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1 A Toolkit for Optimizing Fish Passage Barrier Mitigation Actions

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Summary

1. The presence of dams, stream-road crossings, and other infrastructure often compromises the connectivity of rivers, leading to reduced fish abundance and diversity. The assessment and mitigation of river barriers is critical to the success of restoration efforts aimed at restoring river integrity.
2. In this paper, we present a combined modeling approach involving statistical regression methods and mixed integer linear programming to maximize resident fish species richness within a catchment through targeted barrier mitigation. Compared to existing approaches, our proposed method provides enhanced biological realism while avoiding the use of complex and computationally intensive population/ecosystem models.
3. To estimate barrier passability quickly and at low cost, we further outline a rapid barrier assessment methodology. The methodology is used to characterize potential passage barriers for various fish species common to the UK but can be readily adapted to different planning areas and other species of interest.
4. We demonstrate the applicability of our barrier assessment and prioritization approach based on a case study of the River Wey, located in south-east England. We find that significant increases in species richness can be achieved for modest investment in barrier mitigation. In particular, dams and weirs with low passability located on mid to high order streams are identified as top priorities for mitigation.
5. *Synthesis and applications.* Our study shows the benefits of combining a coarse resolution barrier assessment methodology with state-of-the art optimization modeling to cost-effectively plan fish passage barrier mitigation actions. The modeling approach can help inform on-the-ground river restoration decision making by providing a recommended course of action that best allocates limited resources in order to restore longitudinal connectivity and maximize ecological gains.

Introduction

Longitudinal connectivity is essential to the ecological integrity of river ecosystems (Pringle, 2003). However, human impacts have significantly reduced the connectivity of river systems worldwide through the construction of artificial barriers, such as dams, weirs, culverts, and other stream-road crossings (Nilsson et al., 2005). Anthropogenic fragmentation of river networks is well recognized as a significant threat to the occurrence, abundance, and persistence of many freshwater species (Bednarek, 2001; Bourne et al., 2011). River connectivity plays an important role for fish at the individual and population levels. For individuals,

44 physical obstructions limit movement, access to rearing and spawning habitat, and shelter from predation
45 and disturbances (Lucas and Baras, 2001; Liermann et al., 2012). Artificial barriers also impact metapopula-
46 tion dynamics by isolating local populations and restricting dispersal and genetic exchange (Stanford et al.,
47 1996; Wofford et al., 2005; Minor and Urban, 2007). The result is that fragmented populations often face an
48 increased risk of local extinction and a reduced chance of subsequent recovery because recolonization is no
49 longer possible (Lucas et al., 2009).

50 There is sound evidence that removing artificial barriers is not only a cost-effective means of restoring
51 hydrologic and river ecosystem processes (Roni et al., 2002), but that the benefits of such can be realized
52 quickly (O'Connor et al., 2015). A number of studies have demonstrated significant increases in fish abundance
53 and or diversity (Kanehl et al., 1997; Catalano et al., 2007; Gardner et al., 2013) and a rapid return to
54 more natural flow conditions (East et al., 2015) following barrier removal. Unsurprisingly, there is growing
55 support for and implementation of barrier mitigation schemes, particularly in the US, Canada, parts of
56 the European Union (EU), and Australia. This is evidenced by legislative drivers, such as the EU Water
57 Framework Directive, and by the funding of large-scale restoration programs, like the US National Fish
58 Habitat Partnership, both of which emphasize the need to remove fish passage barriers.

59 Although headway is being made to restore river connectivity, the scale of the problem is nonetheless daunting.
60 It is estimated, for example, that the North American Great Lakes basin is fragmented by no less than 7,000
61 dams and 268,000 road crossings (Januchowski-Hartley et al., 2013). To help direct barrier mitigation efforts,
62 a variety of prioritization methodologies have emerged. Scoring and ranking is by far the most commonly
63 employed approach (Kocovsky et al., 2009; Nunn and Cowx, 2012). A serious weakness with scoring and
64 ranking is that barriers are considered independently. This can lead to a highly inefficient set of barriers
65 being selected for mitigation (O'Hanley and Tomberlin, 2005). Optimization models, by comparison, provide
66 an objective framework for decision making that guarantees maximum benefit given available resources.
67 Coordinated planning is achieved (unlike with scoring and ranking) by considering the spatial relationships
68 among barriers (i.e., their upstream/downstream positions) and the interactive effects that multiple barrier
69 mitigation actions have on longitudinal connectivity.

70 In this paper, we present a novel optimization framework for cost-effectively targeting the mitigation of fish
71 passage barriers in order to maximize resident fish species richness. Given the availability of fish survey
72 data, statistical regression methods are used to capture relationships between fish species richness and river
73 connectivity and then integrated into the optimization framework. We demonstrate the utility of our modeling
74 approach with a case study of the River Wey located in south-east England. To estimate barrier passability
75 quickly and at low cost, we further outline a rapid barrier assessment methodology. Although designed for

76 fish common to the UK, the methodology can be readily adapted to other planning areas and for other species
77 of interest. We anticipate the techniques presented in this paper will be of direct use to practitioners involved
78 in watershed management.

79 A number of features set our current model apart from barrier optimization models already proposed in the
80 literature. For example, most existing models (Paulsen and Wernstedt, 1995; Kuby et al., 2005; O’Hanley
81 and Tomberlin, 2005; Zheng et al., 2009; King and O’Hanley, 2016) are designed exclusively to facilitate
82 passage of diadromous fish (e.g., salmon), which travel upstream from the sea into freshwater. This simplifies
83 the modeling process in that the only dispersal paths that need to be considered are those from the river
84 mouth to areas located above barriers. Our model, in contrast, focuses on potamodromous (aka resident)
85 species fish, which exhibit more complex migration patterns involving internal movements from one area of
86 a river network to another. The only existing studies dealing with resident fish dispersal to our knowledge
87 are O’Hanley (2011) and O’Hanley et al. (2013b). Specifically, O’Hanley (2011) maximizes the single largest
88 subsection of river unimpeded by barriers to promote undirected fish dispersal, while O’Hanley et al. (2013b)
89 maximize river habitat connectivity according to the C metric proposed by Diebel et al. (2015), which
90 accounts for the quality and accessibility of different river habitat types as well as travel distances between
91 habitat areas. In the latter, dispersal paths between each and every pair of habitat patches are considered.

92 The most notable aspect of our model is the integration of statistical methods for the purpose of quantifying
93 river connectivity impacts on fish species richness. This adds a degree of sophistication not normally seen with
94 barrier optimization methods. The standard (simpler) approach is to maximize some form of habitat metric,
95 as with O’Hanley (2011) or O’Hanley et al. (2013b). Two notable exceptions to the use of habitat metrics are
96 Paulsen and Wernstedt (1995) and Zheng et al. (2009). Paulsen and Wernstedt (1995) propose a framework
97 for selecting barrier mitigation and other in-stream habitat restoration actions at minimum cost which satisfy
98 defined escapement and harvesting goals. Zheng et al. (2009), meanwhile, optimize multiple ecological and
99 socioeconomic outcomes of dam removal, including fish productivity gains, adjusted fish biomass ratios,
100 dam removal costs, and invasive species management costs. In both studies, impacts of barrier mitigation
101 actions on fish abundance and community composition are modeled using complex population/ecosystem
102 simulations. Simulation models normally require detailed knowledge of habitat use, demographic rates, and
103 dispersal characteristics. This limits their applicability in most real-world settings, where reliable data of
104 this kind are usually scarce or nonexistent.

105 Our proposed model strikes a good balance between realism and complexity. Maximizing species richness
106 ostensibly has the advantage of being a more ecologically informed and managerially relevant planning goal.
107 At the same time, data requirements are rather modest (i.e., the availability of fish survey data and wide-area

108 geographic information system data). Moreover, unlike the afore mentioned simulation-optimization based
109 approaches, our proposed framework remains highly scalable and computationally efficient, meaning that
110 problems involving large number of barriers still be solved relatively quickly.

111 In what follows, our aim is to give details of the proposed barrier optimization modeling framework, including
112 a formal mathematical formulation of the problem, basic data needs, key statistical analyses required to
113 parametrize the model, and an overview of the rapid barrier assessment protocol. For demonstration purposes,
114 we use a case study of the River Wey catchment. This helps to achieve are second major aim, which is to
115 show how our approach can be used to support smarter and more effective river barrier mitigation planning.

