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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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Abstract

1. Throughout the world, decreased connectivity of fluvial habitats caused by anthropogenic river channel alterations such as culverts, weirs and dykes is pointed out as an important threat to the long term survival of many aquatic species. In addition to assessing habitat quality and abundance, wildlife managers are becoming increasingly aware of the importance of taking into account habitat connectivity when prioritizing restoration efforts. In this paper, a new approach of spatial analysis adapted to rivers and streams is proposed to model 2D functional habitat connectivity, integrating distance, costs and risk of travelling between habitat patches (e.g.. daily-use, spawning, refuge) for particular fish species, size classes and life stages.

2. This approach was applied to a case study in which brown trout (*Salmo trutta*) habitat accessibility was examined and compared under various scenarios of stream restoration in a highly fragmented stream in Ile-de-France. Probabilities of reaching

spawning habitats were estimated from a trout-populated area located downstream of the barriers and from potential daily-use habitat patches across the stream segment.

3. The approach successfully helped prioritize restoration actions by identifying options which yield a maximal increase in accessible spawning habitat areas and connectivity between spawning habitat and daily-use habitat patches. This case study illustrates the practical use of the approach and the software in the context of river habitat management.

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

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Introduction

To survive, grow and complete their life cycle, many fish species need to chronologically access different habitats providing for particular life functions (i.e. feeding, refuge, spawning) and life stages. In rivers and streams, the spatial and temporal variation of flow velocity, bed morphology, vegetation and temperature contribute to creating and maintaining a dynamic mosaic of habitat patches (Statzner, 1981, Pringle *et al.*, 1988). The resulting heterogeneity provides a variety of complementary functional habitats for fish (Schlosser, 1995, Le Pichon *et al.*, 2016). The spatial configuration of complementary habitats and the connectivity between them affects fish dispersion and migration, which in turn have an impact on the spatial variation in genetic diversity, community composition and metapopulation dynamics (Fullerton *et al.*, 2010). Throughout the world, anthropogenic river channel alterations such as dams, culverts, weirs, dykes and derivations have over the years decreased the natural connectivity of fluvial systems, restricting the movement of organisms and threatening biodiversity (Elosegi *et al.*, 2010). To tackle this issue, aquatic conservation and management planners are putting increasing effort in stream restoration aiming at reducing habitat fragmentation (Merenlender and Matella, 2013).

Habitat connectivity describes how the environment facilitates or restricts dispersal or migration of organisms between habitats patches (Taylor *et al.*, 1993). The so-called ‘structural’ habitat connectivity reflects the physical structure of the landscape (i.e. shape, size and relative location of habitat patches, presence of natural and artificial barriers)

(Baudry and Merriam, 1988). In contrast, 'functional' connectivity reflects how organisms respond to the physical structure of the river in terms of mobility between habitats. Being species- and life stage- specific, functional connectivity in riverscapes defines the capacity or the ease at which aquatic organisms can travel from a habitat patch to another depending on their swimming capacities or dispersal behaviour, energy costs and mortality risks involved. Considering its importance for the persistence of populations (Fahrig and Merriam, 1994), gaining knowledge of species-specific functional connectivity for particular rivers is crucial, and provides in many cases a more useful perspective for addressing specific management problems. In particular, assessing functional connectivity might be especially valuable in the context of barrier removal projects, as it could help decision makers to prioritize restoration actions (Branco et al., 2014, Rivers-Moore et al., 2016).

Estimates of functional habitat connectivity can be obtained through empirical measurements of fish dispersion and migration rates using various bio-telemetry and mark-and-recapture techniques (Kanno *et al.*, 2014). At the scale of river networks, population genetics can also be used to determine biological connectivity through its footprints in the reproductive history of individuals and populations (Torterotot *et al.*, 2014). However, acquiring such data is costly and can be logistically challenging. An alternative solution is to model functional habitat connectivity, providing quantitative estimates of accessible habitat area. This approach might be particularly useful as a decision-support tool for wildlife managers and landscape planners.

Terrestrial landscape ecologists have a tradition of modeling connectivity using numerous approaches based on Euclidian distances (Mühlner *et al.*, 2010), diffusion (Reeves and Usher, 1989), corridor definition (Gilbert-Norton *et al.*, 2010) and graph theory (Rayfield *et al.*, 2011). Although connectivity has been widely studied in streams and rivers (e.g. Pringle, 2003, Moilanen *et al.*, 2008), methodologies to model stream habitat connectivity adapted to the longitudinal constraints of a river structure and the directionality imposed by flow velocity are more recent (Fullerton *et al.*, 2010). Among different research paths, 1D methods based on graph- or network theory have recently generated enthusiasm (Eros *et al.*, 2011, Van Looy *et al.*, 2014). While graph-theory is useful for providing a schematic representation of the interconnections between habitat patches at the scale of large river networks, it might not always be the best option to characterize connectivity of smaller-scale continuous habitat maps, particularly to account for areas located outside suitable habitat patches.

An alternative approach to modelling habitat connectivity is to estimate the shortest distance (within wetted area) to or from habitat patches at the pixel level of 2D raster maps (Jensen *et al.*, 2006). As heterogeneous environments might induce variable resistance to movement, cost-distance functions (Knaapen *et al.*, 1992) can be used in order to identify least-cost paths (or functional distances) between locations (Adriaensen *et al.*, 2003). This approach is well suited to analyze continuous aquatic data over large extents, which are becoming increasingly available. In particularly, high resolution remote sensing imagery provides solutions to map numerous variables such as bathymetry and water temperature (McKean *et al.*, 2009, Dugdale *et al.*, 2013, Tamminga *et al.*, 2015). A 2D raster-based approach to analyze connectivity is particularly useful to describe large rivers, fluvial lakes and estuaries with connected waterbodies, where fish can possibly move in every direction rather than only up- or downstream in a network. Hence, by adopting a continuous view of the river and its spatially heterogeneous environment, this approach is in line with a "riverscape perspective", which is increasingly considered as desirable for carrying out effective research and planning conservation (Fausch *et al.*, 2002, Wiens, 2002, Fullerton *et al.*, 2010, White *et al.*, 2014).

The objective of this paper is to (i) describe a free software (Anaqualand 2.0) designed to quantify functional habitat connectivity of mobile organisms in streams and rivers and to (ii) show the usefulness of this approach to evaluate the potential connectivity changes resulting from river modifications. Based on least-cost path modeling, Anaqualand 2.0 software differs from available GIS tools by accounting for fish movement directionality (up- and downstream) and allows converting connectivity between habitat patches into species- and life-stage-specific probability of access. To illustrate this potential, Anaqualand 2.0 was used in a case study to model brown trout (*Salmo trutta*) habitat connectivity and the probability of reaching spawning sites (ie. habitat accessibility) under scenarios of barrier removal to help prioritize connectivity restoration actions.

Anaqualand 2.0 program overview

The software allows the user to quantify the structural and functional connectivity between habitat patches or point coordinates in the upstream, downstream or in both directions (Le Pichon *et al.*, 2006). Structural connectivity can be quantified by calculating instream distances between habitat patches (i.e. shortest path within the channel boundary) and resistance to movement is assumed to be homogeneous across the river. In contrast, functional connectivity integrates the distance between patches and a spatially variable resistance to movement allowing to identify least-cost paths between patches expressed as a minimal cumulative resistance (MCR) (Knaapen *et al.*, 1992, Adriaensen *et al.*, 2003). This approach is based on the general assumptions of optimal foraging theory (Davies *et al.*, 2012) predicting that fish will tend to minimize the energy costs while they travel (Giske *et al.*, 1998). Thus, the least-cost path between two functional habitat patches might sometimes imply travelling a longer distance than the shortest instream distance in order to avoid an obstacle or risky area. Anaqualand 2.0 is freely available and can be downloaded from the internet (http://www6.rennes.inra.fr/sad/Outils-Produits/Outils-informatiques/Anaqualand).

Input data and habitat patch delineation

Anaqualand 2.0 requires to input a raster map (ascii format) describing the physical template of the river. Coordinates of the upstream and downstream ends of the study stream are required to indicate stream flow directionality. Depending on data availability and objectives, it may be a simple binary map displaying the river outline (water/not water) or a more detailed categorical map containing depth classes, morphological units, physical or chemical barriers, etc. Multiple sets of resistance values, for up- and downstream directions, specific to each species and life stage studied, can be uploaded. One or several functional habitats maps can be added to examine the connectivity to or between them (e.g. refuge to foraging habitat or spawning to nursery). Optimally, resistance to movement can be determined through empirical studies of fish mobility in heterogeneous environments (see Beier *et al.*, 2008 for review). However, as such studies are complex to carry out, few empirical resistance estimates have been yet published (but see Turgeon *et al.*, 2010). Therefore, from a management perspective, resistance values based on expert opinion and literature review (Beier *et al.*, 2008) is often considered as a justifiable trade-off.

