

Kent Academic Repository

Full text document (pdf)

Citation for published version

Erős, Tibor and O'Hanley, J.R. and Czeglédi, István (2018) A Unified Model for Optimizing Riverscape Conservation. *Journal of Applied Ecology*. ISSN 0021-8901.

DOI

<https://doi.org/10.1111/1365-2664.13142>

Link to record in KAR

<http://kar.kent.ac.uk/66054/>

Document Version

Author's Accepted Manuscript

Copyright & reuse

Content in the Kent Academic Repository is made available for research purposes. Unless otherwise stated all content is protected by copyright and in the absence of an open licence (eg Creative Commons), permissions for further reuse of content should be sought from the publisher, author or other copyright holder.

Versions of research

The version in the Kent Academic Repository may differ from the final published version.

Users are advised to check <http://kar.kent.ac.uk> for the status of the paper. **Users should always cite the published version of record.**

Enquiries

For any further enquiries regarding the licence status of this document, please contact:

researchsupport@kent.ac.uk

If you believe this document infringes copyright then please contact the KAR admin team with the take-down information provided at <http://kar.kent.ac.uk/contact.html>

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

2

3 **Tibor Erós,^{1,2,3*} Jesse R. O'Hanley,⁴ István Czeglédi¹**

4

5 ¹MTA Centre for Ecological Research, Balaton Limnological Institute, Klebelsberg K. u. 3,

6 H-8237 Tihany, Hungary

7 ²MTA Centre for Ecological Research, Danube Research Institute, Budapest, Hungary

8 ³MTA Centre for Ecological Research, GINOP Sustainable Ecosystems Group, Tihany,

9 Hungary

10 ⁴Kent Business School, University of Kent, Canterbury CT2 7FS, UK

11

12 ***Corresponding author:**

13 Balaton Limnological Institute, MTA Centre for Ecological Research, Klebelsberg K. u. 3

14 H-8237 Tihany, Hungary

15 eros.tibor@okologia.mta.hu

16

17 **Running title:** Optimizing riverscape conservation

18

19 **Word count:** Total (8298), Summary (327), Main Text (5763), Acknowledgements (79),

20 Data Accessibility (18), References (1836), Tables and Figure Legends (275)

21 **No. of tables:** 1

22 **No. of figures:** 7

23 **No. of references:** 69

24

25 **Keywords:** land use planning, ecosystem services, spatial prioritization, protected area

26 networks, river barriers, habitat fragmentation, connectivity restoration, riverscape

27 **Abstract**

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

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

58

59 **Introduction**

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

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

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

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

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

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

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

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

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

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

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

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

145 Lastly, because resources for conservation and connectivity restoration are limited, it is
146 essential for landscape management to allocate resources in the most efficient way possible.
147 The recommendation to use a spatially explicit prioritization approach leaves two reasonable
148 alternatives: graph theory models (Erős et al., 2011) and optimization models (King et al.,
149 2017). Optimization has the distinct advantage over graph theory in being prescriptive rather
150 than descriptive (King & O'Hanley, 2016), meaning that it produces a recommended course
151 of action that aims for the best allocation of limited resources to maximize benefits (i.e.,
152 biggest bang for the buck). Moreover, optimization models are perfectly suited to balancing
153 multiple, potentially competing goals, thus making them ideal for driving negotiation among
154 decision makers and delivering more win-win scenarios that promote biodiversity protection
155 and ecosystem services provision.

156

157 **Materials and Methods**

158 Study Area

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

167 Biodiversity and Ecosystem Services Indicators

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

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

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

$$199 \quad \text{LUI} = \% \text{ pasture} + 2 \times \% \text{ arable land} + 4 \times \% \text{ urban area}$$

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

$$205 \quad \text{ACV} = 6n_{\text{EW}} + 5n_{\text{CR}} + 4n_{\text{EN}} + 3n_{\text{VU}} + 2n_{\text{NT}} + n_{\text{LC}}$$

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

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

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

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

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

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

241 Barrier Survey Data

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

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

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

276 River Protection and Connectivity Optimization Model

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

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

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

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

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

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

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

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

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

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

321

322 **Results**

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

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

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

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

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

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

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

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

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

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

406 **Discussion**

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

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

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

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

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

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

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

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

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

497

498 **Authors' Contributions**

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

503

504 **Acknowledgements**

505 This work was supported by the grants OTKA K104279 and GINOP 2.3.3-15-2016-00019.
506 We thank numerous people for help with field work and other phases of this project, but
507 especially Árpád Tóth, Rita Tóth, Péter Sály, Péter Takács, Gábor Várбірó, Andrea Zagyva,
508 and Bernadett Kern. We also thank the National Water Authority for providing us the barrier
509 dataset as well as Robert M. Hughes, an anonymous referee, and the Associate Editor for very
510 helpful comments made on an earlier draft of this paper.

511

512 **Data Accessibility**

513 Data available from the Dryad Digital Repository. DOI:

514

515 **References**

516 Angermeier, P.L. (2000) The natural imperative for biological conservation. *Conservation*
517 *Biology*, **14**, 373-381.

518 Angermeier, P.L., Karr J.R. (1994) Biological integrity versus biological diversity as policy
519 directives: Protecting biotic resources. *BioScience*, **44**, 690-697.

520 Antal, L., Harka, Á., Sallai, Z., Guti, G. (2015) TAR: Software to evaluate the conservation
521 value of fish fauna. *Pisces Hungarici*, **9**, 71-72.

522 Auerbach, D.A., Deisenroth, D.B., McShane, R.R., McCluney, K.E., Poff N.L. (2014)
523 Beyond the concrete: Accounting for ecosystem services from free-flowing rivers.
524 *Ecosystem Services*, **10**, 1-5.

525 Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., Roni, P.,
526 Pollock, M.M. (2010) Process-based principles for restoring river ecosystems. *BioScience*,
527 **60**, 209-222.

