

Prioritizing barrier removal to improve functional connectivity of rivers

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Summary

1. Freshwater systems are severely impacted by connectivity reduction due to the construction of dams and weirs. The breach of this longitudinal connectivity imperils freshwater fish species world-wide. There is thus an increasing need for numerical tools that help decision-makers correctly allocate resources to prioritize restoration actions.

2. This study provides a methodology for prioritizing the removal of barriers. It is based on spatial graphs, which represent structural units as nodes and relationships between nodes as links, and uses habitat suitability modelling (Boosted Regression Trees) to weight nodes. To exemplify the application of this procedure, we used the Tagus River network and evaluated the impact of the dams (29 built between 1928 and 2004) on the occurrence of each of two fish species (Iberian barbel *Luciobarbus bocagei* – representing large potamodromous fish; and southern Iberian chub *Squalius pyrenaicus* – representing small water-column residents) and on the combination of both.

3. Results show that dam construction on the Tagus was responsible for a 48.4–54.4% reduction in river connectivity for different fish species. Actions to promote connectivity in just seven of the dams would increase connectivity by 35.0–37.2%.

4. The removal of a single barrier chosen through prioritization had a greater overall connectivity increase than the random removal of seven barriers.

5. *Synthesis and applications.* The proposed prioritization method, using spatial graphs and habitat suitability modelling, makes it possible to model the impact of the removal or placement of an insurmountable barrier on the overall functional connectivity of a river network, facilitating resource allocation and minimizing the impact of new barrier implementation.

Key-words: boosted regression trees, dam removal, functional connectivity, habitat suitability, longitudinal connectivity, river restoration, spatial graphs, stream fish

Introduction

Riverine environments are among the most endangered environments on earth (Gleick 2003). Connectivity can be understood as the functional ‘exchange pathway of matter, energy and organisms’ (Ward & Stanford 1995). Its most important role for several freshwater fish species lies in its longitudinal dimension. The origins of the longitudinal connectivity concept are to be found in the river continuum concept (Vannote *et al.* 1980). It is interrelated with the notion of ecological corridors (Formon & Godron 1986), with the theory of habitat fragmentation

(Fischer & Lindemayer 2007) and with ‘The serial discontinuity concept of lotic ecosystems’ (Ward & Stanford 1983), which hypothesizes that the thermal and flow alterations promoted by impoundments create an interruption of continuum processes. A breach of this longitudinal connectivity leads to geographic isolation (Moilanen & Nieminen 2002), which is one of the more pressing factors influencing species distributions (Fahrig & Merriam 1985). Connectivity interruption has led to declines in the populations of half of the threatened European fish species (Northcote 1998). It affects fish movements for reproduction, feeding and habitat colonization, which in turn leads to potential genetic impoverishment and loss of population portions, while promoting the dispersion of exotic fauna (Branco *et al.* 2012). In order for a body of water

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to achieve good ecological status, which is the main goal of the Water Framework Directive (European Commission 2000), the re-establishment of the system's longitudinal connectivity should be seen as a priority (Mader & Maier 2008).

Connectivity can be divided into structural and functional connectivity; structural connectivity refers to the physical relationships between structural elements (habitat patches, segments, etc.) (Keitt, Urban & Milne 1997; Antongiovanni & Metzger 2005; Segurado, Branco & Ferreira 2013). Functional connectivity on the other hand accounts for the response of the biological element (community, population, etc.) to the landscape structure (Tischendorf & Fahrig 2000; Taylor, Fahrig & With 2006), being the result of complex relationships between individuals, populations and landscapes (Crooks & Sanjayan 2006; Vogt *et al.* 2009). Functional connectivity should consider several parameters, such as the structural nature of connectivity, habitat preferences, habitat availability and blockage elements that impede animals from moving from one landscape element to the next (Pe'er *et al.* 2011). To be able to identify relevant habitat variables for conservation actions (e.g. connectivity), there is the need to understand the ecology of the target species (Bowne, Bowers & Hines 2006).