Instream distances and functional distance maps

Instream distances are defined as the shortest paths between a source and a target within the channel boundary. Functional distance, defined as the least-cost path between two locations, is expressed as the minimal cumulative resistance (MCR). Anaqualand 2.0 allows the user to create functional distance maps, in which every pixel values express the minimal cost to reach the closest habitat of the specified type. Functional distance can be calculated: 1) either for all patches or for a selection of patches, 2) either for all patches simultaneously (one map of functional distance to reach the nearest patch) or separately for each patch (several maps of functional distance to reach single patches), 3) either in upstream (functional distance to reach the nearest upstream patch), in downstream (functional distance to reach the nearest downstream patch) or in both directions (functional distance to reach the nearest patch independently of flow direction).

Probability of access maps

As accessibility decreases with functional distance traveled, functional distance maps (MCR) can be converted into accessibility maps using a decreasing probability transformation function and a mobility coefficient (α) (Le Pichon *et al.*, 2006). Four functions are available: 1) linear, 2) Gaussian, 3) exponential or 4) threshold-driven. The function used depends on the behaviour of the target species. In case of uncertainty, multiple curves can be computed as a way to perform a sensitivity analysis. A Gaussian transformation would illustrate a population characterized by most fish reaching moderate distances and few traveling long distances; while an exponential transformation would characterize a population in which few fish that are mobile may travel over longer distances and a threshold driven curve could be used when resistance features present lethal conditions or an absolute physical barriers. The mobility coefficient (α), a parameter estimated in meters is calibrated based on the existing knowledge of the species- and life-stage-specific home range extent or migration distances (Hanski, 1994, Vos *et al.*, 2001).

Case study

Context and objectives

With the adoption of the Water Framework Directive (Council of the European Communities, 2000), European countries have referenced and mapped stream barriers and have set targets of conservation and restoration of water bodies. In this context, the Haute Vallée de Chevreuse Natural Regional Park, France, is carrying out a project aiming at restoring ecological continuity of streams on its territory using barrier removal or channel restoration at the bottom of the valley. However, due to the high number of barriers and the limited resources, action prioritization is crucial to maximize their potential short and medium term ecological benefits (Gangloff, 2013).

Brown trout (*Salmo trutta*) is a European species of salmonid that is considered as a flagship species in France, indicator of good ecological status of rivers and important for sport fishing. In the Ile-de-France region, where streams are highly impacted by human activities and populations have markedly declined, it remains of high conservation importance in stream where small populations still exist. Allowing free passage might be important for freshwater brown trout resident populations, as mature individuals tend to migrate upstream in autumn from their daily-use rearing habitat to suitable spawning grounds (Jonsson and Jonsson, 2011). Outside the spawning season, most individuals display restricted mobility, while a fraction of the population is more mobile and move between suitable daily-use habitat (Jonsson and Jonsson, 2011). Therefore, restoring free passage outside the spawning season might allow fish to colonize upstream areas and increasing stream productivity. The progressive colonization of daily-use habitats might be stepping stones providing access to further spawning habitats. In this context, Anaqualand 2.0 appears to be an ideal tool for quantifying the changes in habitat availability associated with different scenarios of barrier removal in order to guide the allocation of resources in restoration of the Mérantaise. Specifically, this case study aims at estimating 1) accessibility to spawning/daily-use habitat from the downstream end of the study area, providing benefits of connectivity restoration for the downstream population, and 2) accessibility to spawning habitats from any daily-use habitat patches, providing overall habitat gains. To analyze the sensitivity of accessibility estimates, input parameters were varied in terms of a) resistance values adapted to fish life stage, b) mobility coefficients and c) probability transformation functions.

Study area

The Mérantaise is a first order stream draining a 31 km² catchment located 23 km south-west of Paris, in the Ile-de-France region. It is a tributary of the Yvette River belonging to the Seine River catchment (Figure 1a) (48°43’45”; 2°06’02”). The Mérantaise was identified as a priority stream, as it provides a high potential of spawning habitat for brown trout population restricted to a segment located downstream of an impassable mill weir (B3) (Figure 2). This stream is also considered as a reservoir of biological diversity bordered by wetlands and includes twenty-height terrestrial and aquatic protected species. Because of a long history of human impacts, the course of the stream is lined with several barriers originating from hydraulic structures (mill weirs) dating from the XIII to XIX century. The focus of this study is a 6 km–long segment of the Mérantaise contained within the Haute Vallée de Chevreuse Natural Regional Park. This stream segment is around 2-5 m-wide, its maximum depth in pools at low flow is approximately 1.0 m. The channel is generally incised, the average slope is 0.75% and the dominant substrate varies from mixtures of silt and sand to gravel and cobbles.

Field survey

Habitat characterization

Hydromorphological units (HMU) along the stream profile were visually delimited and mapped based on geomorphology and flow type (Newson et al., 1998). Riffle constituted 5%, runs 28%, glides 55% and pools 7% of the total area (Figure 1b). Twelve barriers, potentially restricting fish mobility, were identified, including three impassable mill weirs (1.0-1.5 m high, B3, B11 and B12) and nine barriers (0.1 m and 0.5 m high) created by culverts, crossing of waste water pipes and an old washhouse. Concave underbanks, presence of roots, boulders and aquatic plants, considered to be potential trout shelters, were visually identified and georeferenced using a handheld Garmin GPSMAP 62 (± 5 m). Potential spawning grounds were identified and georeferenced at low flow on the basis of substrate size and HMU, with the expert assistance of a river technician, highly experienced in counting trout redds in the PNRHVC streams.

Fish movement

Between March 2012 and April 2013, thirty-nine individuals were tracked using radio-telemetry in the 2 km-long downstream section of the study segment, limited by the impassable barrier B3. Fish were caught by electrofishing, anesthetized (10% eugenol solution), weighed, measured and tagged intra-peritoneally with radio transmitters (ATS® models F1020, F1040, and F1170 with encapsulated antenna) using the protocol defined by Gosset *et al.*, (2006). Location of individuals was monitored (i) continuously using two fixed-point receivers (ATS®, R4500S) installed on barriers and (ii) once a week with mobile receivers. Scales were collected to determine age and size at first reproduction. As all age 3+ and older trout presented spawning marks, it was further assumed that first reproduction occurred at age 2+. The body length (BL) of immature (1+ non-spawners, n=10) trout ranged from 178 to 226 mm and BL of mature trout (2+ and older, spawners, n=29) varied between 221 to 554 mm.

Data analysis

Habitat mapping

Potential spawning habitat patches were mapped based on georeferenced data using ArcGIS® (ESRI, 2011). Daily-use habitats were modeled using radio-telemetry data (outside the spawning season) and three spatial metrics: distance to pools (DP), distance to riffles (DR) and distance to shelters (DS), generated with Anaqualand 2.0. The three spatial metrics had proved to be predictors of the presence of trout in headwater streams of Ile-de-France (Le Pichon *et al.*, 2013), as the proximity of pools and riffles tend to provide fish with refuge and feeding opportunities (Ovidio, 1999, Ovidio *et al.*, 2002, Armstrong *et al.*, 2003). A generalized linear model was built to predict daily-use habitat using DS, DP and DR extracted at every radio-telemetry fish location and at every point of an equally-sized pseudo absence dataset generated randomly throughout the river segment ($S= -0.116 - (0.099*DS) - (0.445*DP) + (0.0248*DR)$ ($p=0.891, 0.023, 0.003, 0.069$)). To delineate discrete habitat patches, the raster map values were reclassified as a binary map using a probability threshold of 0.4. The resulting longitudinal distribution of the spawning and daily habitat patches are presented in Figure 1c.

Resistance maps

Raster maps of resistance, quantifying how trout mobility may be restricted by physical barriers, variable swimming energy costs and perceived predation risk, were created combining three variables: HMU (five types), barriers (N=12) and shelters (presence/absence). HMU, the twelve barriers and the shelters (5 m diameter circular buffer) were combined to yield 34 possible categories representing the five HMU and the twelve barriers with and without shelters. These classes will be further referred to as mesohabitats. Finally, thirteen resistance maps were generated according to the successive barrier removal scenarios (Figure 3).