528 Bennett, E.M., Cramer, W., Begossi, A., et al. (2015) Linking biodiversity, ecosystem
529 services, and human well-being: Three challenges for designing research for sustainability.
530 *Current Opinion in Environmental Sustainability*, **14**, 76-85.

531 Birk S, Bonne W, Borja A, Brucet S, Courrat A, Poikane S, et al. (2012) Three hundred ways
532 to assess Europe's surface waters: an almost complete overview of biological methods to
533 implement the Water Framework Directive. *Ecological Indicators*, **18**, 31-41.

534 Böhmer, J., Rawer-Jost, C., Zenker, A., Meier, C., Feld, C.K., Biss, R., Hering, D. (2004)
535 Assessing streams in Germany with benthic invertebrates: Development of a multimetric
536 invertebrate based assessment system. *Limnologica*, **34**, 416-432.

537 Branco, P., Segurado, P., Santos, J. M., Ferreira, M. T. (2014) Prioritizing barrier removal to
538 improve functional connectivity of rivers. *Journal of Applied Ecology*, **51**, 1197-1206.

539 Cimon-Morin, J., Darveau, M., Poulin, M. (2013) Fostering synergies between ecosystem
540 services and biodiversity in conservation planning: A review. *Biological Conservation*,
541 **166**, 144–154.

542 Cordingley, J.E., Newton, A.C., Rose R.C., Clarke R.T., Bullock J.M. (2016) Can landscape-
543 scale approaches to conservation management resolve biodiversity ecosystem services
544 trade-offs? *Journal of Applied Ecology*, **53**, 96-105.

545 Cote, D., Kehler, D.G., Bourne, C., Wiersma, Y.F. (2009) A new measure of longitudinal
546 connectivity for stream networks. *Landscape Ecology*, **24**, 101-113.

547 Doody, D.G., Withers, P.J.A., Dils, R.M., McDowell, R.W., Smith, V., McElarney, Y.R.,
548 Dunbar, M., Daly, D. (2016) Optimizing land use for the delivery of catchment ecosystem
549 services. *Frontiers in Ecology and the Environment*, **14**, 325-332.

550 Dynesius, M., Nilsson, C. (1994) Fragmentation and flow regulation of river systems in the
551 northern third of the world. *Science*, **266**, 753-762.

552 Erős, T. (2007) Partitioning the diversity of riverine fish: The roles of habitat types and non-
553 native species. *Freshwater Biology*, **52**, 1400-1415.

554 Erős, T., Schmera, D., Schick, R.S. (2011) Network thinking in riverscape conservation – A
555 graph-based approach. *Biological Conservation*, **144**, 184-192.

556 Erős, T., Olden, J.D., Schick, R.S., Schmera, D., Fortin, M-J. (2012) Characterizing
557 connectivity relationships in freshwaters using patch-based graphs. *Landscape Ecology*,
558 **27**, 303-317.

559 Fattorini, S. (2006) A new method to identify important conservation areas applied to the
560 butterflies of the Aegean Islands (Greece). *Animal Conservation*, **9**, 75-83.

561 Filipe, A.F., Marques, T.A., Seabra, S., Tiago, P., Riberio, F., Moreira da Cost, L., Cowx,
562 I.G., Collares-Pereira, M.J. (2004) Selection of priority areas for fish conservation in
563 Guadiana river basin, Iberian Peninsula. *Conservation Biology*, **18**, 189-200.

564 Gordon, N.D., McMahon, T.A., Finlayson, B.L. (1992) *Stream Hydrology: An Introduction*
565 *for Ecologists*. Wiley, Chichester.

566 Grant E., Lowe, W., Fagan, W. (2007) Living in the branches: Population dynamics and
567 ecological processes in dendritic networks. *Ecology Letters*, **10**, 165-175.

568 Grizetti, B., Lanzanova, D., Liqueste, C., Reynaud, A., Cardoso A.C. (2016) Assessing water
569 ecosystem services for water resource management. *Environmental Science & Policy*, **61**,
570 194-203.

571 Halpern, B.S., Klein, C.J, Brown, C.J., et al. (2013) Achieving the triple bottom line in the
572 face of inherent trade-offs among social equity, economic return, and conservation.
573 Proceedings of National Academy of Sciences, USA, **110**, 6229-6234.

574 Hawkins, C.P., Norris, R.H., Hogue, J.N., Feminella, J.W. (2000) Development and
575 evaluation of predictive models for measuring the biological integrity of streams.
576 Ecological Applications, **10**, 1456-1477.

577 Hermoso, V., Filipe, A.F., Segurado, P., Beja, P. (2017) Freshwater conservation in a
578 fragmented world: Dealing with barriers in a systematic planning framework. Aquatic
579 Conservation: Marine and Freshwater Ecosystems, DOI: 10.1002/aqc.2826

580 Hermoso, V., Linke, S., Prenda, J., Possingham, H.P. (2011) Addressing longitudinal
581 connectivity in the systematic conservation planning of fresh waters. Freshwater Biology,
582 **56**, 57-70.

583 Higgins J.A., Bryer M.T., Khoury M.L., Fitzhugh T.W. (2004) A freshwater classification
584 approach for biodiversity conservation planning. Conservation Biology **19**, 432-445.

585 Holmlund, C.M., Hammer, M. (1999) Ecosystem services generated by fish populations.
586 Ecological Economics, **29**, 253-258.

587 Howe, C., Suich, H., Vira, B., Mace, G.M. (2014) Creating win-wins from tradeoffs?
588 Ecosystem services for human well-being: A meta-analysis of ecosystem service tradeoffs
589 and synergies in the real world. Global Environmental Change, **28**, 263-275.

590 Isaak, D. J., Luce, C. H., Rieman, B. E., Nagel, D. E., Peterson, E. E., Horan, D. L., Parkes,
591 S., Chandler, G. L. (2010) Effects of climate change and wildfire on stream temperatures
592 and salmonid thermal habitat in a mountain river network. Ecological Applications, **20**,
593 1350–1371.