116 **Materials and Methods**

117 **Case Study Background**

118 The River Wey, located in the south-east of England, is a tributary to the River Thames and covers an area
119 of approximately 900km² (Figure 1). The Wey is comprised of two main tributaries that meet approximately
120 15km to the west of Guildford and flows into the non-tidal portion of the Thames at Weybridge. There
121 are three operational canal systems within the catchment: the Wey Navigation (between Guildford and
122 Weybridge), the Godalming Navigation (between Guildford and Godalming), and Basingstoke Canal (heading
123 west from Weybridge). Agriculture is the principal land-use in the south and west of the catchment, while
124 the north is primarily urban (EA, 2008a).

125 The Environment Agency (EA) is the main public body in England with responsibility for managing river
126 ecosystems. The EA's Fisheries Action Plan for the Wey catchment has identified the presence of physical
127 obstructions as a key pressure on fish diversity and abundance (EA, 2008b). An inventory of barriers within
128 the main reaches of the River Wey was prepared by merging three existing datasets:

- 129 1. The EA's obstruction database EA (2010b) containing natural and anthropogenic barriers across Eng-
130 land and Wales, including waterfalls, dams, weirs, sluices, and locks (but not culverts).
- 131 2. The National Flood and Coastal Defense Database (NFCDD), a catalog of weirs, sluice gates, locks,
132 and culverts.
- 133 3. Cross sections and longitudinal profiles of river reaches with labeled structures, including weirs and
134 culverts (provided by the EA).

135 In total, 805 barriers were identified, including weirs, dams, sluices, culverts, locks, fords, bridge aprons,
136 mills, and cascades. The location of each barrier was subsequently matched to the EA's detailed river
137 network (DRN) using standard geographic information system (GIS) procedures.

138 To rationalize the river network for the River Wey catchment, all watercourses identified as a drain on
139 the DRN were removed given their likely low ecological value.¹ Additionally, where man-made channels
140 introduced braids into the system, these were terminated immediately before rejoining the main river stem
141 in order to maintain a dendritic structure (Campbell Grant et al., 2007). Following these adjustments, the
142 final barrier dataset employed in the analysis comprised 1,160km of waterway with 669 artificial and natural
143 barriers (Figure 1).

144 **Rapid Barrier Assessment**

145 A coarse resolution rapid barrier assessment methodology for the UK that is suitable for multiple fish species
146 and considers both up and downstream dispersal was devised by Kemp et al. (2008). This was later revised,
147 following field trials, by the Scotland and Northern Ireland Forum for Environment Research (SNIFFER,
148 2010). The assessment method uses rule based criteria for fish morphology, behavior, and swimming and
149 leaping ability to estimate barrier passability. Barrier passability represents the fraction of fish (in the range
150 0 to 1) that are able to successfully negotiate a given barrier in the upstream or downstream directions. Each
151 barrier is assigned one of four passability levels as follows: 0 is a complete barrier to movement; 0.3 is a high
152 impact partial barrier, passable to a small proportion of fish or passable only for short periods of time; 0.6 is
153 a low impact partial barrier, passable to a high proportion of fish or for long periods of time; and 1 is a fully
154 passable structure. Partial barriers are often created by fluctuating river discharge, which causes variation in
155 water depth and velocity at the barrier, thereby impeding large fish at low flows or individuals with a weaker
156 swimming performance at high flows. The methodology described in SNIFFER (2010) was used to evaluate
157 adult brown trout (*Salmo trutta*) passability for a sample ($n = 63$) of the 669 barriers in our dataset based
158 on a combination of in-field measurements and photographic analysis. Criteria used to assign upstream and
159 downstream barrier passabilities are shown in Tables 1 and 2, respectively.

160 A remote based screening method was subsequently performed to identify any impassable structure. Hy-
161 draulic head data were extracted from the NFCDD and leveling surveys and used to determine which struc-
162 tures had head heights exceeding the 1m leaping ability of adult brown trout. Stepped weirs were also
163 assumed to be impassable unless the total head height was less than 1m and the effective width was less
164 than 2m (i.e., passable in a single leap). This was based on the finding that all stepped weirs surveyed in

¹Drains include any watercourse identified as a ditch, reen, rhyne, or drain on Ordnance Survey maps or by local EA staff.

165 the field had pool depths that were too shallow to allow adult brown trout to leap from one step to another.
166 In all, 93 barriers were designated as impassable in the upstream direction due to excessive height or width
167 and assigned an upstream passability score of 0. Navigation locks ($n = 35$) are not currently included in the
168 rapid barrier assessment method due to limited research into their effects on fish migration. For our study, a
169 provisional score of 0.3 was assigned to locks in each direction as they normally lack attraction flow and can
170 remain empty for long periods of time. Their use without specific alterations to accommodate fish passage
171 is thought to be largely accidental (Travade and Larinier, 2002). For all remaining barriers ($n = 478$), up-
172 stream/downstream passability was set to the median value of the same structural type. A cursory analysis
173 showed relatively little variation in passability for barriers of a given structural type.

174 **Fish Survey Dataset**

175 The EA completed 145 fish surveys within the River Wey catchment between October 1989 and October 2011
176 as part of ongoing monitoring. Surveys were completed using electrofishing methods. The average length
177 and area of river surveyed was approximately 120 m and 1,000 m², respectively. In total, 22 different species
178 were identified, with an average of around 6 species and 96 individual fish identified per survey event.

179 All surveys in which one or zero fish species were recorded were removed from the dataset on the basis
180 that such observations were due to sampling error, a temporal phenomenon, or indicative of highly localized
181 pressures (e.g., pollution). In addition, all observations prior to 2002 (i.e., those from 1989, 1990, and 1991)
182 were excluded in order to maintain a contemporary set of sampling data. This resulted in a final dataset of
183 121 survey observations spread across 29 locations (river reaches) to investigate the significance of subnetwork
184 connectivity on species richness in the River Wey.

185 **Habitat Connectivity**

186 Formally, the area upstream of a barrier up to the next set of barriers or river terminus is termed a river
187 *subnetwork*. Assuming that a river never diverges as it flows downstream (i.e., has a tree structure), each
188 subnetwork can be identified by its bounding downstream barrier. Subnetwork A in Figure 2a, for example,
189 is formed by the section of river between barriers A, B, and C.

190 In what follows, we take the overall passability p_j of a given barrier j (i.e., its *bidirectional* passability) as
191 the product of the barrier's upstream and downstream passabilities. With respect to barrier B shown in
192 Figure 2a, if passability in the upstream direction is 0.5 and passability in the downstream direction is 0.8,
193 then $p_B = 0.5 \times 0.8 = 0.4$. The *cumulative passability* z_{jk} between an origin subnetwork j and destination

194 subnetwork k is equal to the product of all barrier passability values along the shortest path from subnetwork
 195 j to k . Cumulative passability is analogous to the notion of longitudinal connectivity, specifically between
 196 the origin and destination subnetworks of a given route. For instance, fish wanting to access habitat in
 197 subnetwork D starting from subnetwork C (Figure 2a) must negotiate barriers C, B, and D. Consequently,
 198 cumulative passability z_{CD} for this path is the product of the bidirectional passabilities of those three barriers
 199 (i.e., $z_{CD} = 0.3 \times 0.4 \times 0.2 = 0.024$).

200 With this in place, we use the C metric proposed by Diebel et al. (2015) to describe overall habitat connectivity
 201 within a watershed. Unlike simpler connectivity metrics (e.g., DCIP), the C metric takes into account access
 202 to different types of habitat (e.g., spring spawning in headwaters, summer feeding in mid-order streams, and
 203 over-wintering in larger rivers or lakes). Using the notation provided in Table 3, the C metric is constructed
 204 by first determining the total availability A_{jh} of habitat type h accessible from a given river subnetwork j as
 205 follows:

$$A_{jh} = \sum_{k \in J} D_{jk} v_{kh} z_{jk}$$

206 where cumulative passability is calculated as $z_{jk} = \prod_{\ell \in B_{jk}} p_{\ell}$, the product of all barrier passabilities along
 207 the path from subnetwork j to k . The baseline availability A_{jh}^0 of habitat type h accessible from subnetwork
 208 j assuming no barriers exist in the river network is similarly defined as:

$$A_{jh}^0 = \sum_{k \in J} D_{jk} v_{kh}$$

209 The term D_{jk} employed in the calculation of A_{jh} and A_{jh}^0 represents a distance decay factor for the journey
 210 between subnetworks j and k and is given by:

$$D_{jk} = \frac{1}{1 + \left(\frac{d_{jk}}{d_0}\right)^2}$$

211 The connectivity C_j for a given subnetwork j can then be calculated using the ratios of available and baseline
 212 habitat across all habitat types h or more specifically:

$$C_j = \frac{1}{m} \sum_{h=1}^m \frac{A_{jh}}{A_{jh}^0} \tag{1}$$

213 Note that in order to account for all habitat within a river system (specifically the stretch of river below the
 214 first set of barriers), a “dummy” barrier with passability equal to 1 must be introduced at the river mouth if
 215 no such structure exists (e.g., barrier M in Figure 2a). Accordingly, this results in a total of $\frac{n(n-1)}{2}$ unique
 216 subnetwork-to-subnetwork paths, where n is the total number of artificial/natural barriers present plus the
 217 dummy barrier.

