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Historical data to plan the recovery of the European eel

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Summary

1. Long-term perspectives are critical to understand contemporary ecological systems. However, historical data on the distribution of biodiversity have only rarely been used in applied environmental sciences.

2. Here, we use historical sources to reconstruct the historical range of the European eel, a critically endangered species. We then use this baseline range to set range targets for the recovery of the European eel, as opposed to the abundance-based targets established by the European Union, which are constrained by the poor information on pre-collapse stocks.

3. We collected over 10 000 historical freshwater fish records from Spain in the 19th and 16th centuries, as well as over 25 000 records from the global biodiversity information facility (GBIF) to characterize historical and current European eel distribution in the Iberian Peninsula. We converted fish records into an eel presence–absence data set using subcatchment as spatial unit of analysis and modelled eel distribution in the different historical periods.

4. The eel was historically widespread throughout the Iberian Peninsula, but it has lost over 80% of its original range, mainly due to river fragmentation by dams. Distribution models applied to 16th- and 19th-century data showed a high agreement, supporting the use of the 19th-century estimated distribution as a baseline range. We identified the number and identity of dams that should be made passable for accomplishing specific range recovery targets, for example showing that acting upon 20 dams would make available 60% of the baseline eel range.

5. *Synthesis and applications*. This work exemplifies how insights gained from historical ecology can support and guide present-day management of migratory fishes. Similar approaches could be developed throughout Europe to plan the recovery of the eel, since there are large amounts of historical eel records. Historical baseline ranges for the eel range should be incorporated into the European Union legal mandates aimed at the recovery of the species.

Key-words: *Anguilla anguilla*, conservation targets, dams, distribution changes, historical ecology, reference conditions, river fragmentation

Introduction

Long-term information on the characteristics of ecosystems and the distribution of biodiversity is crucial to understand the dynamics of contemporary ecological systems (Swetnam, Allen & Betancourt 1999; Willis & Birks 2006). However, ecological studies are rarely based on information older than 50 years and the past distributions of organisms are seldom incorporated in conservation strategies (Boakes *et al*. 2010; Szabo & Hedl 2011). Ecologists often distrust historical documents, because they are considered imprecise and anecdotal (Scharf 2014), as graphically exemplified by Edmonds (2005: 88): 'chipped, cracked, and fogged, laced with errors, omissions prejudices, silent assumptions, and preconceptions, they [historical texts] do not reflect the past so much as refract it'. Due to this distrust, studies on the long-term dynamics of distributions of organisms are most frequently based on data collected by well-known, trusted naturalists, such as the data set collected by Joseph Grinnell in Sierra Nevada (California, USA) in the early 20th century (Moritz *et al*. 2008; Tingley *et al*. 2009). However,

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high-quality historical data such as Grinnell's are necessarily limited in space, because few people were involved in their collection. Clavero & Revilla (2014) claimed that historical written sources based on citizen science initiatives could provide abundant, fine-grained and large-scale information on the past distribution of several species, opening important new paths for addressing ecological questions, just as contemporary citizen science does for short-term ecology (Duputié, Zimmermann & Chuine 2014). In this work, we use over 10 000 historical records of freshwater fish in Spain to analyse distribution changes of the European eel [*Anguilla anguilla* (Linnaeus, 1758)] and set range targets for its recovery.

The European eel (henceforth simply the eel) breeds in an unknown area in or near the Sargasso Sea and its larval stages are transported by the Gulf Stream to the coasts of Europe and Northern Africa (Tesch 2003). In approaching continental shelves, eels metamorphose into glass eels to colonize freshwater systems as elvers and yellow eels, although they can also remain in coastal areas (Tsukamoto & Nakai 1998). After a variable period, ranging from 2 to 20 years (Tesch 2003), eels metamorphose into silver eels and set forth on the journey back to the breeding grounds. Eel stocks collapsed in the early 1980s across the whole species range, with reductions in eel catches in commercial fisheries frequently exceeding 90% (Feunteun 2002; Kettle, Asbjørn Vøllestad & Wibig 2011). In the present situation, the eel is thought to be outside its safe biological limits (ICES 2013) and has accordingly been listed as critically endangered in the IUCN Red List (Freyhof & Kottelat 2010).

The eel is an economically and culturally important species (Kuroki, Righton & Walker 2014) and one of the few freshwater fish that are professionally exploited in Europe and Northern Africa (Righton & Walker 2013). The importance of the eel is reflected in the unique species-level legislation that the European Union has established to promote its recovery (European Commission 2007). Member states have to develop recovery plans for the eel at the hydrological basin scale, with the explicit target of enabling 'the escapement to the sea of at least 40% of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock'. The obvious difficulty for the implementation of this regulation is to know how pristine eel stocks were (Bevacqua *et al.* 2009). Long-term fisheries records do exist for some locations (Andersson, Florin & Petersson 2012), allowing the estimation of a baseline levels for eel abundance. However, these precious data sets are scarce and the abundance-based descriptions of pristine eel stocks that they provide can hardly be extrapolated among locations. An alternative approach would be to characterize the range of the eel in pristine conditions and use that information to define specific targets for range recovery. This approach implies a change in the paradigm of eel recovery targets, from a definition based on abundance (i.e. stocks) to a focus on the spatial occupancy (i.e. range), a shift that is supported by the consistent occupancy–abundance temporal relationships reported at the intraspecific level (e.g. Zuckerberg, Porter & Corwin 2009).

The drivers of the collapse of the European eel remain a matter of discussion (Feunteun 2002; Kettle, Asbjørn Vøllestad & Wibig 2011). The collapse of eel stocks in the 1980s could have been related to massive habitat loss due to dams in Iberian and Moroccan watercourses because eel stocks in these areas would be disproportionally important due to their proximity to the Sargasso Sea (Kettle, Asbjørn Vøllestad & Wibig 2011). Eels starting their oceanic migration to breeding grounds might be energy-limited (Clevestam *et al.* 2011), and differences in travel distances of more than 2500 km (e.g. between southern Spain and Norway) can make an important difference (Kettle, Asbjørn Vøllestad & Wibig 2011). A different line of analysis proposes that eel collapse was driven by negative conditions of oceanic currents in breeding areas, hampering the connection between the Sargasso Sea and the Gulf Stream (Baltazar-Soares *et al.* 2014). The dynamics in current circulation determined eel recruitment success before the 1980s, but since the onset of the collapse, recruitment has remained consistently low, independently of sea currents. Thus, even if currents led to the population collapse, the inability of the species to recover from that sudden decline episode should be linked to drivers different from current dynamics (Baltazar-Soares *et al.* 2014).