594 Januchowski-Hartley, S.R., McIntyre, P.B., Diebel, M., Doran, P.J., Infante, D.M., Joseph, C.,
595 Allan, D.J. (2013) Restoring aquatic ecosystem connectivity requires expanding

596 inventories of both dams and road crossings. *Frontiers in Ecology and the Environment*,
597 **11**, 211-217.

598 Jax, K., Barton, D.N., Chan, K.M.A., et al. (2013) Ecosystem services and ethics. *Ecological*
599 *Economics*, **93**, 260-268.

600 Karr, J.R. (1999) Defining and measuring river health. *Freshwater Biology*, **41**, 221–234.

601 Kemp, P.S., O’Hanley, J.R. (2010) Procedures for evaluating and prioritising the removal of
602 fish passage barriers: A synthesis. *Fisheries Management and Ecology*, **17**, 297-322.

603 King, S. & O’Hanley, J.R. (2016) Optimal fish passage barrier removal – revisited. *River*
604 *Research and Applications*, **32**, 418-428.

605 King, S., O’Hanley, J.R., Newbold, L., Kemp, P.S., Diebel, M.W. (2017) A toolkit for
606 optimizing barrier mitigation actions. *Journal of Applied Ecology*, **54**, 599-611.

607 Lee, P., Smyth, C. Boutin, S. (2004) Quantitative review of riparian buffer width guidelines
608 from Canada and the United States. *Journal of Environmental Management*, **70**, 165-180.

609 Ligeiro, R., Hughes, R.M., Kaufmann, P.R., et al. (2013) Defining quantitative stream
610 disturbance gradients and the additive role of habitat variation to explain macroinvertebrate
611 taxa richness. *Ecological Indicators*, **25**, 45-57.

612 Linke, S., Kennard, M.J., Hermoso, V., Olden, J.D., Stein, J., Pusey, B.J. (2012) Merging
613 connectivity rules and large-scale condition assessment improves conservation adequacy in
614 river systems. *Journal of Applied Ecology*, **49**, 1036-1045.

615 Maes, J., Liqueste, C., Teller, A., et al. (2016) An indicator framework for assessing ecosystem
616 services in support of the EU Biodiversity Strategy to 2020. *Ecosystem Services*, **17**, 14-23.

617 McDonnell, M.D., Possingham, H.P., Ball, I.R., Cousins, E.A. (2002) Mathematical methods
618 for spatially cohesive reserve design. *Environmental Modeling and Assessment*, **7**, 107-
619 114.

620 McKay, S.K., Cooper, A.R., Diebel, M.W., Elkins, D., Oldford, G., Roghair, C., Wieferich,
621 D. (2017) Informing watershed connectivity barrier prioritization decisions: A synthesis.
622 *River Research and Applications*, **33**, 847-862.

623 Milt, A.W., Doran, P.J., Ferris, M.C., Moody, A.T., Neeson, T.M., McIntyre, P.B. (2017)
624 Local-scale benefits of river connectivity restoration planning beyond jurisdictional
625 boundaries. *River Research and Applications*, **33**, 788-795.

626 Mitchell M.G.E., Bennett E.M., Gonzalez A. (2013) Linking landscape connectivity and
627 ecosystem service provision: Current knowledge and research gaps. *Ecosystems*, **16**, 894-
628 908.

629 Moilanen, A., Leathwick, J., Elith, J. (2008) A method for spatial freshwater conservation
630 prioritization. *Freshwater Biology*, **53**, 577-592.

631 Moody, A.T., Neeson, T.M., Milt, A., et al. (2017) Pet project or best project? Online
632 decision support tools for prioritizing barrier removals in the Great Lakes and beyond.
633 *Fisheries*, **42**, 57-65.

634 Nalle, D.J., Arthur, J.L., Sessions, J. (2002) Designing compact and contiguous reserve
635 networks with a hybrid heuristic approach. *Forest Science*, **48**, 59-68.

636 Neeson, T.M., Ferris, M.C., Diebel, M.W., Doran, P.J., O'Hanley, J.R., McIntyre, P.B. (2015)
637 Enhancing ecosystem restoration efficiency through spatial and temporal coordination.
638 *Proceedings of the National Academy of Sciences, USA*, **112**, 6236-6241.

639 Nelson, E. Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D.R, et al. (2009)
640 Modeling multiple ecosystem services, biodiversity conservation, commodity production,
641 and tradeoffs at landscape scales. *Frontiers in Ecology and Environment*, **7**, 4-11.

642 Newbold, S.C., Siikamäki, J. (2009) Prioritizing conservation activities using reserve site
643 selection methods and population viability analysis. *Ecological Applications*, **19**, 1774-
644 1790.

645 Noonan, M., Grant, J., Jackson, C. (2012) A quantitative assessment of fish passage
646 efficiency. *Fish and Fisheries*, **13**, 450-464.

647 O’Hanley, J.R. (2011) Open rivers: Barrier removal planning and the restoration of free-
648 flowing rivers. *Journal of Environmental Management*, **92**, 3112-3120.

649 O’Hanley, J.R., Scaparra, M.P., Garcia, S. (2013) Probability chains: A general linearization
650 technique for modeling reliability in facility location and related problems. *European*
651 *Journal of Operational Research*, **230**, 63-75.

652 Peipoch, M., Brauns, M., Hauer, F.R., Weitere, M., Valett, M.H. (2015) Ecological
653 simplification: Human influences on riverscape complexity. *Bioscience*, **65**, 1057-1065.

654 Palomo I., Montes C., Martín-López B., González J.A., García-Llorente M, Alcorlo P., Mora
655 M.R.G (2014) Incorporating the socio-ecological approach in protected areas in the
656 Anthropocene. *Bioscience*, **64**, 181-191.

657 Poff, N.L., Olden, J., Meritt, D.M., Pepin, D.M. (2007) Homogenization of regional river
658 dynamics by dams and global biodiversity implications. *Proceedings of the National*
659 *Academy of Sciences, USA*, **104**, 5732-5737.

