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Modelling functional fish habitat connectivity in rivers. A case study for prioritizing restoration actions targeting brown trout

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1   **Modelling functional fish habitat connectivity in rivers: A case study for prioritizing**

2   **restoration actions targeting brown trout**

3

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9

10   **Abstract**

11   1. Throughout the world, decreased connectivity of fluvial habitats caused by

12   anthropogenic river channel alterations such as culverts, weirs and dykes is pointed out as

13   an important threat to the long term survival of many aquatic species. In addition to

14   assessing habitat quality and abundance, wildlife managers are becoming increasingly

15   aware of the importance of taking into account habitat connectivity when prioritizing

16   restoration efforts. In this paper, a new approach of spatial analysis adapted to rivers and

17   streams is proposed to model 2D functional habitat connectivity, integrating distance,

18   costs and risk of travelling between habitat patches (e.g.. daily-use, spawning, refuge) for

19   particular fish species, size classes and life stages.

20   2. This approach was applied to a case study in which brown trout (*Salmo trutta*)

21   habitat accessibility was examined and compared under various scenarios of stream

22   restoration in a highly fragmented stream in Ile-de-France. Probabilities of reaching

1

23   spawning habitats were estimated from a trout-populated area located downstream of the

24   barriers and from potential daily-use habitat patches across the stream segment.

25   3. The approach successfully helped prioritize restoration actions by identifying

26   options which yield a maximal increase in accessible spawning habitat areas and

27   connectivity between spawning habitat and daily-use habitat patches. This case study

28   illustrates the practical use of the approach and the software in the context of river habitat

29   management.

30   **Keywords:** river, stream, habitat management, habitat mapping, fish.

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34 **Introduction**

35

36 To survive, grow and complete their life cycle, many fish species need to chronologically

37 access different habitats providing for particular life functions (i.e. feeding, refuge,

38 spawning) and life stages. In rivers and streams, the spatial and temporal variation of

39 flow velocity, bed morphology, vegetation and temperature contribute to creating and

40 maintaining a dynamic mosaic of habitat patches (Statzner, 1981, Pringle *et al.*, 1988).

41 The resulting heterogeneity provides a variety of complementary functional habitats for

42 fish (Schlosser, 1995, Le Pichon *et al.*, 2016). The spatial configuration of

43 complementary habitats and the connectivity between them affects fish dispersion and

44 migration, which in turn have an impact on the spatial variation in genetic diversity,

45 community composition and metapopulation dynamics (Fullerton *et al.*, 2010).

46 Throughout the world, anthropogenic river channel alterations such as dams, culverts,

47 weirs, dykes and derivations have over the years decreased the natural connectivity of

48 fluvial systems, restricting the movement of organisms and threatening biodiversity

49 (Elosegi *et al.*, 2010). To tackle this issue, aquatic conservation and management

50 planners are putting increasing effort in stream restoration aiming at reducing habitat

51 fragmentation (Merenlender and Matella, 2013).

52

53 Habitat connectivity describes how the environment facilitates or restricts dispersal or

54 migration of organisms between habitats patches (Taylor *et al.*, 1993). The so-called

55 'structural' habitat connectivity reflects the physical structure of the landscape (i.e. shape,

56 size and relative location of habitat patches, presence of natural and artificial barriers)

3

57   (Baudry and Merriam, 1988). In contrast, 'functional' connectivity reflects how

58   organisms respond to the physical structure of the river in terms of mobility between

59   habitats. Being species- and life stage- specific, functional connectivity in riverscapes

60   defines the capacity or the ease at which aquatic organisms can travel from a habitat

61   patch to another depending on their swimming capacities or dispersal behaviour, energy

62   costs and mortality risks involved. Considering its importance for the persistence of

63   populations (Fahrig and Merriam, 1994), gaining knowledge of species-specific

64   functional connectivity for particular rivers is crucial, and provides in many cases a more

65   useful perspective for addressing specific management problems. In particular, assessing

66   functional connectivity might be especially valuable in the context of barrier removal

67   projects, as it could help decision makers to prioritize restoration actions (Branco et al.,

68   2014, Rivers-Moore et al., 2016).

69

70   Estimates of functional habitat connectivity can be obtained through empirical

71   measurements of fish dispersion and migration rates using various bio-telemetry and

72   mark-and-recapture techniques (Kanno *et al.*, 2014). At the scale of river networks,

73   population genetics can also be used to determine biological connectivity through its

74   footprints in the reproductive history of individuals and populations (Torterotot *et al.*,

75   2014). However, acquiring such data is costly and can be logistically challenging. An

76   alternative solution is to model functional habitat connectivity, providing quantitative

77   estimates of accessible habitat area. This approach might be particularly useful as a

78   decision-support tool for wildlife managers and landscape planners.

79

4

80   Terrestrial landscape ecologists have a   tradition of modeling connectivity using

81   numerous approaches based on Euclidian distances (Mühlner *et al.*, 2010), diffusion

82   (Reeves and Usher, 1989), corridor definition (Gilbert-Norton *et al.*, 2010) and graph

83   theory (Rayfield *et al.*, 2011). Although connectivity has been widely studied in streams

84   and rivers (e.g. Pringle, 2003, Moilanen *et al.*, 2008), methodologies to model stream

85   habitat connectivity adapted to the longitudinal constraints of a river structure and the

86   directionality imposed by flow velocity are more recent (Fullerton *et al.*, 2010). Among

87   different research paths, 1D methods based on graph- or network theory have recently

88   generated enthusiasm (Eros *et al.*, 2011, Van Looy *et al.*, 2014). While graph-theory is

89   useful for providing a schematic representation of the interconnections between habitat

90   patches at the scale of large river networks, it might not always be the best option to

91   characterize connectivity of smaller-scale continuous habitat maps, particularly to

92   account for areas located outside suitable habitat patches.

93   An alternative approach to modelling habitat connectivity is to estimate the shortest

94   distance (within wetted area) to or from habitat patches at the pixel level of 2D raster

95   maps (Jensen *et al.*, 2006). As heterogeneous environments might induce variable

96   resistance to movement, cost-distance functions (Knaapen *et al.*, 1992) can be used in

97   order to identify least-cost paths (or functional distances) between locations (Adriaensen

98   *et al.*, 2003). This approach is well suited to analyze continuous aquatic data over large

99   extents, which are becoming increasingly available. In particularly, high resolution

100   remote sensing imagery provides solutions to map numerous variables such as

101   bathymetry and water temperature (McKean *et al.*, 2009, Dugdale *et al.*, 2013, Tamminga

102   *et al.*, 2015). A 2D raster-based approach to analyze connectivity is particularly useful to

5

103   describe large rivers, fluvial lakes and estuaries with connected waterbodies, where fish

104   can possibly move in every direction rather than only up- or downstream in a network.

105   Hence, by adopting a continuous view of the river and its spatially heterogeneous

106   environment, this approach is in line with a "riverscape perspective", which is

107   increasingly considered as desirable for carrying out effective research and planning

108   conservation (Fausch *et al.*, 2002, Wiens, 2002, Fullerton *et al.*, 2010, White *et al.*,

109   2014).