Combining recent hypotheses on the eel collapse, it seems plausible that the significant impact of dams massively built since the 1950s in the Iberian Peninsula and since the 1980s in Morocco (Kettle, Asbjørn Vøllestad & Wibig 2011) may have constrained the capacity of the eel to buffer recruitment fluctuations driven by natural phenomena (Baltazar-Soares *et al.* 2014). If this was the case, southern areas of the eel range that had acted as main sources of breeding individuals would be currently unable to support the large stocks needed to enhance recruitment. Recovering eel populations in Iberian Peninsula and Morocco would thus be critical for the overall recovery of the species.

Here, we analyse the historical distribution of the eel in the Iberian Peninsula based on abundant data provided by historical Spanish citizen science initiatives from the 16th and 19th centuries (Clavero & Revilla 2014) and characterize the spatial component of the species collapse by comparing historical and current ranges. We then used the historical eel range to set a baseline scenario that could support the adoption of realistic conservation targets and management actions for eel recovery. To exemplify this approach, we identified the minimum number of dams that should be modified to allow the recovery of explicit percentages of eel baseline range. This work shows the potential of applied historical ecology approaches to support present-day management of biodiversity (Swetnam, Allen & Betancourt 1999; Szabo & Hedl 2011).

Materials and methods

DATA SOURCES

We collected historical data on freshwater fish distribution from two Spanish historical sources: the geographic dictionary edited by (Madoz 1845-1850; henceforth 'the Madoz') and the late-16th-century *Relaciones Topográficas* (Clavero & Revilla 2014). Although the two sources differ in many aspects (e.g. the Madoz contains information collected by correspondents, while the *Relaciones Topográficas* reports full questionnaires as answered by locals), they both coincide in that they were structured data-gathering initiatives involving thousands of informants and reported short inventories of socioeconomically important species (either for their usefulness or harmfulness). In that sense, the data sets extracted from the Madoz and the *Relaciones Topográficas* differ from *ad hoc* data sets based on the accumulation of records collected in an unstructured manner, with varying sampling effort in space and time, such as those of atlases or herbaria records (Robertson, Cumming & Erasmus 2010). While the latter are uninformative in relation to absences, the non-inclusion of a relevant species in one of the historical inventories can arguably be interpreted as an absence.

The Madoz contains information on most Spanish population centres, rivers and topographical accidents (Clavero & Revilla 2014; Clavero & Villero 2014). It was published between 1845 and 1850 in 16 volumes, with some 11 800 pages and around 75 000 articles. The Madoz was the result of over a decade of work, compiling the information provided by several correspondents and over 1400 local collaborators. It aimed at giving a quantitative, updated description of the Spanish territory, which should serve to the progress of the country. In the words of its author, the dictionary gave to statistic aspects 'all the importance that this science deserves in modern times' (pg. 7; prologue in volume 1). Most fish records in the Madoz are reported either when describing rivers and wetlands or as a 'production', together with crops, livestock and game species.

We searched for citations of freshwater fish in the digitalized copies of the Madoz dictionary available at www.bibliotecavirtualdeandalucia.es, using the search tool in a pdf document reader. Searches were performed using known common names of fish, including all local variants found within the Madoz. The detection of these variants was made easier by the fact that fish records were most often provided in the form of short lists. We found information on fish species in 5982 localities across Spain, with 11 582 records of fish identifiable to at least genus level, most often to species (additionally, 956 records referred simply to 'fish'). We used Google Earth to georeference localities that could be positioned within a map with an acceptable level of precision, including villages, small topographical accidents, small rivers or specific sites commented in articles dealing with larger geographical (e.g. stretches within a river) or administrative units (e.g. judicial districts, provinces). The resulting data set had information from 5427 georeferenced localities, including 10 223 individual fish records. The eel was cited in 2815 sites, that is 51·9% of the georeferenced localities with fish records. The Spanish voice *anguila* was consistently used to name eels across the Madoz. The only variant detected was the term '*orihuelo*', a rare local voice, though still in use today, from central-western Spain, which was found only three times. This consistency in the use of the eel popular name ensures the avoidance of species misidentifications, which can be a serious problem in historical ecology studies (Mladenoff *et al.* 2002).

The *Relaciones Topográficas* (literally, topographic accounts) were a series of questionnaires distributed through Spanish villages between 1574 and 1582, during the reign of Philip II (Clavero & Villero 2014). Questionnaires asked about a diversity of matters, including living means, social organization and history. Although three different versions of the questionnaire were edited, all of them contained specific questions on river systems and their fisheries. The questionnaires were responded by at least two locals, who, according to the instructions that accompanied the questionnaires, had to be 'intelligent and inquisitive'. To date, at least 637 *Relaciones Topográficas* have been found, mainly corresponding to villages in central and southern Spain, and are conserved in the library of the Escorial Monastery, near Madrid. They were copied in the late 18th century, and these copies are kept in the library of the Spanish Royal History Academy, also in Madrid. We used the available transcriptions (see Clavero & Villero 2014) and the 18th-century copy to compile freshwater fish information from 628 *Relaciones Topográficas* (i.e. 98·6% of those conserved). We found data on freshwater fish for 181 villages, of which 121 (66·8%) reported the presence of eels.

Present-day data on freshwater fish distributions in Spain were obtained from the Global Biodiversity Information Facility (GBIF, www.gbif.org, accessed March 2014), which mainly relies on the information provided by the Spanish National Biodiversity Inventory (Clavero & Villero 2014). We searched the GBIF data base for Spanish georeferenced records of the most common freshwater fish taxa to obtain 25 135 records, 2677 of which corresponded to the eel.