218 Barrier Optimization Model

219 The aim of our model is to select barriers for repair or removal (i.e., mitigation) in order to maximize mean
 220 resident fish richness within a given study area. We assume that fish species richness R_j within a subnetwork
 221 j is determined, at least in part, by its connectivity status C_j . Given the availability of sufficient fish survey
 222 and potentially other relevant environmental data, the relationship between fish species richness R_j and
 223 connectivity C_j can be estimated empirically using standard statistical regression techniques.

224 We further assume that multiple mitigation options (e.g., removal, replacement, installing a fish pass, fitting
 225 baffles) may be available at any given barrier, which vary in terms of cost and passability improvement,
 226 but that only one of these can be implemented. In most practical situations, mitigation is restricted to
 227 artificial barriers (i.e., natural barriers like waterfalls cannot be mitigated). Besides producing an increase in
 228 passability, barrier mitigation potentially serves to increase the cumulative passability of each route passing
 229 through a treated barrier and, in turn, an increase in both the connectivity status C_j and fish species richness
 230 R_j of each river subnetwork. Lastly, there is assumed to be a budget b , which limits the total expenditure
 231 on river barrier mitigation actions.

232 To formalize this, we let p_j^0 denote the initial bidirectional passability of barrier j . The set of mitigation
 233 projects available at barrier j is given by S_j and indexed by i . Implementation of mitigation project i at
 234 barrier j costs an amount c_{ji} and results in an increase in passability of p'_{ji} . We also introduce the following
 235 decision variables.

$$x_{ji} = \begin{cases} 1 & \text{if mitigation project } i \text{ is implemented at barrier } j \\ 0 & \text{otherwise} \end{cases}$$

z_{jk} = cumulative passability between origin subnetwork j and destination k

C_j = connectivity status of river subnetwork j

R_j = mean fish species richness of river subnetwork j

236 With this in place, a nonlinear formulation of our optimization model is given below.

$$\max \frac{1}{V} \sum_{j \in J} v_j R_j \quad (2)$$

s.t.

$$R_j = f(C_j, \boldsymbol{\pi}_j) \quad \forall j \in J \quad (3)$$

$$C_j = \sum_{k \in J | k < j} w_{jk} z_{kj} + \sum_{k \in J | k \geq j} w_{jk} z_{jk} \quad \forall j \in J \quad (4)$$

$$z_{jk} = \prod_{\ell \in B_{jk}} \left(p_\ell^0 + \sum_{i \in S_\ell} p'_{\ell i} x_{\ell i} \right) \quad \forall j, k \in J | k \geq j \quad (5)$$

$$\sum_{i \in S_j} x_{ji} \leq 1 \quad \forall j \in J \quad (6)$$

$$\sum_{j \in J} \sum_{i \in S_j} c_{ji} x_{ji} \leq b \quad (7)$$

$$x_{ji} \in \{0, 1\} \quad \forall j \in J, i \in S_j \quad (8)$$

237 In the above model, the objective function (2) maximizes habitat weighted fish species richness across all
 238 subnetworks in the river system. Parameter $V = \sum_{j \in J} v_j$ is the total amount of habitat within the study
 239 area. Equations (3) specify that species richness R_j within a given subnetwork j is assumed to be some
 240 function $f(\cdot)$ of connectivity status C_j along with a set of additional environmental covariates $\boldsymbol{\pi}_j$ influencing
 241 species richness. Connectivity status C_j for any subnetwork j is determined by equations (4), where:

$$w_{jk} = \frac{1}{m} D_{jk} \sum_{h=1}^m \frac{v_{kh}}{A_{jh}^0}$$

242 Assuming that cumulative passability between subnetworks j and k is symmetric (i.e., $z_{jk} = z_{kj}$), it is
 243 straightforward to show that equations (1) and (4) provide equivalent expressions of the C metric. We also
 244 point out that other connectivity metrics could be used in place of the C metric. For example, the popular
 245 DCIP metric of Cote et al. (2009) computed at the individual subnetwork scale (referred to as DCIs by
 246 Mahlum et al., 2014b) could just as easily be integrated into our model by redefining parameter $w_{jk} = \frac{v_k}{V}$.

247 To continue, constraints (5) determine the cumulative passability z_{jk} between subnetworks j and k . This is
 248 equal to the product of all intervening barrier passabilities, where the passability of any barrier ℓ along the
 249 route is equal to initial passability p_ℓ^0 plus the increase in passability $p'_{\ell i}$ if mitigation project i is carried out

250 at the barrier (i.e., $x_{\ell i} = 1$). Constraints (6) ensure only one mitigation project i can be carried out at barrier
 251 j . This prevents the model from nonsensically selecting multiple types of mitigation for any given barrier
 252 (e.g., a barrier cannot be “repaired” and “removed” at the same time). Inequality (7) is the budget constraint,
 253 which stipulates that the total cost of barrier mitigation actions cannot exceed the available budget b . Lastly,
 254 constraints (8) impose binary restrictions on the x_{ji} barrier mitigation decision variables.

255 As detailed in the statistical analysis subsection below, rather than directly estimate species richness R_j , we
 256 employed the following model to evaluate the expected number of “missing” or absent species in subnetwork
 257 j .

$$\bar{R}_j = \exp(\beta'_j + \beta_1 C_j) \quad \forall j \in J \tag{9}$$

258 Equations (9) derive from the use of a generalized Poisson regression model, where β_1 is the coefficient for
 259 connectivity status C_j and β'_j is a parameter that aggregates the constant and other explanatory variables
 260 for species absence \bar{R}_j in subnetwork j . Expected species richness can, in turn, be determined by replacing
 261 equations (3) with:

$$R_j = R^{\max} - \bar{R}_j \quad \forall j \in J \tag{10}$$

262 where R^{\max} represents the total number of species found within the study area.

263 Note that inclusion of equations (9) invariably results in a nonlinear model, as does the multiplication of
 264 the x_{ji} decision variables in equations (5). Nonlinear optimization models are notoriously difficult to solve.
 265 Rather than resort to developing a heuristic or rely on some other specialized solution method, a preferable
 266 option, as recommended by O’Hanley (2009), is to try to linearize the problem. In an appendix (see Appendix
 267 S1 in Supporting Information), we first show how (5) can be transformed to into an equivalent set of linear
 268 constraints using the probability chain method of O’Hanley et al. (2013a). We subsequently detail an approach
 269 for approximating equations (9) as a piece-wise linear curve.

270 For our River Wey case study, the net amount of habitat in each subnetwork (v_j) was characterized as the
 271 net length of stream above a barrier up to the next set of barriers or the river terminus. Only a single habitat
 272 type was considered (i.e., $m = 1$) as over 75% of river stretches in the Wey are classified as primary river
 273 in the DRN. The dispersal distance for fish (d_0) was assumed to be 7.5km based on a preliminary analysis
 274 showing good statistical fit between species richness and the level of connectivity for this distance.

275 In total, there were 650 artificial barriers (out of the 669 total) that had bidirectional passabilities less than
276 1 and, therefore, were considered as candidates for mitigation action. For each of these barriers, a single
277 mitigation project was considered. Barriers outside the middle and lower reaches of the main river stem and
278 navigation sections were considered suitable candidates for complete removal, thereby restoring full passability
279 in both directions (i.e., $p'_j = 1 - p_j^0$) at those locations. Such barriers are typically small, so there is generally
280 little conflict or opportunity cost associated with their removal. Barriers associated with the middle and
281 lower reaches of the main river stem were not considered suitable for removal due to the adverse effect on
282 navigation in this part of the system. These barriers were considered candidates for the provision of fish
283 passes. Fish passes were assumed to increase upstream passability to 0.75 and restore full passability in the
284 downstream direction (i.e., $p'_j = 0.75 - p_j^0$). In our analysis, it was assumed that bidirectional passability at
285 locks could be increased to 0.65 via investment in more regular or improved operations (i.e., $p'_j = 0.65 - p_j^0$).
286 The costs of barrier mitigation were estimated on the basis of costs provided by the River Restoration Council
287 (pers. comm.) for work at similar structures and from information published by the EA (EA, 2010a). The
288 cost of mitigating all 650 candidate barriers within the River Wey was estimated to be £53,355,000.

