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A new method to include fish biodiversity in river connectivity indices with applications in dam impact assessments

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ABSTRACT

Different indices have been developed to quantify the extent and severity of river fragmentation. These indices vary depending on the specific goals of the study. Here, we present a new Conservation Connectivity Index (CCI_P) for potamodromous fish species that considers the conservation value (richness, rarity and vulnerability) of river segments.

The Iberian Peninsula holds > 20 endemic and endangered potamodromous fish species as well as > 1000 large dams (> 1 hm^3 of capacity). The CCI_P was calculated for the eight most important river basins of the Iberian Peninsula and compared to the Dendritic Connectivity Index (DCI_P) developed by Cote et al. in 2009, which uses only river length as a habitat variable. With the use of both DCI_P and CCI_P, the dams were analysed and ranked according to their impacts on the river basin.

The main results show that Iberian river basins are heavily fragmented, with river basin connectivity percentages of less than 20% in most cases using both DCI_P and CCI_P. CCI_P values are slightly higher than DCI_P values in almost all cases. When the impact of individual dams is analysed, differences also appear between the DCI_P and CCI_P. CCI_P highlights the impact of dams located in areas of high fish conservation value while DCI_P emphasize the impact of dams fragmenting large river segments.

The CCI_P appears to be adequate to highlight important sites for conservation in river connectivity studies. It could be applied in different studies and river basins around the world to prioritize dam removals or plan new dam locations.

1. Introduction

River fragmentation due to dams and other man-made obstacles is one of the main threats to river ecosystems (Grill et al., 2019; Olden, 2016; Vörösmarty et al., 2010). There are > 45,000 large dams constructed worldwide, while thousands more are planned or under construction (Zarfl et al., 2014). Globally, only 35% of large river systems are completely unfragmented (Nilsson et al., 2005).

The effects of river fragmentation are very obvious on diadromous fish species as obstacles can block their migrations and consequently reduce and totally extirpate these fish populations from large river systems (Clavero and Hermoso, 2015; Hall et al., 2011; Hitt et al., 2012; Lundqvist et al., 2008; Nieland et al., 2015; Thorstad et al., 2005). However, potamodromous freshwater fishes are also deeply affected by the presence of barriers due to population fragmentation (Almodóvar and Nicola, 1997; Clavero et al., 2004; Kanehl et al., 1997; Kondolf et al., 2006; Perkin and Bonner, 2011; Richter et al., 2010). Small, isolated populations are more vulnerable to extinctions due to loss of genetic variability and the incidence of catastrophic events (Hanski and Gilpin, 1991; Letcher et al., 2007; Levins, 1968; MacArthur and Wilson, 1967; Nislow et al., 2011). Dams have been related to low fish species richness (Dodd et al., 2003; Nislow et al., 2011), low genetic variability (Morita et al., 2009; Wofford et al., 2005; Yamamoto et al., 2004) and even population extirpations (Morita and Yamamoto, 2002).

Due to the extent and magnitude of fragmentation impacts, river connectivity has received growing attention in recent decades, with studies focusing on dam impacts, river fragmentation assessments, river connectivity importance for river conservation or barrier mitigation (Erös et al., 2018; Grill et al., 2019; Hermoso et al., 2017; Magilligan et al., 2016; O'Connor et al., 2015). Different tools developed to study river connectivity fragmentation vary depending on the objectives and scale of the study (Kemp and O'Hanley, 2010; McKay et al., 2017). River connectivity studies are generally focused on understanding the impacts of barriers in river basin fragmentation and organisms, prioritizing obstacles for removal and reporting the best new barrier locations (Diebel et al., 2015; King et al., 2017; King and O'Hanley, 2016;

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Maitland et al., 2016).

Accurately modelling river connectivity is a difficult task due to the large and often difficult to collect array of variables affecting it. As a consequence, indices are generally restricted to use few and simple factors (Bourne et al., 2011; Kemp and O'Hanley, 2010; Maitland et al., 2016). Some of the most applied indices use network analysis to create models that consider barrier passability and location inside a river network. Usually, river length or water volume are used as proxies for habitat quality (Cote et al., 2009; Grill et al., 2015; McKay et al., 2013). However, the results of the indices may vary depending on the variables selected to build them (Bourne et al., 2011; Rodeles et al., 2019). River connectivity modelling methods need to be adapted to the objectives of particular studies to improve the accuracy of their predictions. Some connectivity indices add habitat variables for one (Rodeles et al., 2019) or a group of fish species (Diebel et al., 2015; Maitland et al., 2016; O'Hanley et al., 2013) or other parameters that indicate the quantity and quality of river habitat (Grill et al., 2014). This flexibility allows for index adaptation to different environments and objectives.

More than 70% of Iberian freshwater fish species are endemic, and 59% of all native species are under threat according to the International Union for the Conservation of Nature (IUCN, IUCN, 2019). Dam-related impacts and water extraction affect 60% of Iberian native freshwater fish species (Maceda-Veiga, 2013). However, river connectivity fragmentation studies are scarce and have focused on few river basins (Benejam et al., 2014; Branco et al., 2014, 2012; Segurado et al., 2015, 2013; Solà et al., 2011) or the effects of single dams (Alexandre and Almeida, 2010; Almodóvar and Nicola, 1997).

Our first objective was to develop a new index to assess the structural connectivity of river networks. It is called Conservation Connectivity Index (CCI_P) and includes a conservation value for freshwater fish species. This index is based in the Dendritic Connectivity Index for potamodromous fishes (DCI_P, Cote et al., 2009), and adds the Biodiversity Index (BI) developed by Rey Benayas and De La Montaña (2003). The Biodiversity Index would allow us to identify high-value river segments for the conservation of rare and endangered potamodromous fish species. The CCI_P was designed to highlight the impact of dams in the connectivity of valuable areas for freshwater fish conservation. The impact of each studied dam was assessed with both indices to evaluate the capacity of CCI_P to prioritize important areas for freshwater fish conservation. The second objective of this research was to analyse the river connectivity of the Iberian Peninsula. In this regard, the eight main Iberian river basins were analysed using both DCI_P and CCI_P and the most impacting dams to structural river connectivity of Iberian River basins were identified. This is the first study describing the impact of large dams on river connectivity and conservation at large scales in the Iberian Peninsula.

2. Methods

2.1. Iberian Peninsula and dams

The Iberian Peninsula has an area of 580,000 km^2, with a coastline of 8821 km. It is divided into two countries: Spain, with an area of 506,030 km^2 and Portugal, with an area of 91,152 km^2. The orography of the Iberian Peninsula is abrupt, with numerous mountain ranges oriented east–west and a central high plateau (Antunes et al., 2016).

The eight main river basins in the Iberian Peninsula (Ebro, Duero, Tagus, Guadiana, Guadalquivir, Miño, Jucar and Segura) were used for this study. These eight basins have different sizes and discharges (Table 1). The clash between the Atlantic climate, restricted to the north and with high annual precipitation (> 2500 mm), and the Mediterranean climate, with very low annual precipitation (below 300 mm), creates high discharge variability among these river basins (Lorenzo-Lacruz et al., 2012). The Duero has the largest river network with > 18500 km of streams and the highest mean discharge with > 13,500 hm^3 per year. The smallest river basin is Segura with

Table 1
Main river basins of the Iberian Peninsula and their main characteristics (Lorenzo-Lacruz et al., 2012).

River basin	Main stem length (km)	Drainage area (km^2)	Mean discharge (hm^3/year)	Number of dams	Dams per 100 km of river
Ebro	910	83,876	12,279	167	1.05
Duero	895	91,179	13,788	158	0.84
Tagus	1007	68,167	12,350	206	1.56
Guadiana	778	48,712	4039	130	1.02
Guadalquivir	657	47,212	3780	98	0.94
Miño	310	14,946	10,570	62	1.97
Júcar	498	21,629	1023	17	0.41
Segura	325	15,920	118	36	1.31

2748 km of rivers and a mean annual discharge of 118 hm^3. The Miño River basin has the smallest drainage area but a high mean annual discharge (above 10,000 hm^3) due to a very high annual precipitation (Table 1).