We synthesized historical and current eel distributions using subcatchments as spatial sampling unit, defining them as hydrological units delimited by water divides and river confluences (Hermoso, Ward & Kennard 2013). Subcatchments units are a more appropriate spatial entity to study the distribution patterns of aquatic organisms than equal-sized cells (e.g. UTM cells), because they are the natural areas of influence and boundaries. We used ARC Hydro (Maidment 2002) in ArcGIS 9·1 (ESRI, Redlands, CA, USA) to derive 19 706 subcatchments units in the Iberian Peninsula (i.e. including both Spain and Portugal) from a 90-m digital elevation model. Units had a mean area of 29·1 km^2 (± 23·7 SD). On average, subcatchment units summarized information from 1·1 and 1·6 localities from the *Relaciones Topográficas* (median = 1; range 1–3) and the Madoz (median = 1; range 1–13), respectively.

The information on freshwater fish was translated from point records to subcatchments, to produce a presence–absence data set (Fig. 1). Eel absences derived from localities that reported fish presences using specific common names but did not mention the eel (Fig. 2). Not mentioning a species in a structured data-gathering initiative (as the *Relaciones Topográficas* and the Madoz) may not be a definitive proof of absence, but, in the case of the eel, does suggest it. This assumption is based on the following: (i) the demonstrated knowledge of the informants about the river fish fauna (based on their identification of fish species by their names) and (ii) the fact that the eel was a widely known and an important food resource for Spanish people. In any case, even if there is an imperfect eel detection in this approach (as happens in any survey, also contemporaneous ones), the informative value of absences is larger than that of randomly selected background samples or pseudoabsences used by presence-only distribution

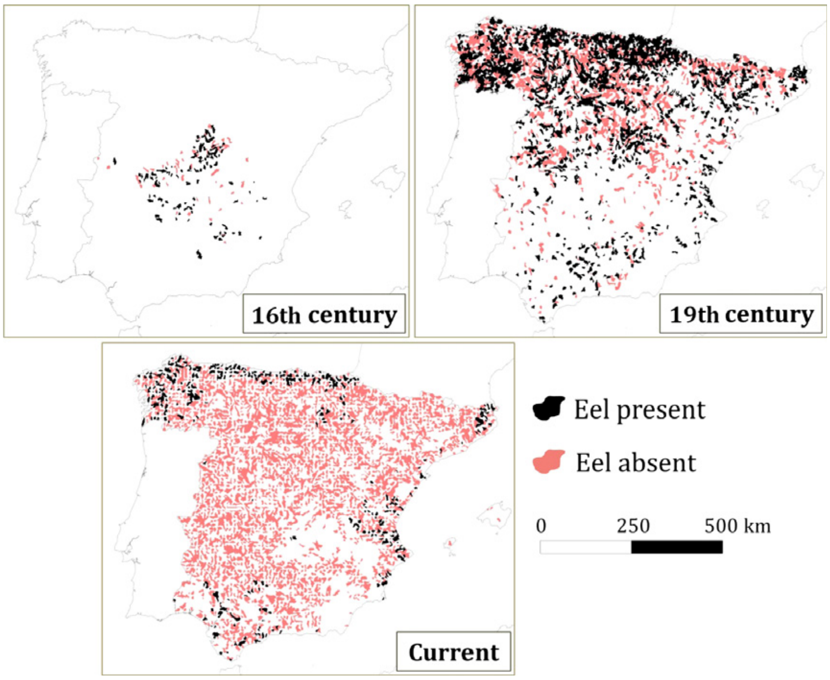

Fig. 1. Data on European eel distribution in Spain in different historical periods. Spatial units are subcatchments, delimited by water divides and river confluences. Black units are those with eel records (presences), while red units are those with freshwater fish records but not eel ones (absences). Data sources: *Relaciones Topográficas* (16th century); Madoz's dictionary15 (19th century); and Global Biodiversity Information Facility (current).

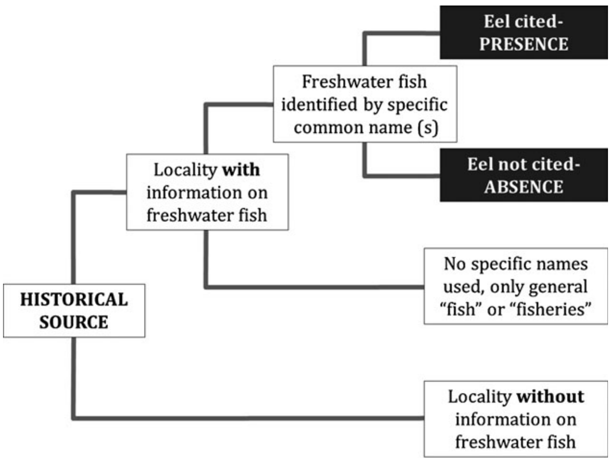

Fig. 2. Strategy followed to define eel presences and absences from historical sources. An eel absence was noted in a locality only when the historical source had good-quality information on freshwater fish (quality being evaluated by the use of specific common names) but the eel was not cited. Only situations included in black boxes were used for the presence–absence data sets.

modelling techniques (Brotons *et al.* 2004). For both the Madoz (19th century) and the *Relaciones Topográficas* (16th century) data, the eel was considered to be present in a given subcatchment if the species was cited in at least one of the localities with fish information included in it. The eel was considered to be absent from a subcatchment unit if it was not cited in any of the localities included in it. Subcatchments that did not contain information on freshwater fish or where the only information referred generically to 'fish' or 'fisheries' were not included in this presence–absence categorization (Fig. 2). We proceeded analogously with the contemporary (GBIF) data, coding as presence units those including at least one eel record, and as absence units those that contained freshwater fish records but not eel ones.

We excluded from all analyses the subcatchments in the arid south-eastern extreme of Spain, where watercourses are ephemeral and there are very few fish records (see Fig. 1), as well as those belonging to the Garonne River basin, which flow northwards into France and biogeographically do not belong to the Iberian Peninsula (the eel was cited in 7 of 10 units with fish data in the Spanish part of the Garonne basin). The final data set had 19 331 subcatchments.