110   The objective of this paper is to (i) describe a free software (Anaqualand 2.0) designed to

111   quantify functional habitat connectivity of mobile organisms in streams and rivers and to

112   (ii) show the usefulness of this approach to evaluate the potential connectivity changes

113   resulting from river modifications. Based on least-cost path modeling, Anaqualand 2.0

114   software differs from available GIS tools by accounting for fish movement directionality

115   (up- and downstream) and allows converting connectivity between habitat patches into

116   species- and life-stage-specific probability of access. To illustrate this potential,

117   Anaqualand 2.0 was used in a case study to model brown trout (*Salmo trutta*) habitat

118   connectivity and the probability of reaching spawning sites (ie. habitat accessibility)

119   under scenarios of barrier removal to help prioritize connectivity restoration actions.

120

121   **Anaqualand 2.0 program overview**

122   The software allows the user to quantify the structural and functional connectivity

123   between habitat patches or point coordinates in the upstream, downstream or in both

124   directions (Le Pichon *et al.*, 2006). Structural connectivity can be quantified by

125   calculating instream distances between habitat patches (i.e. shortest path within the

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126   channel boundary) and resistance to movement is assumed to be homogeneous across the

127   river. In contrast, functional connectivity integrates the distance between patches and a

128   spatially variable resistance to movement allowing to identify least-cost paths between

129   patches expressed as a minimal cumulative resistance (MCR) (Knaapen *et al.*, 1992,

130   Adriaensen *et al.*, 2003). This approach is based on the general assumptions of optimal

131   foraging theory (Davies *et al.*, 2012) predicting that fish will tend to minimize the energy

132   costs while they travel (Giske *et al.*, 1998). Thus, the least-cost path between two

133   functional habitat patches might sometimes imply travelling a longer distance than the

134   shortest instream distance in order to avoid an obstacle or risky area. Anaqualand 2.0 is

135   freely   available   and   can   be   downloaded   from   the   internet

136   (http://www6.rennes.inra.fr/sad/Outils-Produits/Outils-informatiques/Anaqualand).

137

138   *Input data and habitat patch delineation*

139   Anaqualand 2.0 requires to input a raster map (ascii format) describing the physical

140   template of the river. Coordinates of the upstream and downstream ends of the study

141   stream are required to indicate stream flow directionality. Depending on data availability

142   and objectives, it may be a simple binary map displaying the river outline (water/not

143   water) or a more detailed categorical map containing depth classes, morphological units,

144   physical or chemical barriers, etc. Multiple sets of resistance values, for up- and

145   downstream directions, specific to each species and life stage studied, can be uploaded.

146   One or several functional habitats maps can be added to examine the connectivity to or

147   between them (e.g. refuge to foraging habitat or spawning to nursery). Optimally,

148   resistance to movement can be determined through empirical studies of fish mobility in

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149   heterogeneous environments (see Beier *et al.*, 2008 for review). However, as such studies

150   are complex to carry out, few empirical resistance estimates have been yet published (but

151   see Turgeon *et al.*, 2010). Therefore, from a management perspective, resistance values

152   based on expert opinion and literature review (Beier *et al.*, 2008) is often considered as a

153   justifiable trade-off.

154

155   *Instream distances and functional distance maps*

156   Instream distances are defined as the shortest paths between a source and a target within

157   the channel boundary. Functional distance, defined as the least-cost path between two

158   locations, is expressed as the minimal cumulative resistance (MCR). Anaqualand 2.0

159   allows the user to create functional distance maps, in which every pixel values express

160   the minimal cost to reach the closest habitat of the specified type. Functional distance can

161   be calculated: 1) either for all patches or for a selection of patches, 2) either for all

162   patches simultaneously (one map of functional distance to reach the nearest patch) or

163   separately for each patch (several maps of functional distance to reach single patches), 3)

164   either in upstream (functional distance to reach the nearest upstream patch), in

165   downstream (functional distance to reach the nearest downstream patch) or in both

166   directions (functional distance to reach the nearest patch independently of flow direction).

167   *Probability of access maps*

168   As accessibility decreases with functional distance traveled, functional distance maps

169   (MCR) can be converted into accessibility maps using a decreasing probability

170   transformation function and a mobility coefficient (α) (Le Pichon *et al.*, 2006). Four

171   functions are available: 1) linear, 2) Gaussian, 3) exponential or 4) threshold-driven. The

172   function used depends on the behaviour of the target species. In case of uncertainty,

173   multiple curves can be computed as a way to perform a sensitivity analysis. A Gaussian

174   transformation would illustrate a population characterized by most fish reaching

175   moderate distances and few traveling long distances; while an exponential transformation

176   would characterize a population in which few fish that are mobile may travel over longer

177   distances and a threshold driven curve could be used when resistance features present

178   lethal conditions or an absolute physical barriers. The mobility coefficient (α), a

179   parameter estimated in meters is calibrated based on the existing knowledge of the

180   species- and life-stage-specific home range extent or migration distances (Hanski, 1994,

181   Vos *et al.*, 2001).

182

183   **Case study**

184   *Context and objectives*

185   With the adoption of the Water Framework Directive (Council of the European

186   Communities, 2000), European countries have referenced and mapped stream barriers

187   and have set targets of conservation and restoration of water bodies. In this context, the

188   Haute Vallée de Chevreuse Natural Regional Park, France, is carrying out a project

189   aiming at restoring ecological continuity of streams on its territory using barrier removal

190   or channel restoration at the bottom of the valley. However, due to the high number of

191   barriers and the limited resources, action prioritization is crucial to maximize their

192   potential short and medium term ecological benefits (Gangloff, 2013).

193   Brown trout (*Salmo trutta*) is a European species of salmonid that is considered as a

194   flagship species in France, indicator of good ecological status of rivers and important for

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195   sport fishing. In the Ile-de-France region, where streams are highly impacted by human

196   activities and populations have markedly declined, it remains of high conservation

197   importance in stream where small populations still exist. Allowing free passage might be

198   important for freshwater brown trout resident populations, as mature individuals tend to

199   migrate upstream in autumn from their daily-use rearing habitat to suitable spawning

200   grounds (Jonsson and Jonsson, 2011). Outside the spawning season, most individuals

201   display restricted mobility, while a fraction of the population is more mobile and move

202   between suitable daily-use habitat (Jonsson and Jonsson, 2011). Therefore, restoring free

203   passage outside the spawning season might allow fish to colonize upstream areas and

204   increasing stream productivity. The progressive colonization of daily-use habitats might

205   be stepping stones providing access to further spawning habitats.   In this context,

206   Anaqualand 2.0 appears to be an ideal tool for quantifying the changes in habitat

207   availability associated with different scenarios of barrier removal in order to guide the

208   allocation of resources in restoration of the Mérantaise. Specifically, this case study aims

209   at estimating 1) accessibility to spawning/daily-use habitat from the downstream end of

210   the study area, providing benefits of connectivity restoration for the downstream

211   population, and 2) accessibility to spawning habitats from any daily-use habitat patches,

212   providing overall habitat gains. To analyze the sensitivity of accessibility estimates, input

213   parameters were varied in terms of a) resistance values adapted to fish life stage, b)

214   mobility coefficients and c) probability transformation functions.

215

216   *Study area*

217   The Mérantaise is a first order stream draining a 31 km² catchment located 23 km south-

218   west of Paris, in the Ile-de-France region. It is a tributary of the Yvette River belonging to

219   the Seine River catchment (Figure 1a) (48°43'45"; 2°06'02"). The Mérantaise was

220   identified as a priority stream, as it provides a high potential of spawning habitat for

221   brown trout population restricted to a segment located downstream of an impassable mill

222   weir (B3) (Figure 2). This stream is also considered as a reservoir of biological diversity

223   bordered by wetlands and includes twenty-height terrestrial and aquatic protected species.