There are > 1000 large dams in the Iberian Peninsula, 874 in the eight basins selected for this research (Fig. 1, Table 1). The Tagus River has the highest number of dams in total, while the Miño River basin has the highest density per kilometre of stream. The Jucar River basin has the least number and density of dams (Table 1).

River basins were downloaded from HydroSHEDS (Lehner et al., 2008). Information on the dams in Spain was downloaded from the Water Information System (MAGRAMA, 2004), and that of the dams in Portugal was downloaded from the Portuguese official dam database (Agência Portuguesa do Ambiente, 2018). Via ArcGIS 10.5 (ESRI, 2011), all dams were moved to intersect their closest river segment. Then, river segments were split by dam intersections. A segment was defined as the line i) between two stream intersections, ii) an intersection and a dam or iii) two dams (Fig. 2a and 2b). With these resulting segment and dam layers, connectivity indices could be calculated.

2.2. Dendritic Connectivity Index

Longitudinal river connectivity was assessed using the Dendritic Connectivity Index for potamodromous species (DCI_P) developed by Cote et al. (2009). This index uses the passability of each obstacle and "sections", which are calculated as the sum of the length of all segments between two barriers. In this case, all barriers were assumed to be totally impassable because only large dams (> 1 hm^3 capacity) were assessed.

If L is the total length of a river basin, l_i is the length of the i_{th} section, and $i = 1, \ldots, n$, where n is the number of river sections (number of dams + 1), the equation for DCI_P when barrier passability outcome is binary is defined as:

$$DCI_P = \sum_{i=1}^{n} \frac{l_i^2}{L^2} \times 100.$$

The length of a river section between two dams i is calculated as the sum of the length of all river segments that compose it (Fig. 2c). The outcome of the index is a percentage that indicates the proportion of connected river length on a river basin.

The DCI_P was calculated in R 3.4.2 (R Core Team, 2015) using the split segment river network and the dam database (as seen in Fig. 2b) with the packages *raster* (Hijmans et al., 2016), *rgdal* (Bivand et al., 2016), *magrittr* (Bache and Wickham, 2014) and *igraph* (Igraph Core Team, 2015). Then, the river DCI_P was calculated by removing every dam, one by one, to isolate the most impactful obstacles.

This index was used to assess longitudinal connectivity for each of the eight selected basins. Then, it was modified to create a new connectivity index that adds the ecological value of river segments,

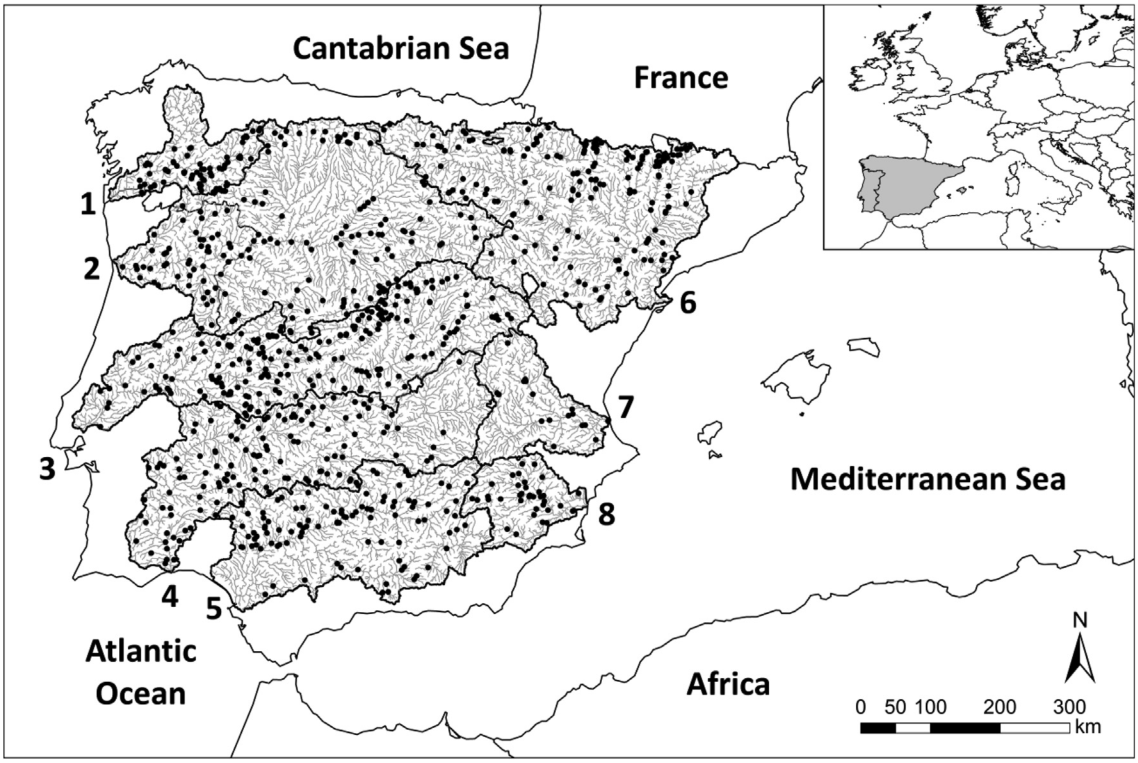

Fig. 1. Main river basins of the Iberian Peninsula with their dams (black dots). Numbers indicate the river mouth of each basin: 1. Miño; 2. Duero; 3. Tagus; 4. Guadiana; 5. Guadalquivir; 6. Ebro; 7. Júcar; 8. Segura.

represented here by the Biodiversity Index (Rey Benayas and De La Montaña, 2003).

2.3. Habitat suitability models and the Biodiversity Index

As a previous step to calculate the Biodiversity Index (BI), the distribution of Iberian freshwater fish species had to be determined. We chose to build ecological niche models to calculate potentially suitable habitats for each fish species. We chose habitat suitability models because they analyse presence and absence data at smaller scales and could generate more refined species distributions. Forty-nine native Iberian freshwater fish species were evaluated (Supplementary Data 1). Estuarine fish species were not included in the analysis. *Cottus hispaniolensis* Bacescu-Mester 1964 was not considered an Iberian fish because it inhabits a French river basin and was removed from the analysis. Last, *Luciobarbus steindachneri* (Almaça 1967) is not considered a