DISTRIBUTION MODELLING

We chose five continuous variables related to topography and distance to the sea to characterize the environmental features of spatial units (see Table S1 in Supporting Information). This set of variables was selected from a larger number of candidate variables by selecting those that would be *a priori* more important for a migratory fish colonizing fresh waters from marine sources, while avoiding highly redundant variable pairs (Leathwick *et al.* 2005). Climatic variables were not used because we could not ensure that the known historical change in absolute values (Rodrigo *et al.* 1999) did not also imply a change in the spatial variability of climatic characteristics across the Iberian Peninsula. Anyway, given the broad climatic niche of the eel (e.g. Tesch 2003), it can be assumed that climatic variables would have little direct effect in the range of the species. Variables were transformed whenever this improved normality, assessed through visual inspection of data distribution.

We used the presence/absence data sets and the original 5 environmental variables to model eel distribution in the three periods analysed (16th and 19th centuries and the present), using ensemble ecological niche modelling approach (Araújo & New 2007). Models were fitted using the BIOMOD2 library (Thuiller, Georges & Engler 2013) within the free statistical software R (R Development Core Team 2011). We used nine different algorithms to model eel distribution: artificial neural networks (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized additive models (GAM), generalized boosting models (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), random forest (RF) and surface range envelope (SRE). The predictive performance of these models was evaluated through the area under receiver operating characteristic curve (AUC), and only models with AUCs above 0·7 were used to build final ensemble models (Table S2). The evaluation of ensemble models was carried out by splitting data in calibration and validation subsets, including 80% and 20% of the data, respectively. The ensemble models were constructed using the weighted mean of probabilities option. Models reported estimates of habitat suitability for the eel in Iberian subcatchments that ranged between 0 and 1, representing worst and optimum habitat, respectively. Throughout the text, we interpreted these values as probabilities of occurrence of the eel. The outputs of models developed for different periods were compared by means of Pearson's correlation (r) and the slopes of standardized major axis (SMA) model II regressions, assuming that matching predictions would have a slope close to one. These comparisons were limited to the geographic area covered by the three data sources used in this study. SMA regressions were analysed with the 'lmodel2' package (Legendre 2014) in R.

DAMS, RECOVERY TARGETS AND MANAGEMENT ACTIONS

We used the ensemble model for the 19th-century data as a reference scenario for eel range in the absence of important anthropogenic impacts in the Iberian Peninsula. For each particular subcatchment unit, we quantified the amount of eel habitat in the reference range scenario as a function of habitat quality and habitat size, using the product of its area and the probability of eel presence (i.e. 19th-century ensemble model). Recovery targets were set in terms of percentage of range recovered, with percentages referring to the total amount of habitat in the Iberian Peninsula (i.e. the sum of the values of all units) in the reference scenario. We compiled information on the distribution of dams in Spain and Portugal to identify the areas currently reachable by upstream migrating eels. A list of reservoirs and their position was obtained from the global reservoir and dam data base (GRanD) (Lehner *et al*. 2011). This list was complemented with the data contained in Web pages on large dams from Spain (http://www.embalses.net/) and Portugal (http://cnpgb.inag.pt/gr_barragens/gbportugal). We considered all dams as insurmountable barriers for eel movements, which is a simplification, since eels are good climbers and are able to overcome relatively small dams (Feunteun 2002). In any case, this assumption is supported by the strong impact of dam blockage on current eel distribution (Fig. S1). All subcatchments situated upstream from a dam were thus considered unreachable for the eel.

We used an optimization approach to maximize the amount of eel habitat made available through management actions affecting the minimum possible number of dams. We quantified the potential for habitat recovery (PR) for any particular dam (focus dam) through an index resulting from the addition of two components. The first component (A) was the amount of habitat that would be available for the eel if management action would make the dam fully permeable for eel movement. This amount of habitat is limited upstream either by other dams or by water divides. The second component (B) was the potential for the recovery of habitat by managing subsequent upstream dams. This was calculated with the following formula:

$$B = \sum_{i=1}^{n} \frac{A_i}{D_i \times 10}$$

where B is the potential for the recovery of suitable habitat by managing the n dams placed upstream from the focus dam, A_i is the amount of habitat that would be available if dam i was made permeable (i.e. component A when dam i is treated as the focus dam), and D_i is the number of dam barriers found between the focus dam and dam i, the latter being counted as number 1. D_i was introduced to penalize for the number of downstream dams that would require modifications in order to make a given upstream habitat accessible, and the factor 10 was used to increase this penalty. Adding this second component to the PR formula increased the efficiency of management actions on any given number of dams (Fig. S2). We performed a sequential selection of those dams not having any other downstream obstacle (i.e. those that would be the first encountered by upstream migrating eels), based on the highest PRs. Once the dam with the highest PR had been selected, the list of dams not having any downstream dam was updated, their A and B parameters were reassessed, and a new dam was selected. This procedure was repeated until the first 100 dams had been chosen.

Results

Distribution models showed that eel had been widely distributed throughout the Iberian Peninsula in the 19th century, being especially common around the coast and in the valleys of large rivers (Fig. 3). The species was only less common in the main mountain areas, although it was not infrequent at elevations above 1000 masl (we collected more than 50 records at higher elevations), reaching a maximum of 1360 masl. The comparison of the 19th century and current eel ranges illustrates the spatial collapse of the species (Fig. 3). The amount of habitat lost by the eel in the Iberian Peninsula between these two periods (estimated from the sums for all subcatchment units of the area $\times$ probability of presence products) surpasses 82%, being thus of a similar magnitude to the approximately 90% decline registered in stocks across the whole species range (Kettle, Asbjørn Vøllestad & Wibig 2011). The range of the eel is currently restricted to a coastal fringe, having disappeared from vast areas in major Iberian rivers, which once were important eel habitat. The probability of occurrence has declined since the 19th century even in lowland areas, with the decline being exacerbated by the presence of dams (Fig. S1).

