

A scale-sensitive connectivity analysis to identify ecological networks and conservation value in river networks

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A scale-sensitive connectivity analysis to identify ecological networks and 1 2 conservation value in river networks. 3 Connectivity analysis in river networks 4 5 Kris Van Looy, Cyril Cavillon, Thierry Tormos, Jérémy Piffady, Philippe Landry and Yves 6 Souchon 7 8 K. Van Looy (kris.van-looy@irstea.fr), National Research Institute of Science and Technology for 9 Environment and Agriculture IRSTEA Lyon, UR MALY, River hydro-ecology unit ONEMA 10 IRSTEA, 5 rue de la Doua - CS70077 - 69626 Villeurbane-Lyon cedex, France 11 C. Cavillon (cyril.cavillon@irstea.fr), National Research Institute of Science and Technology for 12 Environment and Agriculture IRSTEA Lyon 13 T. Tormos (Thierry.tormos@onema.fr), French National Agency for Water and Aquatic Environments 14 (ONEMA), River hydro-ecology unit ONEMA IRSTEA, Lyon France 15 J. Piffady (Jeremy, piffady@irstea.fr), National Research Institute of Science and Technology for 16 Environment and Agriculture IRSTEA Lyon 17 P. Landry (philippe.landry@oncfs.gouv.fr), National Wildlife Office (ONCFS), Research unit, 5 rue 18 Saint Thibaud, Saint Benoît, 78610 Auffargis, France 19 Y. Souchon (Yves.souchon@irstea.fr), National Research Institute of Science and Technology for 20 Environment and Agriculture IRSTEA Lyon. 21 22 Keywords: Ecological Niche Factor Analysis, Integral Index Connectivity, network analysis, 23 hydro-morphological quality, otter

25 Abstract

26 Existing methods for connectivity analysis still lack the accuracy required to cover both the necessary 27 resolution of explanatory factors and the dispersion events to explain functional connectivity over 28 larger territories or complex structures like dendritic river networks. To consider such relationships 29 between network structure and ecological patterns, we propose a method that allows dealing with this 30 problem of scale and resolution in the connectivity analysis of dendritic network structures, here 31 illustrated for the re-colonization of the French Loire river basin by the European otter. The ecological 32 niche factor approach is applied to infer favourable habitat in the river network based on large scale 33 data of land use and hydro-morphology of river segments for the entire river basin. Stressors to the 34 riparian zone of channel straightening, urbanisation and forest fragmentation are identified in this way 35 as the principal factors explaining otter occurrence. Based on this qualification of habitat favourability, 36 the integral index of connectivity quantifies habitat availability and connectivity in the dendritic river 37 network. When we calculate the integral index of connectivity over different spatial extents by 38 constraining network distances, the scale-sensitivity of the network's connectivity emerges. Counting 39 for high mobility (high connection distances) identifies conservation networks and priorities mainly in 40 downstream parts of the river basin, whereas zooming in on smaller network distances sorts more 41 restricted high quality areas in central and upstream parts. Finally, the presented approach performed 42 better than distribution modelling approaches in explaining species occurrence over the river network 43 and confirms the crucial aspect of connectivity in the otter re-colonization.

45 Introduction

46 Recent theoretical and experimental studies revealed how limits in network connectivity represent key 47 constraints for species persistence in dendritic networks (Fagan 2002; Carrara et al. 2012). In the real 48 world this essential role of connectivity still needs to be evidenced, which is hampered by the large 49 variation in temporal and spatial scales of analysis (Hannah 2011), and by the lack of knowledge on 50 relationships between network structure and ecological patterns in dendritic networks (Ganio et al. 51 2005). The association of habitat quality and network structure with colonization processes in different 52 settings and species is still poorly understood, but essential to prioritize conservation and restoration 53 (Robles and Ciudad 2012; McCarthy et al. 2012; Carranza et al. 2012). For this challenge, ecological 54 network analysis shows a remarkable expansion of methods in modelling techniques (Thuiller et al. 55 2009) and concepts like the integration of graph methods (Minor and Urban 2008), but little progress 56 is made in bridging the gap between these methods and their applicability for the identification of 57 conservation networks at large scales (Chetkiewicz et al. 2006; Laita et al. 2011; Carroll et al. 2012). 58 Large-scale analysis for connectivity often still lacks the accuracy to integrate the relevant factors in 59 the coarse-grained maps, and the methods covering small areas cannot be applied over larger 60 territories (Beier et al. 2011).