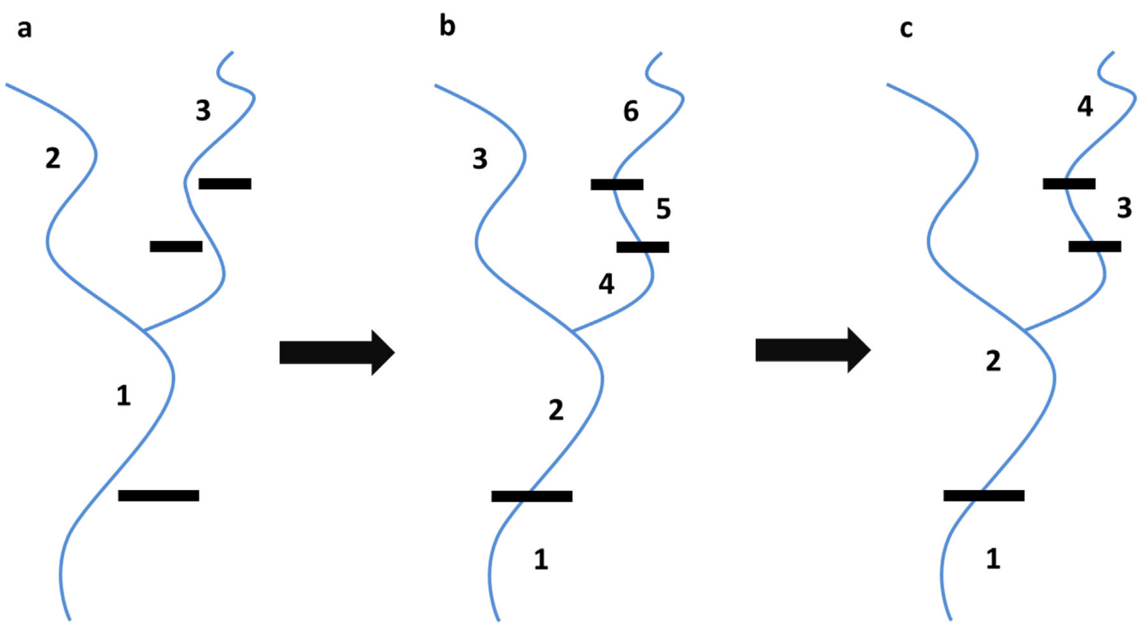

Fig. 2. Representation of a simple river basin with two rivers and three dams. The downloaded rivers were split by their intersections resulting in three segments. In (a) dams were not located on the rivers. In (b) dams were moved to intersect rivers at the nearest point, and segments were split in six segments. In (c) all river segments between two dams were fused together in four sections to calculate the connectivity indices.

valid species in Spain (Doadrio et al., 2011), so it was also not analysed.

Presence and absence fish data were provided by the Iberian Society of Ichthyology (SIBIC, 2015). As environmental variables, nineteen freshwater-specific variables at 1 km grid cell resolution were selected (Domisch et al., 2015). Fourteen are climatic variables, following the "bioclim" structure developed by WorldClim (BIO1, BIO4, BIO5, BIO6, BIO10, BIO11, BIO12, BIO13, BIO14, BIO15, BIO16, BIO17, BIO18 and BIO19) and the other five variables are topographical (average cell elevation and average cell slope) and chemical (mean cell pH, mean cell soil organic carbon and mean cell cation exchange capacity). All variables follow the HydroSHEDS river structure (Hijmans et al., 2005; Lehner et al., 2008). These freshwater-specific variables were selected because they consider the hierarchical nature of river networks and the influence of the surrounding basin areas (Domisch et al., 2015). Five environmental variables related with fish species presence were selected for habitat suitability modeling: mean temperature of the warmest quarter (BIO10), mean temperature of the coldest quarter (BIO11), annual precipitation (BIO12), precipitation seasonality (BIO15) and mean pH. Temperature, precipitation and water chemistry have likely relationships with the presence of Iberian fish species (Doadrio, 2001; Doadrio et al., 2011).

Habitat suitability models for each fish were built on the basins the fish species was found, not the whole Iberian Peninsula, as freshwater fish species distributions are more restricted by historical and geographic limits (Filipe et al., 2009). Species with fewer than 20 occurrences were not modelled because they were considered insufficiently represented. In these cases, distribution models were built using the distribution data provided by the appropriate literature (Doadrio, 2001; Doadrio et al., 2011; Rogado et al., 2004; SIBIC, 2014; Verissimo et al., 2018).

The R package *BIOMOD2* (Thuiller et al., 2016) was used to build habitat suitability models for each species. Following the method used by Clavero et al. (2017), nine model algorithms were used (GBM, GLM, GAM, ANN, CTA, RF, SRE, FDA and MARS). Ten runs of each model were performed, separating 20% of species presences and absences for evaluation. Then, all the algorithms with a mean area under the curve (AUC) $>$ 0.7 were selected to create models with all presences and absences. Then we created an ensemble model with means weighted by the AUC, so models with higher area under the curve weighted more in the ensemble. All ensemble models had an AUC $>$ 0.8. The cutoff threshold that maximizes the true skill statistic (TSS) was selected to transform the outputs of the continuous models (more or less probability of presence) into binary predictions (presence-absence).

In ArcGIS, binary suitability models for all species were added to the HydroSHEDS line river networks. With that, presence/absence data of fish species was added to each segment. A variable number of segments (between 1 and 5%) of Mediterranean River basins (Tagus, Guadiana, Guadalquivir and Segura) were found unsuitable for any fish species. Some of these segments may exist only in winter and spring or may suffer extreme temperatures, droughts, and oxygen scarcity in certain seasons, making the survival of fish species difficult. This is a drawback to using binary habitat suitability models in extreme habitats such as intermittent Mediterranean rivers. With the binary habitat suitability models, the biodiversity index corrected by basin size was calculated for each river segment.

The Biodiversity Index (Rey Benayas and De La Montaña, 2003) combines species richness, rarity and vulnerability. For a given segment r, the Biodiversity Index can be expressed as:

$$BI_r = \sum_{i=1}^{S} \frac{1}{\frac{m_{ri}}{N}} \times V_{ri}$$

where S is the number of fish species in segment r, m_{ri} is the number of segments in which species i was found, N is the total number of segments in the river basin, and V_{ri} is the vulnerability of species i. Species richness is implicit in $\Sigma_{i=1}^{S}$. The vulnerability of species i was determined as its IUCN threat category, ranging from 1 (Least Concern) to 5 (Critically Endangered). There was a not-evaluated fish species (*Squalius pyrenaicus*). For this fish, the "Vulnerable" threat category given in the Spanish Red List books was used (Doadrio, 2001; Doadrio et al., 2011). The result of the Biodiversity Index is a number for each river segment, which is higher when the segment contains a higher number of species, rarer species or more threatened species. The Biodiversity Index was calculated for each river segment in R 3.4.2 with the packages *raster* (Hijmans et al., 2016), *rgdal* (Bivand et al., 2016), and *magrittr* (Bache and Wickham, 2014).

2.4. Conservation Connectivity Index

Using this Biodiversity Index per segment and the Dendritic Connectivity Index (DCI_P), the Conservation Connectivity Index for potamodromous fish species (CCI_P) was developed. In this index, the importance of a segment is not given by segment length but a combination of length and the Biodiversity Index. This is called Conservation Interest of a river segment (*ci*), and for a given segment *r*, it can be expressed as:

$$ci_r = s_r \times BI_r$$

where s_r is the length of segment r and BI_r is the Biodiversity Index of segment r. Then, the ci_r values of all segments of a section (R) are summed to calculate the Conservation Interest *cs* of a section i between dams:

$$cs_i = \sum_{r=1}^{R} ci_r$$

Then, the Conservation Connectivity Index equation is calculated for the river sections of a basin:

$$CCI_P = \sum_{i=1}^{n} \frac{cs_i^2}{CS^2} \times 100$$

where $i = 1, \ldots, n$ is the number of sections present in the river network, cs_i is the Conservation Interest of section i and CS is the Conservation Interest of the whole river network, calculated as the sum of the *cs* of all sections:

$$CS = \sum_{i=1}^{n} cs_i$$

The outcome of the index is a percentage that indicates the proportion of connected habitat (measured here as Conservation Interest, *cs*) on a river basin. As the CCI_P depends on the number of species present on a river basin, its results cannot be compared between river basins. To compare the results of this index between river basins, the results should be standardized by the number of species present in the river basins.

The CCI_P was calculated in R 3.4.2 (R Core Team, 2015) using the split segment river network and the dam database (as seen in Fig. 2b) with the packages *raster* (Hijmans et al., 2016), *rgdal* (Bivand et al., 2016), *magrittr* (Bache and Wickham, 2014) and *igraph* (Igraph Core Team, 2015). Then, the river CCI_P was recalculated by removing one different dam per run to identify the most impactful obstacles. The R code developed to calculate DCI_P, CCI_P and the Biodiversity Index are available in Supplementary Data 2.