Connectivity modelling

Resistance value assignation

Resistance values were determined using a simple model in which normalized values were assigned to HMU by expert opinion, by combining energy costs and predation risk (Table 1). Resistance values associated with energy costs were based on the assumption that resistance increases with flow velocity while predation risk decrease with shelter presence and HMU average depth, as deep flow provides better cover for salmonids than shallow flow (Rosenfeld and Boss, 2001) (Table 1). Resistance yielded values ranging between 0 and 10, calculated as R=log (1/(energy expenses * average depth * shelters). Similarly, resistances were assigned to barriers based on their height and on their passability (Baudoin *et al.*, 2014). Arbitrary high resistance values (2000) were assigned to the three weirs considered impassable (B3, B11 and B12) while resistance attributed to other barriers ranged between 20 and 150. Two separate sets of resistance values were generated for the two fish classes: mature fish (body length > 230 mm), corresponding to the average length of brown trout at maturity in the study stream, and immature fish (body length < 230 mm). For a discussion of alternative methods to determine resistances, see (Beier *et al.*, 2008).

Brown trout mobility coefficient (α)

Home range extents (distance between the two most distant locations), further used as mobility coefficients (α), were estimated from telemetry data. Home range extents were estimated 1) outside the spawning period for immature fish (mean: 143 m, 85th percentile: 338 m, max: 366 m) and mature fish (mean: 170 m, 85th percentile: 398 m, max: 774 m) and 2) during the spawning period for mature fish (mean: 351 m, 85th percentile: 710 m, max: 830 m).

Habitat accessibility

Resistance and functional habitats maps were used to compute functional distance maps expressing at each pixel the least cost for reaching 1) a daily-use habitat from the downstream end of the study section; 2) a spawning habitat from the downstream end of the study section and 3) a spawning habitat from a daily-use habitat. These analyses aimed to compare how easily immature and mature trout can complete their life cycle under different barrier removal scenarios. For each of these analyses, functional distances were then converted to accessibility (probability ranging between 0 and 1) using the mobility coefficients and two transformation curves (Figure 3). Although stream salmonids generally tend to exhibit a spatial behaviour better described by a decreasing exponential (fewer fish moving long distances), this pattern is not always consistent (Rodriguez, 2002). Therefore, a Gaussian transformation was also performed as part of a sensitivity analysis.

Connected functional habitat area

To quantify and visualize the overall accessibility, connected daily-use habitat area (CDHA), connected spawning habitat area (CSHA) and spawning habitat area connected to daily-use habitats (CS2DHA) were estimated as $\sum Ac_i \times A_i$, for i=1 to N (Number of pixels of the corresponding habitat) where A_{ci} stands for the accessibility of a pixel and A_i to pixel area. CDHA was calculated for immature and mature fish while CSHA and CS2DHA were calculated for mature fish.

Results

Cumulative longitudinal profile of (CSHA), accumulated along the longitudinal profile of the stream from downstream to upstream, gives a quantitative estimate of the overall availability of spawning habitat patches weighted by their accessibility for the mature trout under different barrier management scenarios and different levels of trout mobility (Figure 4). Under the scenario of maintaining all barriers, 500 m^2 of CSHA were estimated to be available in the first 1500 m of the stream profile for the fish of average mobility (α= mean) (Figure 4). Allowing fully free passage additionally increased CSHA for the latter by only 80 m^2. Furthermore, the habitat gain was associated with improved connectivity only to spawning habitats located in the first 2200 m, as independently of the barrier presence. In contrast, for the fish of higher mobility (α= 85th percentile and α= max scenarios), allowing free passage both increased connectivity and provided access to spawning habitats located upstream. This was particularly relevant for spawning habitats located between 1500 and 2000 m and to a lesser degree to those between 4000 and 5000 m upstream of the lower end of the study segment (Figure 4).

To estimate the potential gain related to removing each barrier, the total CSHA (Figure 5) and CDHA (Figure 6) were also quantified for successive barrier removal scenarios. While removing the first two barriers did not increase accessibility to CSHA, eliminating the third barrier B3 yielded between 155 and 245 m^2 of additional connected spawning habitats for mobile trout (α= 85th percentile and α=max). Then, removing barriers B5 to B8 provided access to a reach containing further suitable spawning habitats, whereas removing B9 to B12 did not increase CSHA (Figure 5). All together for the mobile fraction of the trout population (α= 85th percentile and α=max), spawning habitat connectivity index was increased from 31 ± 2% with all barriers maintained in place to

44 ± 3% in free passage conditions. In contrast to the results on the CSHA, the potential gains in connected daily-use habitat area (CDHA) for the Mérantaise related to the successive barrier removal were relatively low and varied significantly between fish of different mobility (Figure 6). Removing barriers did not increase the CDHA for lower mobility fish (α=mean) of both size. With high mobility coefficient (α= 85th percentile), an increase of CDHA is observed for both size with the Gaussian transformation function. With the very high mobility coefficient (α= max), a potential gain in CDHA ranging from 2% to 10% was associated with a free passage between B3 and B8 for immature fish with Gaussian transformation function and for mature fish.

With all barriers present, the longitudinal profile of spawning habitat accessibility displayed a decrease in probability of access from 1 to 0.5 from the downstream end of the study reach up to B3, after which the accessibility becomes close to null (Figure 7a). Allowing free fish passage up to B4 provided access to two large patches of spawning habitats located between B3 and B4 (Figure 7b). Lower gains in accessibility were also obtained in the segment between B10 and B11. The removal of barriers B4 to B8 only slightly increased the accessibility to spawning habitats located upstream starting from B6 and between B10 and B11 (Figure 7c). Removing the remaining barriers did not improve further habitat accessibility (Figure 7d).

Overall, even with all barriers present spawning habitat patches in the Mérantaise are generally well connected to daily-use habitats, with accessibility values estimated to be over 0.5 for all patches except those located between B3 and B4 (Figure 8 a). Removing B1 to B4 increased CS2DHA by 140 m^2 (6%) (Figure 8b). Removing further barriers did not provide access to otherwise unreachable habitats, but only slightly increased accessibility values to a few spawning patches (Figure 8 c –d).

Discussion

The presented approach of quantifying connectivity in streams and rivers is novel, adapting a two-dimensional functional landscape model (Adriaensen *et al.*, 2003) to stream ecology and integrating fish movement directionality. This approach provides means to incorporate the behavioural component of connectivity by including fish mobility at specific life stages, a challenge highlighted by Fullerton et al. (2010). Furthermore, the map-based approach might be more suitable than graph-based dendritic network approaches (Saura and Torné, 2009, Van Looy *et al.*, 2014, Segurado *et al.*, 2015) to account for longitudinal and lateral movements along the riverscape and the 2D physical heterogeneity of rivers. These features are of great importance as they allow continuous mapping of habitat variability in a context relevant to particular species and life stages at the intermediate scale of management actions (Le Pichon et al., 2016) that cannot be substituted by discrete data typically obtained from sampling multiple smaller reaches (Fausch *et al.*, 2002, White *et al.*, 2014). Moreover, the presented continuous approach could be complementary with large-scale riverscape approaches, using network drainage lines, for species such as wild salmon whose life-cycle involves movements across large geographic areas (Whited *et al.*, 2012). However, estimating habitat connectivity requires defining resistances and suitable habitat patches at a scale that is relevant to the species and life stages of interest. Therefore, grain size should preferably be smaller than the size of habitat patches and several times smaller than the species capacity of movement. Furthermore, the extent should be larger than the species capacity of movement. The method could be used to examine the small scale mobility of larvae in a reach using a fine scale hydrodynamic model as resistance as well as whale migration in an estuary dominated by large scale tidal currents. Although a limitation of the method consists in obtaining continuous data at the appropriate scale, such 2D riverscape scale data is becoming increasingly available at lower costs through high resolution remote sensing of water temperature (Dugdale *et al.*, 2013), bathymetry (Legleiter *et al.*, 2009), substrate granulometry (Carbonneau *et al.*, 2005) and flow velocity (Tamminga *et al.*, 2015, Hugue *et al.*, 2016).