660 Pont, D., Hugueny B., Beier, U., Goffaux, D., Melcher, A., Noble, R., Rogers, C., Roset, N.,
661 Schmutz, S. (2006) Assessing river biotic condition at a continental scale: A European
662 approach using functional metrics and fish assemblages. *Journal of Applied Ecology*, **43**,
663 70-80.

664 Prager, K., Reed, M., Scott, A. (2012) Encouraging collaboration for the provision of
665 ecosystem services at a landscape scale – Rethinking agri-environmental payments. *Land*
666 *Use Policy*, **29**, 244-249.

667 Reyers, B., Polasky, S., Tallis, H., Mooney, H.A., Larigauderie, A. (2012) Finding common
668 ground for biodiversity and ecosystem services. *BioScience*, **62**, 503-507.

669 Roset, N., Grenouillet, G., Goffaux, D., Kestemont, P. (2007) A review of existing fish
670 assemblage indicators and methodologies. *Fisheries Management and Ecology*, **14**, 393-
671 405.

672 Sály, P., Erős, T. (2016) Ecological assessment of running waters in Hungary: Compilation
673 of biotic indices based on fish. *Pisces Hungarici*, **10**, 15-45.

674 Schröter, M., Remme R.P. (2016) Spatial prioritization for conserving ecosystem services:
675 Comparing hotspots with heuristic optimization. *Landscape Ecology*, **31**, 431-450.

676 Sowa, S.P., Annis, G., Morey, M.E., Diamond, D.D. (2007) A GAP analysis and
677 comprehensive conservation strategy for riverine ecosystems of Missouri. *Ecological*
678 *Monographs*, **77**, 301-334.

679 Taylor, P.D., Fahrig, L., Henein, K., Merriam, G. (1993) Connectivity is a vital element of
680 landscape structure. *Oikos*, **68**, 571-573.

681 Terrado, M., Momblanch, A., Bardina, M., Boithias, L., Munné, A., Sabater, S., Solera, A.,
682 Acuña, V. (2016) Integrating ecosystem services in river basin management plans. *Journal*
683 *of Applied Ecology*, **53**, 865-875.

684 Thorp, J.H., Flotemersch, J.E., Delong, M.D., Casper, A.F. Thoms, M.C., Ballantyne, F.,
685 Williams, B.S., O'Neill, B.J., Haase, C.S. (2010) Linking ecosystem services,
686 rehabilitation, and river hydrogeomorphology. *BioScience*, **60**, 67-74.

687 Vidal-Abarca, M.R., Santos-Martín, F., Martín-López, B., Sánchez-Montoya, M.M., Suárez
688 Alonso, M.L. (2016) Exploring the capacity of Water Framework Directive indices to
689 assess ecosystem services in fluvial and riparian systems: Towards a second
690 implementation phase. *Environmental Management*, **57**, 1139-1152.

691 Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., et al. (2010) Global threats to human water
692 security and river biodiversity. *Nature*, **467**, 555-561.

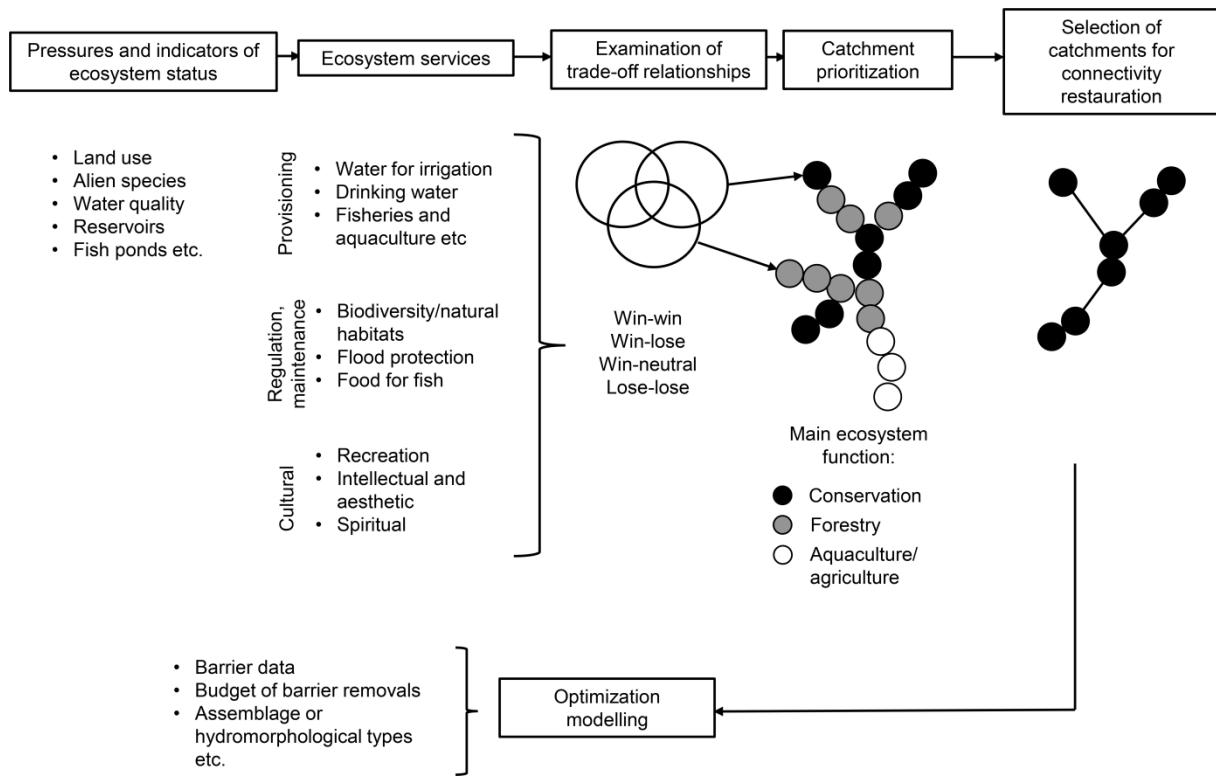
693 Zheng H., Li Y, Robinson BE, Liu G, Ma D, Wang F, Lu F, Ouyang Z, Daily G.C. (2016)
694 Using ecosystem service trade-offs to inform water conservation policies and management
695 practices. *Frontiers in Ecology and the Environment*, **14**, 527–532.

