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

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3   **Tibor Erős,[1,2,3]* Jesse R. O'Hanley,[4] István Czeglédi[1]**

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

6   H-8237 Tihany, Hungary

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

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

9   Hungary

10   [4]Kent 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

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17   **Running title:** Optimizing riverscape conservation

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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

Introduction

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

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

Looking specifically at prioritization in riverine ecosystems, a frequently neglected consideration is the critical role that landscape connectivity plays in the maintenance of both biodiversity and ecosystem services (Taylor *et al.,* 1993; Mitchell *et al.,* 2013). Rivers provide a multitude of vital ecosystem services, such as water supply, navigation, hydropower, fishing, and recreational opportunities (Vörösmarty *et al.,* 2010). Many of these services are 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

6

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 is 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**

Study Area

We selected four river catchments located in Hungary for our study (Fig. 2). These include

Lake Balaton (5775 km^2), the Marcal River (3084 km^2), the Sajó River (5545 km^2), and the

Zagyva River (5677 km^2). Catchments differ considerably in terms of the mix of land uses,

stream habitat type, and number of artificial barriers present (Tab. 1). The dominant land

cover type is agricultural (mainly arable land, vineyards to a smaller extent), but deciduous

forests, pastures, grasslands, and wetlands are also present. Urbanization is primarily confined

to small cities and villages. River habitat can be categorized into five broad types: lowland

river, lowland stream, highland river, highland stream, and submontane stream (Erős, 2007).

Biodiversity and Ecosystem Services Indicators

Conservation area selection methods often use simple biological diversity indicators as

proxies of conservation value (e.g., richness, species occurrences, endemism, species

composition). Rarely is attention given to the biological integrity of the ecosystem, even

though this may be a better indicator of a particular location's value for conservation purposes

(Angermeier & Karr, 1994; Karr, 1999; Peipoch *et al.,* 2015). According to Angermeier and

Karr (1994), "diversity is a collective property of system elements, integrity is a synthetic

property of the system." Diversity quantifies the variety of items in the system (e.g., species

richness, number of functional forms), whereas integrity refers to the number of components

(diversity) and the processes that contribute to the continued functioning of the system in a

natural state. In this sense, integrity emphasizes the degree to which a system has been altered

from its natural (i.e., undisturbed) state (Hawkins *et al.,* 2000; Pont *et al.,* 2006). An

ecosystem with high integrity indicates that natural ecological, evolutionary, and

biogeographic processes are intact (Angermeier & Karr 1994; Angermeier 2000; Beechie *et*

al., 2010). Although biodiversity and biological integrity are often confused, it is important to

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

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

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

16

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.

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512 **Data Accessibility**

513 Data available from the Dryad Digital Repository. DOI:

514

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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