224   Because of a long history of human impacts, the course of the stream is lined with several

225   barriers originating from hydraulic structures (mill weirs) dating from the XIII to XIX

226   century. The focus of this study is a 6 km–long segment of the Mérantaise contained

227   within the Haute Vallée de Chevreuse Natural Regional Park. This stream segment is

228   around 2-5 m-wide, its maximum depth in pools at low flow is approximately 1.0 m. The

229   channel is generally incised, the average slope is 0.75% and the dominant substrate varies

230   from mixtures of silt and sand to gravel and cobbles.

231

232   *Field survey*

233   <u>Habitat characterization</u>

234   Hydromorphological units (HMU) along the stream profile were visually delimited and

235   mapped based on geomorphology and flow type (Newson et al., 1998). Riffle constituted

236   5%, runs 28%, glides 55% and pools 7% of the total area (Figure 1b). Twelve barriers,

237   potentially restricting fish mobility, were identified, including three impassable mill weirs

238   (1.0-1.5 m high, B3, B11 and B12) and nine barriers (0.1 m and 0.5 m high) created by

239   culverts, crossing of waste water pipes and an old washhouse. Concave underbanks,

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240   presence of roots, boulders and aquatic plants, considered to be potential trout shelters,

241   were visually identified and georeferenced using a handheld Garmin GPSMAP 62 (± 5

242   m). Potential spawning grounds were identified and georeferenced at low flow on the

243   basis of substrate size and HMU, with the expert assistance of a river technician, highly

244   experienced in counting trout redds in the PNRHVC streams.

245   <u>Fish movement</u>

246   Between March 2012 and April 2013, thirty-nine individuals were tracked using radio-

247   telemetry in the 2 km-long downstream section of the study segment, limited by the

248   impassable barrier B3. Fish were caught by electrofishing, anesthetized (10% eugenol

249   solution), weighed, measured and tagged intra-peritoneally with radio transmitters

250   (ATS® models F1020, F1040, and F1170 with encapsulated antenna) using the protocol

251   defined by Gosset *et al.*, (2006). Location of individuals was monitored (i) continuously

252   using two fixed-point receivers (ATS®, R4500S) installed on barriers and (ii) once a

253   week with mobile receivers. Scales were collected to determine age and size at first

254   reproduction. As all age 3+ and older trout presented spawning marks, it was further

255   assumed that first reproduction occurred at age 2+. The body length (BL) of immature

256   (1+ non-spawners, n=10) trout ranged from 178 to 226 mm and BL of mature trout (2+

257   and older, spawners, n=29) varied between 221 to 554 mm.

258

259   *Data analysis*

260   <u>Habitat mapping</u>

261   Potential spawning habitat patches were mapped based on georeferenced data using

262   ArcGIS® (ESRI, 2011). Daily-use habitats were modeled using radio-telemetry data

12

263   (outside the spawning season) and three spatial metrics: distance to pools (DP), distance

264   to riffles (DR) and distance to shelters (DS), generated with Anaqualand 2.0. The three

265   spatial metrics had proved to be predictors of the presence of trout in headwater streams

266   of Ile-de-France (Le Pichon *et al.*, 2013), as the proximity of pools and riffles tend to

267   provide fish with refuge and feeding opportunities (Ovidio, 1999, Ovidio *et al.*, 2002,

268   Armstrong *et al.*, 2003). A generalized linear model was built to predict daily-use habitat

269   using DS, DP and DR extracted at every radio-telemetry fish location and at every point

270   of an equally-sized pseudo absence dataset generated randomly throughout the river

271   segment (S= -0.116 - (0.099*DS) - (0.445*DP) + (0.0248*DR) (p=0.891, 0.023, 0.003,

272   0.069)). To delineate discrete habitat patches, the raster map values were reclassified as a

273   binary map using a probability threshold of 0.4. The resulting longitudinal distribution of

274   the spawning and daily habitat patches are presented in Figure 1c.

275   <u>Resistance maps</u>

276   Raster maps of resistance, quantifying how trout mobility may be restricted by physical

277   barriers, variable swimming energy costs and perceived predation risk, were created

278   combining three variables: HMU (five types), barriers (N=12) and shelters

279   (presence/absence). HMU, the twelve barriers and the shelters (5 m diameter circular

280   buffer) were combined to yield 34 possible categories representing the five HMU and the

281   twelve barriers with and without shelters. These classes will be further referred to as

282   mesohabitats. Finally, thirteen resistance maps were generated according to the

283   successive barrier removal scenarios (Figure 3).

284

285   *Connectivity modelling*

13

286   <u>Resistance value assignation</u>

287   Resistance values were determined using a simple model in which normalized values

288   were assigned to HMU by expert opinion, by combining energy costs and predation risk

289   (Table 1). Resistance values associated with energy costs were based on the assumption

290   that resistance increases with flow velocity while predation risk decrease with shelter

291   presence and HMU average depth, as deep flow provides better cover for salmonids than

292   shallow flow (Rosenfeld and Boss, 2001) (Table 1). Resistance yielded values ranging

293   between 0 and 10, calculated as R=log (1/(energy expenses * average depth * shelters).

294   Similarly, resistances were assigned to barriers based on their height and on their

295   passability (Baudoin *et al.*, 2014). Arbitrary high resistance values (2000) were assigned

296   to the three weirs considered impassable (B3, B11 and B12) while resistance attributed to

297   other barriers ranged between 20 and 150. Two separate sets of resistance values were

298   generated for the two fish classes: mature fish (body length > 230 mm), corresponding to

299   the average length of brown trout at maturity in the study stream, and immature fish

300   (body length < 230 mm). For a discussion of alternative methods to determine

301   resistances, see (Beier *et al.*, 2008).

302   <u>Brown trout mobility coefficient (α)</u>

303   Home range extents (distance between the two most distant locations), further used as

304   mobility coefficients (α), were estimated from telemetry data. Home range extents were

305   estimated 1) outside the spawning period for immature fish (mean: 143 m, 85th

306   percentile: 338 m, max: 366 m) and mature fish (mean: 170 m, 85th percentile: 398 m,

307   max: 774 m) and 2) during the spawning period for mature fish (mean: 351 m, 85th

308   percentile: 710 m, max: 830 m).

14

309   Habitat accessibility

310   Resistance and functional habitats maps were used to compute functional distance maps

311   expressing at each pixel the least cost for reaching 1) a daily-use habitat from the

312   downstream end of the study section; 2) a spawning habitat from the downstream end of

313   the study section and 3) a spawning habitat from a daily-use habitat. These analyses

314   aimed to compare how easily immature and mature trout can complete their life cycle

315   under different barrier removal scenarios. For each of these analyses, functional distances

316   were then converted to accessibility (probability ranging between 0 and 1) using the

317   mobility coefficients and two transformation curves (Figure 3). Although stream

318   salmonids generally tend to exhibit a spatial behaviour better described by a decreasing

319   exponential (fewer fish moving long distances), this pattern is not always consistent

320   (Rodriguez, 2002). Therefore, a Gaussian transformation was also performed as part of a

321   sensitivity analysis.