696 **Tables**

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

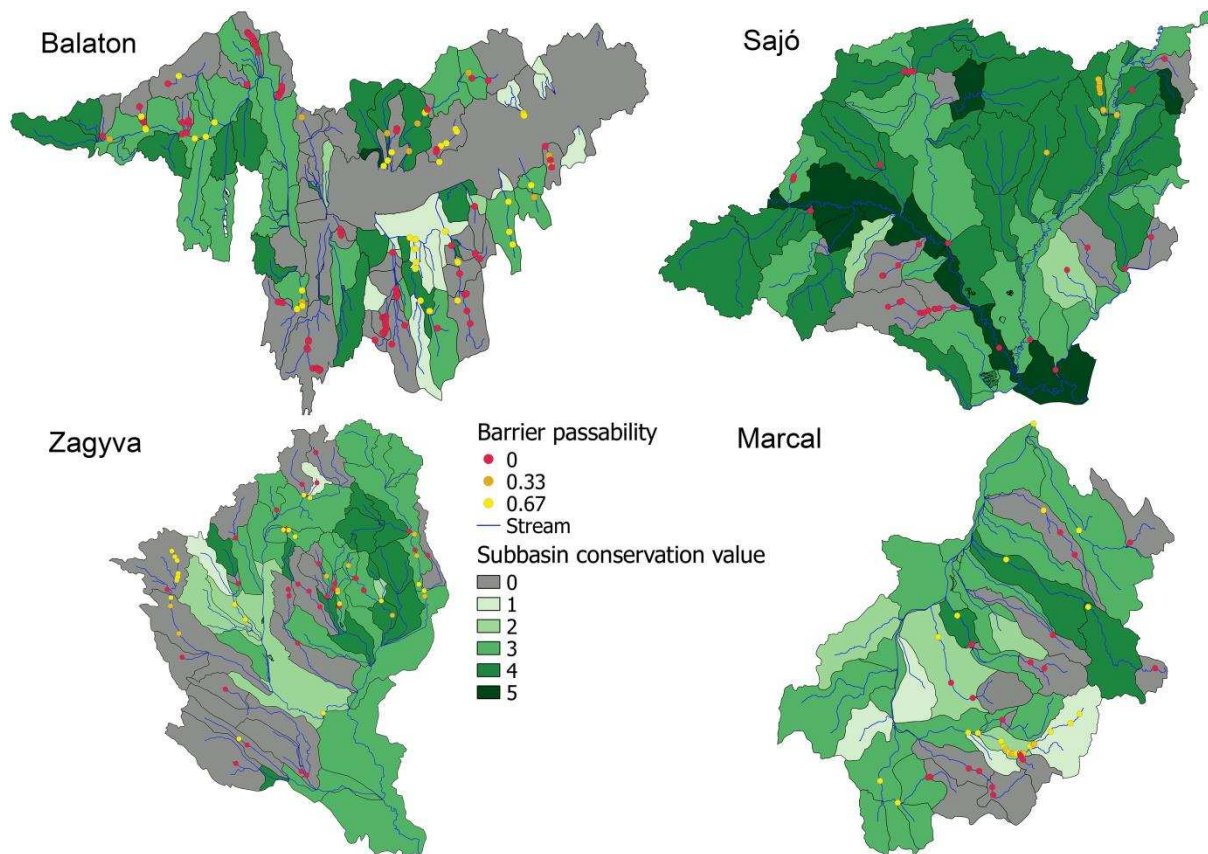
701

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



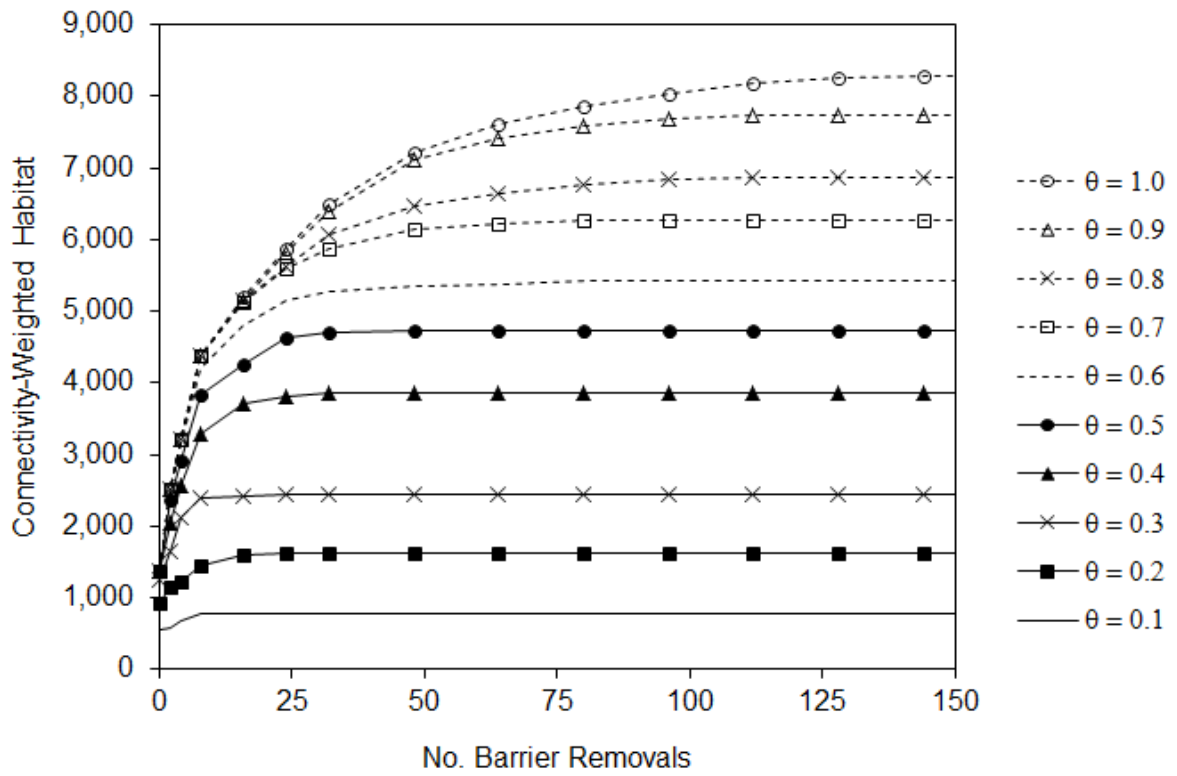
702

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



705

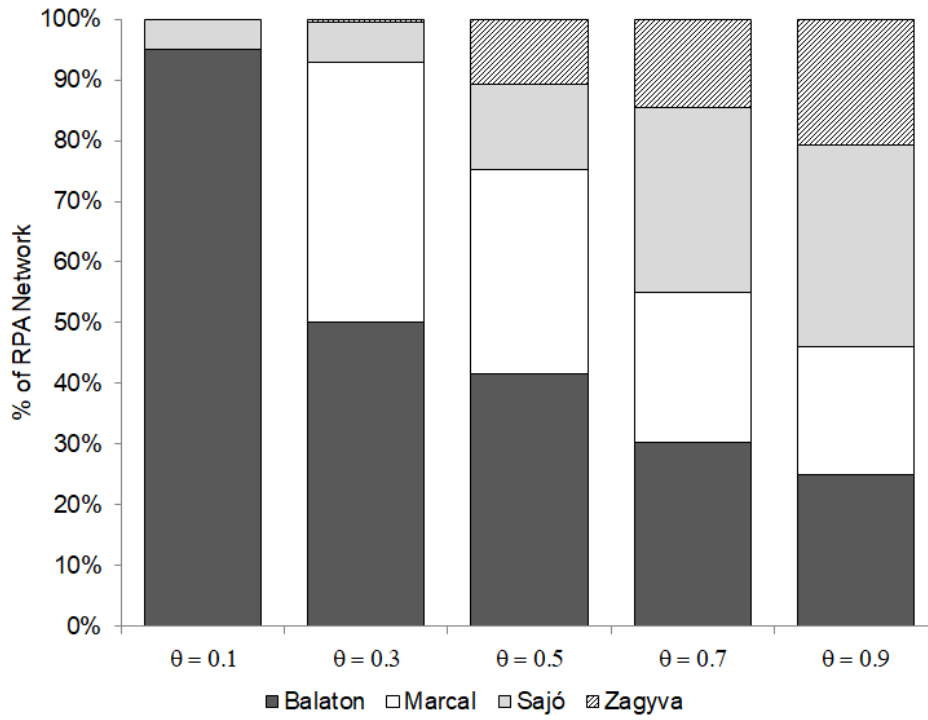
706 **Fig. 2.** Spatial pattern of biological integrity (BII) and distribution of artificial barriers in the