Numerical methods are increasingly being used to simplify data (Harris & Silveira 1999). These methods aid the decision-making process while maintaining scientific accuracy (Paul 2003). Padgham & Webb (2010) propose that the sum of independent impacts of barriers is equal to their joint effect, but it is well accepted that multiple barriers promote cumulative effects on connectivity hindrance (Kemp & O'Hanley 2010; Rolls 2011) – for example, by cumulatively increasing migration delays (Castro-Santos & Haro 2003). Therefore, multiple barriers should be analysed collectively to account for cumulative effects. There are several noteworthy studies that look at barrier removal; the most common approach is the use of scoring-and-ranking techniques (e.g. Taylor & Love 2003; Karle 2005) that use a combination of physical, ecological and economic elements. The main caveat of these scoring-and-ranking systems is that they only account for the impacts of isolated barriers, neglecting the cumulative non-additive impacts of all barriers in a network (O'Hanley & Tomberlin 2005; Kemp & O'Hanley 2010). Alternative methods, that contemplate cumulative impact of barriers, have also been proposed (Kuby *et al.* 2005; Zheng, Hobbs & Koonce 2009; O'Hanley 2011) applying optimization algorithms to define the most favourable barrier removal combinations for different budget limitations. Conyngham *et al.* (2011) advanced by looking at fish passage efficiency of multiple barriers, and Cote *et al.* (2010) and Diebel, Fedora & Cogswell (2010) extended the analysis by incorporating both upstream and downstream barrier passage efficiency for potamodromous and diadromous fish. Nevertheless, most programs developed to prioritize actions

for restoring connectivity do so primarily in order to increase connected river length (Mader & Maier 2008; Kocovsky, Ross & Dropkin 2009), neglecting the habitat suitability/availability for each species or even for the community, and thus favouring structural connectivity over its functional counterpart.

The connectivity among habitat patches at the landscape scale has been extensively addressed using spatial graphs (Urban & Keitt 2001; Dale & Fortin 2010; Galpern, Manseau & Fall 2011). Graph theory is based on simple concepts, and treats spatial elements as nodes and the relationship between nodes as links (Dale & Fortin 2010). Spatial graphs are a special case of graph theory in which the nodes have locations and links are defined by those locations (Fall *et al.* 2007). However, recent works have extended this technique to rivers (Schick & Lindley 2007; Erös, Schmera & Schick 2011; Erös *et al.* 2012; McKay *et al.* 2013; Segurado, Branco & Ferreira 2013), and this has proved to be an excellent tool for assessing the connectivity of river networks. Graphs make it possible to look at a network from two perspectives: a forward approach, understanding how the network became or will become divided (Keitt, Urban & Milne 1997; Urban & Keitt 2001); and a backward approach, understanding how potential restoration actions would result in connectivity increases (Palmer *et al.* 2005). This technique creates the opportunity to study the non-additive cumulative effects of the barriers in a system on the reduction in connectivity by taking into account not only the isolated effect of each barrier, but also the joint effect of all barriers (Segurado, Branco & Ferreira 2013).

The present study aimed to provide a general spatial graph-based framework for prioritizing connectivity restoration actions. To accomplish this, a case study based on the Tagus River network (central Portugal) was used, and the dams therein (29 built between 1928 and 2004) were evaluated considering both their chronological impact and the gains in river connectivity after their simulated removal. This procedure made it possible to rank the dams by priority for removal, taking into account the gains in the functional connectivity of rivers for two fish species with distinct life histories: the Iberian barbel *Luciobarbus bocagei* (Steindachner, 1864) – representing the guild of large potamodromous fish; and the southern Iberian chub *Squalius pyrenaicus* (Günther, 1868) – representing the guild of small water-column residents.

Materials and methods

STUDY AREA

The study area for the proposed case study comprised the Portuguese portion of the Tagus River basin (Lower Tagus), limited upstream by the Cedillo Dam, which is located just across the Portuguese–Spanish border (Fig. 1) (Fig. S1, Supporting information). The Tagus River extends across 1070 km of Portugal and