Along with the general benefits of restoring ecological continuity, stream specific quantitative estimates of increase in habitat accessibility obtained through this raster-based method might provide managers and local decision makers with additional convincing arguments in favor of undertaking stream restoration efforts. Indeed, recently used in a multi-agent platform, connectivity estimates has contributed to overcome water use conflicts by providing a shared vision of the river (Carre et al. 2014).

Through the Water Framework Directive, European countries are recognizing the problem of aquatic habitat fragmentation and allocating budgets to progressively restore river channels and, where necessary, build structures to allow fish passage. Several methods have been recently suggested for prioritizing barrier removal including scoring and ranking barriers, stepwise scoring and ranking, scenario analysis, optimization, or complete enumeration (see McKay et al. 2016 for review). Anaqualand is well suited to perform scenario analyses and can handle either continuous or binary estimates of barrier permeability. The assessment of the cumulative impacts of multiple barriers possible with the software would help prioritizing barrier removal (Branco *et al.*, 2014, Cote *et al.*, 2009) with better efficiency than scoring-and-ranking approaches (Kemp and O'Hanley, 2010).

In this study, connectivity was expressed in terms of connected habitat, providing a decision support tool to compare different scenarios rather than precise estimates of probability of access. In the light of the conducted analysis, efforts in the case of Mérantaise should be concentrated on improving the passability of B3 barrier in order to both increase the area of accessible spawning habitats by 13% of the total habitat area for mobile trout and maximize the connectivity between spawning habitat and daily-use habitat patches. Such change is favorable, as improved connectivity between spawning and daily-use habitats might increase probability of habitat use (Flitcroft *et al.*, 2012). However, removing further barriers upstream would only slightly increase the total accessible habitat area due to more passable barriers and to the lower availability of functional habitats in this upstream reach. Therefore, the removal or modification of these barriers might be considered to be of low priority in terms of brown trout habitat management and conservation. Nevertheless, although removing barriers did not increase CDHA for lower mobility fish, removing barriers might improve future CDHA for these fish, as mobile fish will spawn in the upstream area and produce low mobility fish that in turn will use available daily use habitats.

Overall, caution must be taken when interpreting the results as they are affected by the choice of several parameters, such as the estimates of up- and downstream mobility, resistance assigned to barriers and probability distribution functions. For instance, the resistance assigned to barriers could vary according to water discharge and have an impact on connectivity for brown trout (Denic and Geist 2010). Furthermore, since there is a generally fairly high uncertainty associated with these input parameters, in addition to estimating connectivity for a plausible range of mobility parameters, it might be appropriate to assess the sensitivity of the results to different resistance model formulations and to interpret the results accordingly. In recent decades, knowledge of mobility behaviour and of the characteristics affecting barrier passability for many species has improved significantly (Ovidio and Philippart, 2002, Baudoin *et al.*, 2014). Nevertheless, more field studies quantifying the effect of physical habitat on fish mobility are still needed in order to properly calibrate spatially variable resistance to movement at different fish size and life stages. In cases where resistance values are unavailable, connectivity can still be estimated using a distance and mobility data only. In the future application of the model, it should also be considered that in parallel to increasing connectivity, additional benefits of barrier removal can include restoring channel morphology and bed granulometry. Such possible changes in both upstream and downstream habitats were not taken into account in this case study, but could be addressed by coupling Anaqualand with a two-dimensional hydraulic modelling.

Anaqualand could be useful for future work aiming at improving estimates of stream carrying capacities, in particular for species exhibiting distinct ontogenic shifts in habitat requirements during their life cycle. For instance, for brown trout, estimating successively the connectivity of adult daily use habitats to spawning habitats, of connected spawning to nursery habitats and of connected nursery habitats to juvenile daily use habitats might be useful to get a portrait of how habitats are linked through the life cycle. Comparing the habitat connectivity levels associated with each life stage might help to identify bottlenecks caused by habitat limitation and obtain better estimates of carrying capacity. Furthermore, the approach could also be used to improve habitat quality models of species using complementary habitats over a daily cycle, such as feeding habitats and shelters. This paper presented a case applied to fish but the method could as well be applied to other mobile organisms which dispersal is restricted by natural or anthropogenic constraints, such as aquatic invertebrates (Datry et al., 2016). Overall, Anaqualand may become a timely tool particularly helpful to fisheries managers, as evidence showing the critical importance of connectivity between habitats used throughout the life cycle for the productivity and persistence of fish populations is accumulating (Flitcroft *et al.*, 2012, Falke *et al.*, 2013, Bergeron et al. 2016). Finally, in addition to increased accessible habitat area as assessed in this case study, prioritisation of management efforts might also be established based on issues related to costs, the social context, local politics and to the cultural heritage designation associated with particular streams or historical obstacles (most often mill weirs; Kemp and O'Hanley, (2010).

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References

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E. 2003. The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning* **64**: 233-247.

Armstrong J, Kemp P, Kennedy G, Ladle M, Milner N. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* **62**: 143-170.

Baudoin, J.-M., Burgun, V., Chanseau, M., Larinier, M., Ovidio, M., Sremski, W., Steinbach, P., Voegtle, B., 2014. Informations sur la Continuité Ecologique-ICE, Evaluer le franchissement des obstacles par les poissons. Principes et méthodes. Onema, Paris. 204pp.

Baudry J, Merriam HG. 1988. Connectivity and connectedness: functional versus structural patterns in landscapes. In *Connectivity in Landscape Ecology*, Schreiber KF (ed). in Schreiber, K. F. ed. Connectivity in landscape ecology, Proceedings of the 2nd International Association for Landscape Ecology. Munstersche Geographische Arbeiten 29, p.23-28.

Beier P, Majka DR, Spencer WD. 2008. Forks in the Road: Choices in procedures for designing wildland linkages. *Conservation Biology* **22**: 836-851.

Bergeron N, Roy M, Le Pichon C, Gillis CA, Bujold JN, Mingelbier M, 2016. Functional habitat chronology analysis: integrating life stages habitat requirements and habitat connectivity for estimating river production potential. Paper 26203 in, Webb JA, Costelloe JF, Casas-Mulet R, Lyon JP, Stewardson MJ (eds.) *Proceedings of the 11th International Symposium on Ecohydraulics*. Melbourne, Australia, 7-12 February 2016. The University of Melbourne, ISBN: 978 0 7340 5339 8.

Branco P, Segurado P, Santos JM, Ferreira MT. 2014. Prioritizing barrier removal to improve functional connectivity of rivers. *Journal of Applied Ecology* **51**: 1197-1206.

Carbonneau PE, Bergeron N, Lane SN. 2005. Automated grain size measurements from airborne remote sensing for long profile measurements of fluvial grain sizes. *Water Resources Research* **41:** 1-9, W11426 (doi: 10.1029/2005WR003994).

Carre C, Haghe J-P, De Coninck A, Becu N, Deroubaix J, Pivano C, Flipo N, Le Pichon C, Tallec G. 2014. How to integrate scientific models in order to switch from flood control river management to multifunctional river management? *International Journal of River Basin Management* **12**: 1-30.

Cote D, Kehler D, Bourne C, Wiersma Y. 2009. A new measure of longitudinal connectivity for stream networks. *Landscape Ecology* **24**: 101-113.

Council of the European Communities. 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Communities.

Datry T, Pella H, Leigh C, Bonada N, Hugueny B. 2016. A landscape approach to advance intermittent river ecology. *Freshwater Biology* **61**: 1200-1213.

Davies NB, Krebs JR, West SA. 2012. *An introduction to behavioural ecology*. John Wiley & Sons.

Denic M, Geist J. 2010. Habitat suitability analysis for lacustrine brown trout (Salmo trutta) in Lake Walchensee, Germany: implications for the conservation of an endangered flagship species. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**: 9-17.

Dugdale SJ, Bergeron NE, St-Hilaire A. 2013. Temporal variability of thermal refuges and water temperature patterns in an Atlantic salmon river. *Remote Sensing of Environment* **136**: 358-373.

Elosegi A, Diez J, Mutz M. 2010. Effects of hydromorphological integrity on biodiversity and functioning of river ecosystems. *Hydrobiologia* **657**: 199-215.

Eros T, Schmera D, Schick RS. 2011. Network thinking in riverscape conservation - A graph-based approach. *Biological Conservation* **144**: 184-192.

ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Fahrig L, Merriam G. 1994. Conservation of Fragmented populations. *Conservation Biology* **8**: 50-59.