 707 four case study catchments: Lake Balaton, the Marcal River, the Sajó River, and the Zagyva
 708 River. BII is shown on a five-point scale, where a darker shade of green indicates higher
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



713

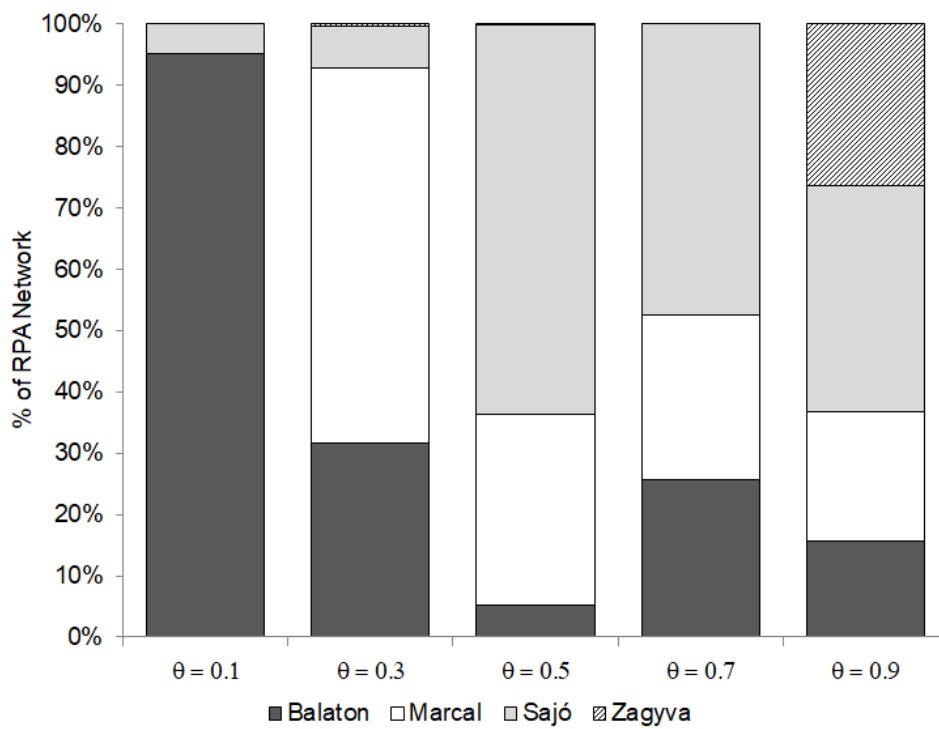
714 **Fig. 3.** Connectivity-weighted habitat versus number of barrier removals for various sized
 715 river protected area (RPA) networks.