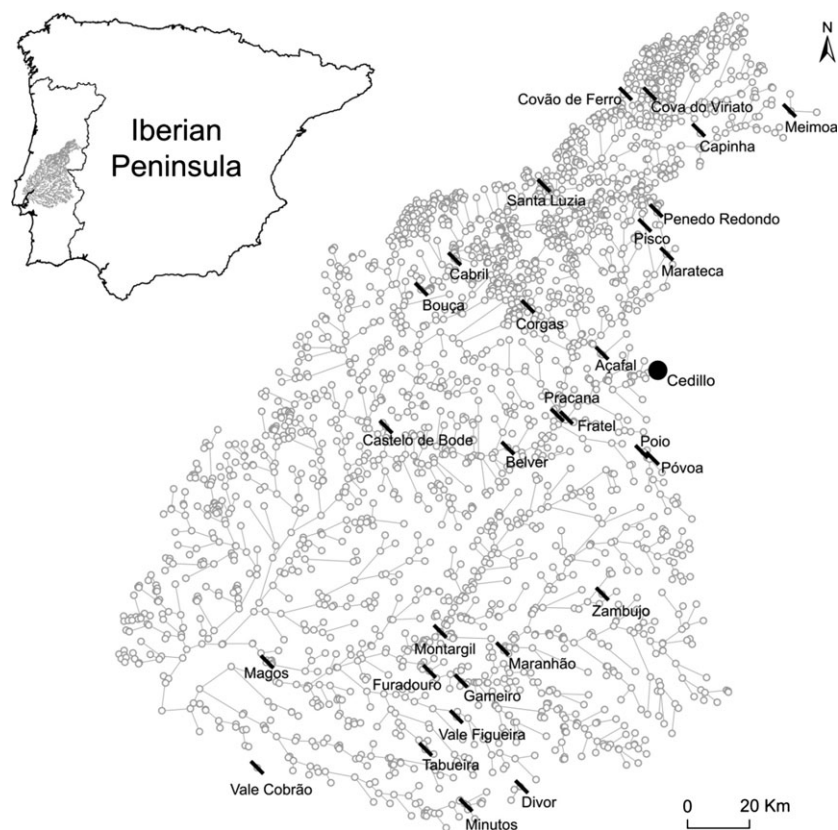


Fig. 1. Study area and representation of the graph model of the Tagus River network. The dams considered in this study are represented as black bold lines (—).

Spain. It represents the largest basin on Portuguese territory and the third largest one in the Iberian Peninsula, with an area of c. 80 000 km², of which 24 800 km² are in Portugal (INAG I.P. 2012). The river runs westwards towards the Atlantic coast, presenting a marked seasonal and interannual variability in flow. The lower Tagus system (study area) has been modified by dam construction since the first quarter of the 20th century (see Appendix S1, Supporting information).

SPECIES SELECTION

Iberian rivers are dominated by cyprinid fishes, ranging from large benthic potamodromous to small resident pelagic species. Therefore, two model species were selected: the Iberian barbel (*L. bocagei*, barbel hereafter) was selected to represent large potamodromous (obligatory reproduction migrations exclusively in fresh water) benthic cyprinids; and the southern Iberian chub (*S. pyrenaicus*, chub hereafter) was selected to represent small water-column resident cyprinids. The barbel is a potamodromous fish that relies on the ability to freely progress upstream to complete the life cycle. So, in the lower Tagus systems, at least part of the population is severely limited in their ability to reach suitable spawning grounds, and is, as such, limited in their ability to complete the life cycle. The chub is a resident species with an endangered status in the Portuguese red list (Cabral *et al.* 2005), where it is clearly stated that the main cause of threat is habitat degradation due to the building of dams.

FISH SAMPLING

A total of 456 sites in Portugal were selected and sampled between 1996 and 2012. These sites were located in several basins

within the known species distribution range to allow for a wide environmental gradient to increase model predictive ability. The sampling was performed by electrofishing – the least biased method for sampling stream fish (Cowx 1989) – following standard procedures similar to the one adopted by the European Committee for Standardization (CEN norm 14011 March 2003). Data analysis was based on presence/absence data, which is less susceptible to interseason and year variations (Magalhães *et al.* 2007). Additionally, this data transformation reduces the bias present in abundance data analyses when the sampling effort has disparities among sites, homogenizing data and increasing the accuracy and predictability of the analyses.

HABITAT ASSESSMENT AND SUITABILITY MODELLING

The Tagus River network was divided into its constituent segments, a segment being a stretch of river between confluences. The river network segmentation followed the GIS riverscape theme of the ‘Catchment Characterisation and Modelling – River and Catchment database for Europe’ (CCM2) (Vogt *et al.* 2007) and defined 2542 river segments.