61

62 To tackle this problem of scale and resolution in the design of conservation networks, we propose a 63 scale-sensitive approach based on a connection-constrained analysis of network connectivity. We 64 illustrate the developed approach with the distribution data of the European otter in the Loire River 65 basin. In the last 2 decades a recovery of otter is observed for most of its West-European distribution. 66 This recovery is recorded for Spain (Cortés et al. 1998), Italy (Loy et al. 2009) and France (Janssens et 67 al. 2008) after many decades of decline (Lodé 1993). In the Loire river basin a core of historical 68 population persisted and a strong re-colonization is observed (Janssens et al. 2008). We cross-examine 69 the species' distribution with land cover and environmental variables both at the river segment and the 70 sub-catchment scale, to identify available habitat with a graph-based method for connectivity analysis 71 (Saura and Rubio 2010; Eros et al. 2011; Minor and Urban 2008). Quantifying available habitat and 72 connections in networks over larger scales necessitates the integration of environmental variables at

73	different scales (Rouget et al. 2006). The choice of target species for prioritizing conservation
74	determines the resolution of environmental data needed and the connectivity required (Arponen et al.
75	2012), both with regard to resource selection and mobility (Moilanen and Hanski 2001), as to potential
76	biotic interactions (Godsoe et al. 2012). The otter is often presented as target species and indicator for
77	the connectivity and quality of the river ecosystem (Robitaille and Laurance 2002). Population
78	dynamics of the otter plays at the river basin scale, while individuals experience the local habitat and
79	its connectivity at the river segment scale. These two scale levels are the relevant scales to gather data
80	for the assessment of river corridor quality and functions (Allan 2004; Wiens 2002).
81	In this contribution we describe the proposed method of integrated network connectivity and habitat
82	availability assessment and compare it to more commonly used distribution model approaches both in
83	its power to predict species occurrence in the river network, and to its ability to highlight the
84	contribution of connectivity in relationship to the observed ecological pattern of the otter re-
85	colonization over the river network. For this validation the importance of connectivity for otter was
86	tested in a part of the river basin where the re-colonization was fully accomplished.
87	

89 Methods

90 **Observational data for otter**

Data of otter presence was gathered in the Loire Basin by a network of associations' volunteers 91 92 gathered under the Loire Basin Mammal Network, and assembled by the services of the National 93 Wildlife Office (ONCFS). Harmonised protocols in data collection were adopted following the 94 internationally agreed otter census protocol (Lodé 1993). For the otter, presence was confirmed from 95 the observation of spraints (otter's droppings). The otter is a highly mobile animal with home ranges 96 of 2 - 100km (Ruiz-Olmo et al. 2001). In accordance to guidelines for the confirmation of otter 97 presence and to avoid overestimating accidental visits of individuals to small water courses (Kruuk 98 2006), only main water courses in fluvial systems and rivers starting from a minimum catchment of 99 >10km² were retained for the analysis. As otter spraints cannot provide information on otter 100 abundance, only about presence (Mason and Macdonald 1987; Sulkava et al. 2007), and furthermore 101 the frequency of spraints may be very low when otters are at low densities (Macdonald and Mason 102 1983), the species distribution analysis was limited to a presence only approach. 103 The consistent observation effort over the last 25 years allowed for a reconstruction in well-defined 104 time-steps (5 survey periods) of otter presence and the re-colonization of the river basin. Although the 105 re-colonization is surely not fully accomplished for the Loire basin - only 37% of the surveyed 17 106 000km are occupied - the outer bounds are all reached by now (Fig. 1). And as dispersing individuals 107 will preferably chose the best available sites as a residence, this analysis of non-fully achieved re-108 colonization of the river network offered good perspectives to discriminate the essential factors in 109 dispersal and habitat selection (Clavero et al. 2010; Ruiz-Olmo et al. 2001). For the analysis of the 110 habitat selection, the presence in the most recent survey was retained (Fig. 1).