716 (a)



717

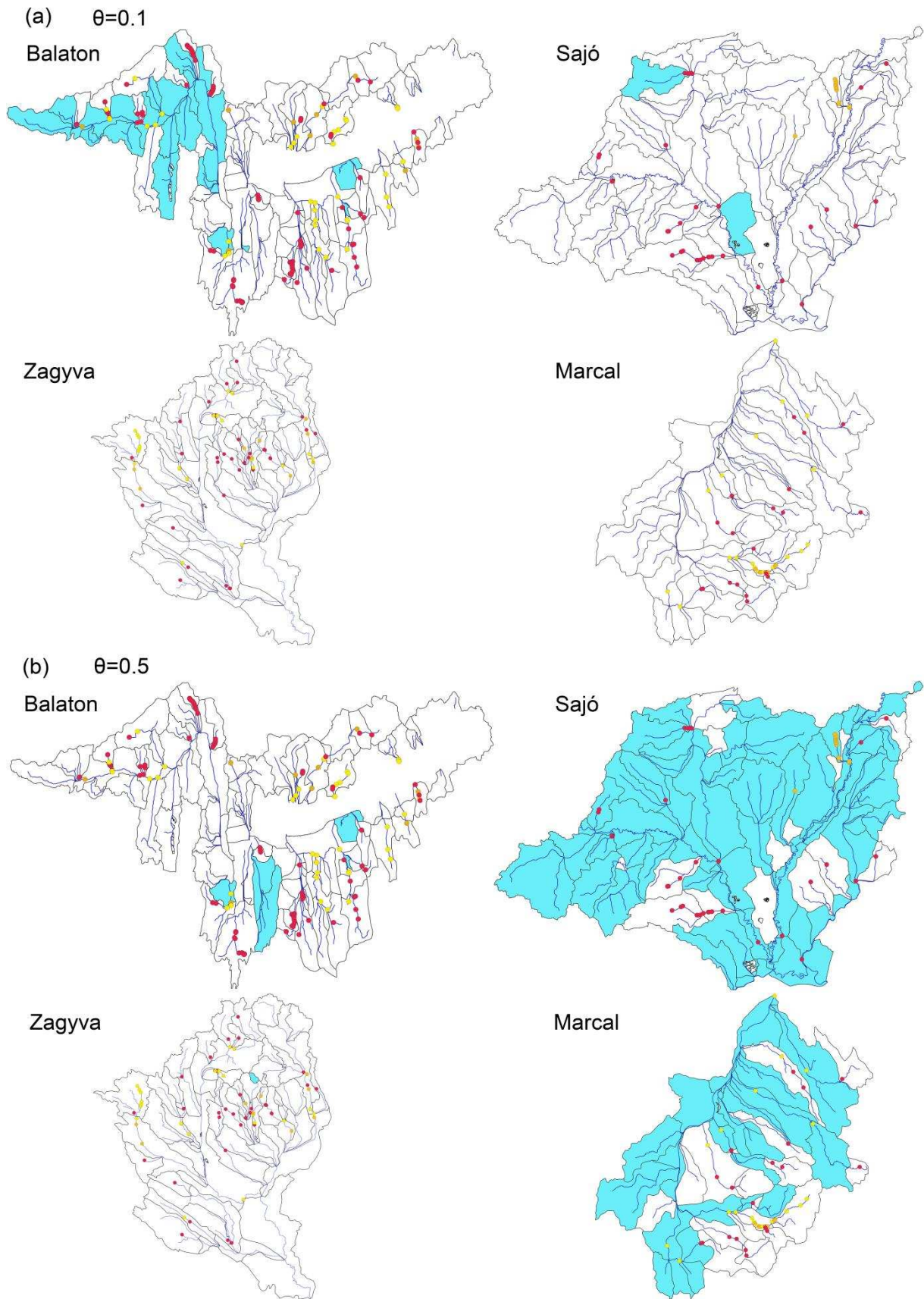
718 (b)