289 The barrier optimization model was coded in the OPL modeling language using CPLEX studio version 12.5
290 (IBM, 2013). CPLEX is a state-of-art commercial software package that employs branch-and-cut methods
291 to solve mixed integer linear programs (MILPs). All experiments were run on the same dual-core Toshiba
292 Satellite Pro R850-15F laptop (Intel i3 processor, 2.10 GHz per chip) with 8GB of RAM.

293 Species Richness Statistical Analysis

294 To parametrize our optimization model, it is necessary to estimate the magnitude and confirm the significance
295 of the effect of subnetwork connectivity on fish species richness. In the analysis that follows, we investigate the
296 significance of the C metric in determining fish species absence (the complement to species richness) using
297 the fish survey dataset for the River Wey described above. Estimation of species absence (\bar{R}_j) produced
298 better fitting models than those in which species richness (R_j) was used as the dependent variable.

299 Our *a priori* expectation is that fish species absence is influenced by both subnetwork connectivity and size,
300 with the later being quantified as the square root of total upstream river length ($\sqrt{USL_j}$). We also include
301 dummy variables for time in the estimation procedure to control for temporal variation across survey years
302 and to increase the accuracy of the parameter estimates. Consequently, our theoretical model of species
303 absence for the River Wey takes the following form.

$$\log_e(\bar{R}_j) = \beta_0 + \beta_1 C_j^0 + \beta_2 \sqrt{USL_j} + \sum_{t=1}^T \beta_{2+t} year_{jt} \quad (11)$$

304 In the above equation, variable \bar{R}_j is the expected number of unobserved species during a survey event, β_0 is
 305 a constant, C_j^0 is the current connectivity status of subnetwork j with associated parameter β_1 , and $year_{jt}$,
 306 $t = 1, \dots, T$, are a series of dummy variables for the year fish surveys were undertaken (T being the total
 307 number of years) with associated parameters β_{2+t} .

308 We employ a Poisson regression model, rather than ordinary least squares (OLS), given the discrete nature
 309 of the dependent variable \bar{R}_j and the fact that it is not normally distributed. A good summary of Poisson
 310 regression is provided in Green (2008). The theoretical model specified in equation (11) was estimated using
 311 the LIMDEP version 10 software package (Green, 2012). To avoid the restriction of equal mean and variance
 312 (equidispersion), we rely on the generalized Poisson modeling approach proposed by Consul and Jain (1973).
 313 This generalized model relaxes the assumption of equidispersion by allowing the variance for the distribution
 314 of the dependent variable to be characterized as a function of the regression mean and an associated scaling
 315 factor θ . In adopting a generalized Poisson model, the regression equation for estimating species absence \bar{R}_j
 316 takes on the basic form given by (9), where $\beta'_j = \beta_0 + \beta_2 \sqrt{USL_j} + \sum_{t=1}^T \beta_{2+t} year_{jt}$.

317 Results

318 Regression Model Results

319 Results of the fish species richness statistical analysis are summarized in Table 4. The dummy variables for
 320 survey years are omitted from the table as their inclusion was purely to control for temporal variation. A
 321 conventional OLS regression reveals that approximately half the variation observed in missing fish species
 322 count \bar{R} is explained by the model ($R^2 = 0.46$) and that the key explanatory variables are significant at
 323 the 1 to 5% level. For the preferred generalized Poisson regression, the scale parameter θ is negative and
 324 significant at the 1% level, confirming underdispersion of the data. The likelihood ratio test confirmed that
 325 the explanatory variables are jointly significant at the 1% level. More importantly, the coefficient for variable
 326 C^0 (parameter β_1) is significant at the 1% level. This estimate is not directly comparable to the OLS estimate
 327 as it represents the effect on $\log_e(\bar{R})$ of a one unit increase in C^0 . However, a comparable *partial* effect (i.e.,
 328 local gradient) can be calculated for C^0 by evaluating the effect this variable has on the expected value of
 329 \bar{R} by fixing each independent variable at its mean within the sample data. These results are reported in the

330 final column (dy/dx) of Table 4. The partial effect of -14.28 for C^0 is significant at the 5% level. Besides
331 being close to the OLS estimate of -12.73, its magnitude indicates that potentially large reductions (gains)
332 in species absence (richness) can be achieved with increased connectivity.

333 Optimization Model Results

334 Gains in mean species richness within the River Wey produced by the barrier optimization model are shown
335 in Figure 3. An overall pattern of diminishing returns is observed, whereby increases in species richness
336 become progressively smaller with increased budget. Given a budget of just £5M, for example, mean richness
337 can increase by roughly 2.3 above the baseline value of 5.2 fish species. This represents close to a 50% increase
338 in species diversity. To achieve nearly a doubling in species richness, however, requires a four-fold increase
339 in the budget (i.e., £20M for an increase of 5.0 in species richness).

340 The spatial distribution of species richness for these two solutions as well as the baseline (£0 budget) are
341 shown in Figure 4. At present (£0 budget), middle and lower portions of the River Wey are predicted to have
342 comparatively higher richness (7-10 species), particularly along main stem river segments. Richness in most
343 of the upper reaches is quite low (2-4 species), in part because of their smaller size but mostly do to limited
344 connectivity. This is evident by looking at the species richness maps for the £5M and £20M solutions. Initial
345 gains in species richness are primarily seen first in the upper reaches (£5M), followed by gains in the middle
346 to lower sections of the river catchment (£20M).

347 In Table 5, we examine some of the basic characteristics of barriers that were selected for mitigation by our
348 model. Dams/weirs and culverts are the dominant types of barriers in the Wey system, comprising 265 and
349 268, respectively, out of the 650 total candidate barriers. In spite of being roughly equally common, however,
350 we find that dams/weirs are targeted for mitigation action much more often than culverts at lower budgets
351 (\leq £25M). For instance, 57 structures are targeted for mitigation at a budget of £5M, 37 (65%) of which are
352 dams/weirs but only 13 (23%) of which are culverts. No locks and relatively few screens are selected at lower
353 budget levels. Locks, in fact, are almost never selected until the budget is large enough to remove nearly
354 all barriers. Meanwhile, sluices and “other” barriers are comparatively over represented at lower budgets.
355 Sluices and “other” barriers, for example, make up just 6% and 2% of all barriers, respectively, but account
356 for 10% and 5% of selected barriers at the £20M budget.

357 Inspection of Table 5 further reveals that barriers on high order streams to be high priority targets. At
358 a budget of £5M, almost no barriers on order 1-2 streams are selected. Even when the budget reaches as
359 high as £25M, just 14% of selected barriers are located on order 1-2 streams. Figure 5, which displays the

360 £5M and £15M solutions spatially, shows that many of the barriers selected for mitigation are also in areas
361 with high degrees of bifurcation, notably in the central portion of the river network between Weybridge and
362 Guildford where several tributaries converge. In contrast, areas with limited bifurcation (e.g., to the west of
363 Guildford and along stretches of river from Alton to Farnham) are not selected for mitigation.

364 Given all this, it comes as little surprise that barriers targeted for mitigation at lower budget levels (\leq £25M)
365 tend to be large (\geq 1m head height), have lower than average initial passability, and are generally more costly
366 to mitigate compared to barriers as a whole. These characteristics are all typical of barriers located on high
367 order streams. Looking at Table 5, 43% of all large barriers are selected at a budget of £15M. Average
368 passability of selected barriers is 0.10, slightly less than the overall average of 0.12. Further, the average cost
369 of selected barriers is £98k, which is significantly higher than the £82k average for all barriers.

370 A final observation that can be made with respect to Table 5 is that at lower budget levels, the optimization
371 model targets barriers with large upstream subnetworks. For example, the average length of river immediately
372 above selected barriers (Net USL) goes from 7.5km at a budget of £5M to 3.3km at a budget of £25M. The
373 average subnetwork size, in contrast, is only 1.7km. This suggests that at lower budget amounts, a simple
374 rule of thumb may be to sequentially mitigate the barrier obstructing access between the two largest adjacent
375 subnetworks until the budget is expended.

