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

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## Abstract

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

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

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## 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

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

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

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

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

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

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

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

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

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

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

## **Materials and Methods**



## *Study Area*

We selected four river catchments located in Hungary for our study (Fig. 2). These include Lake Balaton (5775 km<sup>2</sup>), the Marcal River (3084 km<sup>2</sup>), the Sajó River (5545 km<sup>2</sup>), and the Zagyva River (5677 km<sup>2</sup>). 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

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

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

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

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

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

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

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

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

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

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

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

#### *Barrier Survey Data*

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

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

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

#### *River Protection and Connectivity Optimization Model*

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

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

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

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

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

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

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

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

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

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

## Results

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

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

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

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



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

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

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

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

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

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

## Discussion

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

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

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

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

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

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

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

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

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

## **Authors' Contributions**

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

## **Acknowledgements**

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## **Data Accessibility**

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

## **References**

- Angermeier, P.L. (2000) The natural imperative for biological conservation. *Conservation Biology*, **14**, 373-381.
- Angermeier, P.L., Karr J.R. (1994) Biological integrity versus biological diversity as policy directives: Protecting biotic resources. *BioScience*, **44**, 690-697.
- Antal, L., Harka, Á., Sallai, Z., Guti, G. (2015) TAR: Software to evaluate the conservation value of fish fauna. *Pisces Hungarici*, **9**, 71-72.

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

526 Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., Roni, P.,  
 527 Pollock, M.M. (2010) Process-based principles for restoring river ecosystems. *BioScience*,  
 528 **60**, 209-222.

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

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

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

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

540 Cimon-Morin, J., Darveau, M., Poulin, M. (2013) Fostering synergies between ecosystem  
 541 services and biodiversity in conservation planning: A review. *Biological Conservation*,  
 542 **166**, 144–154.

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

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



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

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

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

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

557 Erős, T., Olden, J.D., Schick, R.S., Schmera, D., Fortin, M-J. (2012) Characterizing  
558 connectivity relationships in freshwaters using patch-based graphs. *Landscape Ecology*,  
559 **27**, 303-317.

560 Erős, T., O’Hanley, J.R., Czeglédi, I. (2018) Data from: A unified model for optimizing  
561 riverscape conservation. Dryad Digital Repository: <https://doi.org/10.5061/dryad.41pj936>

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

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

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

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

571 Grizetti, B., L Lanzanova, D., Lique, C., Reynaud, A., Cardoso A.C. (2016) Assessing water  
572 ecosystem services for water resource management. *Environmental Science & Policy*, **61**,  
573 194-203.

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

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

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

583 Hermoso, V., Linke, S., Prenda, J., Possingham, H.P. (2011) Addressing longitudinal  
584 connectivity in the systematic conservation planning of fresh waters. *Freshwater Biology*,  
585 **56**, 57-70.

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

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

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

593 Isaak, D. J., Luce, C. H., Rieman, B. E., Nagel, D. E., Peterson, E. E., Horan, D. L., Parkes,  
594 S., Chandler, G. L. (2010) Effects of climate change and wildfire on stream temperatures

595 and salmonid thermal habitat in a mountain river network. *Ecological Applications*, **20**,  
596 1350–1371.

597 Januchowski-Hartley, S.R., McIntyre, P.B., Diebel, M., Doran, P.J., Infante, D.M., Joseph, C.,  
598 Allan, D.J. (2013) Restoring aquatic ecosystem connectivity requires expanding  
599 inventories of both dams and road crossings. *Frontiers in Ecology and the Environment*,  
600 **11**, 211-217.

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

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

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

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

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

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

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

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

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

620 McDonnell, M.D., Possingham, H.P., Ball, I.R., Cousins, E.A. (2002) Mathematical methods  
 621 for spatially cohesive reserve design. *Environmental Modeling and Assessment*, **7**, 107-  
 622 114.

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

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

629 Mitchell M.G.E., Bennett E.M., Gonzalez A. (2013) Linking landscape connectivity and  
 630 ecosystem service provision: Current knowledge and research gaps. *Ecosystems*, **16**, 894-  
 631 908.