719

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

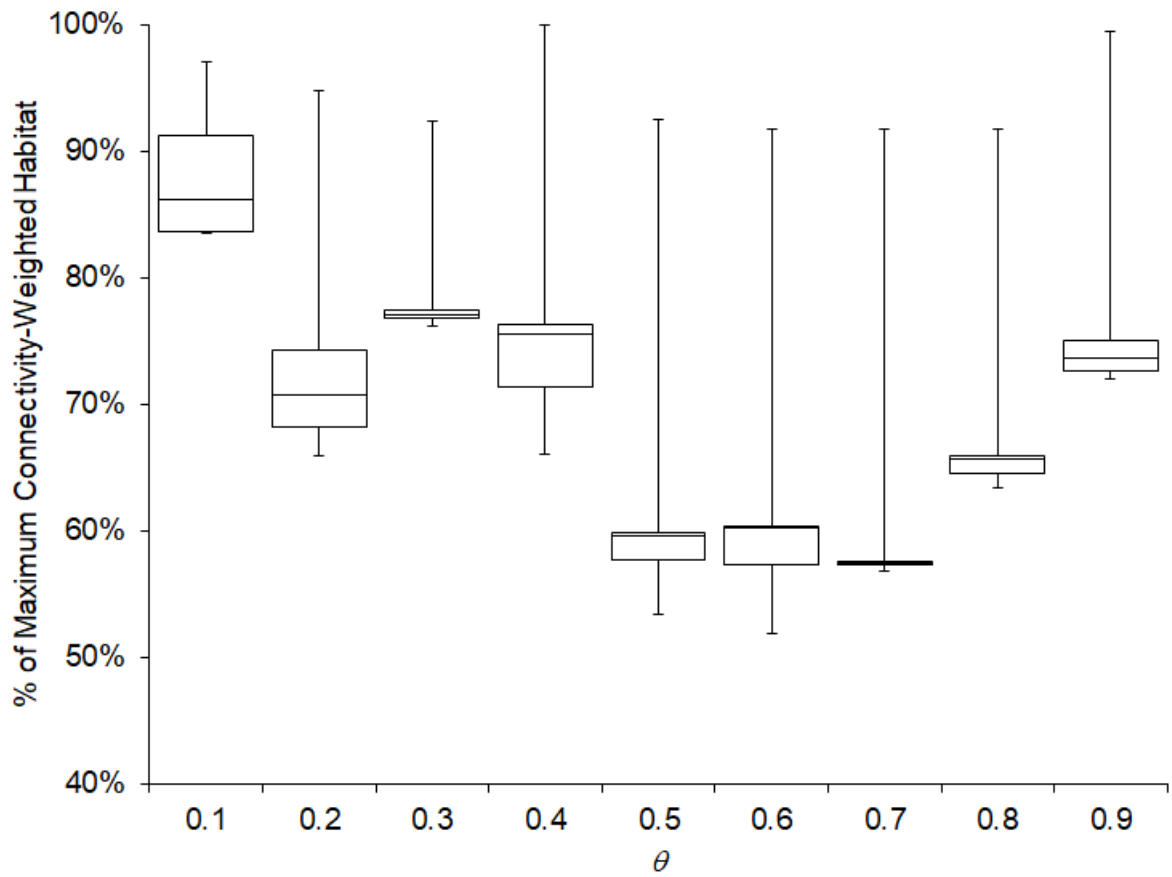
722



723

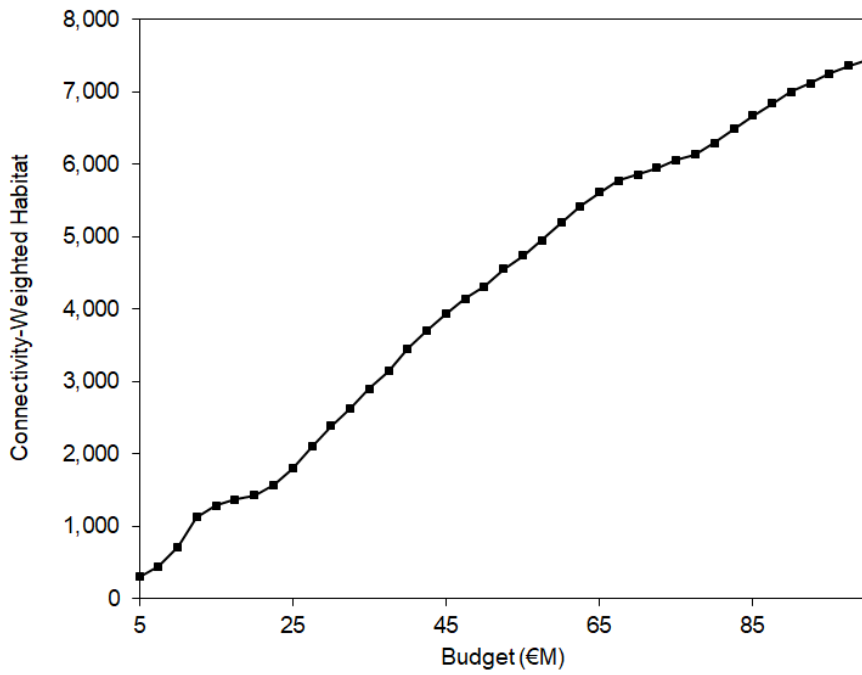
724 **Fig. 5.** Maps showing selected subcatchments for RPA networks of size $\theta = 0.1$ (a) and $\theta =$
 725 0.5 (b) given unlimited barrier removals.

726



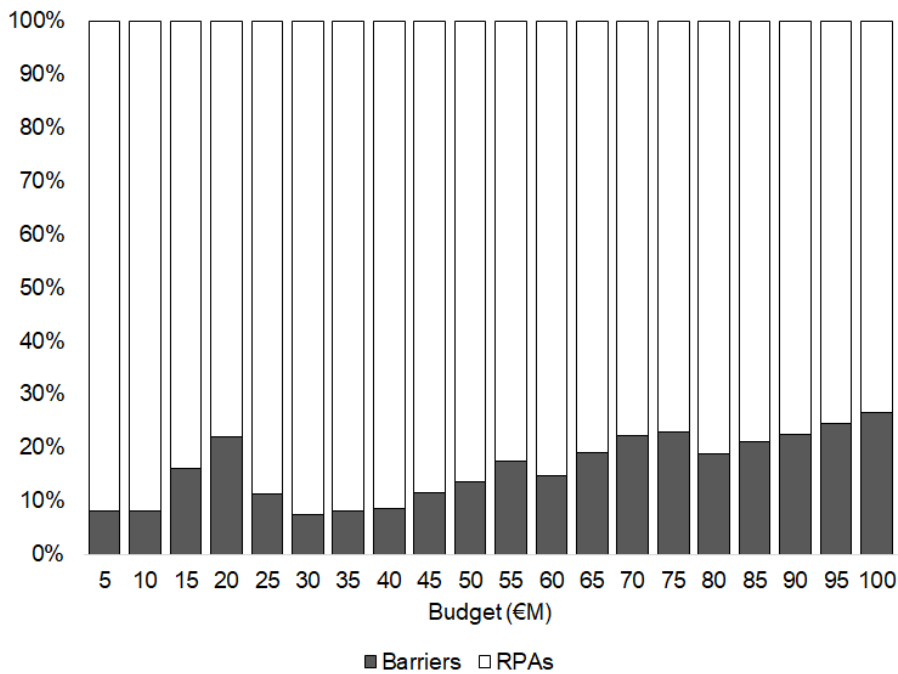
727
 728 **Fig. 6.** Box plots showing the median, lower/upper quartiles, and minimum/maximum
 729 (whiskers) amount of connectivity-weighted habitat as a percentage of maximum for various
 730 RPA network sizes based on a sequential, two-stage approach to conservation and restoration
 731 planning (river protection decisions made first, barrier removal decisions second).

732 (a)



733

734 (b)



735

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