|	Habitat Amount (km)						Land Use (%)						
Catchment	SMS	HLS	HLR	LLS	LLR	Total	ART	AG	FOR	NFOR	WET	WB	No. of Barriers
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
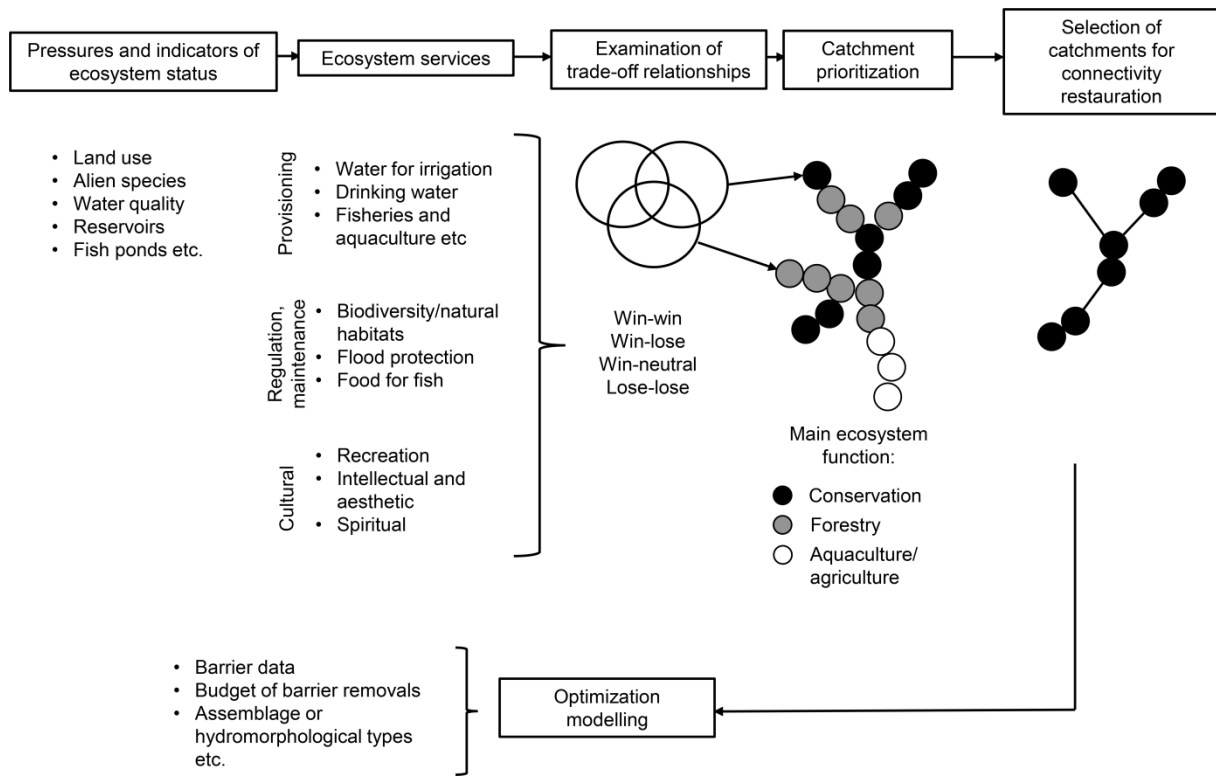
Fig. 1. A general framework for prioritizing catchments for biodiversity conservation versus ecosystem services and targeting connectivity restoration actions.

705
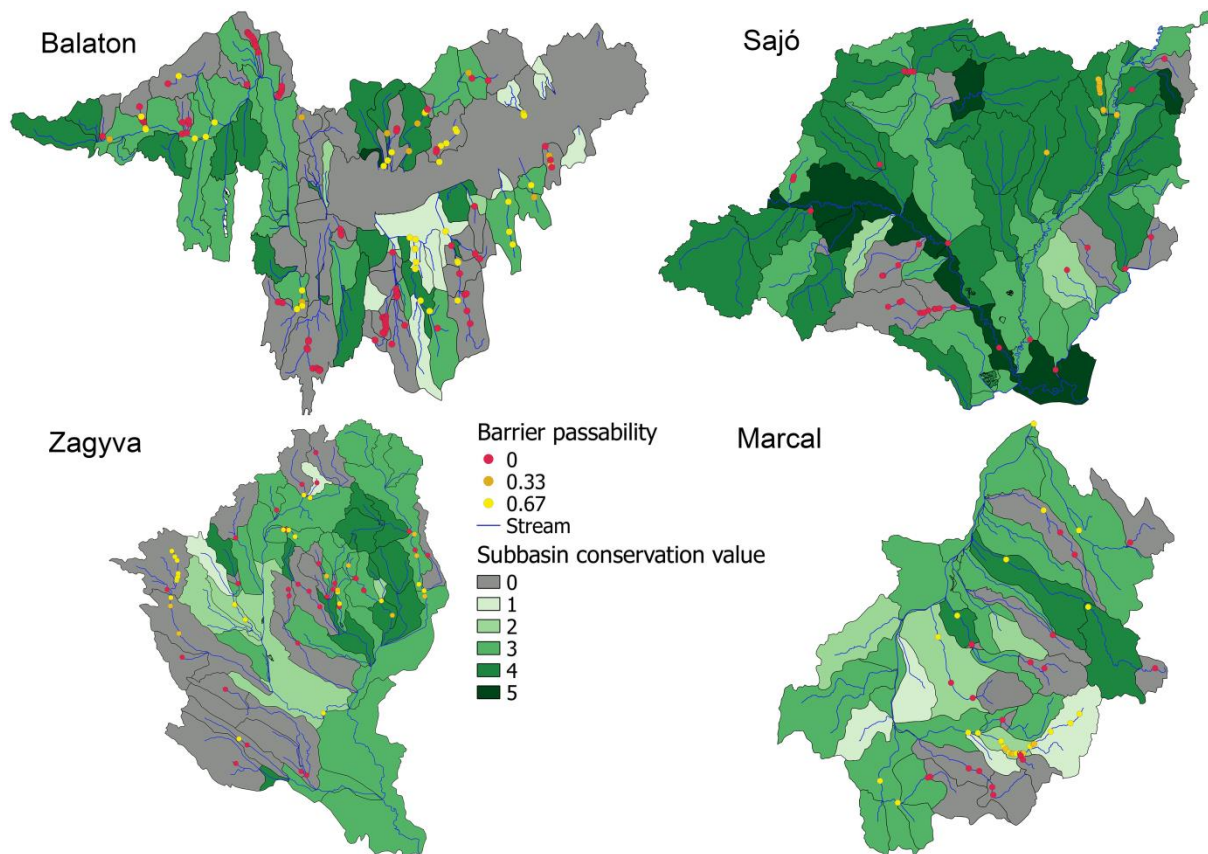
Fig. 2. Spatial pattern of biological integrity (BII) and distribution of artificial barriers in the four case study catchments: Lake Balaton, the Marcal River, the Sajó River, and the Zagyva River. BII is shown on a five-point scale, where a darker shade of green indicates higher integrity. Grey colored catchments have been assigned an integrity score of zero, indicating they were deemed better suited to land use functions other than conservation/connectivity restoration (e.g., agriculture). Note, that fully passable barriers (i.e. where barrier passability value equals 1) are not shown on the maps.