Falke JA, Dunham JB, Jordan CE, McNyset KM, Reeves GH. 2013. Spatial ecological processes and local factors predict the distribution and abundance of spawning by Steelhead (Oncorhynchus mykiss) across a complex riverscape. *Plos One* **8,** e79232, 1-11.

Fausch KD, Torgersen CE, Baxter CV, Li HW. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *BioScience* **52**: 483-498.

Flitcroft RL, Burnett KM, Reeves GH, Ganio LM. 2012. Do network relationships matter? Comparing network and instream habitat variables to explain densities of juvenile coho salmon (Oncorhynchus kisutch) in mid-coastal Oregon, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* **22**: 288-302.

Fullerton AH, Burnett KM, Steel EA, Flitcroft RL, Pess GR, Feist BE, Torgersen CE, Miller DJ, Sanderson BL. 2010. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. *Freshwater Biology* **55**: 2215-2237.

Gangloff MM. 2013. Taxonomic and ecological tradeoffs associated with small dam removals. *Aquatic Conservation: Marine and Freshwater Ecosystems* **23**: 475-480.

Gilbert-Norton L, Wilson R, Stevens JR, Beard KH. 2010. A meta-analytic review of corridor effectiveness. *Conservation Biology* **24**: 660-668.

Giske J, Huse G, Fiksen O. 1998. Modelling spatial dynamics of fish. *Reviews in Fish Biology and Fisheries* **8**: 57-91.

Gosset C, Rives J, Labonne J. 2006. Effect of habitat fragmentation on spawning migration of brown trout (Salmo trutta L.). *Ecology of Freshwater Fish* **15**: 247-254.

Hanski I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**: 151-162.

Hugue F, Lapointe M, Eaton BC, Lepoutre A. 2016. Satellite-based remote sensing of running water habitats at large riverscape scales: Tools to analyze habitat heterogeneity for river ecosystem management. *Geomorphology* **253**: 353-369.

Jensen OP, Christman MC, Miller TJ. 2006. Landscape-based geostatistics: a case study of the distribution of blue crab in Chesapeake Bay. *Environmetrics* **17**: 605-621.

Jonsson, B & Jonsson, N. (2011) Ecology of Atlantic salmon and brown trout: Habitat as a template for life histories. Fish and Fisheries Series 33, Springer, Dordrecht, The Netherlands, 708 pp.

Kanno Y, Letcher BH, Coombs JA, Nislow KH, Whiteley AR. 2014. Linking movement and reproductive history of brook trout to assess habitat connectivity in a heterogeneous stream network. *Freshwater Biology* **59**: 142-154.

Kemp PS, O'Hanley JR. 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. *Fisheries Management and Ecology* **17**: 297-322.

Knaapen JP, Scheffer M, Harms B. 1992. Estimating habitat isolation in landscape planning. *Landscape and Urban Planning* **23**: 1-16.

Le Pichon C, Gorges G, Faure T, Boussard H. 2006. Anaqualand 2.0 : freeware of distances calculations with frictions on a corridor. In. Cemagref: Antony; https://www6.rennes.inra.fr/sad/Outils-Produits/Outils-informatiques/Anaqualand.

Le Pichon C, Talès E, Clément F, Leclerc N, Gorges G, Zahm A. 2013. Effet des discontinuités physiques sur la distribution spatiale des poissons en tête de bassin : cas de l'Orgeval. In *L'observation long terme en environnement: Exemple du bassin versant de l'Orgeval*. Editions QUAE: Versailles.

Le Pichon C, Tales É, Gorges G, Baudry J, Boët P. 2016. Using a continuous riverscape survey to examine the effects of the spatial structure of functional habitats on fish distribution. *Journal of Freshwater Ecology* **31**: 1-19.

Legleiter CJ, Roberts DA, Lawrence RL. 2009. Spectrally based remote sensing of river bathymetry. *Earth Surface Processes and Landforms* **34**: 1039-1059.

McKay, S. K., Cooper, A. R., Diebel, M. W., Elkins, D., Oldford, G., Roghair, C., and Wieferich, D. 2016. Informing watershed connectivity barrier prioritization decisions: A Synthesis. *River Research and Applications*, doi: 10.1002/rra.3021.

McKean J, Nagel D, Tonina D, Bailey P, Wright CW, Bohn C, Nayegandhi A. 2009. Remote sensing of channels and riparian zones with a narrow-beam aquatic-terrestrial LIDAR. *Remote Sensing* **1**: 1065-1096.

Merenlender AM, Matella MK. 2013. Maintaining and restoring hydrologic habitat connectivity in mediterranean streams: an integrated modeling framework. *Hydrobiologia* **719**: 509-525.

Moilanen A, Leathwick J, Elith J. 2008. A method for spatial freshwater conservation prioritization. *Freshwater Biology* **53**: 577-592.

Mühlner S, Kormann U, Schmidt-Entling M, Herzog F, Bailey D. 2010. Structural versus functional habitat connectivity measures to explain bird diversity in fragmented orchards. *Journal of Landscape Ecology* **3**: 52-64.

Newson MD, Harper DM, Padmore CL, Kemp JL, Vogel B. 1998. A cost-effective approach for linking habitats, flow types and species requirements. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 431-446.

Ovidio M. 1999. Annual activity cycle of adult brown trout (*Salmo trutta* L.): A radio-telemetry study in a small stream of the Belgian Ardenne. *Bulletin francais de la peche et de la pisciculture* **352**: 1-18.

Ovidio M, Baras E, Goffaux D, Giroux F, Philippart JC. 2002. Seasonal variations of activity pattern of brown trout (*Salmo trutta*) in a small stream, as determined by radio-telemetry. *Hydrobiologia* **470**: 195-202.

Ovidio M, Philippart JC. 2002. The impact of small physical obstacles on upstream movements of six species of fish - Synthesis of a 5-year telemetry study in the River Meuse basin. *Hydrobiologia* **483**: 55-69.

Pringle C. 2003. The need for a more predictive understanding of hydrologic connectivity *Aquatic Conservation: Marine and Freshwater Ecosystems* **13**: 467-471.

Pringle CM, Naiman RJ, Bretschko G, Karr JR, Oswood MW, Webster JR, Welcomme RL, Winterbourn MJ. 1988. Patch dynamics in lotic systems : the stream as a mosaic. *Journal of North American Benthological Society* **7**: 503-524.

Rayfield B, Fortin M-J, Fall A. 2011. Connectivity for conservation: a framework to classify network measures. *Ecology* **92**: 847-858.

Reeves SA, Usher MB. 1989. Application of diffusion-model to the spread of an invasive species:the coypu in Great-Britain. *Ecological Modelling* **47**: 217-232.

Rivers-Moore N, Mantel S, Ramulifo P, Dallas H. 2016. A disconnectivity index for improving choices in managing protected areas for rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems* **26**: 29-38.

Rosenfeld JS, Boss S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 585-593.

Saura S, Torné J. 2009. Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. *Environmental Modelling & Software* **24**: 135-139.

Schlosser IJ. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia* **303**: 71-81.

Segurado P, Branco P, Avelar AP, Ferreira MT. 2015. Historical changes in the functional connectivity of rivers based on spatial network analysis and the past occurrences of diadromous species in Portugal. *Aquatic Sciences* **77**: 427-440.

Statzner B. 1981. The Relation Between' Hydraulic Stress' and Microdistribution of Benthic Macroinvertebrates in a Lowland Running Water System, the Schierenseebroks(North Germany). *Archiv für Hydrobiologie* **91**: 23-33.

Tamminga A, Hugenholtz C, Eaton B, Lapointe M. 2015. Hyperspatial remote sensing of channel reach morphology and hydraulic fish habitat using an unmanned aerial vehicule (UAV): a first assessment in the context of river research and management. *River Research and Applications* **31**: 379-391.

Taylor PD, Fahrig L, Henein K, Merriam G. 1993. Connectivity is a vital element of landscape structure. *Oikos* **68**: 571-573.

Torterotot J-B, Perrier C, Bergeron NE, Bernatchez L. 2014. Influence of forest road culverts and waterfalls on the fine-scale distribution of Brook trout genetic diversity in a boreal watershed. *Transactions of the American Fisheries Society* **143**: 1577-1591.

Turgeon K, Robillard A, Grégoire J, Duclos V, Kramer DL. 2010. Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. *Ecology* **91**: 3332-3342.