322   Connected functional habitat area

323   To quantify and visualize the overall accessibility, connected daily-use habitat area

324   (CDHA), connected spawning habitat area (CSHA) and spawning habitat area connected

325   to daily-use habitats (CS2DHA) were estimated as $\sum Ac_i \times A_i$, for i=1 to N (Number of

326   pixels of the corresponding habitat) where A_{ci} stands for the accessibility of a pixel and

327   A_i to pixel area. CDHA was calculated for immature and mature fish while CSHA and

328   CS2DHA were calculated for mature fish.

329

330   *Results*

331 Cumulative longitudinal profile of (CSHA), accumulated along the longitudinal profile of

332 the stream from downstream to upstream, gives a quantitative estimate of the overall

333 availability of spawning habitat patches weighted by their accessibility for the mature

334 trout under different barrier management scenarios and different levels of trout mobility

335 (Figure 4). Under the scenario of maintaining all barriers, 500 m^2 of CSHA were

336 estimated to be available in the first 1500 m of the stream profile for the fish of average

337 mobility (α= mean) (Figure 4). Allowing fully free passage additionally increased CSHA

338 for the latter by only 80 m^2. Furthermore, the habitat gain was associated with improved

339 connectivity only to spawning habitats located in the first 2200 m, as independently of

340 the barrier presence. In contrast, for the fish of higher mobility (α= 85th percentile and

341 α= max scenarios), allowing free passage both increased connectivity and provided

342 access to spawning habitats located upstream. This was particularly relevant for spawning

343 habitats located between 1500 and 2000 m and to a lesser degree to those between 4000

344 and 5000 m upstream of the lower end of the study segment (Figure 4).

345 To estimate the potential gain related to removing each barrier, the total CSHA (Figure 5)

346 and CDHA (Figure 6) were also quantified for successive barrier removal scenarios.

347 While removing the first two barriers did not increase accessibility to CSHA, eliminating

348 the third barrier B3 yielded between 155 and 245 m^2 of additional connected spawning

349 habitats for mobile trout (α= 85th percentile and α=max). Then, removing barriers B5 to

350 B8 provided access to a reach containing further suitable spawning habitats, whereas

351 removing B9 to B12 did not increase CSHA (Figure 5). All together for the mobile

352 fraction of the trout population (α= 85th percentile and α=max), spawning habitat

353 connectivity index was increased from $31 \pm 2\%$ with all barriers maintained in place to

16

354     $44 \pm 3\%$ in free passage conditions. In contrast to the results on the CSHA, the potential

355   gains in connected daily-use habitat area (CDHA) for the Mérantaise related to the

356   successive barrier removal were relatively low and varied significantly between fish of

357   different mobility (Figure 6). Removing barriers did not increase the CDHA for lower

358   mobility fish (α=mean) of both size. With high mobility coefficient (α= 85th percentile),

359   an increase of CDHA is observed for both size with the Gaussian transformation

360   function. With the very high mobility coefficient (α= max), a potential gain in CDHA

361   ranging from 2% to 10% was associated with a free passage between B3 and B8 for

362   immature fish with Gaussian transformation function and for mature fish.

363   With all barriers present, the longitudinal profile of spawning habitat accessibility

364   displayed a decrease in probability of access from 1 to 0.5 from the downstream end of

365   the study reach up to B3, after which the accessibility becomes close to null (Figure 7a).

366   Allowing free fish passage up to B4 provided access to two large patches of spawning

367   habitats located between B3 and B4 (Figure 7b). Lower gains in accessibility were also

368   obtained in the segment between B10 and B11. The removal of barriers B4 to B8 only

369   slightly increased the accessibility to spawning habitats located upstream starting from

370   B6 and between B10 and B11 (Figure 7c). Removing the remaining barriers did not

371   improve further habitat accessibility (Figure 7d).

372   Overall, even with all barriers present spawning habitat patches in the Mérantaise are

373   generally well connected to daily-use habitats, with accessibility values estimated to be

374   over 0.5 for all patches except those located between B3 and B4 (Figure 8 a). Removing

375   B1 to B4 increased CS2DHA by 140 m^2 (6%) (Figure 8b). Removing further barriers did

17

376   not provide access to otherwise unreachable habitats, but only slightly increased

377   accessibility values to a few spawning patches (Figure 8 c –d).

378

379   **Discussion**

380   The presented approach of quantifying connectivity in streams and rivers is novel,

381   adapting a two-dimensional functional landscape model (Adriaensen *et al.*, 2003) to

382   stream ecology and integrating fish movement directionality. This approach provides

383   means to incorporate the behavioural component of connectivity by including fish

384   mobility at specific life stages, a challenge highlighted by Fullerton et al. (2010).

385   Furthermore, the map-based approach might be more suitable than graph-based dendritic

386   network approaches (Saura and Torné, 2009, Van Looy *et al.*, 2014, Segurado *et al.*,

387   2015) to account for longitudinal and lateral movements along the riverscape and the 2D

388   physical heterogeneity of rivers. These features are of great importance as they allow

389   continuous mapping of habitat variability in a context relevant to particular species and

390   life stages at the intermediate scale of management actions (Le Pichon et al., 2016) that

391   cannot be substituted by discrete data typically obtained from sampling multiple smaller

392   reaches (Fausch *et al.*, 2002, White *et al.*, 2014). Moreover, the presented continuous

393   approach could be complementary with large-scale riverscape approaches, using network

394   drainage lines, for species such as wild salmon whose life-cycle involves movements

395   across large geographic areas (Whited *et al.*, 2012). However, estimating habitat

396   connectivity requires defining resistances and suitable habitat patches at a scale that is

397   relevant to the species and life stages of interest. Therefore, grain size should preferably

398   be smaller than the size of habitat patches and several times smaller than the species

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399   capacity of movement. Furthermore, the extent should be larger than the species capacity

400   of movement. The method could be used to examine the small scale mobility of larvae in

401   a reach using a fine scale hydrodynamic model as resistance as well as whale migration

402   in an estuary dominated by large scale tidal currents. Although a limitation of the method

403   consists in obtaining continuous data at the appropriate scale, such 2D riverscape scale

404   data is becoming increasingly available at lower costs through high resolution remote

405   sensing of water temperature (Dugdale *et al.*, 2013), bathymetry (Legleiter *et al.*, 2009),

406   substrate granulometry (Carbonneau *et al.*, 2005) and flow velocity (Tamminga *et al.*,

407   2015, Hugue *et al.*, 2016).

408   Along with the general benefits of restoring ecological continuity, stream specific

409   quantitative estimates of increase in habitat accessibility obtained through this raster-

410   based method might provide managers and local decision makers with additional

411   convincing arguments in favor of undertaking stream restoration efforts. Indeed, recently

412   used in a multi-agent platform, connectivity estimates has contributed to overcome water

413   use conflicts by providing a shared vision of the river (Carre et al. 2014).

414

415   Through the Water Framework Directive, European countries are recognizing the

416   problem of aquatic habitat fragmentation and allocating budgets to progressively restore

417   river channels and, where necessary, build structures to allow fish passage. Several

418   methods have been recently suggested for prioritizing barrier removal including scoring

419   and ranking barriers, stepwise scoring and ranking, scenario analysis, optimization, or

420   complete enumeration (see McKay et al. 2016 for review). Anaqualand is well suited to

421   perform scenario analyses and can handle either continuous or binary estimates of barrier

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422   permeability. The assessment of the cumulative impacts of multiple barriers possible with

423   the software would help prioritizing barrier removal (Branco *et al.*, 2014, Cote *et al.*,

424   2009) with better efficiency than scoring-and-ranking approaches (Kemp and O'Hanley,

425   2010).