3. Results

According to the DCI_P results, all major Iberian river basins are heavily fragmented by large dams, with low percentages (3.49 – 19.94%) of river connectivity showed in all cases (Table 2). The most fragmented river basin is the Duero, with a DCI_P of 3.49%, followed by the Tagus River basin (3.76%). The most connected river basin is the Jucar, with a DCI_P of nearly 20%. When CCI_P is calculated, river

Table 2

DCI_P and CCI_P results for the analysed river basins, with the number of sections, mean length and total river basin length.

River basin	Number of sections	Section mean length (km)	Basin length (km)	DCI_P (%)	CCI_P (%)	Number of species
Ebro	168	95.0	15,958.5	6.28	7.33	12
Duero	159	118.2	18,777.9	3.49	8.03	11
Tagus	207	63.7	13,181.3	3.76	8.67	18
Guadiana	131	97.5	12,778.7	8.41	7.57	11
Guadalquivir	99	105.5	10,446.1	7.05	9.88	10
Miño	63	50.0	3150.5	9.71	11.50	5
Júcar	18	228.4	4111.8	19.94	17.89	9
Segura	37	74.3	2748.2	7.16	7.97	4

connectivity appears higher than when the DCI_P is used in all river basins except two (Guadiana and Júcar River basins, Table 2). Only the Jucar and Miño River basins surpass a CCI_P of 10%. The most fragmented river basin in absolute numbers is Ebro, with a CCI_P of 7.33%. When the number of species of each basin is considered to standardize the CCI_P results, the Tagus river basin is the most fragmented by species, with a CCI_P of 0.48% per species and the most connected is the Miño river basin, with a CCI_P of 2.3% per species.

The calculated impact of dams on river fragmentation changed from DCI_P to CCI_P. Dams isolating smaller sections with higher Conservation Interest (*cs*) are more impactful than dams isolating larger sections with a poor Biodiversity Index (Fig. 3).

When creating ranks, the most impactful dams are different from DCI_P to CCI_P (Table 4). When river basin connectivity is calculated with DCI_P, the most impactful dam is Alcalá del Río, in the Guadalquivir River, close to the river mouth. The second is José Bautista, which isolates a large river section of the Segura River basin. Other main stem dams are very impactful, such as Pignatelli and Mequinenza in the Ebro River basin, José María de Oriol in the Tagus River basin and Alqueva in the Guadiana basin (Table 3). There are no Tagus, Duero or Miño dams among the ten most impacting dams of all studied river basins (Supplementary Data 3). The removal of the two most impacting dams in the Duero and Miño River basins increases river basin connectivity by less than one point (Table 3).

When CCI_P is used, the most impactful dam in absolute numbers is Santarem, in the lower Tagus River basin, which isolates sections with critically endangered endemic fishes (Fig. 3). This dam does not appear among the most impacting dams of the Tagus River basin according to DCI_P (Table 3). Pignatelli and Mequinenza are the two most impacting dams of the Ebro River basin according to both DCI_P and CCI_P. Alcalá del Río, Alqueva and José Bautista are also the most impacting dams in their river basins according to both indices (Tables 3 and 4). However, the two most impacting dams in the Duero River basin are different from DCI_P to CCI_P. The complete lists of dams ranked by impact can be found in the Supplementary Data 3.

4. Discussion

Numerous river basin connectivity indices have been developed over the last two decades to help understand the impacts of river fragmentation by dams and other obstacles (Kemp and O'Hanley, 2010; McKay et al., 2017). In this paper, a connectivity index (DCI_P) to analyse the structural connectivity of river basins for potamodromous fishes was modified to develop a new connectivity index (CCI_P) that considers the conservation value of river segments for freshwater fish species. This new index should highlight dams impacting important conservation areas for freshwater fish species and, thus, aid in dam mitigation prioritization decisions. At the same time, we analysed the connectivity of the eight main river basins of the Iberian Peninsula.

According to our results, CCI_P is always slightly higher than DCI_P except in the Guadiana and Júcar River basins. This may be due to the presence of segments not suitable for any fish species resulting from the habitat suitability models fitted. However, it may also indicate that Guadiana and Júcar dams are in river stretches with high Conservation Interest values (Fig. 3). Other river basins, such as the Ebro or Duero (that contain fish species in all segments), may have a higher CCI_P than DCI_P due to the presence of numerous dams in headstreams where the Biodiversity Index is lower (Figs. 1 and 3).

The contribution of each section to the total river basin index changes between the two indices as does the importance of each dam for connectivity (Tables 3 and 4). The presence of many of the same dams among the most impactful of each river basin when using both indices may indicate that the effect of the Conservation Interest added to the index might not be strong enough to completely offset the effect of river section length in the connectivity index outcome. However, some dams appear in the CCI_P list due to the high Conservation Interest of their locations only (Table 4). This is especially true for the lower Tagus River basin, home to endangered and rare endemic fish species such as *Iberochondrostoma olisiponensis* or *I. lusitanicum*. The high conservation value of this area (Fig. 3) makes the Santarem dam the most impactful obstacle of the Tagus River basin when CCI_P is used (Table 4). The Tagus River connectivity increases 4.32 points when the Santarem dam is removed according to CCI_P. However, using DCI_P, the Tagus River connectivity increases only 0.34 points when the Santarem dam is removed (Supplementary Data 3). This indicates that the Conservation Interest of this area is high enough to compensate for the short river length of the section. There are numerous other dams in a similar situation (Pocinho, etc., Supplementary Data 3). Following these results, we think that this new connectivity index (CCI_P) effectively emphasizes river sections with a high conservation value.

However, there are a few drawbacks to this study. The most important one is the use of habitat suitability models with a binary outcome as a previous step to Biodiversity Index calculation. Habitat suitability models allow the creation of potential habitat maps at small scales. However, the accuracy of the results depends on numerous factors (Guisan et al., 2017). The first one is the quantity and quality of presence and absence data. The fish sampling data used to build the models were collected from thousands of different projects and researchers scattered randomly across the Iberian Peninsula. Some rare species were under-sampled, and others may not be well represented across their whole distribution area, skewing the result of the habitat suitability models. Generalist species are also more difficult to model (Gu and Swihart, 2004; Hortal et al., 2008; Meynard and Quinn, 2007). Spatial autocorrelation may also be an issue, although we tried to reduce its impact by removing presence points that were too close to each other (Araújo and Guisan, 2017; Meynard and Quinn, 2007). Ensemble models were created to soften the differences between models, as there is not an ideal modelling method for all circumstances (Segurado and Araújo, 2004). The ensemble model area under the curve (AUC) was high in all cases (> 0.8), but that only means the models correctly discriminate presences from absences (Lobo et al., 2008). Moreover, the conversion of the continuous habitat suitability to binary (suitable/non-suitable) categories simplifies the calculation of the connectivity index, but it is also a source for error because it uses a threshold to transform the model, and no threshold selection method is perfect. The method used here (maximizing the true skill statistic, TSS) may overestimate rare species (Freeman and Moisen, 2008). Furthermore, as explained in the Methods section, some species could not be modelled so their habitat suitability maps were performed selecting river segments with occurrences according to the available literature. These maps have their own sources of errors, different from the habitat suitability models, which need to be considered when making decisions at the local scale. On the other hand, fishes may live in less-than-ideal environmental situations, so binary suitability models could underrepresent the potential habitat for some fish species. However, this is not a shortcoming of the CCI_P, but a problem with the examples used to calculate it, as