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

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

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

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

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

645 Newbold, S.C., Siikamäki, J. (2009) Prioritizing conservation activities using reserve site  
646 selection methods and population viability analysis. *Ecological Applications*, **19**, 1774-  
647 1790.

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

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

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

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

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

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

663 Pont, D., Hugueny B., Beier, U., Goffaux, D., Melcher, A., Noble, R., Rogers, C., Roset, N.,  
664 Schmutz, S. (2006) Assessing river biotic condition at a continental scale: A European  
665 approach using functional metrics and fish assemblages. *Journal of Applied Ecology*, **43**,  
666 70-80.

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

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

672   Roset, N., Grenouillet, G., Goffaux, D., Kestemont, P. (2007) A review of existing fish  
673       assemblage indicators and methodologies. *Fisheries Management and Ecology*, **14**, 393-  
674       405.

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

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

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

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

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

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

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

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

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

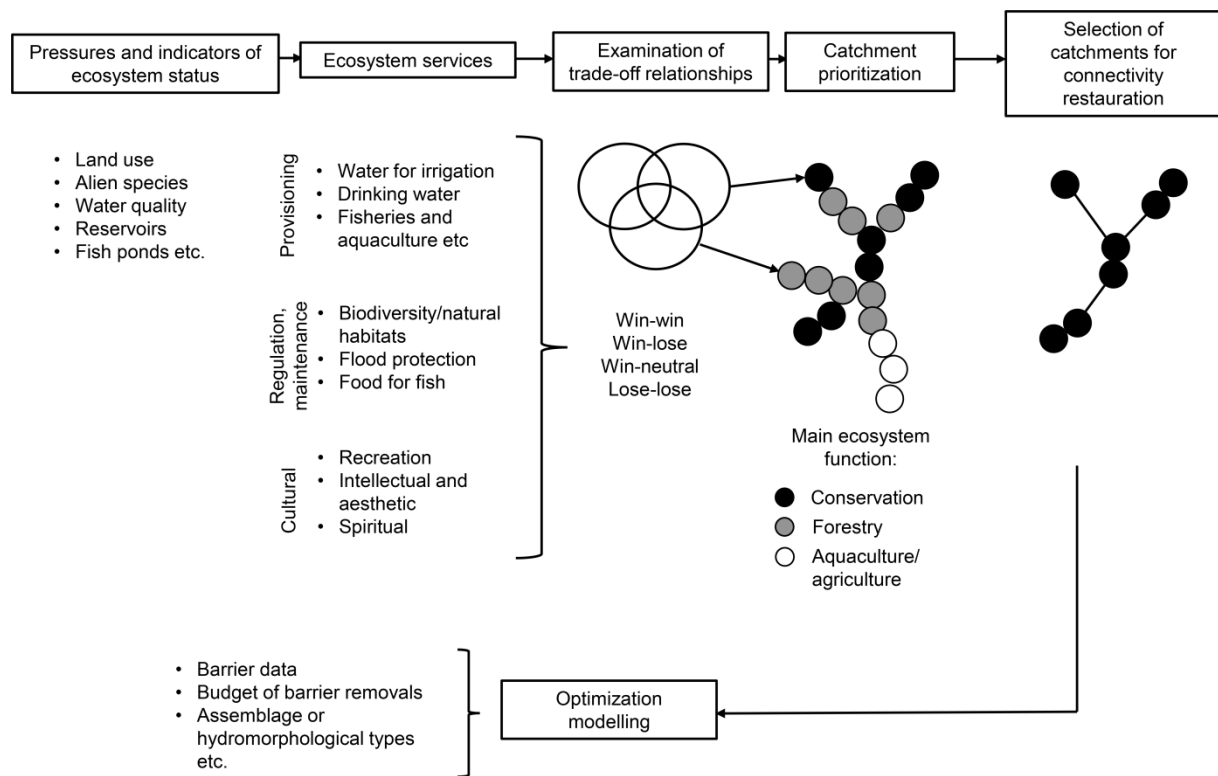
699 **Tables**

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

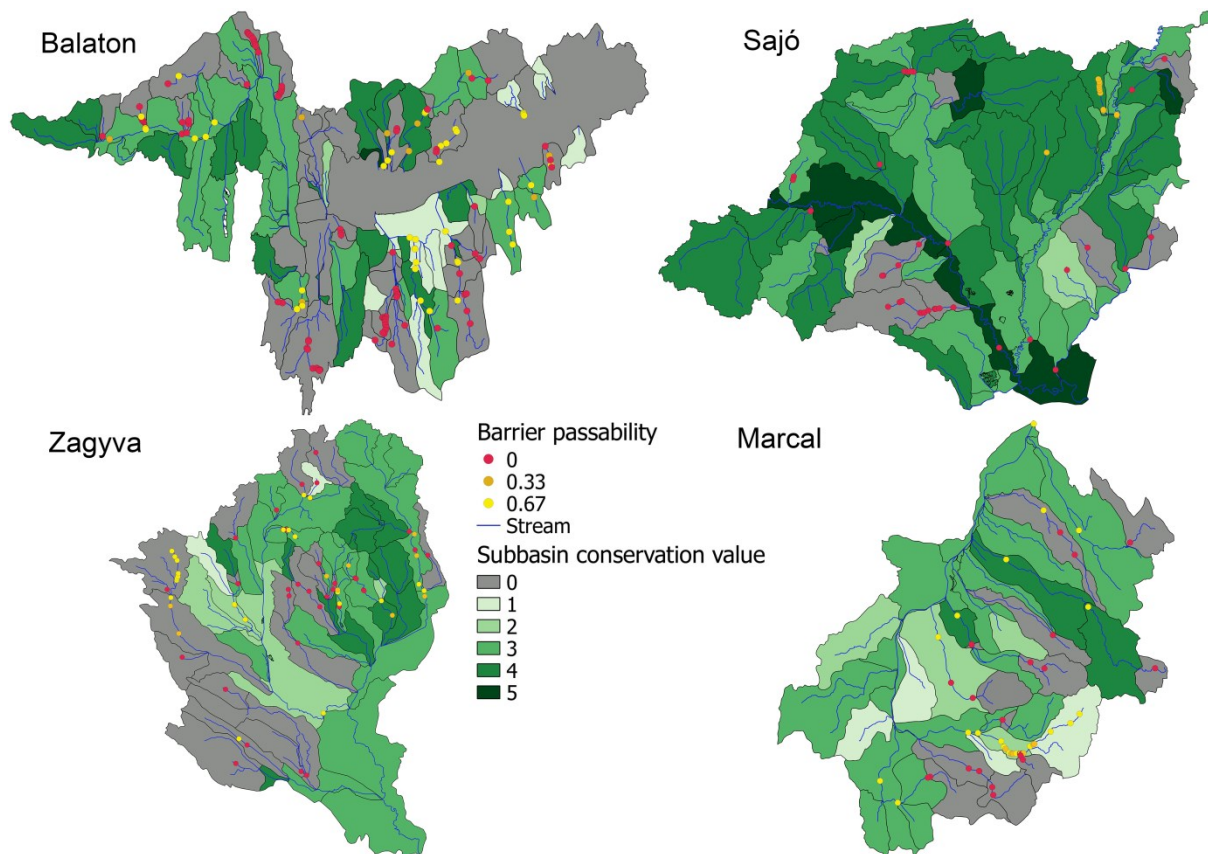
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Catchment	Habitat Amount (km)						Land Use (%)						No. of Barriers
	SMS	HLS	HLR	LLS	LLR	Total	ART	AG	FOR	NFOR	WET	WB	
Balaton	0.0	321.1	49.3	189.0	37.8	597.2	6.1	44.6	27.0	5.6	2.7	13.9	138
Marcal	20.9	157.9	0.0	252.6	70.4	501.8	5.5	64.9	24.2	5.2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