426   In this study, connectivity was expressed in terms of connected habitat, providing a

427   decision support tool to compare different scenarios rather than precise estimates of

428   probability of access. In the light of the conducted analysis, efforts in the case of

429   Mérantaise should be concentrated on improving the passability of B3 barrier in order to

430   both increase the area of accessible spawning habitats by 13% of the total habitat area for

431   mobile trout and maximize the connectivity between spawning habitat and daily-use

432   habitat patches. Such change is favorable, as improved connectivity between spawning

433   and daily-use habitats might increase probability of habitat use (Flitcroft *et al.*, 2012).

434   However, removing further barriers upstream would only slightly increase the total

435   accessible habitat area due to more passable barriers and to the lower availability of

436   functional habitats in this upstream reach. Therefore, the removal or modification of these

437   barriers might be considered to be of low priority in terms of brown trout habitat

438   management and conservation. Nevertheless, although removing barriers did not increase

439   CDHA for lower mobility fish, removing barriers might improve future CDHA for these

440   fish, as mobile fish will spawn in the upstream area and produce low mobility fish that in

441   turn will use available daily use habitats.

442   Overall, caution must be taken when interpreting the results as they are affected by the

443   choice of several parameters, such as the estimates of up- and downstream mobility,

444   resistance assigned to barriers and probability distribution functions. For instance, the

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445   resistance assigned to barriers could vary according to water discharge and have an

446   impact on connectivity for brown trout (Denic and Geist 2010). Furthermore, since there

447   is a generally fairly high uncertainty associated with these input parameters, in addition to

448   estimating connectivity for a plausible range of mobility parameters, it might be

449   appropriate to assess the sensitivity of the results to different resistance model

450   formulations and to interpret the results accordingly. In recent decades, knowledge of

451   mobility behaviour and of the characteristics affecting barrier passability for many

452   species has improved significantly (Ovidio and Philippart, 2002, Baudoin *et al.*, 2014).

453   Nevertheless, more field studies quantifying the effect of physical habitat on fish mobility

454   are still needed in order to properly calibrate spatially variable resistance to movement at

455   different fish size and life stages. In cases where resistance values are unavailable,

456   connectivity can still be estimated using a distance and mobility data only. In the future

457   application of the model, it should also be considered that in parallel to increasing

458   connectivity, additional benefits of barrier removal can include restoring channel

459   morphology and bed granulometry. Such possible changes in both upstream and

460   downstream habitats were not taken into account in this case study, but could be

461   addressed by coupling Anaqualand with a two-dimensional hydraulic modelling.

462   Anaqualand could be useful for future work aiming at improving estimates of stream

463   carrying capacities, in particular for species exhibiting distinct ontogenic shifts in habitat

464   requirements during their life cycle. For instance, for brown trout, estimating

465   successively the connectivity of adult daily use habitats to spawning habitats, of

466   connected spawning to nursery habitats and of connected nursery habitats to juvenile

467   daily use habitats might be useful to get a portrait of how habitats are linked through the

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468   life cycle. Comparing the habitat connectivity levels associated with each life stage might

469   help to identify bottlenecks caused by habitat limitation and obtain better estimates of

470   carrying capacity. Furthermore, the approach could also be used to improve habitat

471   quality models of species using complementary habitats over a daily cycle, such as

472   feeding habitats and shelters. This paper presented a case applied to fish but the method

473   could as well be applied to other mobile organisms which dispersal is restricted by

474   natural or anthropogenic constraints, such as aquatic invertebrates (Datry et al., 2016).

475   Overall, Anaqualand may become a timely tool particularly helpful to fisheries managers,

476   as evidence showing the critical importance of connectivity between habitats used

477   throughout the life cycle for the productivity and persistence of fish populations is

478   accumulating (Flitcroft *et al.*, 2012, Falke *et al.*, 2013, Bergeron et al. 2016). Finally, in

479   addition to increased accessible habitat area as assessed in this case study, prioritisation

480   of management efforts might also be established based on issues related to costs, the

481   social context, local politics and to the cultural heritage designation associated with

482   particular streams or historical obstacles (most often mill weirs; Kemp and O'Hanley,

483   (2010).

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485   **Acknowledgments**

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689

690 Table 1. Values assigned to predation risk (average depth and shelter) and energy costs

691 associated with each mesohabitat to calculate resistance (R

692 (R=log (1/(energy costs * predation risk)). Note that higher scores yields lower resistance

693 values.

	Energy costs	Predation risk	Energy costs	Predation risk
	Immature fish		Mature fish	
Pool	1	1	1	1
Glide	1	1	1	0.5
Run	0.6	0.7	0.8	0.55
Riffle head	0.45	0.5	0.7	0.45
Riffle	0.4	0.6	0.5	0.45
Shelter (P/A)	(1/0.65)		(1/0.45)	

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700   Figure 1. Study area, a) Location of the study site (star), the Merantaise stream in the

701   Seine River Basin, b) pseudo three-dimensional representation of the river profile with

702   location of spawning and daily use habitat patches c) longitudinal profile of barriers and

703   hydromorphological units (HMU) indicated as white bars.

704   Figure 2. Mérantaise stream study site. a. View of a riffle during the winter. b. View of

705   the Seuil d'Ors mill weir (B3) during the summer.

706   Figure 3. Flowchart used to model brown trout habitat accessibility. a) Input data, b)

707   Input parameters and c) Connected habitat availability output for the three analyses

708   yielding estimates of 1) connected daily use habitat area (CDHA) from downstream 2)

709   connected spawning habitat area from downstream (CSHA) and 3) connected spawning

710   to daily use habitat area (CS2DHA). Connected habitat availability was estimated for

711   varying functional habitat connectivity (N=3), scenarios of successive upstream barrier

712   removal (N=13), fish size for CDHA (N=2), mobility coefficients (N=3) and probability

713   of access transform function (N=2).

714   Figure 4. Cumulative longitudinal profile of connected spawning habitat area (CSHA)

715   (m^2) accessible to mature trout during the spawning period. Symbol shapes represent

716   degrees of trout mobility: including average (mean), high (p85: 85th percentile) and very

717   high (maximum) mobility; line type corresponds to two management scenarios: with all

718   twelve barriers present (barriers) and in free passage conditions (no barriers); symbol

719   color reflects the probability transform function: Gaussian (ga) or exponential (ex). B1 to

720   B12 indicate barrier locations. "0" at the x-axis corresponds to the downstream end of the

721   study segment.

722   Figure 5. Spawning habitat accessibility index, expressing the ratio between the

723   connected spawning habitat area (CSHA) and the total spawning habitat area in

724   percentage, for mature trout. Average mobility trout (mean), high mobility trout (p85:

725   85th percentile) and very high mobility trout (max) are represented by different symbol

726   shapes; symbol color reflects the probability transform function used: Gaussian (ga) or

727   exponential (ex). Grey area displays the envelope of accessibility values for mobile trout

728   (85th percentile and max).

729   Figure 6. Daily-use habitat accessibility index, expressing the ratio between the

730   connected daily-use habitat area (CDHA) and the total daily-use habitat area in

731   percentage. Symbol size reflects two fish size classes considered: mature fish (m); and

732   immature trout (i). Symbol type allows to distinguish between average mobility trout

733   (mean), high mobility trout (p85: 85th percentile) and very high mobility trout (max),

734   outside the spawning season. Symbol color reflects the probability transform functions

735   used: Gaussian (ga) and exponential (ex). Grey area displays the range of connectivity

736   values for mobile trout (85th percentile and max).