Van Looy K, Piffady J, Cavillon C, Tormos T, Landry R, Souchon Y. 2014. Integrated modelling of functional and structural connectivity of river corridors for European otter recovery. *Ecological Modelling* **273**: 228-235.

Vos CC, Verboom J, Opdam PFM, TerBraak CJF. 2001. Toward ecologically scaled landscape indices. *American Naturalist* **157**: 24-41.

White SM, Giannico G, Li H. 2014. A 'behaviorscape' perspective on stream fish ecology and conservation: linking fish behavior to riverscapes. *Wiley Interdisciplinary Reviews: Water* **1**: 385-400.

Whited DC, Kimball JS, Lucotch JA, Maumenee NK, Wu H, Chilcote SD, Stanford JA. 2012. A Riverscape analysis tool developed to assist wild salmon conservation across the North Pacific Rim. *Fisheries* **37**: 305-314.

Wiens JA. 2002. Riverine landscapes: Taking landscape ecology into the water. *Freshwater Biology* **47**: 501-515.

Table 1. Values assigned to predation risk (average depth and shelter) and energy costs associated with each mesohabitat to calculate resistance (R (R=log (1/(energy costs * predation risk)). Note that higher scores yields lower resistance 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)

Figure 1. Study area, a) Location of the study site (star), the Merantaise stream in the Seine River Basin, b) pseudo three-dimensional representation of the river profile with location of spawning and daily use habitat patches c) longitudinal profile of barriers and hydromorphological units (HMU) indicated as white bars.

Figure 2. Mérantaise stream study site. a. View of a riffle during the winter. b. View of the Seuil d'Ors mill weir (B3) during the summer.

Figure 3. Flowchart used to model brown trout habitat accessibility. a) Input data, b) Input parameters and c) Connected habitat availability output for the three analyses yielding estimates of 1) connected daily use habitat area (CDHA) from downstream 2) connected spawning habitat area from downstream (CSHA) and 3) connected spawning to daily use habitat area (CS2DHA). Connected habitat availability was estimated for varying functional habitat connectivity (N=3), scenarios of successive upstream barrier removal (N=13), fish size for CDHA (N=2), mobility coefficients (N=3) and probability of access transform function (N=2).

Figure 4. Cumulative longitudinal profile of connected spawning habitat area (CSHA) (m^2) accessible to mature trout during the spawning period. Symbol shapes represent degrees of trout mobility: including average (mean), high (p85: 85th percentile) and very high (maximum) mobility; line type corresponds to two management scenarios: with all twelve barriers present (barriers) and in free passage conditions (no barriers); symbol color reflects the probability transform function: Gaussian (ga) or exponential (ex). B1 to B12 indicate barrier locations. "0" at the x-axis corresponds to the downstream end of the study segment.

Figure 5. Spawning habitat accessibility index, expressing the ratio between the connected spawning habitat area (CSHA) and the total spawning habitat area in percentage, for mature trout. Average mobility trout (mean), high mobility trout (p85: 85th percentile) and very high mobility trout (max) are represented by different symbol shapes; symbol color reflects the probability transform function used: Gaussian (ga) or exponential (ex). Grey area displays the envelope of accessibility values for mobile trout (85th percentile and max).

Figure 6. Daily-use habitat accessibility index, expressing the ratio between the connected daily-use habitat area (CDHA) and the total daily-use habitat area in percentage. Symbol size reflects two fish size classes considered: mature fish (m); and immature trout (i). Symbol type allows to distinguish between average mobility trout (mean), high mobility trout (p85: 85th percentile) and very high mobility trout (max), outside the spawning season. Symbol color reflects the probability transform functions used: Gaussian (ga) and exponential (ex). Grey area displays the range of connectivity values for mobile trout (85th percentile and max).

Figure 7. Pseudo two-dimensional profile of the accessibility of spawning habitat from the downstream end of the study section. Different management scenarios are presented: a) all barriers are maintained, b) accessibility gain (increase) when removing B1-B4 compared to the scenario a), c) accessibility gain when removing B1-B8 compared to the scenario b), d) accessibility gain when removing B1-B12 compared to the scenario c). The cases shown were calculated for mature fish with very high mobility (α=max) and using the exponential function of decrease in probability of access. B1 to B12 and stars indicated the location of barriers.

Figure 8. Pseudo two-dimensional profile of the accessibility of spawning habitat patches from daily use habitat patches located upstream or downstream. Different management scenarios are presented: a) all barriers are maintained, b) accessibility gain (increase) when removing B1-B4 compared to the scenario a), c) accessibility gain when removing B1-B8 compared to the scenario b), d) accessibility gain when removing B1-B12 compared to the scenario c). The cases shown were calculated for mature trout with very high mobility (α=max) and using the exponential function of decrease in probability of access. B1 to B12 and stars indicated the location of barriers.

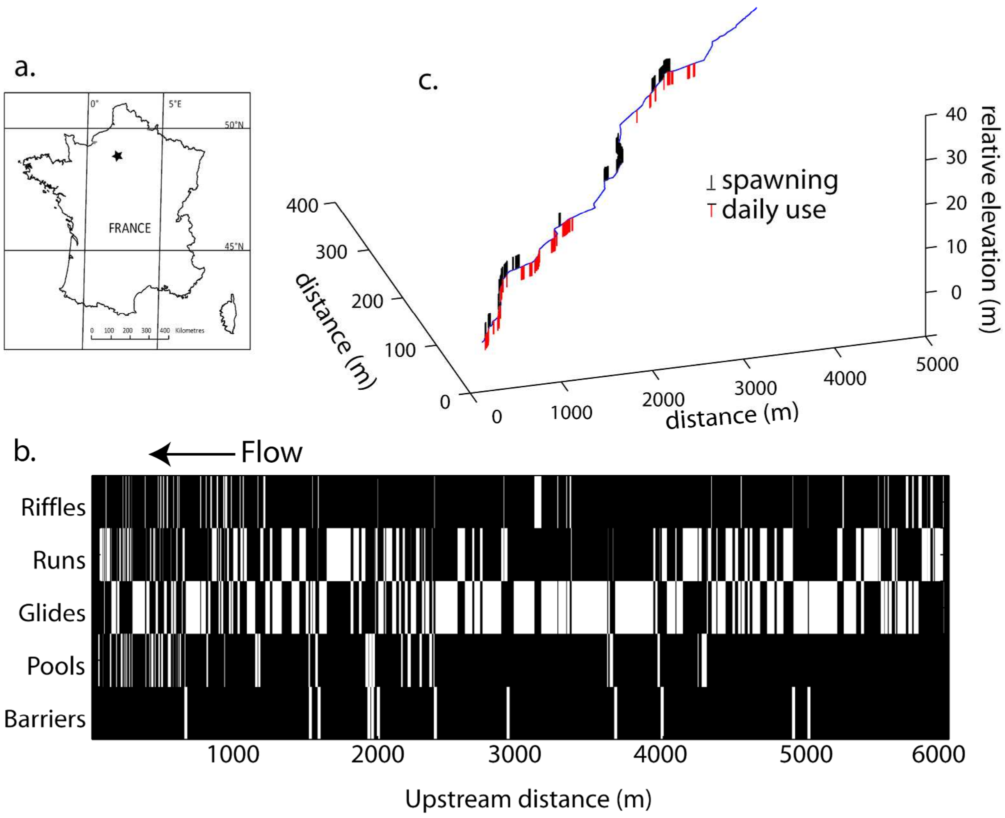
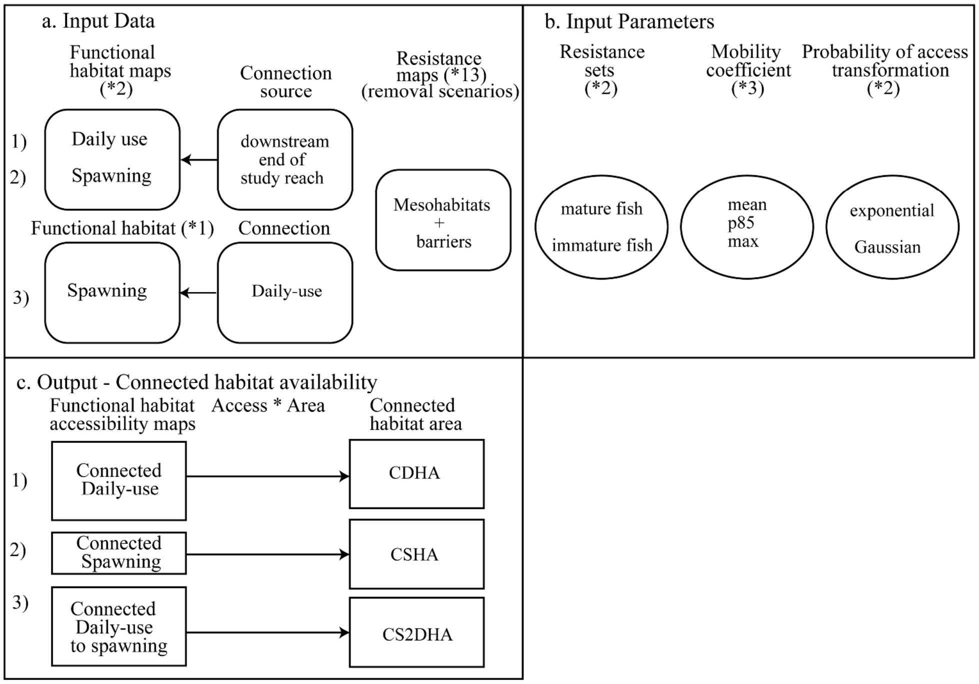


