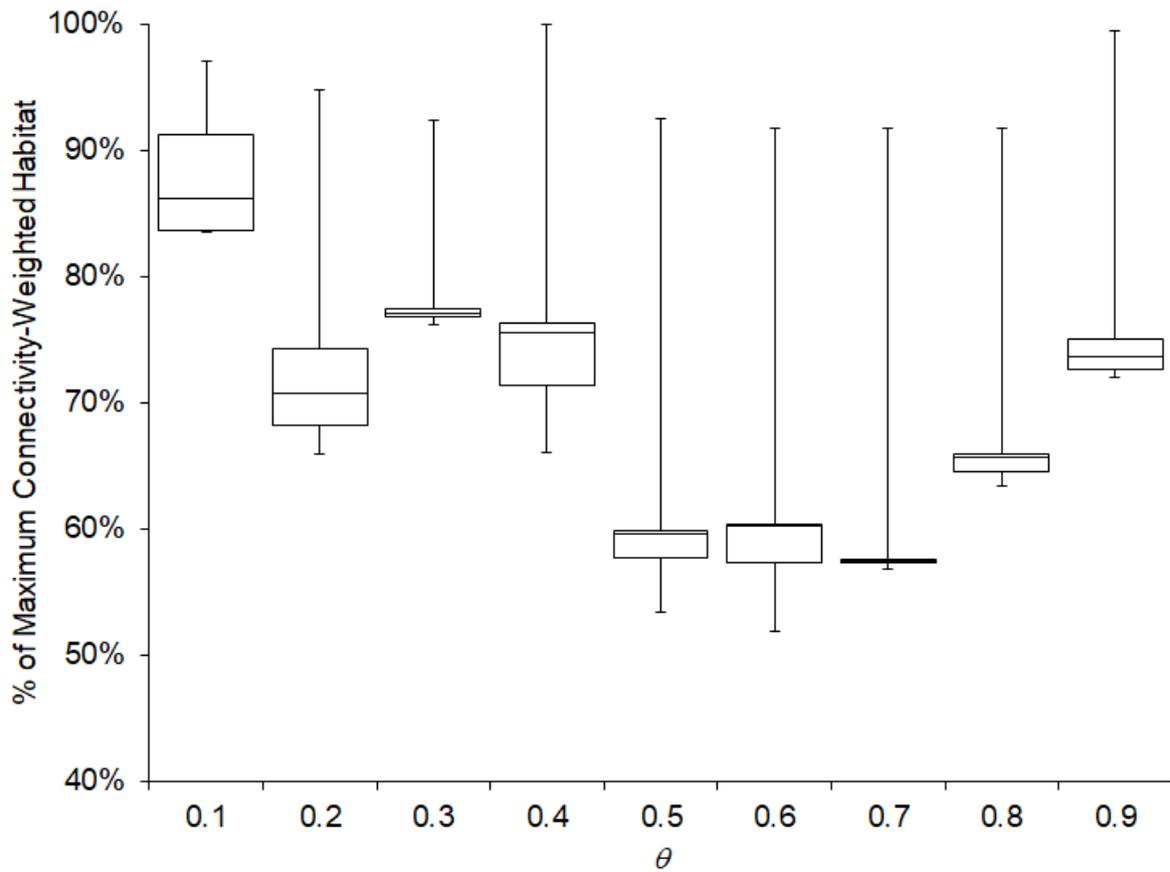
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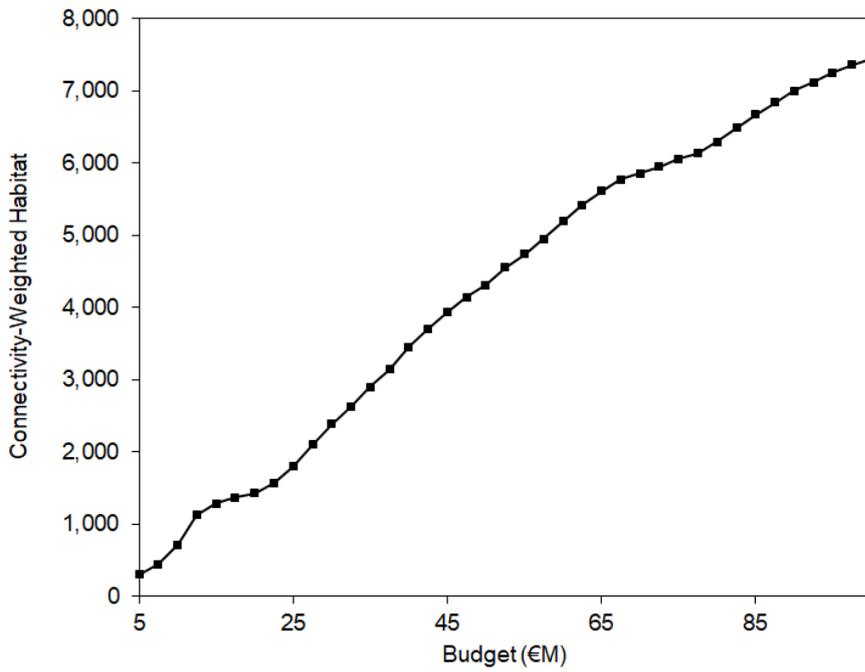
727 **Fig. 5.** Maps showing selected subcatchments for RPA networks of size $\theta = 0.1$ (a) and
 728 $\theta = 0.5$ (b) given unlimited barrier removals.