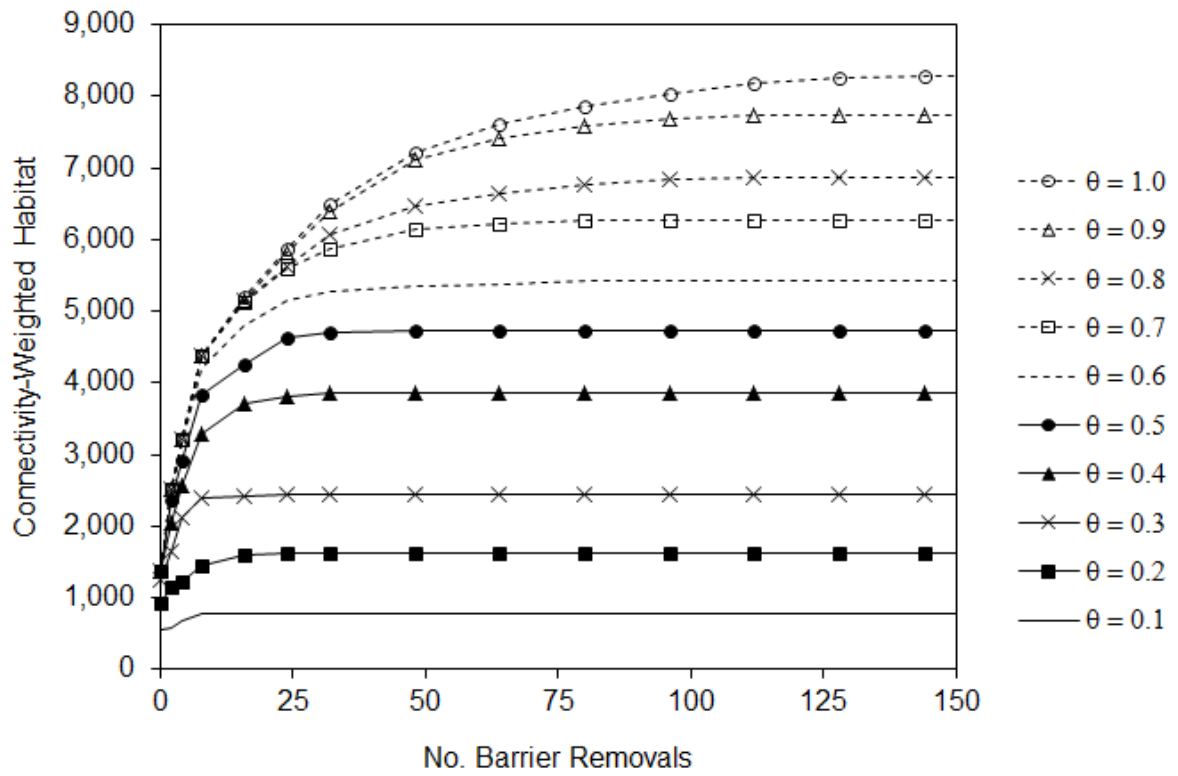




**Fig. 1.** A general framework for prioritizing catchments for biodiversity conservation versus ecosystem services and targeting connectivity restoration actions.