713
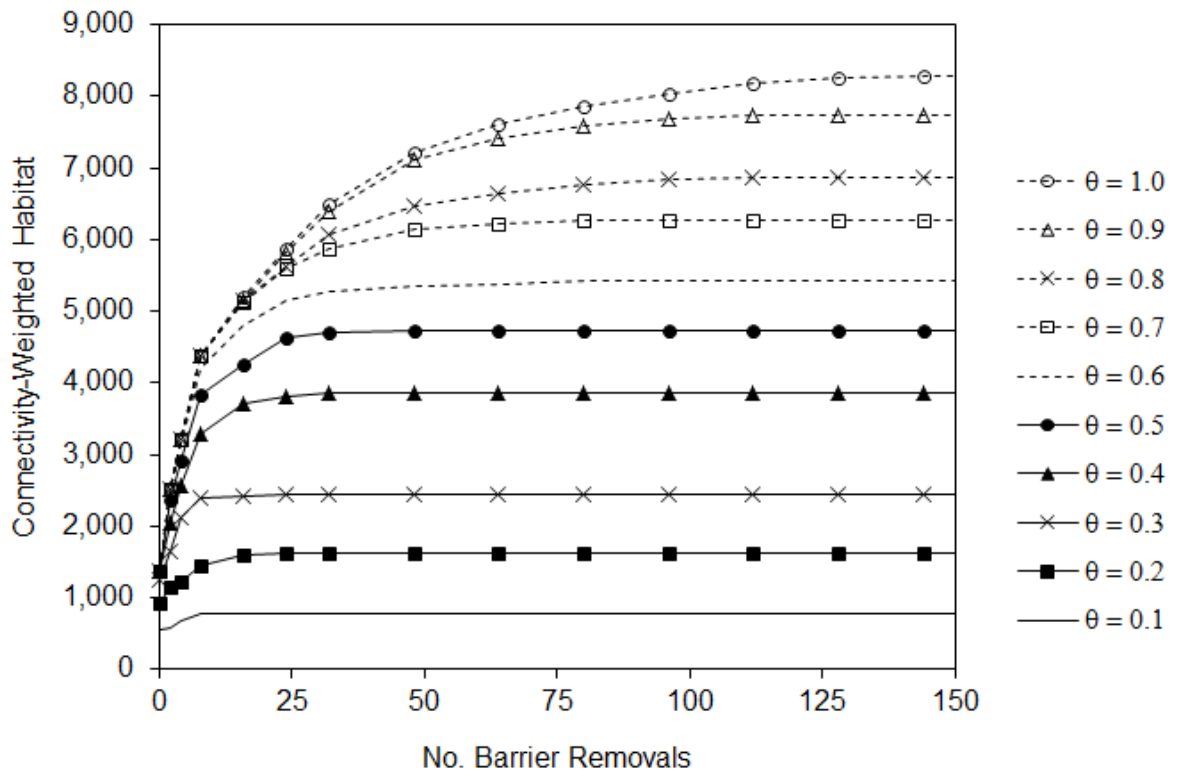
Fig. 3. Connectivity-weighted habitat versus number of barrier removals for various sized