737   Figure 7. Pseudo two-dimensional profile of the accessibility of spawning habitat from

738   the downstream end of the study section. Different management scenarios are presented:

739   a) all barriers are maintained, b) accessibility gain (increase) when removing B1-B4

740   compared to the scenario a), c) accessibility gain when removing B1-B8 compared to the

741   scenario b), d) accessibility gain when removing B1-B12 compared to the scenario c).

742   The cases shown were calculated for mature fish with very high mobility (α=max) and

743   using the exponential function of decrease in probability of access. B1 to B12 and stars

744   indicated the location of barriers.

745   Figure 8. Pseudo two-dimensional profile of the accessibility of spawning habitat patches

746   from daily use habitat patches located upstream or downstream. Different management

747   scenarios are presented: a) all barriers are maintained, b) accessibility gain (increase)

748   when removing B1-B4 compared to the scenario a), c) accessibility gain when removing

749   B1-B8 compared to the scenario b), d) accessibility gain when removing B1-B12

750   compared to the scenario c). The cases shown were calculated for mature trout with very

751   high mobility (α=max) and using the exponential function of decrease in probability of

752   access. B1 to B12 and stars indicated the location of barriers.

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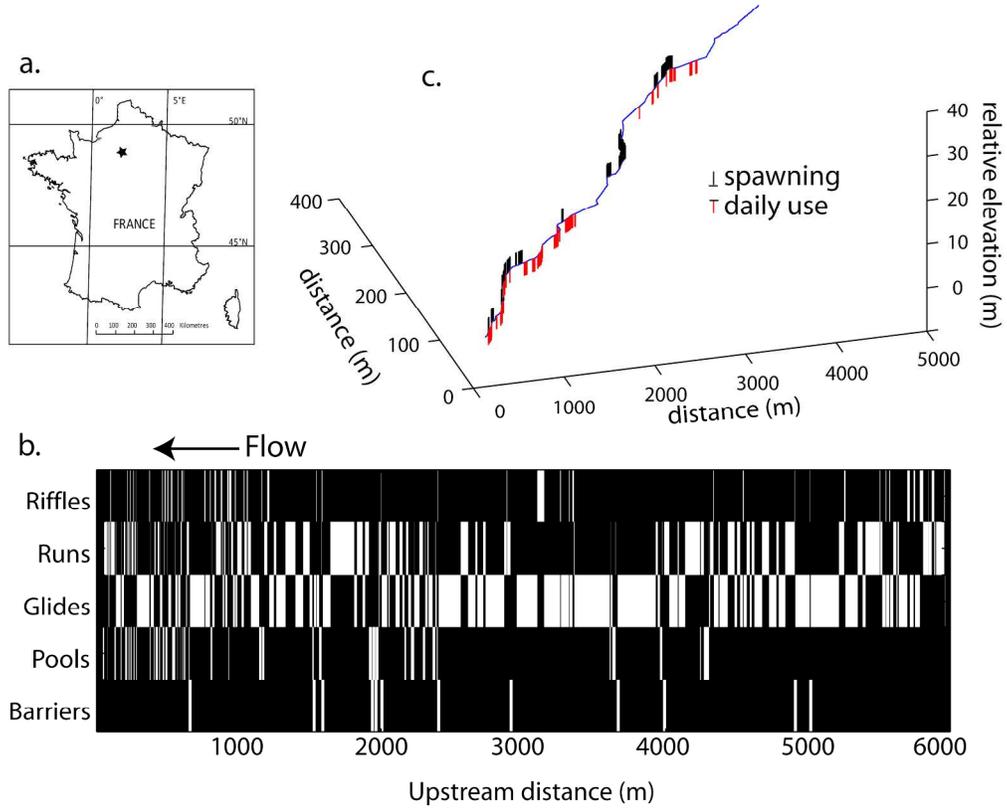
Figure 1
120x109mm (600 x 600 DPI)

Figure 2
161x65mm (300 x 300 DPI)

a. Input Data

Functional habitat maps (*2)   Connection source   Resistance maps (*13) (removal scenarios)

1) Daily use
2) Spawning

downstream end of study reach

Mesohabitats + barriers

Functional habitat (*1)   Connection

3) Spawning   Daily-use

b. Input Parameters

Resistance sets (*2)   Mobility coefficient (*3)   Probability of access transformation (*2)