It is remarkable that ancient water retention structures found in Spain and Portugal, such as dams from Roman or Arabic periods (Hooke 2006), did not constitute important barriers for eel movements along river systems. For example, the Arabic Xerta weir in the lower Ebro River's main channel (Prats *et al*. 2011) did not impede the penetration of the eel into the Ebro River basin (Fig. 1). We thus interpreted the probability of occurrence map of the eel in 19th century as a baseline for the eel range in a pristine state. This assumption was further supported by

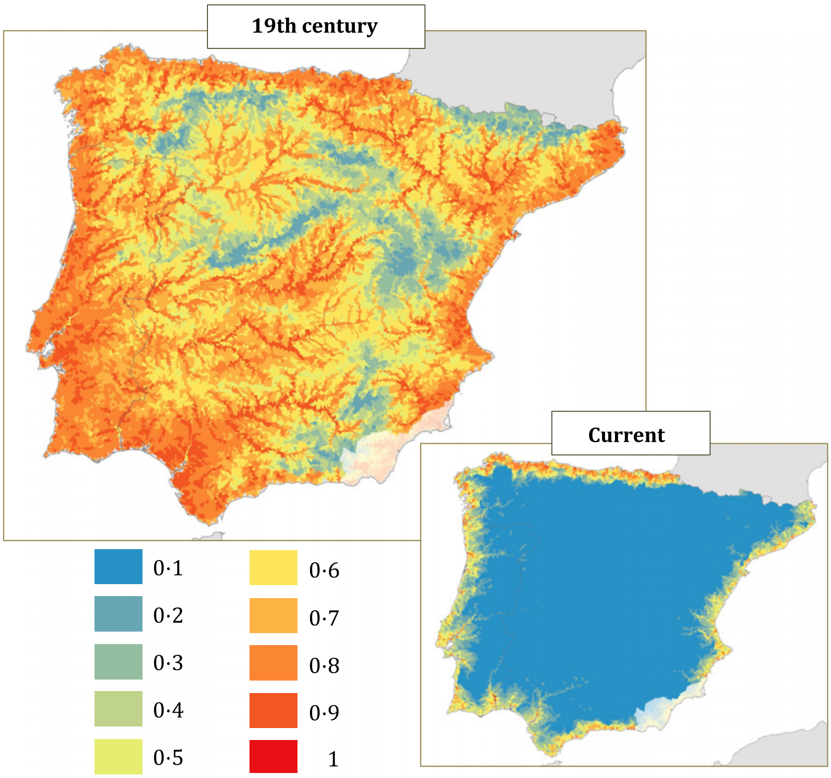

Fig. 3. Probability of occurrence of the eel in the Iberian Peninsula in the 19th century and the present. Estimates derive from the ensemble species distribution models using BIOMOD2. A semi-transparent layer is placed over the arid south-western Spain, where there are no permanent rivers and all fish records (either historical or contemporaneous) are extremely rare (see Fig. 1). AUCs: 19th century = 0·81; current = 0·94. Note that projections over Portugal are based on data collected exclusively in Spain.

the strong relationship and general agreement between the predictions of distribution models based on data from the 19th and 16th centuries (Pearson's $r = 0{\cdot}63$; SMA slope = 1·31; Fig. 4). This consistency is notable, since the two models were sourced from totally independent compilations of popular knowledge separated by almost 300 years. The eel has nowadays completely disappeared from vast areas in inland Spain where it had been commonly recorded in the 19th century. The relationship between the predictions for these two periods was weaker ($r = 0{\cdot}27$) and the slope of the SMA regression was close to zero (slope = 0·08) (Fig. 4).

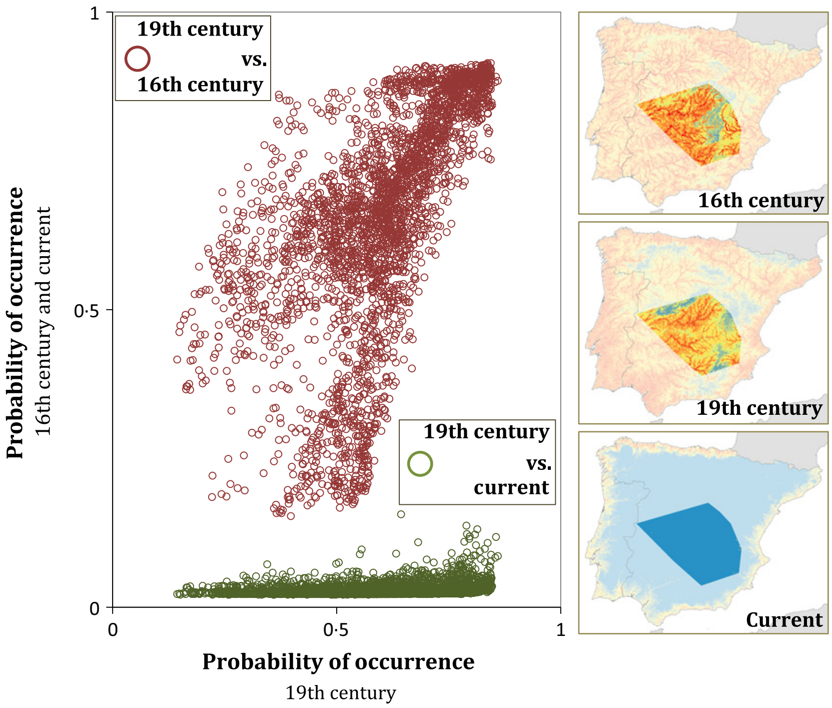

Fig. 4. Relationships between the probabilities of occurrence of the eel in different historical periods. Estimates refer only the area limited by the minimum convex polygon enclosing the information provided by the *Relaciones Topográficas* (see Fig. 1), as shown in right panels (codes for probabilities of occurrence as in Fig. 3). For descriptors of the ensemble models, see Table S2. Data sources as in Fig. 1.

Based on the eel baseline range (Fig. 3), we followed an optimization approach to select the minimum number of dam barriers that should be made passable for eels in order to achieve explicit spatial, instead of abundance-based, recovery targets (Fig. 5). We found that it would be necessary to make 12 dams permeable to eel movements in two river basins to recover the species access to at least 40% of its baseline range in the Iberian Peninsula. Recovering access to 60% of the original amount of habitat would imply acting on 20 dams while reaching an 80% habitat recovery would need modifications on 76 dams (Fig. 5).