river protected area (RPA) networks.
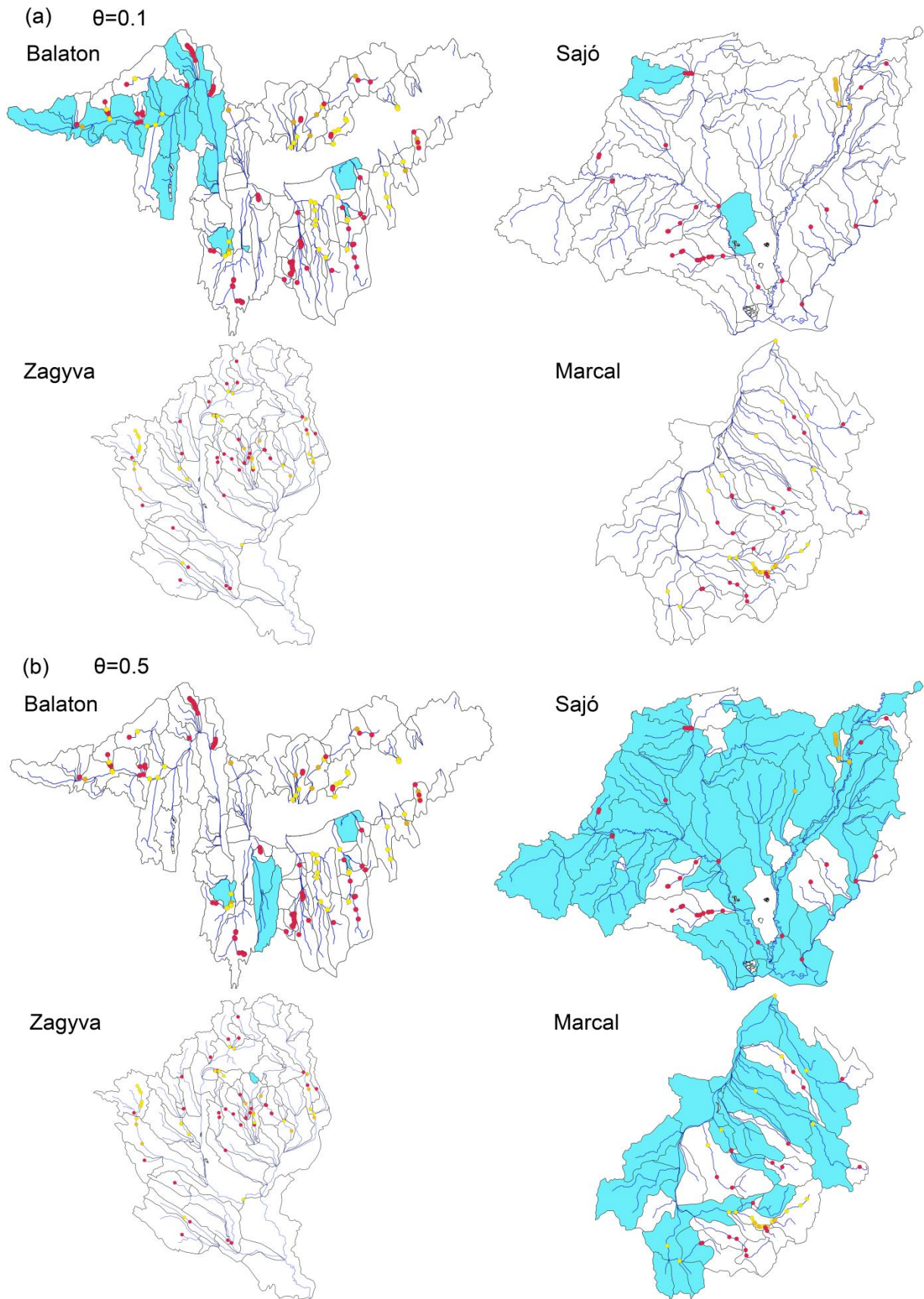
716 (a)
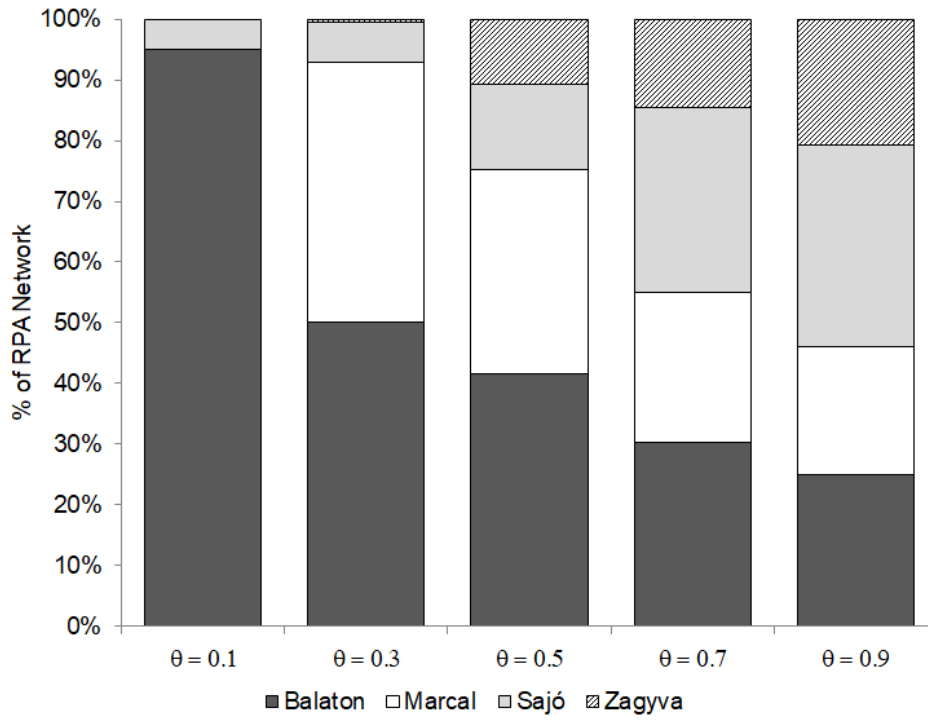
717