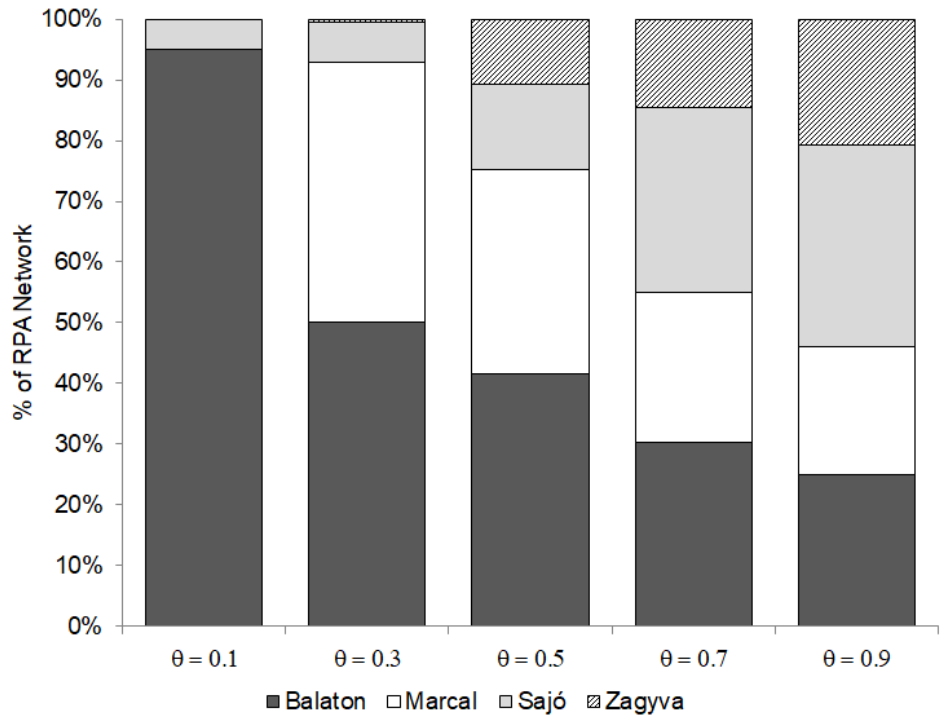
**Fig. 2.** Spatial pattern of biological integrity (BII) and distribution of artificial barriers in the four case study catchments: Lake Balaton, the Marcal River, the Sajó River, and the Zagyva River. BII is shown on a five-point scale, where a darker shade of green indicates higher integrity. Grey 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.



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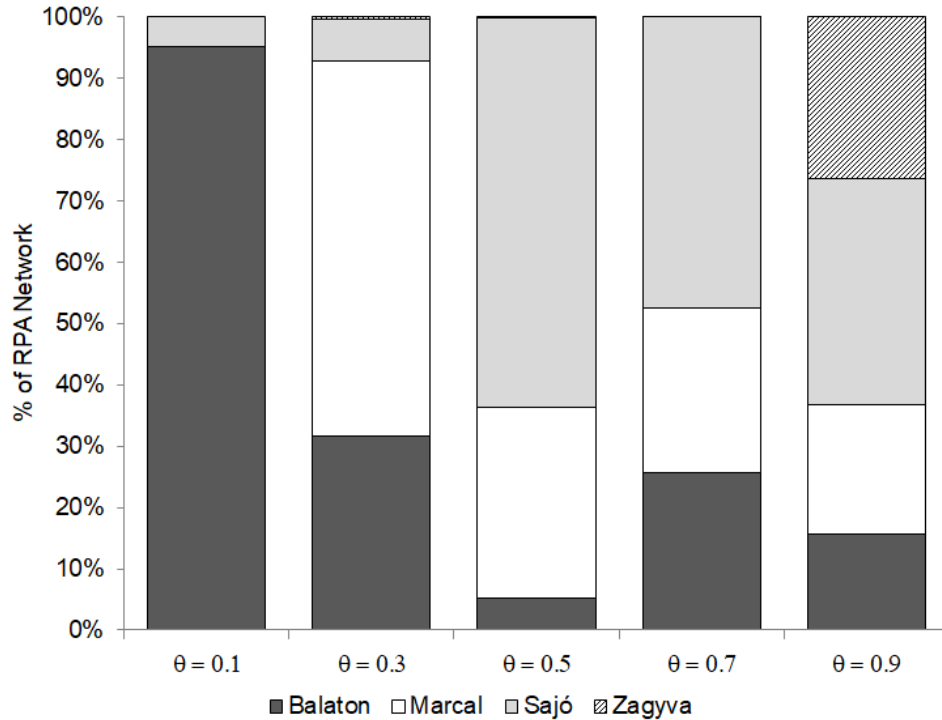
717 **Fig. 3.** Connectivity-weighted habitat versus number of barrier removals for various sized  
 718 river protected area (RPA) networks.