Discussion

In the global context of intense and increasing regulation of river flows (Nilsson *et al.* 2005), the Iberian Peninsula has some of the more regulated and fragmented river systems world-wide (Liermann *et al.* 2012). Several diadromous fishes have declined dramatically due to dam construction (Limburg & Waldman 2009), and neither the eel nor the Iberian Peninsula is exceptions to this pattern. Even though several factors (e.g. overfishing, changes in oceanic circulation or parasites) may have had a role in the decline of the eel, the spatial patterns in the local extinctions of the eel across the Iberian Peninsula are neatly linked to river fragmentation (Fig. 3; Fig. S1). In contrast to the loss of the eel from inland Iberia, the species still performs deep penetrations into several central European river systems (Aprahamian & Walker 2008; Imbert *et al.* 2008). Our results thus support the idea that the role of dams in the decline of the eel might have been underestimated because dam effects have been especially acute only in the southern, water-scarce part of the species range (Kettle, Asbjørn Vøllestad & Wibig 2011). Restoring river connectivity would hence be critical to recover eel stocks in the Iberian Peninsula, probably as well as in other important parts of the eel range, such as Morocco.

We identified the dam barriers which should be modified to ensure eel access to given proportions of its baseline range, but we did not propose the specific actions, such as dam removal (O'Hanley *et al.* 2013), fish passages (Katopodis & Williams 2012) or the more integrative bypass channels (Pander, Mueller & Geist 2013). This is because technical solutions for management actions

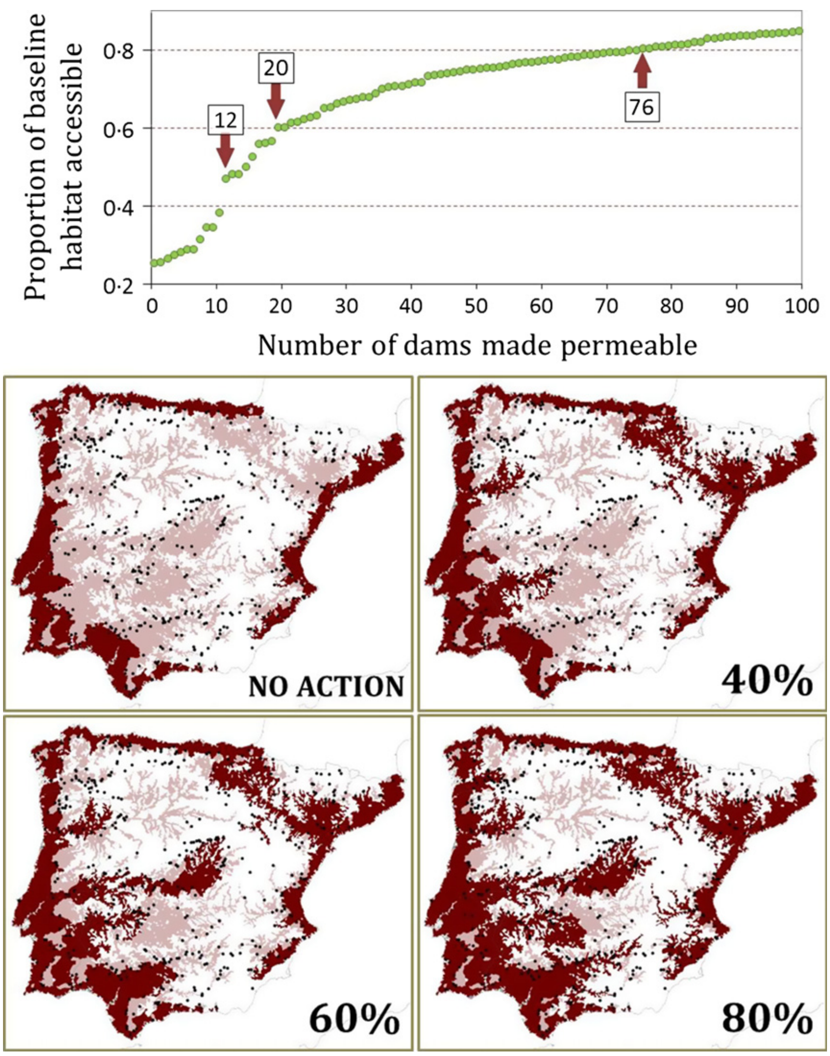

Fig. 5. Identification of dams needed to be made passable in order to achieve specific range recovery targets for the eel. The upper panel shows the proportion of the baseline eel range made accessible with management actions directed towards an increasing number of dams. As an example, recovery targets (broken lines) were set at 0·4, 0·6 and 0·8 of the baseline eel range. The number of dams requiring management to achieve these targets is shown in the boxes. Maps show the location of the dams (black dots) in the Iberian Peninsula. Dark red areas mark the estimated occupancy area in the 19th century baseline scenario, using a cut-off limit in a probability of 0·6 (specificity = sensitivity). Note, however, that the optimization procedure used continuous probability of occurrence values and the presence–absence dichotomy is used only to simplify the graphical representation. In the four maps, a semi-transparent layer covers the area unreachable for eels due to river fragmentation by dams.

should be analysed in a dam-specific basis. Our approach is blind with respect to dam characteristics, but further developments should explicitly assess the cost efficiency of management actions by incorporating the features of each barrier (e.g. O'Hanley *et al*. 2013; Hoenke, Kumar & Batt 2014), such as the cost of building passages in relation to dam height or the permeability for seaward eel migration. For example, dams without hydroelectric uses or with the possibility to establish modifications to avoid fish mortality (Feunteun 2002) should be prioritized. In this sense, it must be taken into account that although the blockage of upstream migration is the most studied and most easily solved impact of dams, the impediment of downstream movement of the eel and other migratory fish is an equally important problem that must also be addressed (e.g. Pelicice, Pompeu & Agostinho 2015).