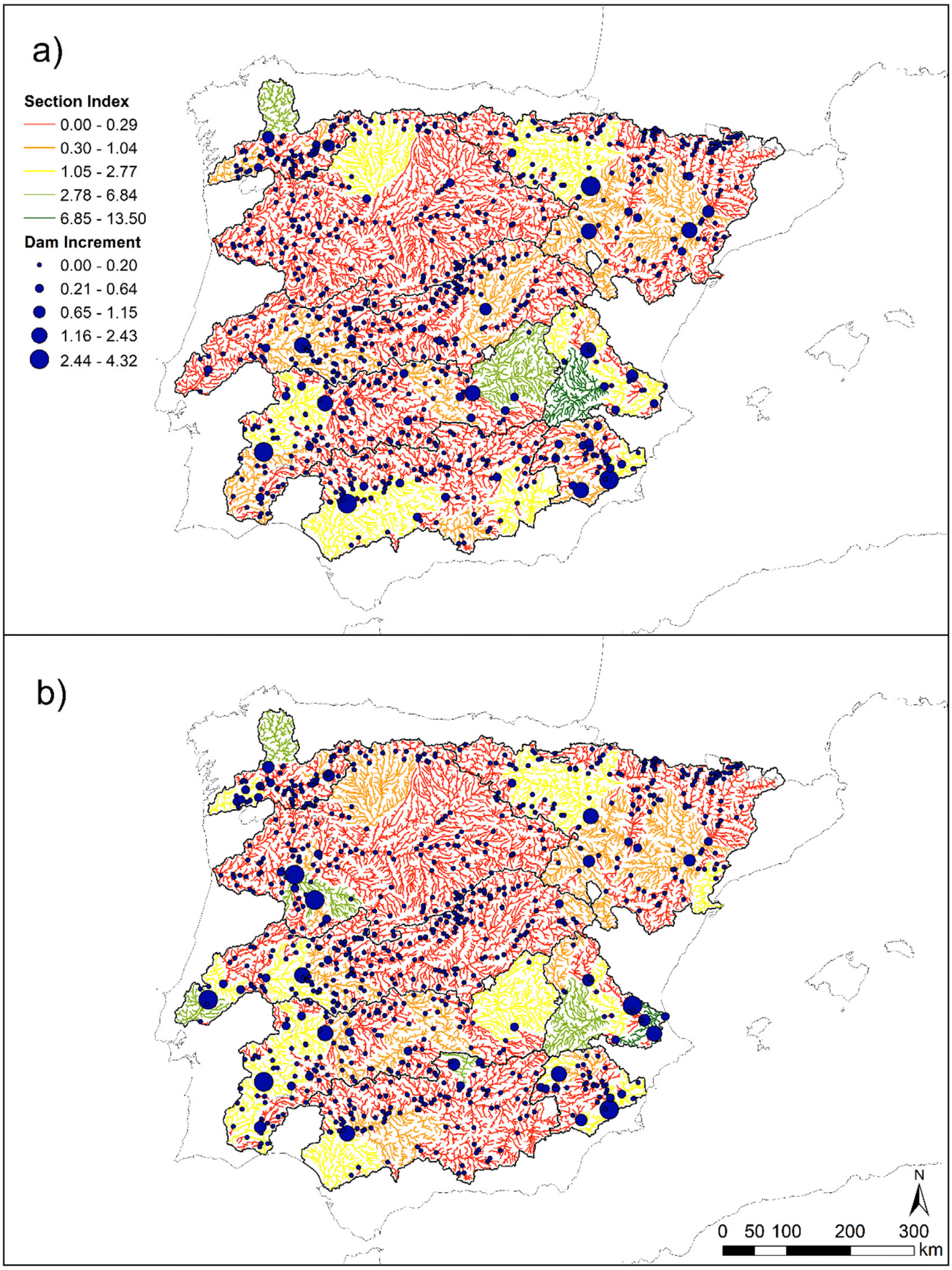

Fig. 3. Studied river basins with coloured river sections between dams. The differences between connectivity values using a) the DCI_P and b) the CCI_P can be seen for both river sections and dams. The value assigned to each section varies from DCI_P to CCI_P, with CCI_P increasing the value of smaller river sections (green lines) with a higher Biodiversity Index and decreasing the value assigned to large river sections with lower Biodiversity Index (orange and red lines). The value assigned to each dam varies in the same way, with more value given to dams located between river sections with high Biodiversity Index when using CCI_P. In color.

there were not accurate species distribution maps for the analysed river basins at the required spatial scale. For areas with adequate species distribution maps, the CCI_P should not present this source of error.

Another problem is the presence of intermittent and seasonal Mediterranean rivers, which are not distinguished in the river segment layers used to create the habitat suitability models. Some rivers that appear suitable for a fish species may be dry for a variable part of the year, making fish presence impermanent or even impossible. As intermittent rivers are by nature disconnected during a variable time of the year, the fragmentation caused by dams measured in this study may be overestimated. This special type of river should require additional site-specific connectivity assessments to ensure more accurate dam fragmentation analyses.

This is the first large-scale assessment of river basin connectivity in the Iberian Peninsula. This study puts numbers to a widely recognized but understudied impact, showing the severity of dam fragmentation of the largest Iberian river basins. Seven out of eight of the Iberian River systems studied have an average of ~ 1 large dam or more per 100 km

Table 3
The two most impactful dams of each Iberian river basin studied according to the DCI_P. The increment represents the difference between the connectivity indices without the dam and the connectivity indices with all the dams.

River basin	Dam name	Coord. X	Coord. Y	Increment (points)
Ebro	Pignatelli	−1.560165	42.026832	3.00
Ebro	Mequinenza	0.275141	41.366526	1.48
Duero	Santa Eulalia de Tábara (Tail Dam)	−5.795833	41.824135	0.41
Duero	Quintana	−4.222999	42.077004	0.37
Tagus	José María De Oriol (Alcántara II)	−6.891230	39.725438	1.17
Tagus	Del Rey	−3.537500	40.298529	1.08
Guadiana	Alqueva	−7.495833	38.197466	2.50
Guadiana	Puente Navarro	−3.762500	39.112500	1.34
Guadalquivir	Alcalá del Río	−5.974037	37.517631	4.31
Guadalquivir	Vadomojón	−4.229167	37.638893	0.50
Miño	Belesar	−7.714073	42.630740	0.86
Miño	Montearenas	−6.554306	42.554027	0.77
Júcar	El Batanejo	−1.656490	39.714824	1.46
Júcar	Forata	−0.859441	39.342775	1.14
Segura	José Bautista	−1.316645	37.879167	3.38
Segura	Puentes IV	−1.819172	37.737500	1.26

Table 4
The two most impacting dams per river basin according to the CCI_P. Due to the different number of fish species present on each river basin, the results of CCI_P cannot be accurately compared between basins.

River basin	Dam name	Coord. X	Coord. Y	Increment (points)
Ebro	Pignatelli	−1.558904	42.027957	2.15
Ebro	Mequinenza	0.276344	41.367659	1.15
Duero	Pocinho	−7.110845	41.137985	3.69
Duero	Puerto Seguro	−6.717282	40.794398	3.34
Tagus	Santarem	−8.572013	39.311137	4.32
Tagus	José María de Oriol (Alcántara II)	−6.889860	39.726661	1.86
Guadiana	Alqueva	−7.494469	38.198715	4.00
Guadiana	Montijo	−6.427385	38.922501	1.76
Guadalquivir	Alcalá del Río	−5.972698	37.518889	1.86
Guadalquivir	Montoro III	−4.094530	38.526478	0.81
Miño	Montearenas	−6.552864	42.555167	1.00
Miño	Belesar	−7.712587	42.631893	0.79
Júcar	Forata	−0.858228	39.343965	3.03
Júcar	Bellus	−0.477968	38.941535	2.43
Segura	José Bautista	−1.315431	37.880395	2.99
Segura	Fuensanta	−2.207115	38.392855	2.11

of stream and most river basins have DCI_P and CCI_P values of 10% or less (Table 3). This high degree of fragmentation may be crucial for numerous Iberian fish populations in the long term (Morita et al., 2009; Morita and Yamamoto, 2002). It must be considered that river fragmentation is a "recent" impact (few decades old), so population extirpations of potamodromous fish species due to genetic and stochastic events may not have been manifested yet (Olden et al., 2010). This delayed extinction is called "extinction debt" and refers to lagged population extirpation as populations reach a new ecological equilibrium following an impact (MacArthur & Wilson 1967; Ewers & Didham 2006; Kuussaari et al. 2009). The CCI_P developed in this study appears to be effective in highlighting the most impacted river sections according to their length and conservation value, despite the shortcomings of the methodology described above.