719 (a)



720

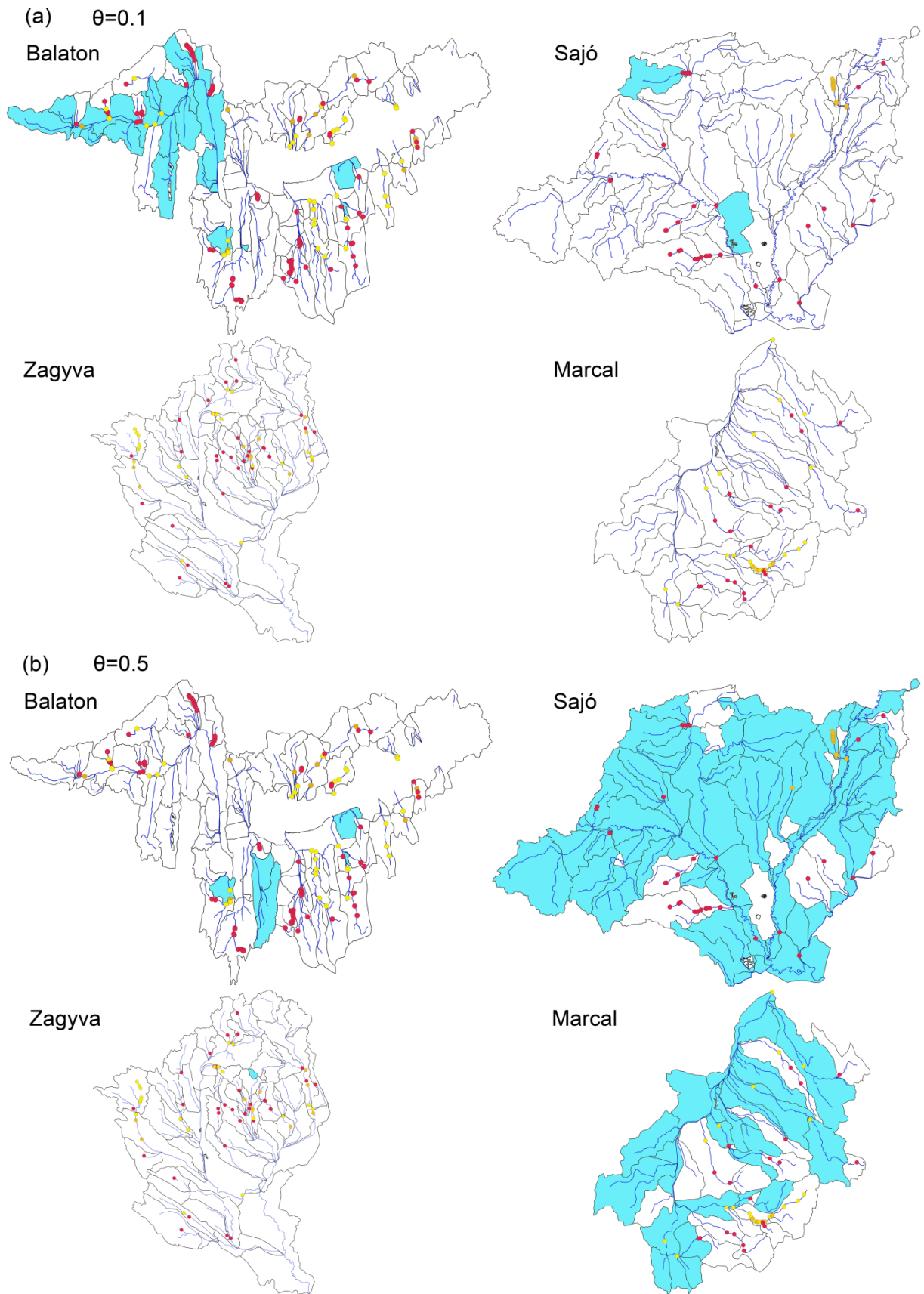
721 (b)