111

112 Environmental and anthropogenic stressor data of the riparian corridor

113 A systematic sectioning into river segments and assembling of hydromorphological and land cover

114 data for the riparian corridor in different buffer sizes (valley floor, floodplain, 100m, 30m, 10m) was

- 115 realised for the entire river network (Chandesris et al. 2008). Rivers were subdivided into hydro-
- 116 morphological units based on a semi-automatic sectioning that distinguished changes in geological

117	entities, channel form, sinuosity and valley floor width. Resulting river segments range from 1km on
118	average for small streams and up to 20km on average for large rivers. For each of these river
119	segments, information was collected from two spatial scales: the catchment's land cover information
120	was gathered for regional sub-catchments (i.e. hydrological units delimited by water divides and river
121	confluences) and locally information on land cover and hydromorphology was extracted for the
122	individual river segment in different dimensions for the riparian corridor (Table 1).
123	
124	Ecological niche factor network analysis
125	The restriction to presence only data was the reason to apply the ecological niche factor analysis
126	(ENFA) in the definition of ecological networks for the species (Hirzel et al. 2001). This method also
127	allowed inferring key habitat factors from incomplete distribution data as was obviously the case for
128	this colonizing species' distribution (Clavero et al. 2010). ENFA allowed integrating the inferred
129	habitat factors in a network analysis to mark the potential network occupied by the species (Basille et
130	al. 2009). The marginality and specialisation of the species' presences was determined for the
131	environmental variables over the river segments to describe the ecological niche of the species. The
132	95% confidence intervals of the variables with significant marginality and specialisation for occupied
133	segments were selected as boundary values to consider segments as favourable. An extrapolation of
134	this ecological niche over the entire river basin was carried out. Distance criteria were applied to join
135	favourable segments based on the minimum home range values of 2km for otter, and this resulted in
136	networks of non-fragmented habitat patches over the river basin.

138 Ecological network design based on connectivity analysis

The dendritic river network structure needed an adequate topological definition for the analysis of its potential as ecological network for the species (Grant et al. 2007). For this purpose and in agreement with terrestrial network frameworks, the river segments were regarded as habitat nodes whereas the true river network nodes (confluences and segment junctions) were considered as connectors in the network (Eros et al. 2011). As we investigated species movement both in up- and downstream direction, the full complexity of dendritic networks came in the picture. Starting from the topological

definition of the river segments in GIS, scripts were developed to derive neighbourhood matrices that
depicted the network structure. Figure 2 illustrates the resulting network structure that was applied in
the analysis.

148 We adopted the graph method of weighing network importance of nodes (Urban 2005), defined as

149 river segments in our case, by a specified application of the Integral Index of Connectivity (Pascual-

150 Hortal and Saura 2006). This index offered a measure that integrates the habitat quality of nodes with

151 the complexity and connectivity of the landscape. For our specific river network implementation,

152 integrating the habitat suitability output of the ENFA, the general formula of the Integral Index of