Figure 1
120x109mm (600 x 600 DPI)

Figure 2
161x65mm (300 x 300 DPI)



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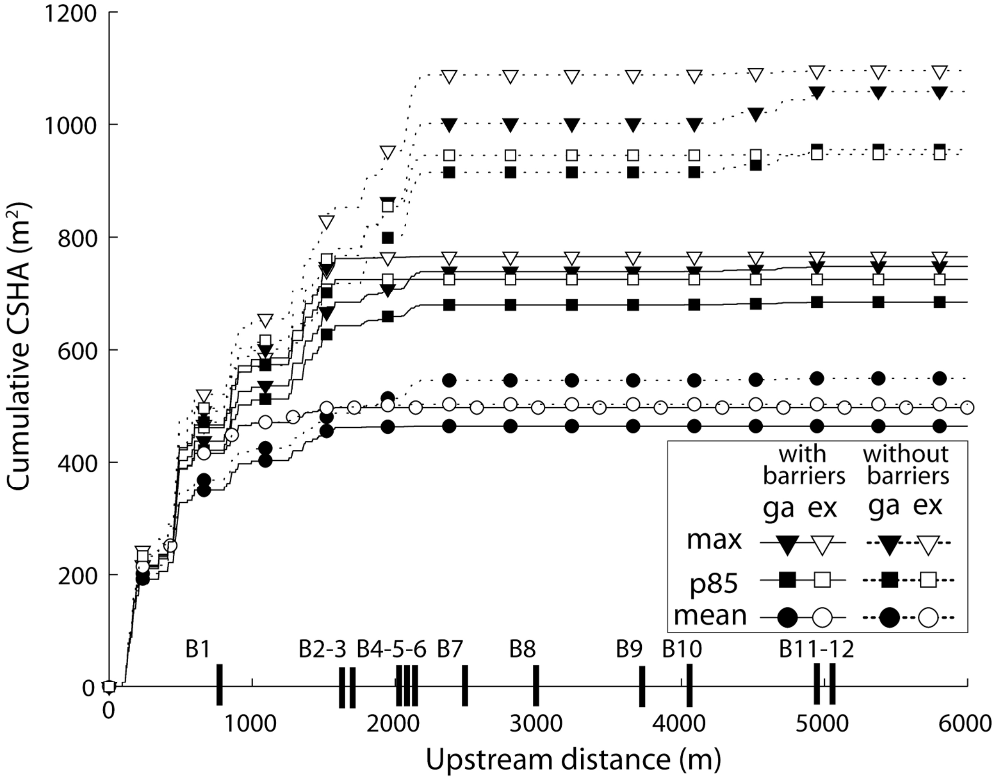

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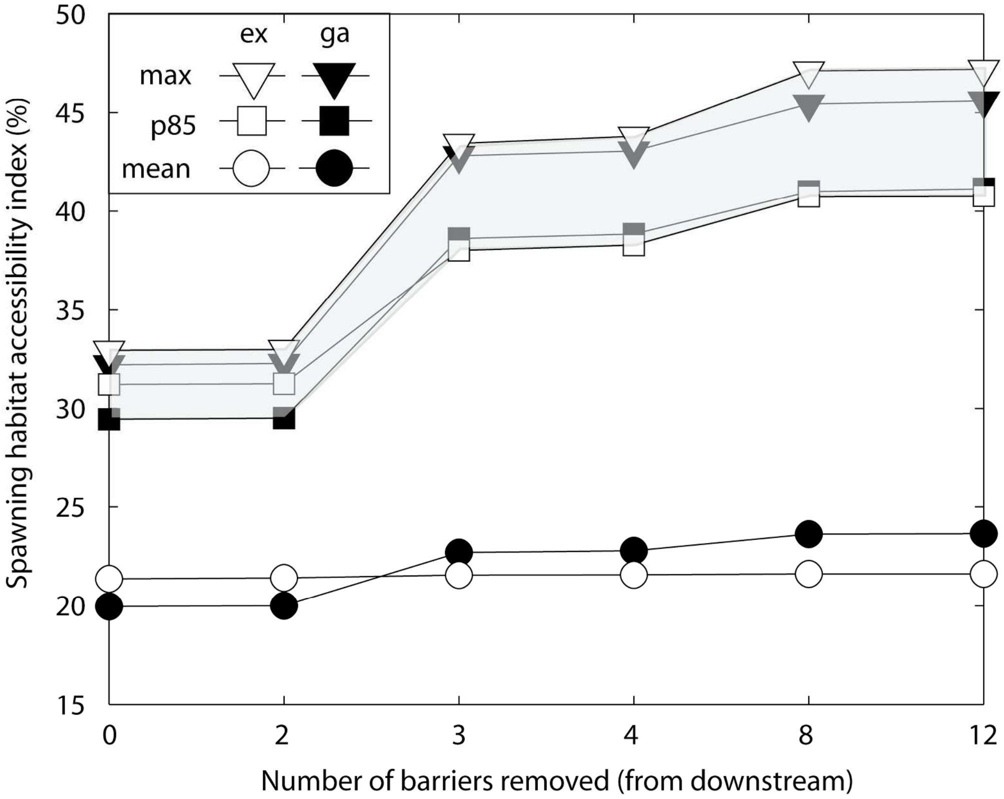

Figure 5
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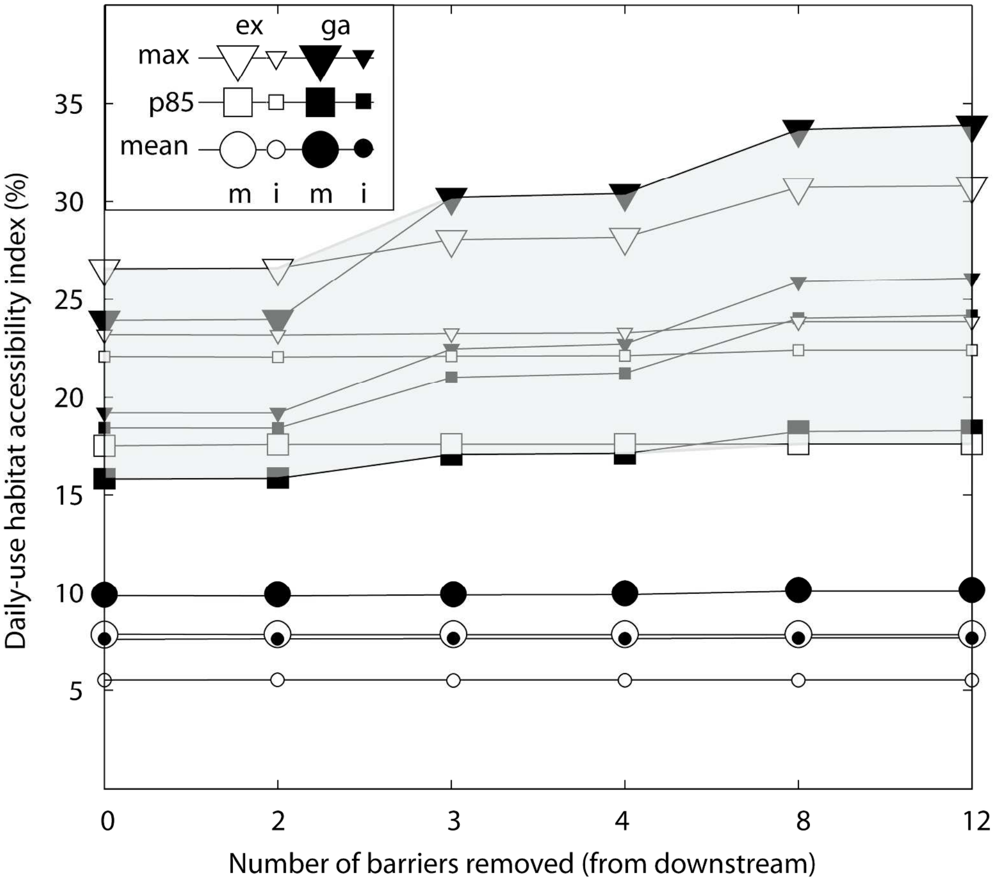