376 Discussion

377 The presence of river barrier infrastructure across the world has substantially reduced the longitudinal, lateral,
378 and even vertical connectivity of fluvial ecosystems (Nilsson et al., 2005; Grill et al., 2015). The negative
379 impacts that artificial barriers have on fish populations are well-known (Stanford et al., 1996; Bednarek, 2001;
380 Pringle, 2003). There is now increasing interest amongst ecologists, river managers and policy makers to
381 remove or otherwise mitigate these barriers in order to improve the ecological integrity of river environments.
382 In this paper, we present a toolkit for the rapid assessment and cost-effective prioritization of resident fish
383 passage barriers to restore longitudinal connectivity.

384 A large number of barrier passability assessment methods have been developed (Taylor and Love, 2003;
385 WDFW, 2009; Gargan et al., 2011). Despite the varied impact that structures can have on different fish
386 (Ovidio and Philippart, 2002; MacPherson et al., 2012), few methodologies account for multiple species and
387 structure types and even fewer consider downstream movements (Kemp and O’Hanley, 2010). The rapid
388 barrier assessment methodology proposed in SNIFFER (2010) and used in the current study is an exception.
389 We apply this methodology on a catchment scale and demonstrate its potential in helping to prioritize barrier

390 mitigation work.

391 Although the passability values generated relate to flow conditions at the time of surveying, this compromise
392 is necessary to create a rapid assessment tool for maximizing the number of structures that can be surveyed
393 in the field. A good indication of barrier passability is obtained and more detailed surveys can be conducted
394 if necessary. For barriers surveyed in the field, a mean of 5.7 barriers were evaluated each day using two
395 surveyors and readily available equipment. Thus, the method can reduce the time and cost required to
396 inventory river barriers compared to more detailed surveys. In situations where the number of barriers to
397 be surveyed is prohibitive, a sampling procedure can be employed, as done in Januchowski-Hartley et al.
398 (2014), whereby a subset of barriers are assessed for passability and the data used to build regression models
399 for predicting passability at unsurveyed sites based on simple structural information combined with easy-to-
400 obtain remote sensing data.

401 In our case study, the rapid barrier assessment was used to assess passabilities for adult brown trout (*S.*
402 *trutta*). Normally, specification of a focal species can have a strong influence on the barrier prioritization
403 process. A barrier to one species or life-stage may not be a barrier to another. Indeed, trout can typically pass
404 barriers that fish with weaker swimming/jumping abilities cannot. This, in turn, can bias which barriers are
405 selected for repair/removal. With our modeling approach, the choice of a focal species is largely arbitrary. Our
406 main concern is overall species richness. To estimate this, a statistical analysis is performed to determine how
407 species richness correlates with the connectivity status of a chosen focal species. Using a different focal species
408 will invariably affect the raw level of connectivity being measured but only has a minor effect on predicted
409 fish species richness due to the high degree of correlation in connectivity status for different species. Indeed,
410 a statistical/optimization analysis using common carp (*Cyprinus carpio*) as the focal species (results not
411 shown) produced qualitatively similar findings.

412 It is also worth noting that while the barrier assessment methodology is based on up-to-date fisheries research,
413 it has not been validated against observed fish passage data. This is a common problem with most barrier
414 assessment methods, which requires further attention in the literature. Consequently, it is important to bear
415 in mind that inconsistencies between predicted and actual passability may lead to sub-optimal management
416 decisions with resulting economic and ecological costs (Mahlum et al., 2014a).

417 It is vital for barrier prioritization methods, if they are to be applied in the real world, that they be capable
418 of producing cost-effective solutions using easy to obtain data. Ideally, they should also be fairly easy
419 to implement, computationally efficient, and flexible in meeting different planning goals. In this regard,
420 the model we present here makes a valuable contribution to the growing literature on barrier optimization
421 methods. Specifically, we propose an efficient and scalable model that can be implemented using off-the-shelf

422 optimization software. The model is noteworthy for integrating statistical methods in order to maximize
423 gains in mean species richness across a watershed. In this regard, it provides a simplified way of focusing on
424 an ecologically relevant goal (species richness) without the need to integrate data hungry and computationally
425 intensive population/ecosystem simulation models (Paulsen and Wernstedt, 1995; Zheng et al., 2009).

426 We demonstrate the applicability of our barrier optimization model using a dataset of 669 fish passage barriers
427 from the River Wey in the UK. For the River Wey system, roughly a doubling in mean species richness can be
428 achieved with a mitigation budget of £20M. Investments above £30M may not be cost-effective; approximately
429 85% of potential ecological improvements (equivalent to 6.23 additional species on average) can be obtained
430 at this budget level. Beyond this point, one observes diminishing marginal returns. An analysis of the types
431 of barriers selected for mitigation action under different budget scenarios indicates that it is the larger, low
432 passability barriers located on mid to high order streams, particularly in areas of dense river branching, that
433 are prioritized for action in the River Wey system. These results are generally in line with Cote et al. (2009)
434 and O’Hanley et al. (2013b), which both found that it is the removal of barriers in the central portion of a
435 river network that usually yield the largest connectivity gains for resident fish. In the case of the Wey, these
436 barriers are far more likely to be dams/weirs, sluices, or “other,” rather than culverts, screens, or locks.

437 We believe that the methods presented here can be of direct use to decision makers involved in river ecosystem
438 management. The optimization model readily generates prescriptive solutions for barrier mitigation action
439 that maximize restoration gains given available resources. These solutions can, in turn, be implemented *in*
440 *toto* or form the basis for more detailed modeling and fine-tuning later on. This is a distinct advantage
441 compared to other barrier prioritization methods, such as scoring and ranking or graph theoretic approaches,
442 which are either highly inefficient or merely descriptive (i.e., solutions proposed by an analyst can be evaluated
443 but no recommended best course of action is provided).

444 Optimization models are especially useful for generating Pareto optimal trade-off curves, which reveal how
445 environmental improvements vary with different levels of investment. They can also be useful in driving
446 insightful economic analyses. For example, the economic benefit associated with barrier mitigation due to
447 improvements in mean fish species richness (or other biophysical attributes) can be fairly easily estimated us-
448 ing established non-market valuation techniques (Morrison and Bennett, 2004; MacDonald et al., 2011). This
449 suggests that our optimization model could be readily integrated into a bio-economic modeling framework
450 to determine optimal levels of investment in barrier mitigation. Often used in cost-benefit analysis studies
451 related to fisheries management (e.g., Adams et al., 1993), bio-economic models overlay economics with pop-
452 ulation modeling with the aim of assessing the monetary benefit of increased fish production derived from
453 proposed management interventions (e.g., changes in harvesting rules or habitat conservation/restoration

454 activities) relative to the cost of the proposed interventions. Given the increasing use of cost-benefit analysis
455 in environmental decision making, this is anticipated to be especially useful to government agencies involved
456 in river management and policy. Research is ongoing in this regard.

457 With regard to other lines of future research, the optimization models presented here could be extended in a
458 number of ways. For example, it is assumed in our model that the river network is strictly dendritic, meaning
459 that there is only a single direct path between any two subnetworks. Moving away from this assumption
460 would be useful, especially for the River Wey, which is heavily modified by man-made navigation channels
461 that result in a braided river structure. Another interesting pursuit might be to consider different functional
462 forms for describing the relationship between connectivity and fish species richness and then try to incorporate
463 this into an optimization model. It is likely, if the resulting formulations were to involve complex, nonlinear
464 functions, that specially designed heuristics would need to be developed to solve such problems.

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472 the paper.

473 **Data Accessibility**

474 Fish sampling data, barrier data, and OPL optimization model code used in used in this study are available
475 from the Dryad Digital Repository doi: 10.5061/dryad.46vf8 (King et al., 2016)

476 **References**

477 Adams, R., Berrens, R., Cerda, A., Li, H., P, K., 1993. Developing a bioeconomic model for riverine man-
478 agement: Case of the John Day River, Oregon. *Rivers* 4 (3), 213–226.

479 Bednarek, A. T., 2001. Undamming rivers: A review of the ecological impacts of dam removal. *Environmental*
480 *Management* 27 (6), 803–814.