718 (b)
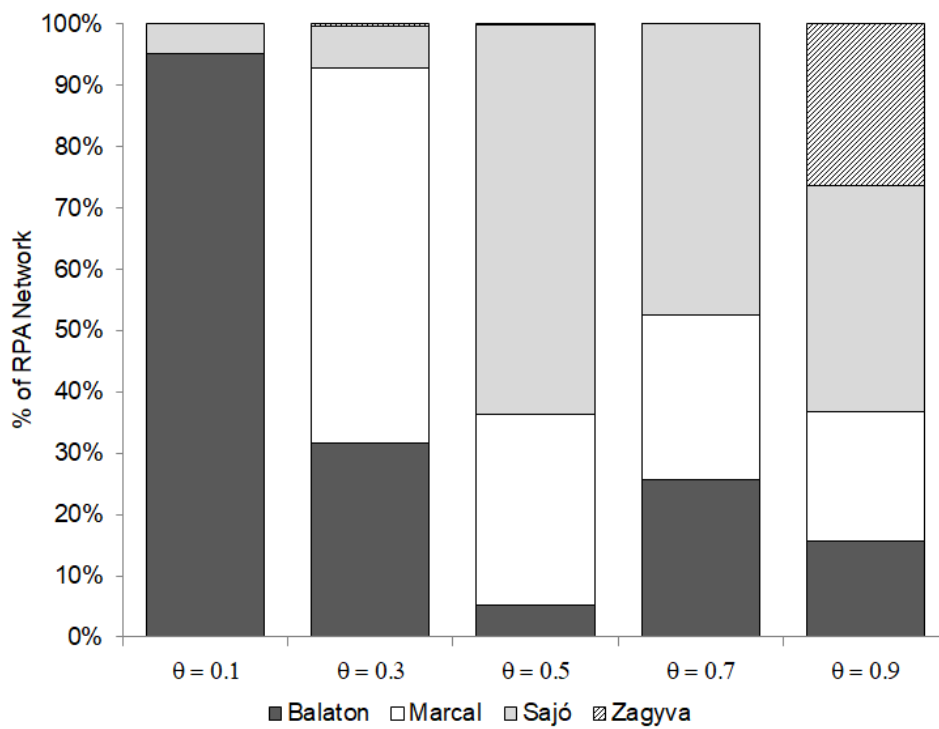
719

720 **Fig. 4.** Fraction of the RPA network in each river catchment given no barrier removal (a) and
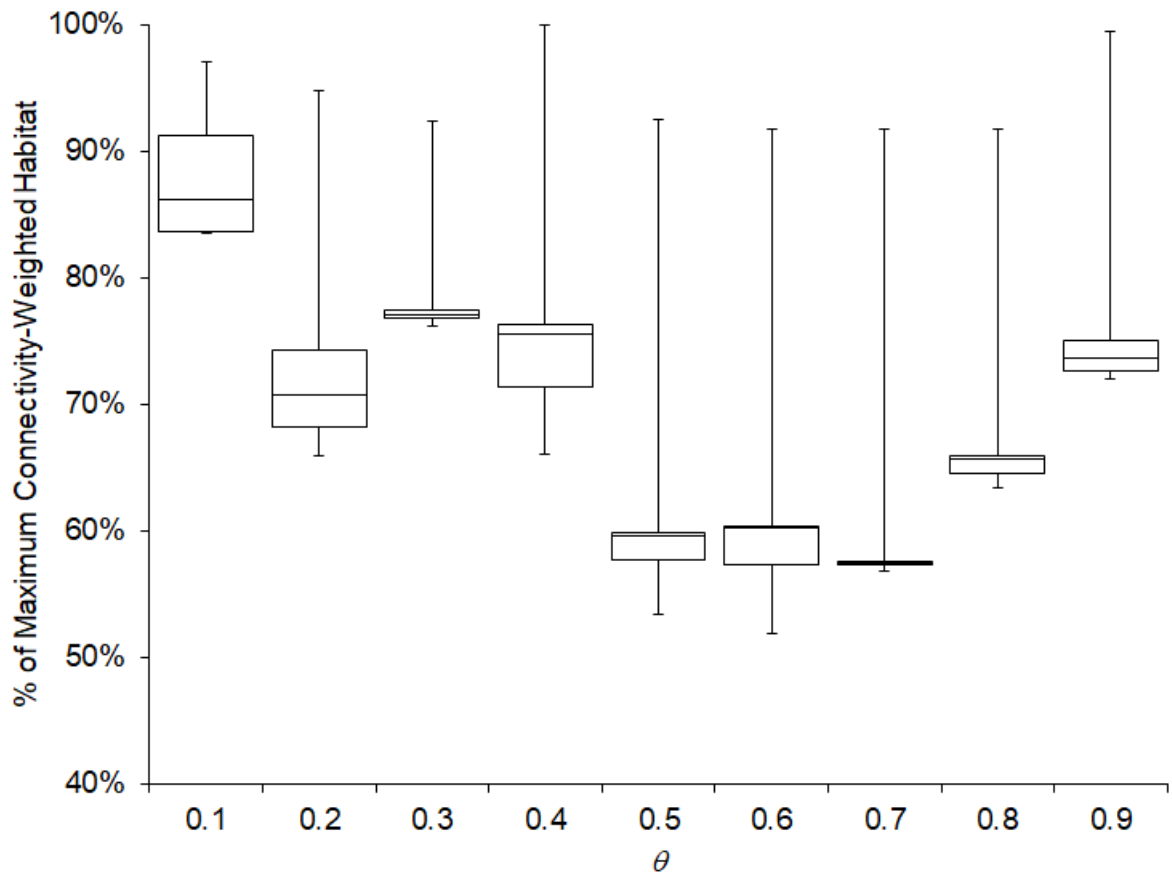721 unlimited barrier removals (b) for various RPA network sizes.
722