Habitat suitability models were based on 24 environmental variables, including five variables compiled at the segment scale and 19 variables compiled at the watershed scale associated with each segment (see Appendix S2, Supporting information). Only regionalized variables (distributed in space and available for all the study area) were used in habitat suitability models, in order to allow predictions for non-sampled segments. We integrated all the information using the CCM2 river network data base (Vogt *et al.* 2007). This data base includes two main GIS themes: river segments (line theme); and the respective associated watershed (polygon theme). Except for the five landcover variables, all

variables were readily available in the CCM2 data base, including segment hydromorphologic features, topography and climate. Landcover variables were compiled from Corine Land Cover 2006 (EEA 2010), by computing the proportion of area occupied by each relevant landcover type (forest, non-irrigation crops, irrigation crops, agro-forestry systems and urban) in the watershed polygons linked to each segment.

In order to estimate the potential habitat suitability of each species in each of the river segments in the study area, fish sampling data were modelled using boosted regression trees (BRT) (Elith, Leathwick & Hastie 2008). This technique is known to produce highly predictive models, usually outperforming generalized linear models, generalized additive models and generalized linear mixed models (Elith, Leathwick & Hastie 2008; Leathwick *et al.* 2008; McCue, McGrath & Wiersma 2013). To fit BRT models, we followed the procedure recommended by Elith, Leathwick & Hastie (2008): in order to optimize the number of trees, we carried out a stepwise process based on 10-fold cross-validations (Leathwick *et al.* 2008) using the area under the receiver operational curve (AUC; Fielding & Bell 1997) as the accuracy measure. The AUC assesses how far from chance the model predicts species occurrence, varying from 0.5 (random classification) to 1.0 (perfect classification). Two important parameters determine the number of trees required for optimal predictions: the learning rate (lr), which determines the contribution of each tree to the growing model; and the tree complexity (tc), which controls the number of interactions among variables (i.e. the number of splits of individual trees). We set lr and tc to 0.003 and 3, respectively, which are within the suggested range for the data set size and ensured that at least 1000 trees were achieved after the stagewise process, as recommended by Elith, Leathwick & Hastie (2008). After adjusting the model, we proceed with the model simplification by removing the lowest contributing predictors. This procedure was based on cross-validations to identify the subset of variables that did not contribute to significant changes in the predictive deviance (Elith, Leathwick & Hastie 2008). We used a random subset of 80% of presences and absences to calibrate the models and used the remaining data as the validation subset. Model accuracy was based on the mean AUC values of the 10-fold cross-validations, as well as the estimated AUC value and True Skill Statistics (TSS; Allouche, Tsoar & Kadmon 2006) using the validation subset. The TSS measures the accuracy of the classification into presence and absence and, compared to other measures, is considered to be less influenced by the species prevalence (Allouche, Tsoar & Kadmon 2006). It ranges from -1 (no skill) to 1 (perfect classification skill). We used species prevalence as the classification cut-off probability.

The BRT models were then used to predict (using segment and catchment-scale variables – see Appendix S2, Supporting information) the probability of occurrence (between 0 and 1) for each species in each river segment in the Tagus River network. These probability values were considered surrogates for habitat suitability. To estimate the habitat suitability of each segment for the combination of the two studied species, the respective probabilities of occurrence were multiplied. The resulting values favour segments with high probability values for both species and penalize segments with low probability values for one, and especially both species.

Variable extraction was performed at both the segment and catchment scales using the ARCGIS 10.0 software (ESRI 2011). BRT habitat suitability modelling and prediction were performed

in R 2.15.1 (R Development Core Team 2012), using the GBM (Ridgeway 2007) and DISMO (Elith, Leathwick & Hastie 2008; Hijmans *et al.* 2013) packages.

RIVER NETWORK TOPOLOGY

In order to understand the effects of dams as river longitudinal connectivity fragmenting structures, we used an approach based on spatial graph theory (Fall *et al.* 2007; Erös *et al.* 2012), where the graph network is represented by $G = (N, L)$, where N represents a set of n nodes and L a set of l links (Erös, Schmera & Schick 2011). In the proposed methodology, river segments were represented as nodes and confluences as links. Dams were placed at river segments (nodes) and considered to be insurmountable barriers (impervious to fish movements in both directions) that broke up the original network into sub-networks. Each node was attributed its suitability score (derived from BRT), and the connection between nodes was considered to be binary (linked/unlinked) and undirected (connected both upstream and downstream).

In this graph-based approach, the integral index of connectivity (IIC) was used as the overall connectivity metric. The IIC measures the degree of connectivity of a given network, increasing with augmented connectivity and ranging from 0 – no connection between landscape elements – to 1 – full connection of the landscape elements (Pascual-Hortal & Saura 2006; Saura & Pascual-Hortal 2007). Unlike several connectivity indices, this metric has the advantage of evaluating the importance of landscape elements, individually or in combination, to the maintenance of the system's connectivity (Pascual-Hortal & Saura 2006). It quantifies a segment's importance using both graph structures and habitat availability/suitability.