481 Bourne, C., Kehler, D., Wiersma, Y., Cote, D., 2011. Barriers to fish passage and barriers to fish passage as-
482 sessments: The impact of assessment methods and assumptions on barrier identification and quantification
483 of watershed connectivity. *Aquatic Ecology* 45, 389–403.

484 Campbell Grant, E., Lowe, W., Fagan, W., 2007. Living in the branches: population dynamics and ecological
485 processes in dendritic networks. *Ecology Letters* 10 (2), 165–175.

486 Catalano, M. J., Bozek, M. A., Pellett, T. D., 2007. Effects of dam removal on fish assemblage structure and
487 spatial distributions in the Baraboo River, Wisconsin. *North American Journal of Fisheries Management*
488 27 (2), 519–530.

489 Consul, P., Jain, G., 1973. A generalization of the Poisson distribution. *Technometrics* 15 (4), 791–799.

490 Cote, D., Kehler, D. G., Bourne, C., Wiersma, Y. F., 2009. A new measure of longitudinal connectivity for
491 stream networks. *Landscape Ecology* 24 (1), 101–113.

492 Diebel, M., Fedora, M., Cogswell, S., O’Hanley, J. R., 2015. Effects of road crossings on habitat connectivity
493 for stream-resident fish. *River Research and Applications* 31 (10), 1251–1261.

494 EA, 2008a. The Wey catchment abstraction management strategy. Tech. rep., Environment Agency, Bristol,
495 UK.

496 EA, 2008b. The Wey Valley fisheries action plan. Tech. rep., Environment Agency, Bristol, UK.

497 EA, 2010a. Environment Agency fish pass manual. Bristol, UK.

498 EA, 2010b. Mapping hydropower opportunities and sensitivities in England and Wales: Final report. Tech.
499 rep., Environment Agency, Bristol, UK.

500 East, A., Pess, G., Bountry, J., et al., 2015. Large-scale dam removal on the Elwha River, Washington, USA:
501 River channel and floodplain geomorphic change. *Geomorphology* 228, 765–786.

502 Gardner, C., Coghlan, S., Zydlewski, J., Saunders, R., 2013. Distribution and abundance of stream fishes in
503 relation to barriers: Implications for monitoring stream recovery after barrier removal. *River Research and*
504 *Applications* 29 (1), 65–78.

505 Gargan, P. G., Roche, W. K., Keane, S., King, J. J., Cullagh, A., Mills, P., Keeffe, J. O., 2011. Comparison
506 of field- and GIS-based assessments of barriers to Atlantic salmon migration: A case study in the Nore
507 catchment, Republic of Ireland. *Journal of Applied Ichthyology* 27 (s3), 66–72.

508 Green, W., 2008. *Econometric Analysis*, 6th Edition. Pearson Prentice Hall, Upper Saddle River, New Jersey.

509 Green, W., 2012. LIMDEP version 10. Econometric Software, Inc., Plainview, New York.

510 Grill, G., Lehner, B., Lumsdon, A., MacDonald, G., Zarfl, C., Liermann, C., 2015. An index-based framework
511 for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple
512 scales. *Environmental Research Letters* 10, 015001.

513 IBM, 2013. IBM ILOG CPLEX Optimization Studio V12.5.1 documentation. [http://www-01.ibm.com/
514 support/knowledgecenter/SSSA5P_12.5.1/maps/ic-homepage.html](http://www-01.ibm.com/support/knowledgecenter/SSSA5P_12.5.1/maps/ic-homepage.html), accessed 16/11/2015.

515 Januchowski-Hartley, S., Diebel, M., Doran, P., McIntyre, P., 2014. Predicting road culvert passability for
516 migratory fishes. *Diversity and Distributions* 20 (12), 1414–1424.

517 Januchowski-Hartley, S. R., McIntyre, P. B., Diebel, M., Doran, P. J., Infante, D. M., Joseph, C., Allan,
518 D. J., 2013. Restoring aquatic ecosystem connectivity requires expanding inventories of both dams and
519 road crossings. *Frontiers in Ecology and the Environment* 11 (4), 211–217.

520 Kanehl, P., Lyons, J., Nelson, J., 1997. Changes in the habitat and fish community of the Milwaukee River,
521 Wisconsin, following removal of the Woolen Mills Dam. *River Research and Applications* 17 (2), 387–400.

522 Kemp, P. S., O’Hanley, J. R., 2010. Procedures for evaluating and prioritising the removal of fish passage
523 barriers: A synthesis. *Fisheries Management and Ecology* 17 (4), 297–322.

524 Kemp, P. S., Russon, I. J., Waterson, B., O’Hanley, J. R., Pess, G. R., 2008. Recommendations for a
525 "Coarse-Resolution Rapid-Assessment" methodology to assess barriers to fish migration and associated
526 prioritization tools - Final report. Tech. rep., Scottish Environment Protection Agency, Stirling, UK.

527 King, S., O’Hanley, J. R., 2016. Optimal fish passage barrier removal - Revisited. *River Research and Appli-
528 cations* 32 (3), 418–4289.

529 Kocovsky, P. M., Ross, R. M., Dropkin, D. S., 2009. Prioritizing removal of dams for passage of diadromous
530 fishes on a major river system. *River Research and Applications* 25 (2), 107–117.

531 Kuby, M. J., Fagan, W. F., ReVelle, C. S., Graf, W. L., 2005. A multiobjective optimization model for dam
532 removal: An example trading off salmon passage with hydropower and water storage in the Willamette
533 basin. *Advances in Water Resources* 28 (8), 845–855.

534 Liermann, C., Nilsson, C., Robertson, J., Ng, R., 2012. Implications of dam obstruction for global freshwater
535 fish diversity. *Bioscience* 62 (6), 539–548.

536 Lucas, M., Baras, E., 2001. Migration of freshwater fishes. Blackwell Science, Oxford, UK.

537 Lucas, M., Bub, D., Minh-Ho, J., Kyong, H., Masters, J., 2009. Availability of and access to critical habitats
538 in regulated rivers: Effects of low-head barriers on threatened lampreys. *Freshwater Biology* 54, 621–634.

539 MacDonald, D., Morrison, M., Rose, J., Boyle, K., 2011. Valuing a multistate river: The case of the River
540 Murray. *The Australian Journal of Agricultural and Resource Economics* 55, 374–392.

541 MacPherson, L. M., Sullivan, M. G., Foote, A. L., 2012. Effects of culverts of stream fish assemblages in the
542 Alberta foothills. *North American Journal of Fisheries Management* 32 (3), 480–490.

543 Mahlum, S., Cote, D., Wiersma, Y. F., Kehler, D., Clarke, K. D., 2014a. Evaluating the barrier assessment
544 techniques derived from FishXing software and the upstream movement of brook trout through road
545 culverts. *Transactions of the American Fisheries Society* 143 (1), 39–58.

546 Mahlum, S., Kehler, D., Cote, D., Wiersma, Y. F., Stanfield, L., 2014b. Assessing the biological relevance
547 of aquatic connectivity to stream fish communities. *Canadian Journal of Fisheries and Aquatic Sciences*
548 71 (12), 1852–1863.

549 Minor, E., Urban, D., 2007. Graph theory as a proxy for spatially explicit population models in conservation
550 planning. *Ecological Applications* 17 (6), 1771–1782.

551 Morrison, M., Bennett, J., 2004. Valuing New South Wales rivers for use in benefits transfer. *The Australian*
552 *Journal of Agricultural and Resource Economics* 48 (4), 591–611.

553 Nilsson, C., Reidy, C. A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world’s
554 large river systems. *Science* 308 (5720), 405–408.

555 Nunn, A., Cowx, I., 2012. Restoring river connectivity: Prioritizing passage improvements for diadromous
556 fishes and lampreys. *Ambio* 41, 402–409.

557 O’Connor, J., Duda, J., Grant, G., 2015. 1000 dams down and counting. *Science* 348 (6234), 496–497.

558 O’Hanley, J., 2009. Using the right tool to get the job done - Recommendations on the use of exact and
559 heuristics methods for solving resource allocation problems in environmental planning and management.
560 *Biological Conservation* 142 (4), 697–698.

561 O’Hanley, J. R., 2011. Open rivers: Barrier removal planning and the restoration of free-flowing rivers.
562 *Journal of Environmental Management* 92 (12), 3112–3120.

563 O'Hanley, J. R., Scaparra, P. M., Garcia, S., 2013a. Probability chains: A general linearization technique for
564 modelling reliability in facility location and related problems. *European Journal of Operational Research*
565 230 (1), 63–75.