mature fish
immature fish

mean
p85
max

exponential
Gaussian

c. Output - Connected habitat availability

Functional habitat accessibility maps   Access * Area   Connected habitat area

1) Connected Daily-use → CDHA
2) Connected Spawning → CSHA
3) Connected Daily-use to spawning → CS2DHA
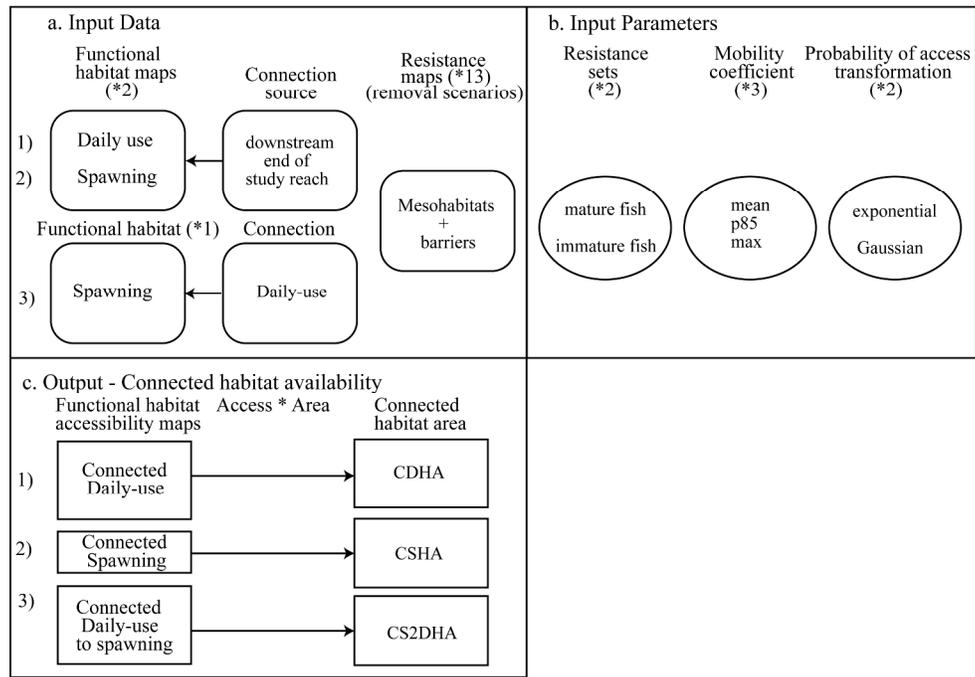
Figure 3
136x96mm (600 x 600 DPI)