Of the various connectivity metrics, Baranyi *et al.* (2011) consider that the IIC and another commonly used metric – the betweenness centrality (BC) (Minor & Urban 2007) – as encapsulating most of the variability in patch ranking. However, these two metrics were shown to be highly correlated in river networks (Segurado, Branco & Ferreira 2013) and, in order to simplify the overall procedure, the BC was therefore not computed. The IIC was computed using CONEFOR v2.6 (Saura & Torné 2009; Saura & Rubio 2010).

PRIORITIZING DAM REMOVAL

First, in order to understand how dam construction incrementally impacted fish habitat availability and connectivity, we pursued a historical approach in which the impact of barriers was determined by following the temporal sequence of dam building, removing links (placing dams) sequentially until the current situation (29 dams) was achieved. Secondly, to prioritize connectivity restitution, we used the actual scenario as the starting point and added links (removing dams) in a backwards stepwise manner. We performed this stepwise approach by iteratively removing dams at each step, with reposition after each removal, in order to determine the isolated effect of removing a single dam. Afterwards, at each step, the dam whose removal had a higher positive impact on overall connectivity, measured as the percentage of IIC increase, was removed permanently, and the process repeated until connectivity was 100% re-established.

To ascertain the validity of the proposed prioritization technique, the results of connectivity increase attained through the

barrier removal prioritization scheme were compared to the results attained by a random removal of barriers. The pursued randomization process consists of randomly choosing the barriers and the removal order of the first seven steps. This process was repeated 30 times, and the percentage of overall connectivity averaged at each step.

Results

According to the graph model of the current topological connectivity of the Tagus network (Fig. 1), each dam – each of which represents a complete barrier to fish passage – divided the original fully connected Tagus River network into several sub-networks (Fig. S1, Supporting information). The BRT modelling technique made it possible to produce habitat suitability maps (Fig. 2) that corresponded to the probability values of the occurrence of a given species predicted for the whole set of river segments. The resultant maps are directly influenced by the physical habitat present in each of the river segments. The estimated accuracy measures (see Appendix S3, Supporting information) indicate that the models had good predictive ability (Lane, Raimondi & Kudela 2009). The resulting habitat suitability map for barbel (Fig. 2a) shows that this species has a wide homogeneous distribution, occurring in

higher order streams, and a limited probability of occurrence at low-order number streams near the extremes of the network. The chub on the other hand (Fig. 2b) presents a more localized potential distribution, occurring in the northern portion of the Tagus River network, especially in small tributaries, and having a low affinity with high-order number river segments. Barbel presence is more affected by the cumulative length of the upstream network and by the area drained by the river segment, whereas chub is more influenced by elevation and rain variables (see Appendix S3, Supporting information). When the probability of occurrence of both species is combined (Fig. 2c), the northern portion of the Tagus network is the primary area for the sympatric occurrence of both species. Here, the intermediate segments gain preponderance over high- and low-order number segments.

The construction of dams had a clear impact on the connectivity of the Tagus River network (Fig. 3). The current 29 dams have produced an overall connectivity reduction (measured as the variation in IIC) of 54.4% for the barbel, 48.4% for the chub and 50.0% for both species combined. It is also shown that, besides the similarity in the overall connectivity reduction between species, the general pattern of reduction was also very similar. The first five dams to be placed had little impact

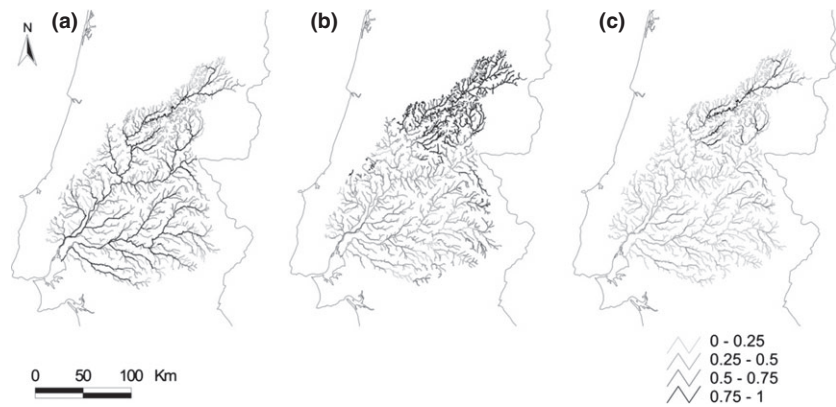


Fig. 2. Map representation of the habitat suitability models, expressed as modelled probability of occurrence, of the Tagus River network for the (a) barbel, (b) chub, (c) combination of the two species.