It also must be mentioned that there are thousands of small dams and weirs in the Iberian Peninsula, many of them not mapped. For example, there are > 3000 small obstacles on the Spanish side of the Duero River basin and almost 2000 in the Ebro River basin (Rodeles et al., 2017). Together, these small obstacles may have very similar effects on connectivity as the larger dams. As a result, river basin connectivity is likely to be much lower than what was shown by DCI_P and CCI_P. Management and conservation plans at smaller scales should consider the presence of these small obstacles in river connectivity calculation.

Moreover, DCI_P and CCI_P only assess the structural river connectivity (the connectivity between the structural elements of the river basin, i.e. river segments), not the functional connectivity (the connectivity due to the transfer of organisms between the segments). The migration capacity between populations of the different fish species analysed in this study is not considered as it is beyond the scope of the CCI_P.

The CCI_P adds a new dimension to the study of river connectivity because it models the effects of fragmentation for valuable areas for the conservation of freshwater fishes. This allows the union of river conservation management with river connectivity. River connectivity and ecological value must be assessed together to achieve efficient river area conservation (Hermoso et al., 2017, 2012). It is also necessary to remember that connectivity indices do not assess other profound dam impacts, such as erosion, lack of sediment and nutrient transport, the facilitation of exotic species invasions or hydrological regime changes, which have to be considered in river conservation plans (Clavero and Hermoso, 2011; Liermann et al., 2012; Timpe and Kaplan, 2017). However, we hope this first step in the joint study of connectivity and conservation will contribute to the understanding of river fragmentation effects and will help in the development of methods for conservation area prioritization.

5. Data statement

R code developed for the calculation of DCI and DCI will be available in Supplementary Data 2 file, as well as the results of dam prioritization calculations. Presence/absence data used to create habitat suitability models belong to the SIBIC and are available under request to sibic@sibic.org and can be visualized at http://www.cartapiscicola.es/#/home.

CRediT authorship contribution statement

Amaia A. Rodeles: Conceptualization, Methodology, Formal analysis, Writing - original draft. **David Galicia:** Methodology, Writing - review & editing. **Rafael Miranda:** Conceptualization, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

Agência Portuguesa do Ambiente As barragens em Portugal [WWW Document] https://www.apambiente.pt/index.php?ref=16&subref=7&sub2ref=31&sub3ref=1285 2018 accessed 5.16.18.

Alexandre, C.M., Almeida, P.R., 2010. The impact of small physical obstacles on the structure of freshwater fish assemblages. River Res. Appl. 26, 977–994. https://doi.org/10.1002/rra.

Almodóvar, A., Nicola, G.G., 1997. Effects of a small hydroelectric power station on brown trout (*Salmo trutta* L.) population in the Hoz Seca river (Tagus River, Spain). Regul. rivers Res. Manag. 484, 477–484.

Antunes, C., Cobo, F., Araújo, M.J., 2016. Iberian inland fishes. In: Craig, J.F. (Ed.), Freshwater Fisheries Ecology. vol. 268. Wiley & Sons, Singapore, pp. 282.

Araújo, M.B., Guisan, A., 2017. Five (or so) challenges for species distribution modelling. R. Soc. B Biol. Sci. Proc. https://doi.org/10.1111/j.1365-2699.2006.01584.x.

Bache, S.M., Wickham, H., 2014. magrittr: a forward-pipe operator for R [WWW Document]. URL https://cran.r-project.org/web/packages/magrittr/index.html (accessed 9.12.18).

Benejam, L., Saura-Mas, S., Bardina, M., Solà, C., Munné, A., García-Berthou, E., 2014. Ecological impacts of small hydropower plants on headwater stream fish: from individual to community effects. Ecol. Freshw. Fish 25, 295–306. https://doi.org/10.1111/eff.12210.

Bivand, R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., Rouault, E., 2016. rgdal: bindings for the "Geospatial" Data Abstraction Library [WWW Document]. URL https://cran.r-project.org/web/packages/rgdal/index.html (accessed 9.28.16).

Bourne, C.M., Kehler, D.G., Wiersma, Y.F., Cote, D., 2011. Barriers to fish passage and barriers to fish passage assessments: the impact of assessment methods and assumptions on barrier identification and quantification of watershed connectivity. Aquat. Ecol. 45, 389–403. https://doi.org/10.1007/s10452-011-9362-z.

Branco, P., Segurado, P., Santos, J.M., Ferreira, M.T., 2014. Prioritizing barrier removal to improve functional connectivity of rivers. J. Appl. Ecol. 51, 1197–1206. https://doi.org/10.1111/1365-2664.12317.

Branco, P., Segurado, P., Santos, J.M., Pinheiro, P., Ferreira, M.T., 2012. Does longitudinal connectivity loss affect the distribution of freshwater fish? Ecol. Eng. 48, 70–78. https://doi.org/10.1016/j.ecoleng.2011.05.008.

Clavero, M., Blanco-Garrido, F., Prenda, J., 2004. Fish fauna in Iberian Mediterranean river basins: biodiversity, introduced species and damming impacts. Aquat. Conserv. Mar. Freshw. Ecosyst. 14, 575–585. https://doi.org/10.1002/aqc.636.

Clavero, M., Hermoso, V., 2015. Historical data to plan the recovery of the European eel. J. Appl. Ecol. 52, 960–968.

Clavero, M., Hermoso, V., 2011. Reservoirs promote the taxonomic homogenization of fish communities within river basins. Biodivers. Conserv. 20, 41–57. https://doi.org/10.1007/s10531-010-9945-3.

Cote, D., Kehler, D.G., Bourne, C., Wiersma, Y.F., 2009. A new measure of longitudinal connectivity for stream networks. Landsc. Ecol. 24, 101–113.

Diebel, M.W., Fedora, M., Cogswell, S., O'Hanley, J.R., 2015. Effects of road crossings on habitat connectivity for stream-resident fish. River Res. Appl. 31, 1251–1261. https://doi.org/10.1002/rra.

Doadrio, I., 2001. Atlas y libro rojo de los peces continentales de España, Second. ed. Ministerio de Medio Ambiente, Madrid.

Doadrio, I., Perea, S., Garzón-Heydt, P., González, J.L., 2011. Ictiofauna continental española. Bases para su seguimiento, First. ed. Ministerio de Medio Ambiente, Medio Rural y Marino, Madrid.

Dodd, H.R., Hayes, D.B., Baylis, J.R., Carl, L.M., Goldstein, J.D., McLaughlin, R.L., Noakes, D.L.G., Porto, L.M., Jones, M.L., 2003. Low-head sea lamprey barrier effects on stream habitat and fish communities in the Great Lakes basin. J. Great Lakes Res. 29, 386–402. https://doi.org/10.1016/S0380-1330(03)70502-4.

Domisch, S., Amatulli, G., Jetz, W., 2015. Near-global freshwater-specific environmental variables for biodiversity analyses in 1 km resolution. Sci. Data 2, 1–13. https://doi.org/10.1038/sdata.2015.73.