Figure 6
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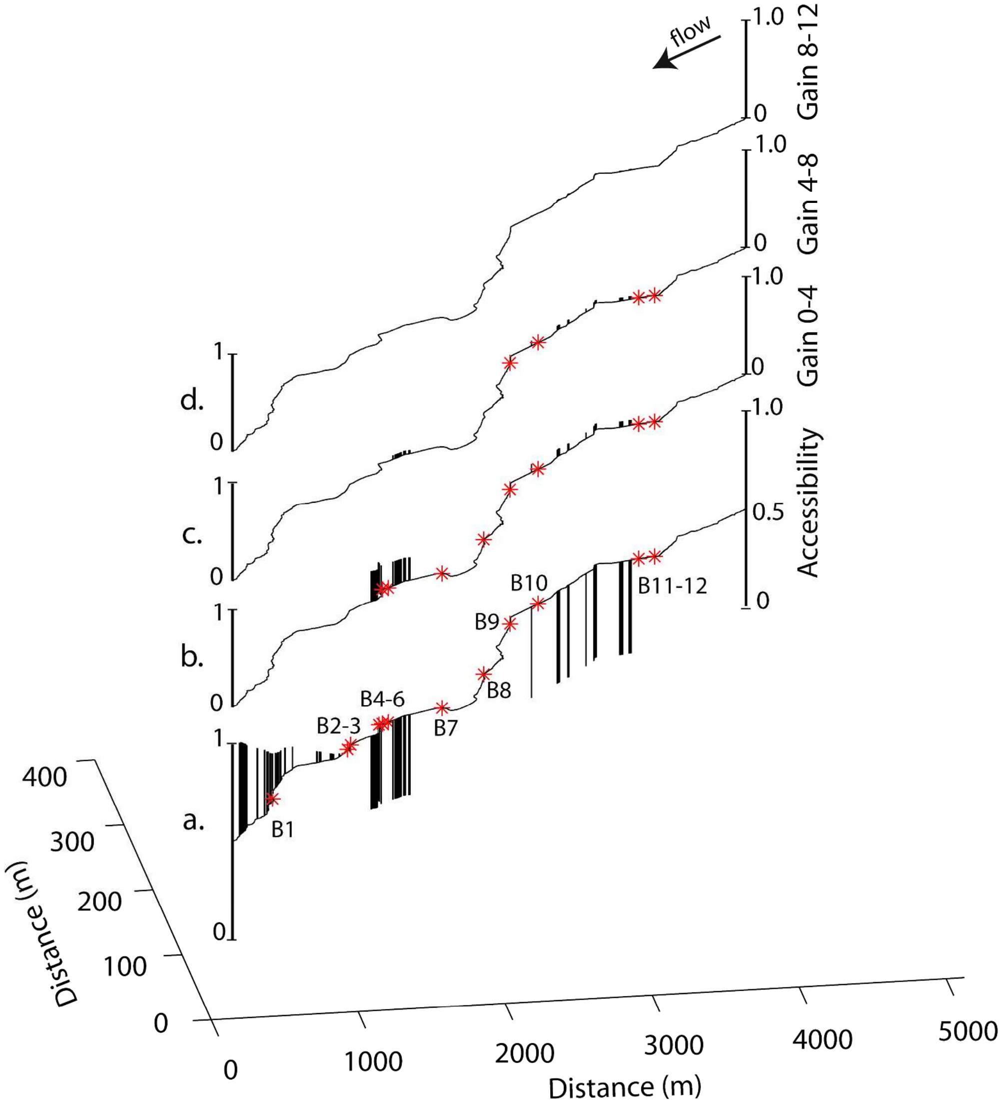

Figure 7
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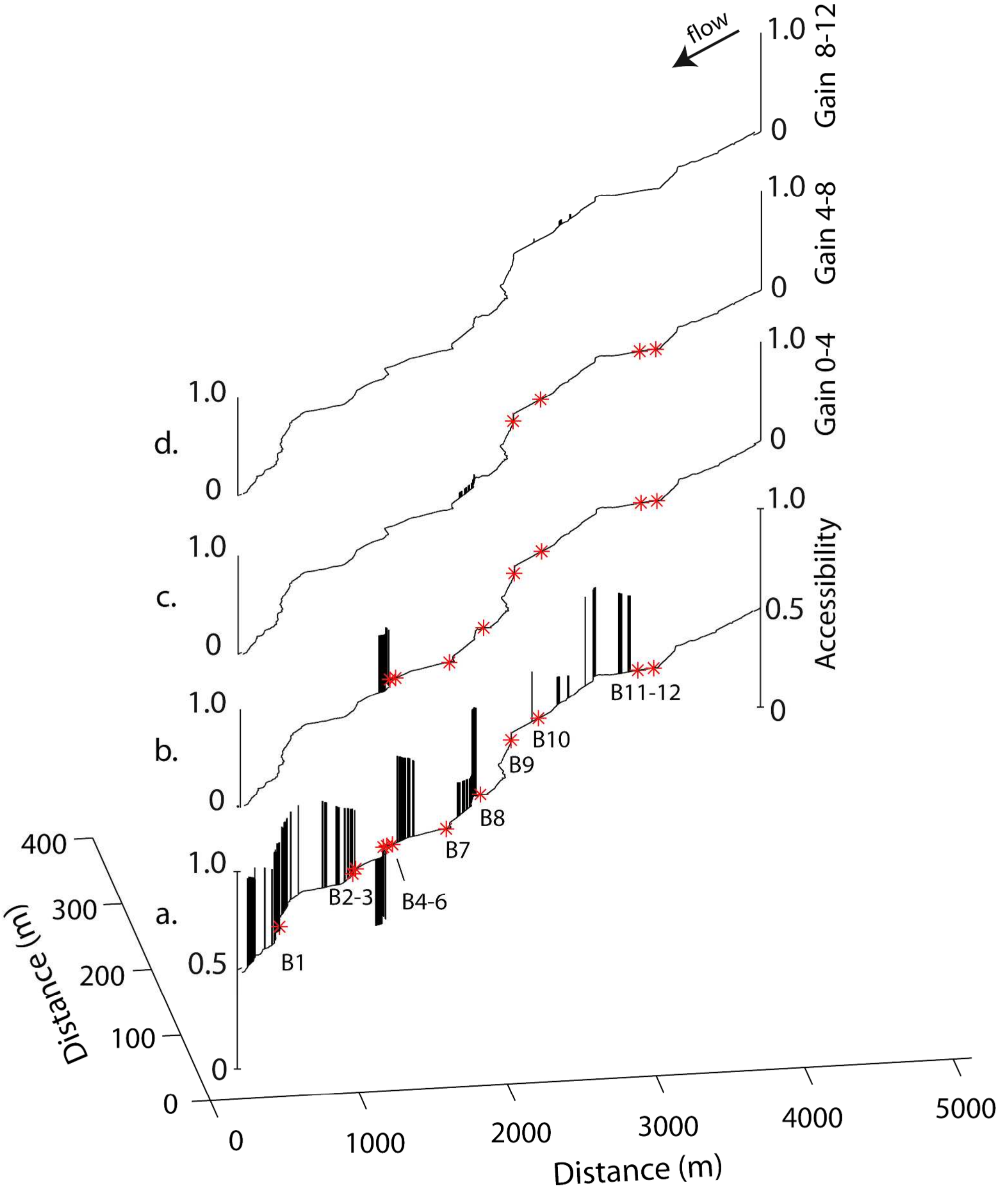

Figure 8
155x185mm (600 x 600 DPI)