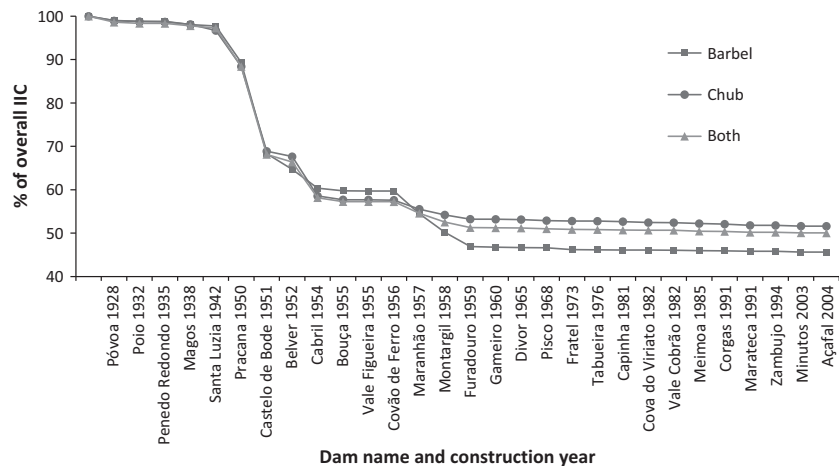


Fig. 3. Percentage of change in the overall connectivity (IIC) of the Tagus River network following the chronological sequence of dam construction.

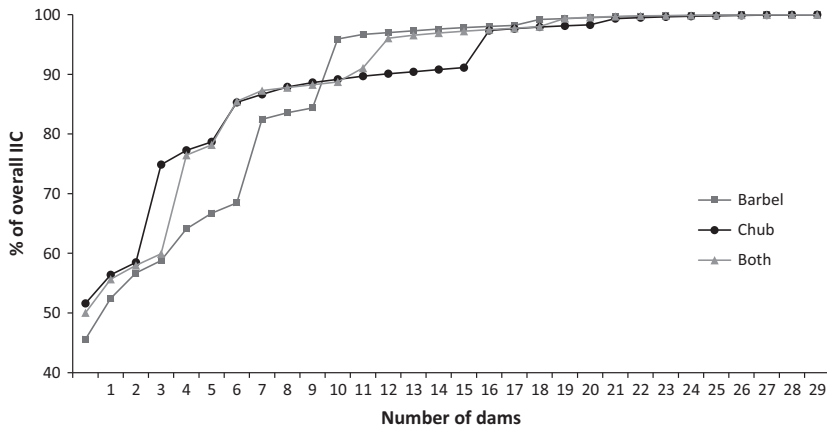


Fig. 4. Percentage of change in the overall connectivity (IIC) of the Tagus River network following the barrier removal sequence defined by the stepwise procedure.

(2.3–3.3% of overall IIC variation), while the following four had a large impact (37.4–39.1% of overall IIC variation). The remaining 20 dams had a comparatively low impact on connectivity, being responsible for just 7.0–14.7% of overall IIC variation.

The backwards-stepped process of dam removal selected a different sequence of dams for barbel, chub and both species combined (see Appendix S1, Supporting information). However, the first dam to be chosen for removal was Castelo de Bode according to all three approaches. Additionally, the removal of the first seven dams contributed to a large connectivity increase (35.0–37.2% of overall IIC variation), while the remaining 22 dam removals only accounted for 12.7–17.5% of overall IIC variation. According to the stepped increase in overall IIC variation for the two species and for the combination of both (Fig. 4), the general pattern of overall IIC variation is similar among the three cases, that is, there is a rapid increase in IIC until a point at which the variation flattens, at around the seventh dam removed. Nonetheless, the barbel's pattern of variation differs slightly from the other two patterns (chub and both), which display a closer variation, especially between the third and the ninth removals.