Erös, T., O'Hanley, J.R., Czeglédi, I., 2018. A unified model for optimizing riverscape conservation. J. Appl. Ecol. 1871–1883. https://doi.org/10.1111/1365-2664.13142.

ESRI, 2011. ArcGIS.

Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. 81, 117–142. https://doi.org/10.1017/S1464793105006949.

Filipe, A.F., Araújo, M.B., Doadrio, I., Angermeier, P.L., Collares-Pereira, M.J., 2009. Biogeography of Iberian freshwater fishes revisited: the roles of historical versus contemporary constraints. J. Biogeogr. 36, 2096–2110. https://doi.org/10.1111/j.1365-2699.2009.02154.x.

Freeman, E.A., Moisen, G.G., 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. Ecol. Modell. 217, 48–58. https://doi.org/10.1016/j.ecolmodel.2008.05.015.

Grill, G., Lehner, B., Lumsdon, A.E., MacDonald, G.K., Zarfl, C., Reidy Liermann, C., 2015. An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. Environ. Res. Lett. 10, 015001. https://doi.org/10.1088/1748-9326/10/1/015001.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., Olden, J.D., Opperman, J.J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P.H., van Soesbergen, A., Zarfl, C., 2019. Mapping the world's free-flowing rivers. Nature 569, 215–221. https://doi.org/10.1038/s41586-019-1111-9.

Grill, G., Ouellet Dallaire, C., Fluet Chouinard, E., Sindorf, N., Lehner, B., 2014. Development of new indicators to evaluate river fragmentation and flow regulation at large scales: a case study for the Mekong River basin. Ecol. Indic. 45, 148–159. https://doi.org/10.1016/j.ecolind.2014.03.026.

Gu, W., Swihart, R.K., 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. Biol. Conserv. 116, 195–203. https://doi.org/10.1016/S0006-3207(03)00190-3.

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat suitability and distribution models. With applications in R, First. ed. Cambridge University Press, Cambridge.

Hall, C.J., Jordaan, A., Frisk, M.G., 2011. The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. Landsc. Ecol. 26, 95–107. https://doi.org/10.1007/s10980-010-9539-1.

Hanski, I., Gilpin, M., 1991. Metapopulation dynamics: brief history and conceptual domain. Biol. J. Linn. Soc. 42, 3–16.

Hermoso, V., Filipe, A.F., Segurado, P., Beja, P., 2017. Freshwater conservation in a fragmented world: dealing with barriers in a systematic planning framework. Aquat. Conserv. Mar. Freshw. Ecosyst. 28, 17–25.

Hermoso, V., Kennard, M.J., Linke, S., 2012. Integrating multidirectional connectivity requirements in systematic conservation planning for freshwater systems. Divers. Distrib. 18, 448–458. https://doi.org/10.1111/j.1472-4642.2011.00879.x.

Hijmans, R.J., Cameron, S., Parra, J., Jones, P., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hijmans, R.J., van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J.A., Perminan Lamigueiro, O., Bevan, A., Racine, E.B., Shortridge, A., 2016. raster: geographic data analysis and modeling [WWW Document] (accessed, 9.27.16)..

Hitt, N.P., Eyler, S., Wofford, J.E.B., 2012. Dam removal increases American eel abundance in distant headwater streams. Trans. Am. Fish. Soc. 141, 1171–1179. https://doi.org/10.1080/00028487.2012.675918.

Hortal, J., Jiménez-Valverde, A., Gómez, J.F., Lobo, J.M., Baselga, A., 2008. Historical bias in biodiversity inventories affects the observed environmental niche of the species. Oikos 117, 847–858. https://doi.org/10.1111/j.0030-1299.2008.16434.x.

Igraph Core Team, 2015. igraph: the network analysis package [WWW Document]. accessed 9.28.16. http://igraph.org/.

IUCN, 2019. The IUCN Red List of Threatened Species [WWW Document]. accessed 1.26.19. http://www.iucnredlist.org/.

Kanehl, P.D., Lyons, J., Nelson, J.E., 1997. Changes in the habitat and fish community of the Milwaukee River, Wisconsin, following removal of the Woolen Mills dam. North Am. J. Fish. Manag. 17, 387–400. https://doi.org/10.1577/1548-8675(1997)017.

Kemp, P.S., O'Hanley, J.R., 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. Fish. Manag. Ecol. 17, 297–322. https://doi.org/10.1111/j.1365-2400.2010.00751.x.

King, S., O'Hanley, J.R., 2016. Optimal fish passage barrier removal - revisited. River Res. Appl. 32, 418–428. https://doi.org/10.1002/rra.

King, S., O'Hanley, J.R., Newbold, L.R., Kemp, P.S., Diebel, M.W., 2017. A toolkit for optimizing fish passage barrier mitigation actions. J. Appl. Ecol. 54, 599–611. https://doi.org/10.1111/1365-2664.12706.

Kondolf, G.M., Boulton, A.J., O'Daniel, S., Poole, G.C., Rahel, F.J., Stanley, E.H., Wohl, E., Bang, A., Carlstrom, J., Cristoni, C., Huber, H., Koljonen, S., Louhi, P., K., N, 2006. Process-based ecological river restoration: visualizing three-dimensional connectivity and dynamic vectors to recover lost linkages. Ecol. Soc. 11, 5.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2009. Extinction debt: a challenge for biodiversity conservation. Trends Ecol. Evol. 24, 564–571. https://doi.org/10.1016/j.tree.2009.04.011.

Lehner, B., Verdin, K., Jarvis, A., 2008. New global hydrography derived from spaceborne elevation data. Eos Trans. https://doi.org/10.1029/2008EO100001.

Letcher, B.H., Nislow, K.H., Coombs, J.A., O'Donnell, M.J., Dubreuil, T.L., 2007. Population response to habitat fragmentation in a stream-dwelling brook trout population. PLoS One 2. https://doi.org/10.1371/journal.pone.0001139.

Levins, R., 1968. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Am. 15, 237–240. https://doi.org/10.1016/j.jinoche.2007.06.005.

Liermann, C.R., Nilsson, C., Robertson, J., Ng, R.Y., 2012. Implications of dam obstruction for global freshwater fish diversity. Bioscience 62, 539–548. https://doi.org/10.1525/bio.2012.62.6.5.

Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: A misleading measure of the performance of predictive distribution models. Glob. Ecol. Biogeogr. 17, 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x.

Lorenzo-Lacruz, J., Vicente-Serrano, S.M., López-Moreno, J.I., Morán-Tejeda, E., Zabalza, J., 2012. Recent trends in Iberian streamflows (1945–2005). J. Hydrol. 414–415, 463–475. https://doi.org/10.1016/j.jhydrol.2011.11.023.

Lundqvist, H., Rivinoja, P., Leonardsson, K., McKinnell, S., 2008. Upstream passage problems for wild Atlantic salmon (*Salmo salar* L.) in a regulated river and its effect on the population. Hydrobiologia 602, 111–127. https://doi.org/10.1007/s10750-008-9282-7.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton, USA.

Maceda-Veiga, A., 2013. Towards the conservation of freshwater fish: Iberian Rivers as an example of threats and management practices. Rev. Fish Biol. Fish. 23, 1–22. https://doi.org/10.1007/s11160-012-9275-5.

Magilligan, F.J., Graber, B.E., Nislow, K.H., Chipman, J.W., Sneddon, C.S., Fox, C.A., 2016. River restoration by dam removal: enhancing connectivity at watershed scales. Elem. Sci. Anthr. 4, 000108. https://doi.org/10.12952/journal.elementa.000108.

MAGRAMA, 2004. Descargas SIA [WWW Document]. accessed 2.22.16. http://servicios2.marm.es/sia/visualizacion/descargas/mapas.jsp.