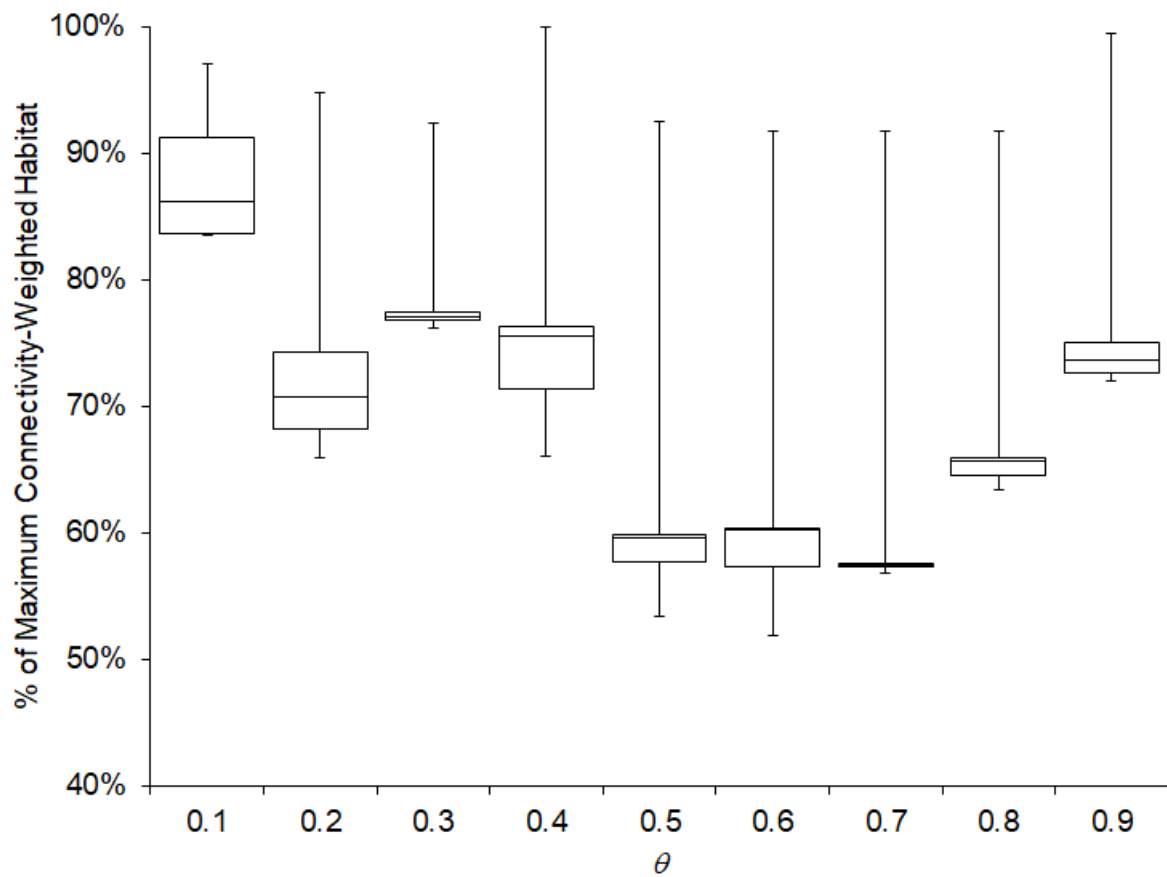
722

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

725

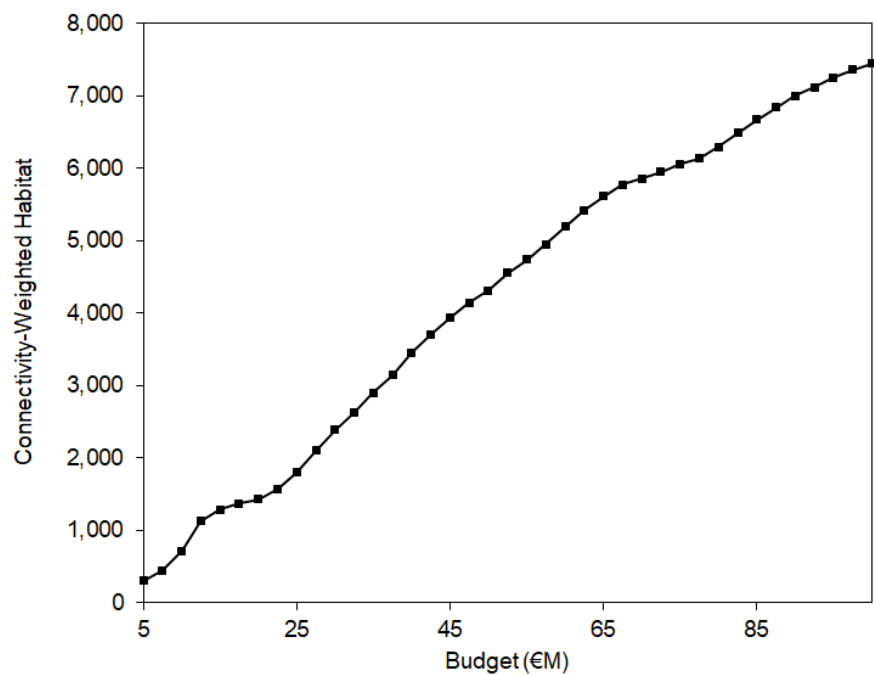


**Fig. 5.** Maps showing selected subcatchments for RPA networks of size  $\theta = 0.1$  (a) and  $\theta = 0.5$  (b) given unlimited barrier removals.



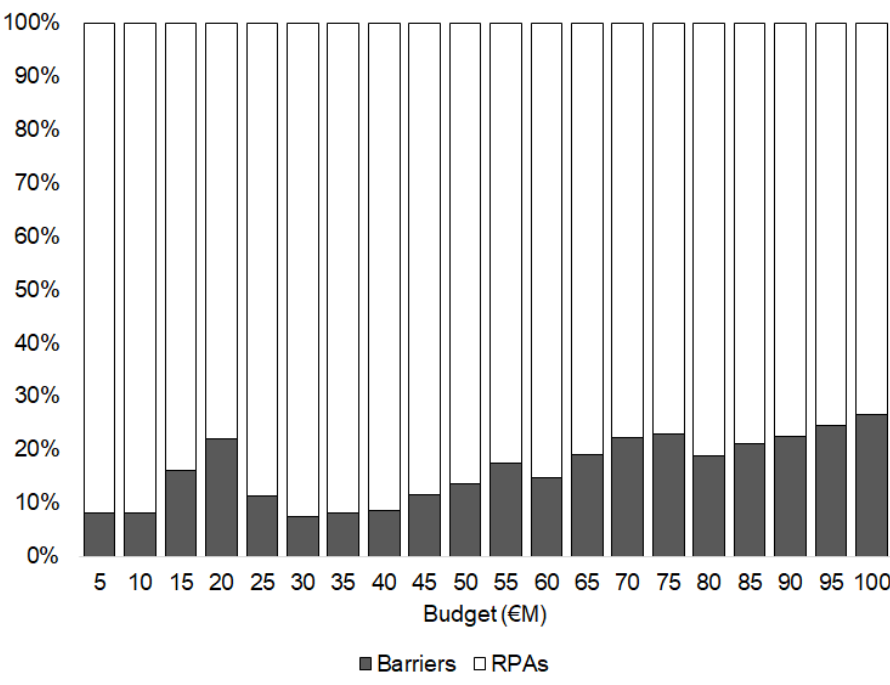
**Fig. 6.** Box plots showing the median, lower/upper quartiles, and minimum/maximum (whiskers) amount of connectivity-weighted habitat as a percentage of maximum for various RPA network sizes based on a sequential, two-stage approach to conservation and restoration planning (river protection decisions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

735 (a)



736

737 (b)



738

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