566 O'Hanley, J. R., Tomberlin, D., 2005. Optimizing the removal of small fish passage barriers. *Environmental*
567 *Modelling and Assessment* 10, 85–98.

568 O'Hanley, J. R., Wright, J., Diebel, M., Fedora, M., Soucy, C., 2013b. Restoring stream habitat connectivity:
569 A proposed method for prioritizing the removal of resident fish passage barriers. *Journal of Environmental*
570 *Management* 125, 19–27.

571 Ovidio, M., Philippart, J. C., 2002. The impact of small physical obstacles on upstream movements of six
572 species of fish. *Hydrobiologia* 483, 55–69.

573 Paulsen, C., Wernstedt, K., 1995. Cost-effectiveness analysis for complex managed hydrosystems: An appli-
574 cation to the Columbia River basin. *Journal of Environmental Economics and Management* 28, 388–400.

575 Pringle, C., 2003. What is hydrologic connectivity and why is it ecologically important? *Hydrological Pro-*
576 *cesses* 17 (13), 2685–2689.

577 Roni, P., Beechie, T. J., Bilby, R. E., Leonetti, F. E., Pollock, M. M., Pess, G. R., 2002. A review of
578 stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest
579 watersheds. *North American Journal of Fisheries Management* 22 (1), 1–20.

580 SNIFFER, 2010. Trialling of the methodology for quantifying the impacts of obstacles to fish passage: Final
581 report, WFD111 Phase 2a. Tech. rep., Scotland & Northern Ireland Forum for Environmental Research,
582 Edinburgh, UK.

583 Stanford, J. A., Ward, J., Liss, W. J., Frissell, C. A., Williams, R. N., Lichatowich, J. A., Coutant, C. C.,
584 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research & Management*
585 12, 391 – 413.

586 Taylor, R. N., Love, M., 2003. Part IX: Fish passage evaluation at stream crossings. California Department
587 of Fish and Game, Sacramento.

588 Travade, F., Larinier, M., 2002. Fish locks and fish lifts. *Bulletin Francais De La Peche et de la Pisciculture*
589 364 (1), 102–118.

590 WDFW, 2009. Fish passage and surface water diversion screening assessment and prioritization manual.
591 Washington Department of Fish and Wildlife, Olympia, WA.

592 Wofford, J., Gresswell, R., Banks, M., 2005. Influence of barriers to movement on within watershed genetic
593 variation of coastal cutthroat trout. *Ecological Applications* 15 (2), 628–637.

594 Zheng, P. Q., Hobbs, B. F., Koonce, J. F., 2009. Optimizing multiple dam removals under multiple objectives:
595 Linking tributary habitat and the Lake Erie ecosystem. *Water Resources Research* 45 (12), W12417.

596 **Supporting Information**

597 Additional supporting information may be found in the online version of this article.

598 **Appendix S1.** Linearization of the barrier optimization model.

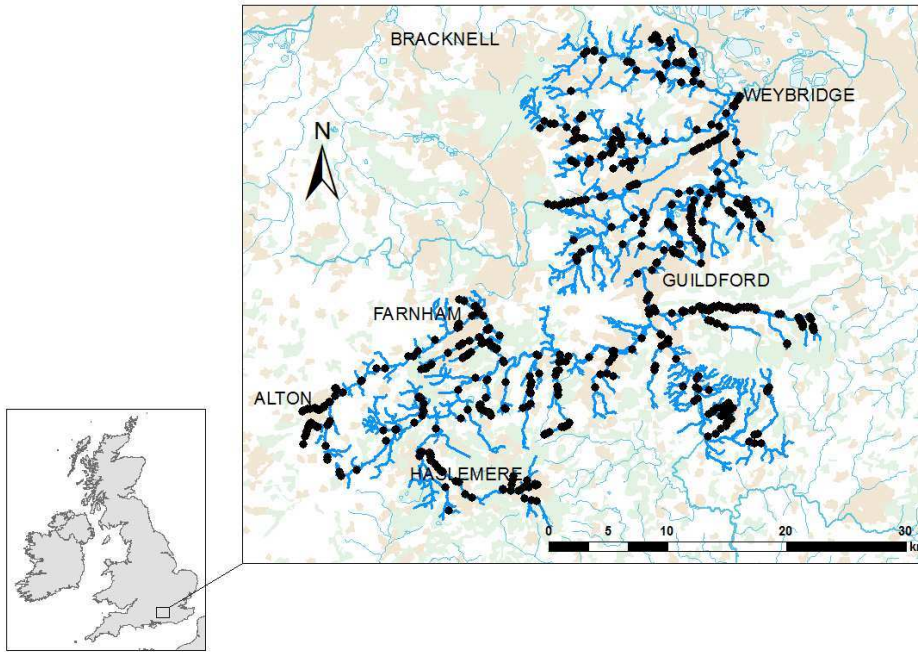


Figure 1: Location and extent of the River Wey catchment. Barriers are represented by black dots.

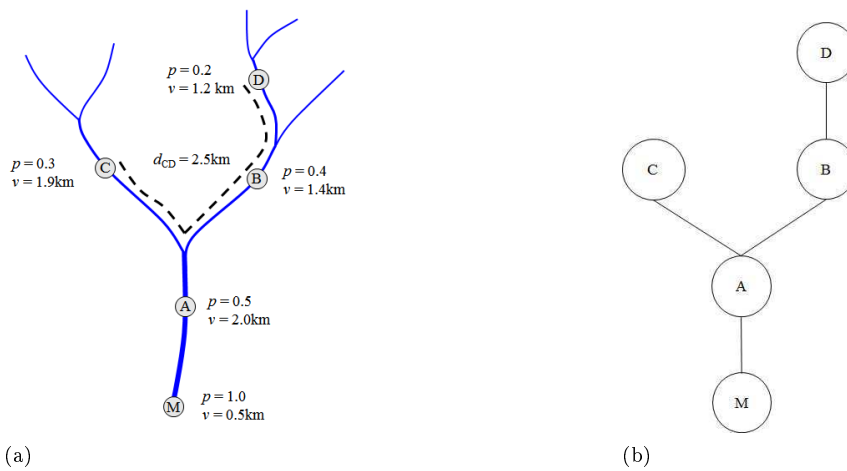


Figure 2: Example of a river barrier network represented spatially (a) and as an equivalent dendritic ecological network (DEN) (b). Note that barrier M is a dummy barrier located at the river mouth with initial passability 1 to ensure that all habitat in the river system is captured in the DEN. In (a), the bidirectional passability p of each barrier and the amount of river habitat v in the subnetwork above each barrier are provided. The value d_{CD} denotes the minimum distance from subnetwork C to D.

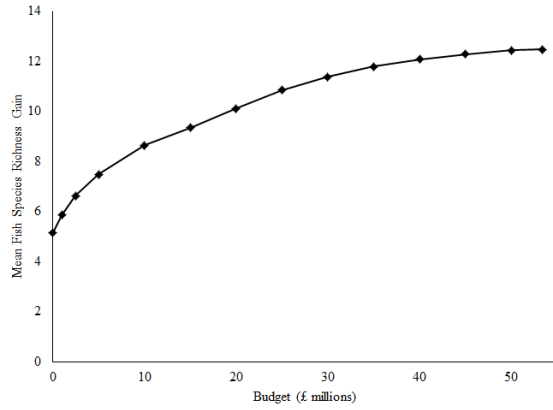
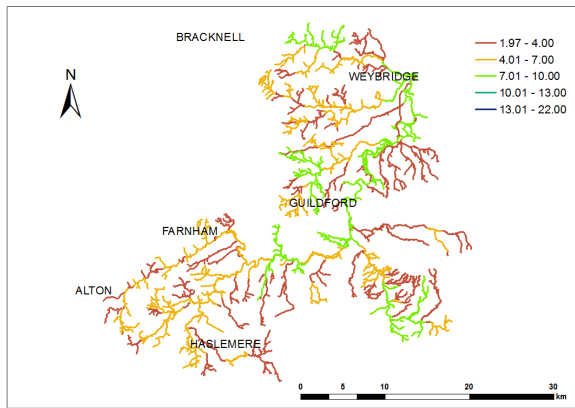
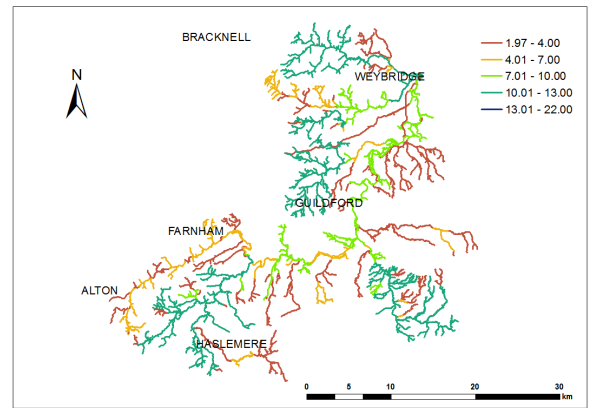