Our proposed optimization approach to increase eel accessibility to suitable habitat at the whole Iberian Peninsula level could be implemented in the basin-specific plans for eel recovery, which are a legal mandate in the European Union (European Commission 2007), or applied to any other spatial unit of interest (e.g. regions or countries). The recovery of the eel would not only restore an important socio-economic resource, but would also imply the recovery of a keystone species. Before its collapse, the eel was the only widespread native piscivorous fish in the Iberian Peninsula (Doadrio 2002) and the staple prey for several predators (Callejo & Delibes 1987). It is thus arguable that the disappearance of the eel across most of the Iberian Peninsula would have had important effects on the functioning of river ecosystems, especially considering the role of predatory fish in structuring aquatic communities (Turner & Mittelbach 1990; Winkelmann *et al*. 2011) and the fact that the eel frequently constituted important proportions of the fish biomass in freshwater systems (Feunteun 2002). However, the description of the impacts of the disappearance of the eel remains elusive, because detailed accounts of freshwater communities in pristine conditions usually do not exist. The socio-economic importance of the eel and the consequent interest in its recovery can become an opportunity to address several of the environmental issues related to dams (Mueller, Pander & Geist 2011).

SYNTHESIS AND APPLICATIONS

This work demonstrates the potential of historical data on species distributions extracted from written sources for understanding the characteristics of natural systems before critical anthropogenic impacts (Li *et al*. 2015). It is also an example of how the knowledge generated through historical ecology approaches may have direct applications on present-day biodiversity management (Willis *et al*. 2007; Szabo & Hedl 2011). The approach followed in this work can be adopted in other regions within the eel range, since historical, large-scale information on freshwater fish distribution is included in the several compilations of geographically structured information available in Europe for the 18th and 19th centuries (Clavero & Revilla 2014), as well as in other, more disperse sources (Beslagic, Marinval & Belliard 2013). Gathering and georeferencing historical records may be a hard, tedious and challenging task, but it is probably the most straightforward option to establish valid baseline scenarios and realistic conservation targets for several threatened species, especially for those species that, like the eel, have been socio-economically relevant. We strongly recommend that the European Union revises legal mandates and targets regarding eel recovery in the light of applied historical ecology approaches.

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Data accessibility

European eel presence–absence data for localities included in the Madoz and the *Relaciones Topográficas* is available from the Dryad Digital Repository: doi: 10.5061/dryad.7vs0v (Clavero & Hermoso 2015).

References

Andersson, J., Florin, A.B. & Petersson, E. (2012) Escapement of eel (*Anguilla anguilla*) in coastal areas in Sweden over a 50-year period. *ICES Journal of Marine Science*, **69**, 991–999.

Aprahamian, M. & Walker, A. (2008) Status of eel fisheries, stocks and their management in England and Wales. *Knowledge and Management of Aquatic Ecosystems*, **390-391**, 07.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, **22**, 42–47.

Baltazar-Soares, M., Biastoch, A., Harrod, C., Hanel, R., Marohn, L., Prigge, E. *et al*. (2014) Recruitment collapse and population structure of the European eel shaped by local ocean current dynamics. *Current Biology*, **24**, 104–108.

Beslagic, S., Marinval, M.C. & Belliard, J. (2013) CHIPS: a database of historic fish distribution in the Seine River basin (France). *Cybium*, **37**, 75–93.

Bevacqua, D., Melia, P., Crivelli, A.J., Gatto, M. & de Leo, G.A. (2009) Assessing management plans for the recovery of the European eel: a need for multi-objective analyses. *American Fisheries Society Symposium*, **69**, 637–647.

Boakes, E.H., McGowan, P.J., Fuller, R.A., Chang-Qing, D., Clark, N.E., O'Connor, K. *et al*. (2010) Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biology*, **8**, e1000385.

Brotons, L., Thuiller, W., Araújo, M.B. & Hirzel, A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, **27**, 437–448.

Callejo, A. & Delibes, M. (1987) Dieta de la nutria *Lutra lutra* (Linnaeus, 1758) en la cuenca del alto Ebro, norte de España. *Miscel lània Zoològica*, **11**, 353–362.

Clavero, M. & Revilla, E. (2014) Biodiversity data: mine centuries-old citizen science. *Nature*, **510**, 35.

Clavero, M. & Villero, D. (2014) Historical ecology and invasion biology: long-term distribution changes of introduced freshwater species. *BioScience*, **64**, 145–153.

Clavero, M. & Hermoso, V. (2015) Data from: Historical data to plan the recovery of the European eel. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.7vs0v.

Clevestam, P.D., Ogonowski, M., Sjöberg, N.B. & Wickström, H. (2011) Too short to spawn? Implications of small body size and swimming distance on successful migration and maturation of the European eel *Anguilla anguilla*. *Journal of Fish Biology*, **78**, 1073–1089.

Doadrio, I. (2002) *Atlas y libro rojo de los peces continentales de España*. Dirección General de Conservación de la Naturaleza, Madrid.

Duputié, A., Zimmermann, N.E. & Chuine, I. (2014) Where are the wild things? Why we need better data on species distribution. *Global Ecology and Biogeography*, **23**, 457–467.

Edmonds, M. (2005). The pleasures and pitfalls of written records. *The Historical Ecology Handbook: A Restorationist's Guide to Reference Ecosystems* (eds D. Egan & E.A. Howell), pp. 73–100. Island Press, Washington, DC.

European Commission (2007) Council Regulation (EC) No 1100/2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel. *Official Journal of the European Union*, **248**, 17–23.

Feunteun, E. (2002) Management and restoration of European eel population (*Anguilla anguilla*): an impossible bargain. *Ecological Engineering*, **18**, 575–591.

Freyhof, J. & Kottelat, M. (2010) *Anguilla anguilla*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. www.iucnredlist.org. Accessed April 2014.

Hermoso, V., Ward, D.P. & Kennard, M.J. (2013) Prioritizing refugia for freshwater biodiversity conservation in highly seasonal ecosystems. *Diversity and Distributions*, **19**, 1031–1042.

Hoenke, K.M., Kumar, M. & Batt, L. (2014) A GIS based approach for prioritizing dams for potential removal. *Ecological Engineering*, **64**, 27–36.

Hooke, J.M. (2006) Human impacts on fluvial systems in the Mediterranean region. *Geomorphology*, **79**, 311–335.

ICES (2013) *Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL)*. ICES, Sukarrieta, Spain, and Copenhagen, Denmark.