Maitland, B.M., Poesch, M., Anderson, A.E., 2016. Prioritising culvert removals to restore habitat for at-risk salmonids in the boreal forest. Fish. Manag. Ecol. 23, 489–502. https://doi.org/10.1111/fme.12188.

McKay, S.K., Cooper, A.R., Diebel, M.W., Elkins, D., Oldford, G., Roghair, C., Wieferich, D., 2017. Informing watershed connectivity barrier prioritization decisions: a synthesis. River Res. Appl. 33, 847–862.

McKay, S.K., Schramski, J.R., Conyngham, J.N., Fischenich, J.C., 2013. Assessing upstream fish passage connectivity with network analysis. Ecol. Appl. 23, 1396–1409. https://doi.org/10.1890/12-1564.1.

Meynard, C.N., Quinn, J.F., 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. J. Biogeogr. 34, 1455–1469. https://doi.org/10.1111/j.1365-2699.2007.01720.x.

Morita, K., Morita, S.H., Yamamoto, S., 2009. Effects of habitat fragmentation by damming on salmonid fishes: lessons from white-spotted charr in Japan. Ecol. Res. 24, 711–722. https://doi.org/10.1007/s11284-008-0579-9.

Morita, K., Yamamoto, S., 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling Charr populations. Conserv. Biol. 16, 1318–1323.

Nieland, J.L., Sheehan, T.F., Saunders, R., 2015. Assessing demographic effects of dams on diadromous fish: a case study for Atlantic salmon in the Penobscot River. Maine. ICES J. Mar. Sci. 72, 2423–2437.

Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. Science 308, 405–408.

Nislow, K.H., Hudy, M., Letcher, B.H., Smith, E.P., 2011. Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. Freshw. Biol. 56, 2135–2144. https://doi.org/10.1111/j.1365-2427.2011.02634.x.

O'Connor, J.E., Duda, J.J., Grant, G.E., 2015. 1000 dams down and counting. Science 348, 496–497. https://doi.org/10.1126/science.aaa9204.

O'Hanley, J.R., Wright, J., Diebel, M., Fedora, M.A., Soucy, C.L., 2013. Restoring stream habitat connectivity: a proposed method for prioritizing the removal of resident fish passage barriers. J. Environ. Manage. 125, 19–27. https://doi.org/10.1016/j.jenvman.2013.02.055.

Olden, J.D., 2016. Challenges and opportunities for fish conservation in dam-impacted waters. In: Closs, G.P., Krkosek, M., Olden, J.D. (Eds.), Conservation of Freshwater Fishes. Cambridge University Press, Cambridge, pp. 107–148.

Olden, J.D., Kennard, M.J., Leprieur, F., Tedesco, P.A., Winemiller, K.O., García-Berthou, E., 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. Divers. Distrib. 16, 496–513. https://doi.org/10.1111/j.1472-4642.2010.00655.x.

Perkin, J.S., Bonner, T.H., 2011. Long-term changes in flow regime and fish assemblage composition in the Guadalupe and San Marcos rivers of Texas. River Res. Appl. 27, 566–579. https://doi.org/10.1002/rra.1373.

Core Team, R., 2015. R: a language and environment. for statistical computing.

Rey Benayas, J.M., De La Montaña, E., 2003. Identifying areas of high-value vertebrate diversity for strengthening conservation. Biol. Conserv. 114, 357–370. https://doi.org/10.1016/S0006-3207(03)00064-8.

Richter, B.D., Postel, S., Revenga, C., Scudder, T., Lehner, B., Churchill, A., Chow, M., 2010. Lost in development's shadow: the downstream human consequences of dams. Water Altern. 3, 14–42. https://doi.org/10.1007/s11195-009-9131-2.

Rodeles, A.A., Galicia, D., Miranda, R., 2017. Recommendations for monitoring freshwater fishes in river restoration plans: a wasted opportunity for assessing impact. Aquat. Conserv. Mar. Freshw. Ecosyst. 27, 880–885. https://doi.org/10.1002/aqc.2753.

Rodeles, A.A., Leunda, P.M., Elso, J., Ardaiz, J., Galicia, D., Miranda, R., 2019. Consideration of habitat quality in a river connectivity index for anadromous fishes. Inl. Waters 9, 278–288. https://doi.org/10.1080/20442041.2018.1544817.

Rogado, L., Alexandrino, P., Almeida, P.R., Alves, M.J., Bochechas, J., Cortes, R., Domingos, I., Filipe, A.F., Madeira, J., Magalhaes, M.F., 2004. Peixes. In: Livro Vermelho Dos Vertebrados de Portugal. Instituto da Conservação da Natureza 57–114.

Segurado, P., Araújo, M.B., 2004. An evaluation of methods for modelling species distributions. J. Biogeogr. 31, 1555–1568. https://doi.org/10.1111/j.1365-2699.2004.01076.x.

Segurado, P., Branco, P., Avelar, A.P., Ferreira, M.T., 2015. Historical changes in the functional connectivity of rivers based on spatial network analysis and the past occurrences of diadromous species in Portugal. Aquat. Sci. 77, 427–440. https://doi.org/10.1007/s00027-014-0371-6.

Segurado, P., Branco, P., Ferreira, M.T., 2013. Prioritizing restoration of structural connectivity in rivers: a graph based approach. Landsc. Ecol. 28, 1231–1238. https://doi.org/10.1007/s10980-013-9883-z.

SIBIC, 2015. SIBIC [WWW Document]. accessed 1.26.16. http://www.sibic.org/sibic.html.

SIBIC, 2014. Carta Piscícola Española [WWW Document]. Electron. Publ. (version 01/2015). URL http://www.cartapiscicola.es/#/home (accessed 1.26.16).

Solà, C., Ordeix, M., Pou-Rovira, Q., Sellarès, N., Queralt, A., Bardina, M., Casamitjana, A., Munné, A., 2011. Longitudinal connectivity in hydromorphological quality assessments of rivers. The ICF index: a river connectivity index and its application to Catalan rivers. Limnetica 30, 273–292.

Thorstad, E.B., Fiske, P., Aarestrup, K., Hvidsten, N.A., Harsaker, K., Heggberget, T.G., Økland, F., 2005. Upstream migration of Atlantic salmon in three regulated rivers. In: Spedicato, M.T., Lembo, G., Marmulla, G. (Eds.), Proceedings of the Fifth Conference on Fish Telemetry Held in Europe. FAO/COISPA, pp. 111–121.

Thuiller, W., Georges, D., Engler, R., Breiner, F., 2016. Package BIOMOD2. Ensemble platform for species distribution modeling.

Timpe, K., Kaplan, D., 2017. The changing hydrology of a dammed Amazon. Sci. Adv. 3, 1–14. https://doi.org/10.1126/sciadv.1700611.

Verissimo, A., Gante, H.F., Santos, C.D., Cheoo, G., Oliveira, J.M., Cereja, R., Ribeiro, F., 2018. Distribution and demography of the critically endangered Lisbon arched-mouth nase. *Iberochondrostoma olisiponense*. Fishes Mediterr. Environ. 2018, 1–13. https://doi.org/10.29094/FiSHMED.2018.002.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature 467, 555–561. https://doi.org/10.1038/nature09549.

Wofford, J.E.B., Gresswell, R.E., Banks, M.A., 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. Ecol. Appl. 15, 628–637. https://doi.org/10.1890/04-0095.

Yamamoto, S., Morita, K., Koizumi, I., Maekawa, K., 2004. Genetic differentiation of white-spotted charr (*Salvelinus leucomaenis*) populations after habitat fragmentation: spatial-temporal changes in gene frequencies. Conserv. Genet. 5, 529–538. https://doi.org/10.1023/B:COGE.0000041029.38961.a0.

Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., Tockner, K., 2014. A global boom in hydropower dam construction. Aquat. Sci. 77, 161–170. https://doi.org/10.1007/s00027-014-0377-0.