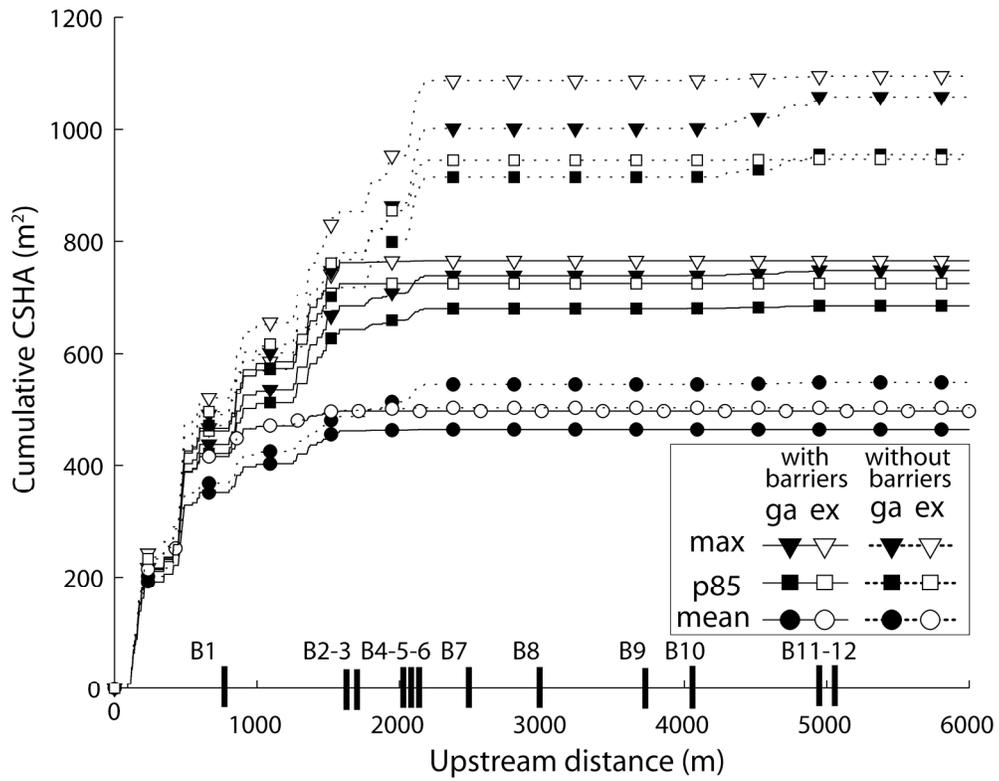
Figure 4
104x81mm (600 x 600 DPI)
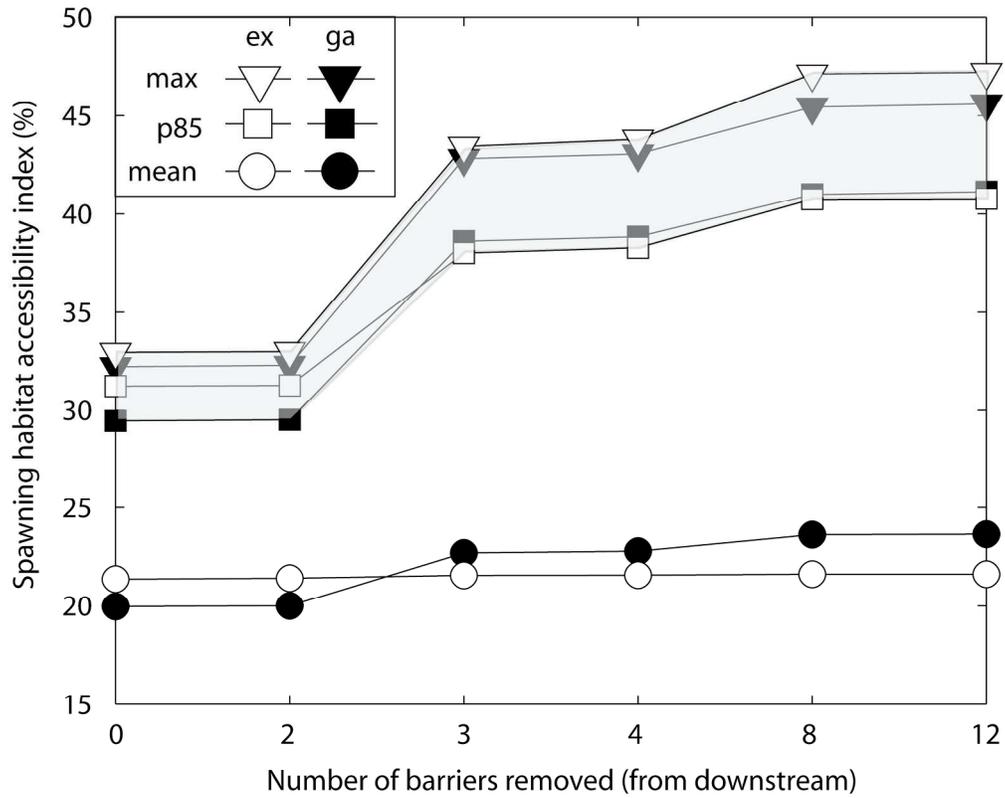
Figure 5
104x83mm (600 x 600 DPI)
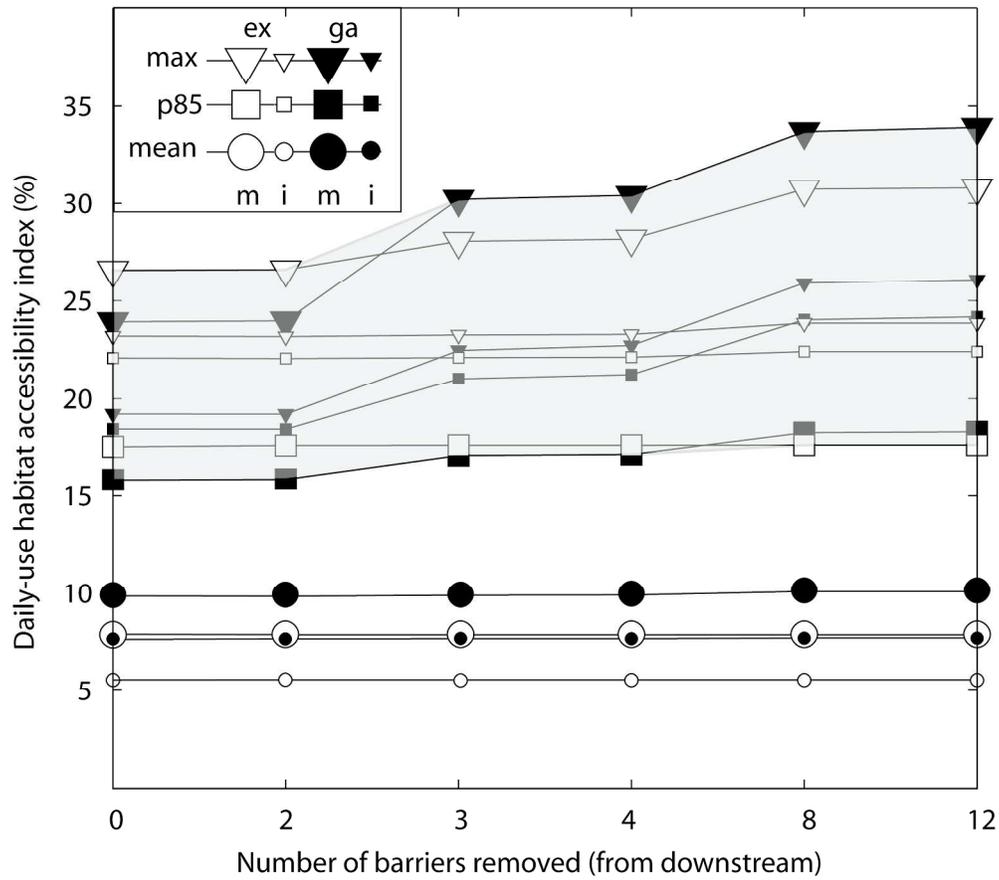
Figure 6
121x110mm (600 x 600 DPI)
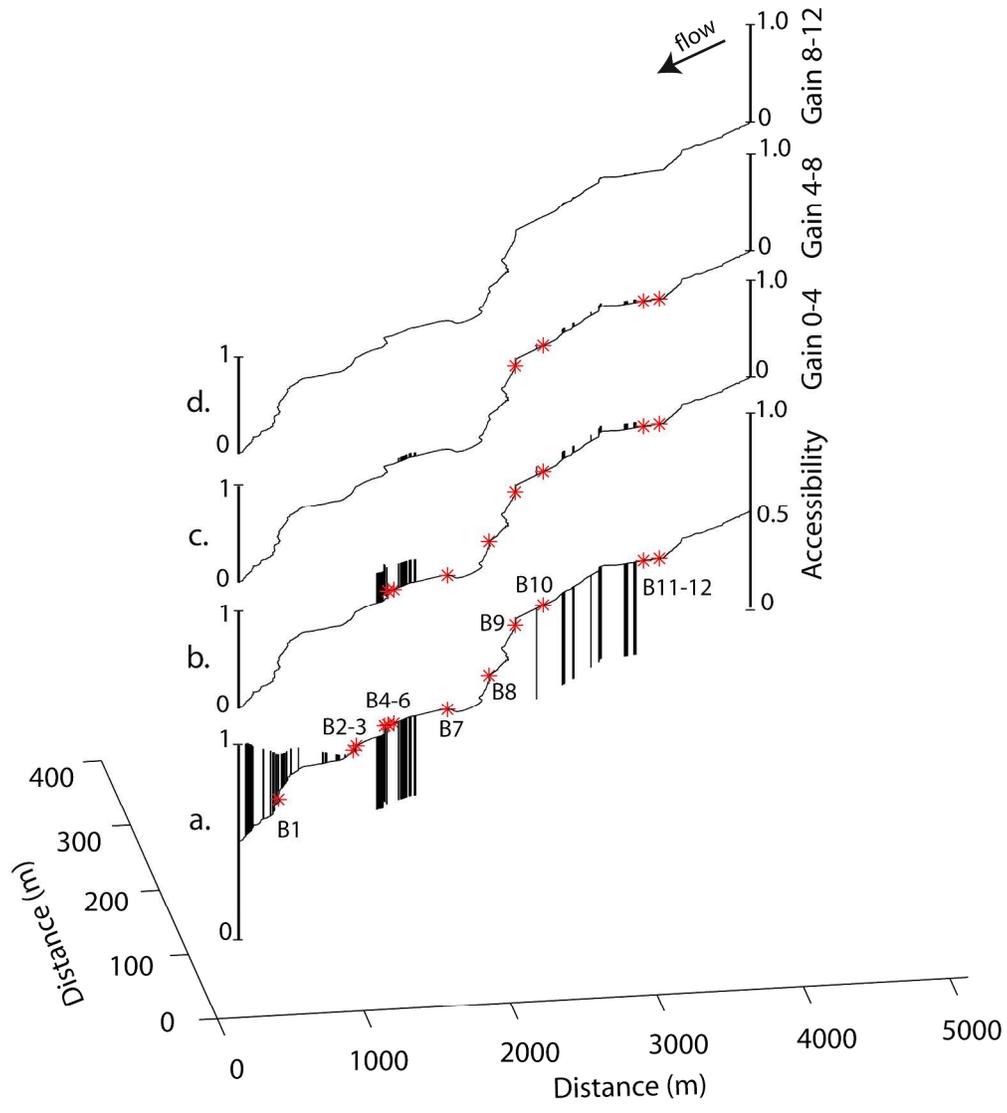
Figure 7
144x159mm (600 x 600 DPI)
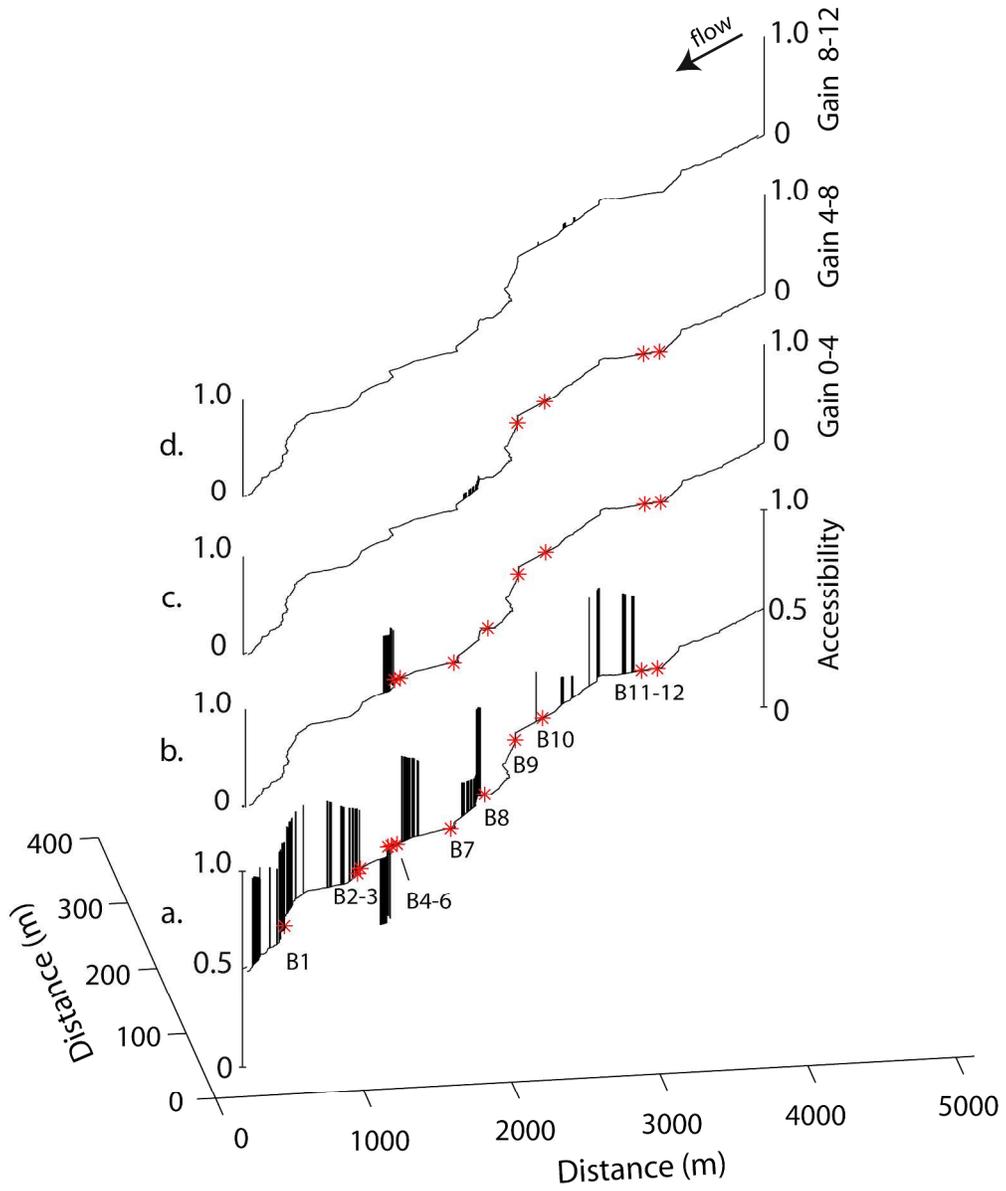
Figure 8
155x185mm (600 x 600 DPI)