Imbert, H., de Lavergne, S., Gayou, F., Rigaud, C. & Lambert, P. (2008) Evaluation of relative distance as new descriptor of yellow European eel spatial distribution. *Ecology of Freshwater Fish*, **17**, 520–527.

Katopodis, C. & Williams, J.G. (2012) The development of fish passage research in a historical context. *Ecological Engineering*, **48**, 8–18.

Kettle, A.J., Asbjørn Vøllestad, L. & Wibig, J. (2011) Where once the eel and the elephant were together: decline of the European eel because of changing hydrology in southwest Europe and northwest Africa? *Fish and Fisheries*, **12**, 380–411.

Kuroki, M., Righton, D. & Walker, A. (2014) The importance of Anguillids: a cultural and historical perspective introducing papers from the World Fisheries Congress. *Ecology of Freshwater Fish*, **23**, 2–6.

Leathwick, J.R., Rowe, D., Richardson, J., Elith, J. & Hastie, T. (2005) Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. *Freshwater Biology*, **50**, 2034–2052.

Legendre, P. (2014) lmodel2: Model II Regression. http://cran.r-project.org/web/packages/lmodel2 R package version 1.7-2.

Lehner, B., Liermann, C.R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P. *et al.* (2011) *Global Reservoir and Dam (GRanD) Database*. Technical Documentation, Version 1.

Li, X., Jiang, G., Tian, H., Xu, L., Yan, C., Wang, Z. *et al.* (2015) Human impact and climate cooling caused range contraction of large mammals in China over the past two millennia. *Ecography*, **38**, 74–82.

Liermann, C.R., Nilsson, C., Robertson, J. & Ng, R.Y. (2012) Implications of dam obstruction for global freshwater fish diversity. *BioScience*, **62**, 539–548.

Limburg, K.E. & Waldman, J.R. (2009) Dramatic declines in North Atlantic diadromous fishes. *BioScience*, **59**, 955–965.

Madoz, P. (1845-1850) *Diccionario Geográfico, Estadístico y Histórico de España, y sus Posesiones de Ultramar*, vols. 16. P. Madoz, Madrid.

Maidment, D.R. (2002) *Arc Hydro: GIS for Water Resources*. ESRI Press, Redlands.

Mladenoff, D.J., Dahir, S.E., Nordheim, E.V., Schulte, L.A. & Guntenspergen, G.G. (2002) Narrowing historical uncertainty: probabilistic classification of ambiguously identified tree species in historical forest survey data. *Ecosystems*, **5**, 539–553.

Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, **322**, 261–264.

Mueller, M., Pander, J. & Geist, J. (2011) The effects of weirs on structural stream habitat and biological communities. *Journal of Applied Ecology*, **48**, 1450–1461.

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.

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. *Journal of Environmental Management*, **125**, 19–27.

Pander, J., Mueller, M. & Geist, J. (2013) Ecological functions of fish bypass channels in streams: migration corridor and habitat for reophilic species. *River Research and Applications*, **29**, 441–450.

Pelicice, F.M., Pompeu, P.S. & Agostinho, A.A. (2015) Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. *Fish and Fisheries*, doi: 10.1111/faf.12089.

Prats, J., Armengol, J., Marcé, R., Sánchez-Juny, M. & Dolz, J. (2011) Dams and reservoirs in the lower Ebro River and its effects on the river thermal cycle. *The Ebro River Basin* (eds D. Barceló & M. Petrovic), pp. 77–95. Springer, Berlin, Heidelberg.

R Development Core Team. (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Righton, D. & Walker, A.M. (2013) Anguillids: conserving a global fishery. *Journal of Fish Biology*, **83**, 754–765.

Robertson, M.P., Cumming, G.S. & Erasmus, B.F.N. (2010) Getting the most out of atlas data. *Diversity and Distributions*, **16**, 363–375.

Rodrigo, F.S., Esteban-Parra, M.J., Pozo-Vázquez, D. & Castro-Díez, Y. (1999) A 500-year precipitation record in Southern Spain. *International Journal of Climatology*, **19**, 1233–1253.

Scharf, E.A. (2014) Deep time: the emerging role of archaeology in landscape ecology. *Landscape Ecology*, **29**, 563–569.

Swetnam, T.W., Allen, C.D. & Betancourt, J.L. (1999) Applied historical ecology: using the past to manage for the future. *Ecological Applications*, **9**, 1189–1206.

Szabo, P. & Hedl, R. (2011) Advancing the integration of history and ecology for conservation. *Conservation Biology*, **25**, 680–687.

Tesch, F.W. (2003) *The eel*. Blackwell Publishing, Oxford.

Thuiller, W., Georges, D. & Engler, R. (2013) BIOMOD2: ensemble platform for species distribution modelling. R package version 2(7), r560.

Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. (2009) Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19637–19643.

Tsukamoto, K. & Nakai, I. (1998) Do all freshwater eels migrate? *Nature*, **396**, 635–636.

Turner, A.M. & Mittelbach, G.G. (1990) Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology*, **71**, 2241–2254.

Willis, K.J. & Birks, H.J.B. (2006) What is natural? The need for a long-term perspective in biodiversity conservation. *Science*, **314**, 1261–1265.

Willis, K.J., Araújo, M.B., Bennett, K.D., Figueroa-Rangel, B., Froyd, C.A. & Myers, N. (2007) How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B*, **362**, 175–187.

Winkelmann, C., Hellmann, C., Worischka, S., Petzoldt, T. & Benndorf, J. (2011) Fish predation affects the structure of a benthic community. *Freshwater Biology*, **56**, 1030–1046.

Zuckerberg, B., Porter, W.F. & Corwin, K. (2009) The consistency and stability of abundance–occupancy relationships in large-scale population dynamics. *Journal of Animal Ecology*, **78**, 172–181.

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Supporting Information

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

Fig. S1. Probability of eel occurrence in the 19th century and the present in relation to altitude and accessibility.

Fig. S2. Percentage of baseline eel range made accessible through different approaches to select management actions.

Table S1. List of the environmental variables used as predictors in the eel distribution models.

Table S2. Summary of AUCs for the 8 algorithms used to model eel distribution.