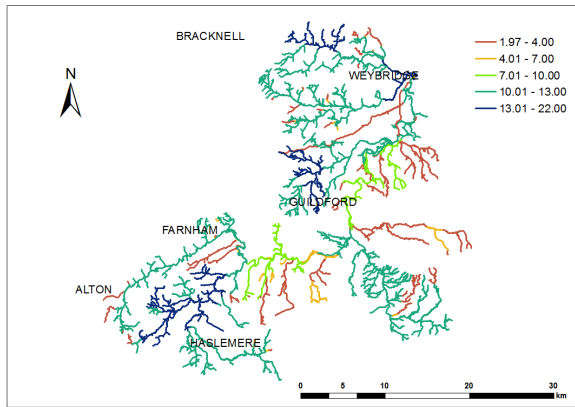
Figure 3: Mean species richness versus budget for the River Wey catchment.



(a)

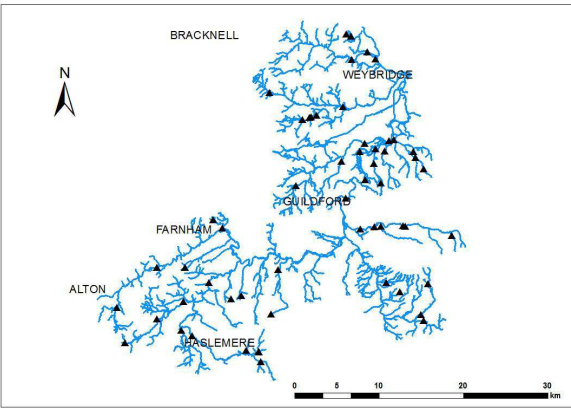


(b)

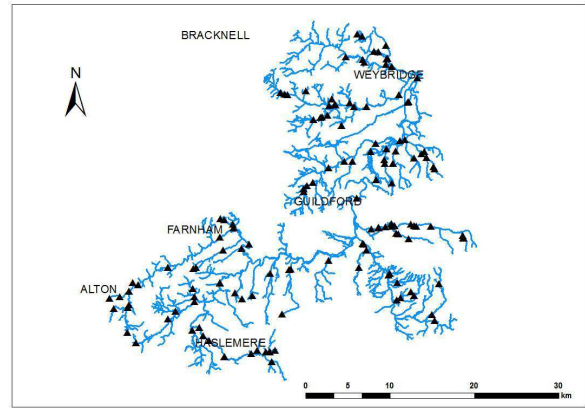


(c)

Figure 4: Distribution of species richness in the River Wey catchment at budgets of £0M (a), £5M (b), and £20M (c).



(a)



(b)

Figure 5: Barriers targeted for mitigation in the River Wey catchment at budgets of £5M (a) and £15M (b). Selected barriers are represented by black triangles.

600 **Tables**

601

Table 1: Barrier assessment criteria for assigning adult brown trout (*S. trutta*) upstream passability scores. Additional criteria used for determining passability scores not presented here include the availability of resting locations, level of turbulence, the presence of lips, standing waves, or debris, the gap width, and the minimum step length.

Assessment Criteria	Passability Score			
	1.0	0.6	0.3	0.0
All structures				
Water depth (m)	≥ 0.10	0.075 - 0.09	0.06 - 0.074	≤ 0.05
Velocity (m/s)	≤ 2	2.1 - 2.5	2.6 - 2.9	≥ 3
If leap barrier				
Hydraulic head (m)	≤ 0.40	0.41 - 0.60	0.61 - 0.99	≥ 1.0
Pool depth (% hydraulic head)	≥ 100	≥ 80	≥ 30	< 30
If slope/swim barrier				
Effective length (m)	≤ 10	11 - 30	31 - 99	≥ 100
Slope (%)				
If effective length $\leq 3m$	≤ 25	26 - 40	41 - 59	≥ 60
If effective length 4-9m	≤ 15	16 - 20	21 - 39	≥ 40
If effective length $\geq 10m$	≤ 5	6 - 10	11 - 14	≥ 15

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Table 2: Barrier assessment criteria for assigning adult brown trout (*S. trutta*) downstream passability scores. Hazards include the presence of any features damaging to downstream migrants.

Assessment Criteria	Passability Score			
	1.0	0.6	0.3	0.0
Crest/inlet water depth (m)	≥ 0.1	0.075 - 0.09	0.06 - 0.074	≤ 0.05
Minimum gap width (m)	> 0.3	0.20 - 0.30	0.10 - 0.19	< 0.10
Hazards	Not present		Present	
Debris	Unrestricted passage	Restricted passage		Prevents passage

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Table 3: Notation used in the C metric.

Symbol	Definition
J	Set of all natural and artificial barriers (aka subnetworks), indexed by j , k , and ℓ
m	The number of habitat types within the study area, indexed by h
v_{jh}	Amount of habitat type h in subnetwork j
v_j	Total amount of habitat in subnetwork j
p_j	Bidirectional passability of barrier j
B_{jk}	The set of barriers along the path from origin subnetwork j to destination subnetwork k
d_{jk}	Distance between subnetworks j and k
d_0	Dispersal distance of the focal fish species, taxa, guild, etc.

Table 4: Statistical model results for predicting fish species absence in the River Wey.

Parameter	OLS	Generalized Poisson	
	Est. (s.e.)	Est. (s.e.)	dy/dx (s.e.)
β_0	17.65 (0.90)**	2.89 (0.076)**	-
β_1	-12.73 (5.25)*	-0.93 (0.32)**	-14.28 (4.96)*
β_2	-0.0052 (6.2×10^{-4})**	-0.00037 (4.6×10^{-5})**	-0.0056 (6.7×10^{-4})**
θ	-	-0.035 (0.0025)**	
R ²	0.46	-	
pseudo-R ²	-	0.16	
AIC	510.6	509.6	

*Significant at the 5% level.

**Significant at the 1% level.

Table 5: Key attributes of barrier mitigation solutions at selected budget values. The column ‘‘All’’ provides a breakdown, by attribute, of the 650 artificial candidate barriers in the River Wey catchment. In the upper portion of the table, the number of selected barriers of a particular category is shown. The category ‘‘Other’’ comprises bridge aprons, mills, and a man-made cascade. In the middle portion of the table, the relative position (Strahler stream order) of targeted barriers within the river network is shown. In the lower portion of the table, selected attributes are provided. This includes the number of barriers with head differences $\geq 1\text{m}$ (Large), average initial passability (Passability), average cost of barrier mitigation (Cost), and the average net upstream length of river immediately above a barrier (Net USL).

Attribute	All	Budget (£M)										
		5	10	15	20	25	30	35	40	45	50	53.4
Dams / Weirs	265	37	55	80	106	121	134	160	178	220	253	265
Culverts	268	13	34	48	65	97	133	163	202	213	253	268
Sluices	41	3	7	14	20	25	27	31	32	37	39	41
Screens	30	1	3	3	7	8	9	12	19	23	30	30
Locks	34	0	0	0	0	0	0	2	4	4	5	34
Other	12	3	7	8	11	12	12	12	12	12	12	12
Total	650	57	106	153	209	263	315	380	447	509	592	650
Order 1-2	315	2	14	20	22	37	68	114	161	185	258	315
Order 3-4	278	42	64	96	148	183	200	209	229	267	277	278
Order 5-6	57	13	28	37	39	43	47	57	57	57	57	57
Large	67	7	17	29	36	42	59	59	62	67	67	67
Passability	0.12	0.06	0.11	0.10	0.10	0.10	0.11	0.11	0.12	0.12	0.12	0.12
Cost (£k)	82.1	87.6	93.8	97.7	95.6	95.0	95.2	92.1	89.5	88.4	84.4	82.1
Net USL (km)	1.7	7.5	5.7	4.6	3.8	3.3	3.0	2.6	2.3	2.1	1.8	1.7