Figure 5 presents the results of the random removal of seven barriers (the number of dams responsible for the largest portion of connectivity increase when using the prioritization technique) on the overall connectivity increase for the three studied cases. There is a clear difference between the random removal and the prioritized removal, the former showing a much poorer performance in increasing connectivity. In fact, the stepped increase of connectivity through random barrier removal has a very low slope, a clear counterpoint to the more rapid increase observed when barriers were removed using the prioritization approach. When comparing the specific connectivity gains attained by both techniques, the advantage of prioritizing becomes even more evident – the random removal of all seven dams attains an overall connectivity increase of 4.1–5.1% which is less than the increase attained by removing a single dam chosen through the prioritization method.

Discussion

Rivers represent a particular case of spatial graph analysis, as the network is already defined and rivers have a high degree of directionality imposed by flow. In opposition to landscape level analysis, in which protection is provided by hubs (group of highly connected nodes), meaning that some networks are able to maintain connectivity even with the loss of several nodes (Urban & Keitt 2001), and river network connection suffers severely from node loss, due to the lack of alternative paths. The present article provides a new spatial graph-based approach that will help decision-makers to prioritize connectivity restoration actions in such a way as to help systems recover from past human-induced impacts. This method offers major advantages: it is a direct approach using spatial graphs that have proven to apply well to aquatic environments (Schick & Lindley 2007; Erös, Schmera & Schick 2011; Pereira, Segurado & Neves 2011; Erös *et al.* 2012); it is able to incorporate habitat suitability of a single species or a group of species into overall connectivity

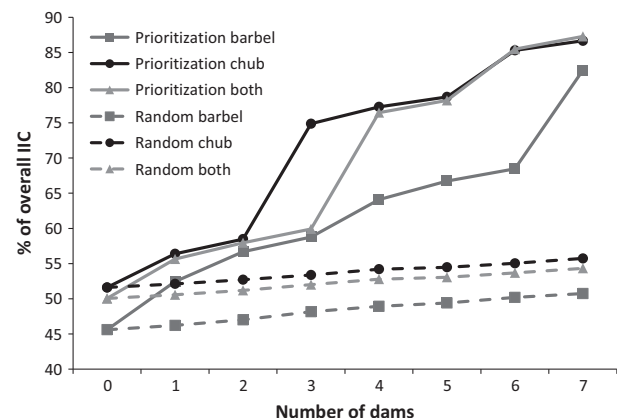


Fig. 5. Percentage of change in the overall connectivity (IIC) of the Tagus River network of the first seven barriers to be removed according to the stepwise procedure and of the random removal of seven dams (30 randomizations).

availability; and finally, it uses simple free software (Ridgeway 2007; Saura & Torné 2009; Saura & Rubio 2010; R Development Core Team 2012; Hijmans *et al.* 2013).

The results showed that the barriers' impact on overall connectivity in the Tagus River network was higher (albeit only slightly) for the barbel. Its wider distribution and preference for larger segments mean that the barbel suffered a more pronounced overall impact, as dams tend to be built in larger river segments. We verified that the first five barriers to be constructed had a small impact on overall connectivity, something also found by Segurado, Branco & Ferreira (2013) in terms of structural connectivity for the same study area. According to a simulation model, Cote *et al.* (2010) showed that largest losses of connectivity in a river network occurred after the implementation of the first barriers. However, the same authors further recognized that the position of the barriers may affect their relative impact on connectivity, something that we observed as well. Although structural connectivity is an important overall river attribute, functional connectivity needs to be evaluated when connectivity restoration actions are focused on specific targets. Our work shows that dams produce a real decrease in the longitudinal connectivity of a river network and that although the extent of this decrease varies among target species, in overall terms it is generally the same.

BRT models were robust, producing predictive models with substantial accuracy, which supports previous findings that ensemble learning techniques, by including a randomization element, have a high predictive performance (Caruana & Niculescu-Mizil 2006; Olden, Lawler & Poff 2008). This methodology's plasticity and robustness made it possible to predict the suitability of each segment of the network for each of the studied species. This technique has applications that can be extended to management problems, identifying areas of conservation priority and facilitating the definition of fishery areas.