723

Fig. 5. Maps showing selected subcatchments for RPA networks of size $\theta = 0.1$ (a) and $\theta = 0.5$ (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)
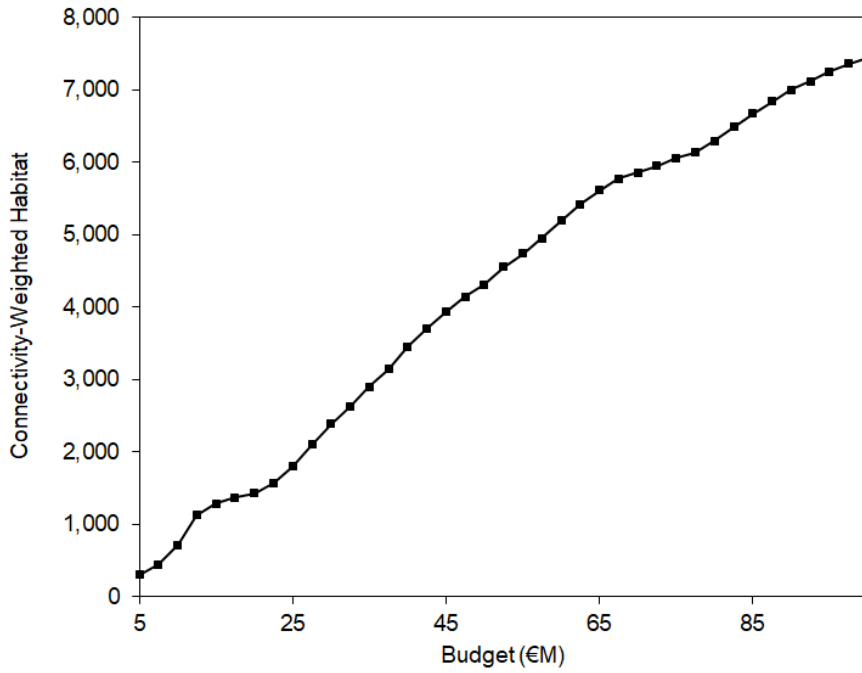
733

734   (b)
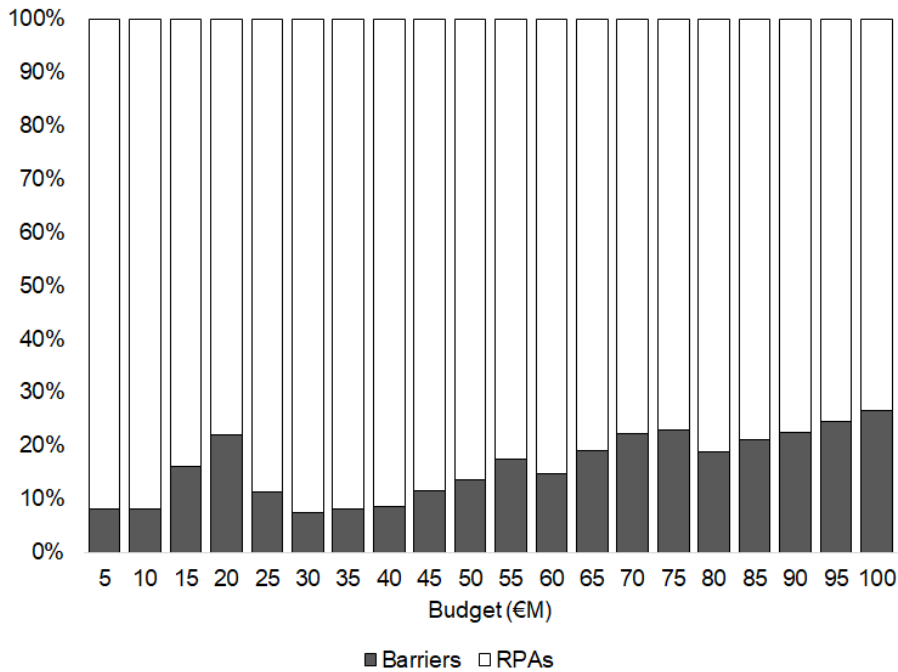
735

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).