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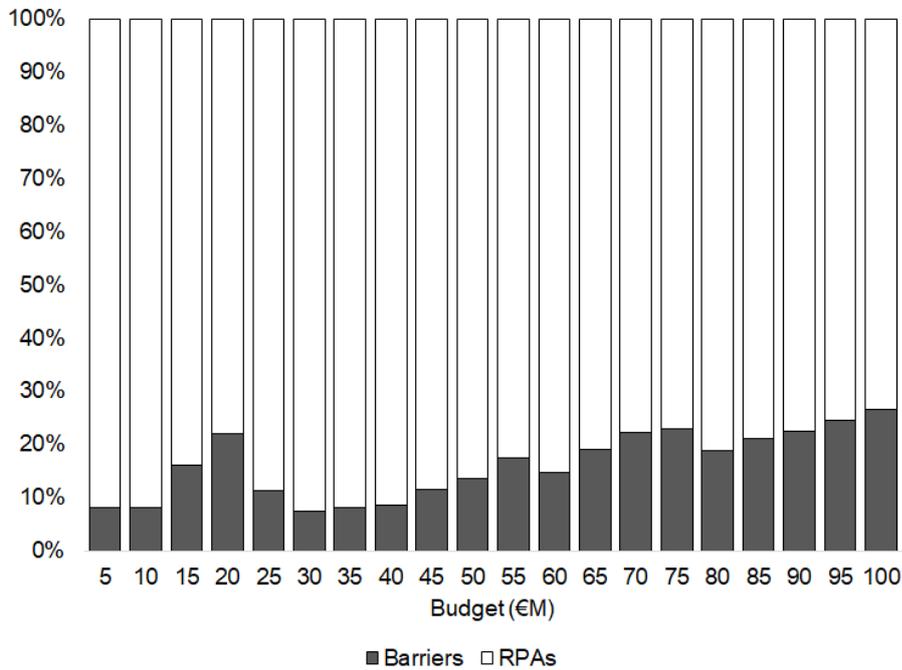
730
 731 **Fig. 6.** Box plots showing the median, lower/upper quartiles, and minimum/maximum
 732 (whiskers) amount of connectivity-weighted habitat as a percentage of maximum for various
 733 RPA network sizes based on a sequential, two-stage approach to conservation and restoration
 734 planning (river protection decisions made first, barrier removal decisions second).

735 (a)



736

737 (b)



738

739 **Fig. 7.** Connectivity-weighted habitat versus combined budget for RPA acquisition and
740 barrier removals (a) and relative spend on RPA acquisition versus barrier removal for various
741 budget amounts (b).