This work, when compared to a solely structural approach (Segurado, Branco & Ferreira 2013), shows that applying a functional connectivity approach to connectivity restoration yields different results, highlighting the importance of accounting for species ecology when planning connectivity enhancement actions. When defining the ranking order of dams for removal, there was a variation among species. Even though we found the same general pattern of variation in connectivity metrics following removals, dams had different degrees of impact on the different target species. One way to circumvent this specificity is to model all species present in the network, or at least a representative of each morpho-ecological guild (Leonard & Orth 1986; Fauth *et al.* 1996) – a method deemed suitable for multi-species approaches (Leonard & Orth 1986) – and to multiply the suitability scores in such a way to permit a holistic definition of restoration priorities. The fact that the random removal of barriers resulted in a small increase in connectivity and that the removal of only one well-chosen barrier

is more beneficial to connectivity than the removal of seven randomly chosen barriers demonstrates that the proposed methodology to prioritize the removal of barriers is an effective way to allocate resources, which are often limited or scarce, and should be considered in connectivity restoration plans and basin management plans.

In this study, we decided to use only insurmountable barriers that limited fish movements completely in both directions. This is, however, a limitation, as even small obstacles can have a significant effect on flow, temperature regime, movement of animals and habitat quality (Larinier 2001), thereby potentially causing changes, though to a lesser extent (Santos *et al.* 2006), in the composition, structure and distribution of fish assemblages (Alexandre & Almeida 2010). In order to increase prioritization accuracy, incorporating barrier permeability should be considered for small and large instream obstacles, as is the case in Cote *et al.* (2010), which although not using a graph methodology followed a similar approach. Metrics along the lines of probability of connectivity (Pascual-Hortal & Saura 2006; Saura & Pascual-Hortal 2007), or the attribution of different values to the links between pairs of nodes according to their permeability (Schick & Lindley 2007; Urban *et al.* 2009), can facilitate the incorporation of these concerns into this spatial graph methodology. Dispersal probabilities should also be included, as different species have different life cycles and different movement abilities.

The presented case study, although used merely to exemplify the proposed method, is limited by only looking at the lower portion of the river basin. This limitation was imposed by the Cedillo Dam placed near the Portuguese–Spanish border that divides the original Tagus-wide graph network into two sub-graphs. We only evaluated the downstream sub-graph and scaled the original functional connectivity of this sub-graph to 100% to derive a single case study. For exemplification purposes, it is adequate, but ideally when applying this technique to management plans, whole rivers should be considered, allowing a more accurate understanding of how basin-wide connectivity infringements affect species.

Variables associated with large spatial scales similar to the ones used in the present study tend to have a higher explanatory capacity, in term of species distribution compared to local-scale variables (Roth, Allan & Erickson 1996; Marsh-Matthews & Matthews 2000; Santos *et al.* 2011). Of course, there may have been other 'local' factors which were not accounted for in the present study, such as instream habitat and/or water quality variables which might have improved habitat suitability analyses. In addition, biotic interactions, such as competition and predation, which are inherently local in scale, are also likely to affect local species distribution. However, given the broad extent of this study, their contribution to the habitat suitability models is unlikely to be significant, as the importance of biotic factors is thought to decrease with increases in spatial scale (Tonn *et al.* 1990).

This article proposes a connectivity rehabilitation prioritization methodology that integrates spatial graphs and habitat suitability in a real-world application to model the impact of the removal or placement of an insurmountable barrier in a river network. This methodology will aid decision-making processes by prioritizing actions in relation to the actual overall connectivity increase and can also be a useful tool for determining how to place new instream structures with fewer impacts. To increase connectivity at a given barrier, the more realistic solution is to build a fish passage device that allow fish to move both upstream and downstream freely, while accommodating an environmental flow that serves as a modulation of the real river flow to allow processes to be maintained.

Even though this study was devised for fish, the methodology is applicable to other biological groups. Future studies should focus on improving the method's ability to identify the habitat increment provided by the re-establishment of the connectivity that was previously limited by a barrier. To accomplish this goal, special attention should be paid to the links between contiguous elements of the river network and to asymmetries in barrier permeability both upstream and downstream.

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Data accessibility

Sampling sites: Data available by request – http://efi-plus.boku.ac.at/Leading_data_owners.htm; <http://www.apambiente.pt/?ref=16&subref=7&sub2ref=9&sub3ref=834>

Variables (CCM2): Available online <http://ccm.jrc.ec.europa.eu/php/index.php?action=view&id=23>

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Characteristics of the dams present in the study area.

Appendix S2. Variables used to model species habitat suitability at different spatial scales.

Appendix S3. Model accuracy measures.

Fig. S1. Study area and representation of the subnetworks created by the dams.