153 Connectivity was defined as follows:

154 IIC= $\Sigma_i \Sigma_j$ [favourability i x favourability /(1 + nl_{ij})]/ A_L^2

155

156 With A_L the overall sum of favourability for all the segments of the entire river basin, and \mathbf{n}_{ii} the 157 number of segments between segments i and j, as connection distance present in the neighbourhood 158 matrix. The overall index ranges from 0 to 1 and increases with improved connectivity (Pascual-Hortal 159 and Saura 2006, 2008). The relative ranking of segments by their contribution to the overall index 160 value is the individual segment's qualification that is useful in this conservation approach. To 161 calculate the importance of each individual segment, we systematically removed each particular 162 segment and recalculated the IIC index. The percentage of index value loss (delta value dIIC) 163 measured the contribution of each segment to the overall index value (Pascual-Hortal and Saura 2008). 164 This dIIC can be considered a habitat availability index (Pascual-Hortal and Saura 2006). We 165 used the recently developed Conefor Sensinode 2.2 software (Saura and Torné 2009) to calculate dIIC 166 values for each river segment. 167

107

168 Constraining the connection distance **n**l_{ij} of number of segments, and thus the extent of the

169 neighbourhood matrix, allowed a scale-sensitive calculation of the index. With connection distance 0,

170 no integration took place of connectivity and habitat quality of the surrounding segments. In this way,

171 the classical habitat network analysis was performed as described above, based on local habitat

172	quality. For a connection distance of 2 and 5, local network structure integrating the habitat quality of
173	the segments was considered. With regard to the otter's home range this measure of 2 to 5
174	neighbouring segments corresponded to a relevant ecological network scale level covering river
175	lengths from 5 up to 100km, which was in agreement with the species' home range. To infer the scale-
176	sensitivity of this network qualification approach, the calculation was also performed with
177	constraining connection distances to 10.
178	
179	Validation importance of connectivity
180	To evaluate the merits of the proposed connectivity analysis, its outcome was compared to both the
181	ENFA approach described above and more dynamic distribution modelling approaches. We generated
182	five different data sets for this comparison. One set consisted of the presence-absence data directly.
183	Four other sets are probabilities of occurrence, generated with respectively the ENFA, a logistic
184	regression and the IIC with connection distances 2 and 5.
185	The dynamic logistic regression model was obtained from the otter presences over the five surveys.
186	The determining habitat factors detected with ENFA were entered in a logistic regression model to
187	derive a colonization likelihood estimate. For each time step (5 steps of 5 year) the neighbouring river
188	segments at the colonization front were simulated and confronted with the observed progression. With
189	this model probability of occurrence was inferred over the entire river network, and confronted with
190	the results of the other analyses for occurrence probability. For this comparison correlations were
191	tested for the river segments of the entire river network between the modelled ENFA habitat
192	favourability, the regression model occurrence probability and the integrated connectivity measures.
193	Afterwards, the model results were confronted with the recorded colonization process for the fully-
194	colonized upstream part of the basin, based on the detailed dataset of the regional nature park of the
195	Livradois-Forez (PNRLF). A measure of colonization speed for the PNRLF river network was
196	calculated over the three recent time steps in which the re-colonization took place: 1995-1999, 2000-
197	2004, and 2005-2009. Each newly occupied river segment was attributed a value of colonization
198	speed, by counting the number of segments traversed at first occurrence to the nearest previously

- 199 occupied segment. Correlation of the different model outputs to this colonization speed over the
- 200 PNRLF river network finally revealed the best predictor of otter occurrence.

202 **Results**

203 Species niche

204 Only 5 out of 22 environmental variables showed discriminating scores in the analysis of marginality 205 and specialisation (Fig. 3). The strongest explaining factor for species presence was the rate of channel 206 normalization ('channel straightening') with significant marginality and specialisation (M = 0.12, S =207 1.16). This factor showed in the niche factor analysis the highest discriminating power on the river 208 network, as it qualifies 12% of the river segments as unfavourable. Strong marginality with little 209 specialisation though is observed for the forest cover in the floodplain (M = -0.13, S = 0.97) and in the 210 30m buffer (M = -0.16, S = 0.96). Urbanisation in the 100m buffer showed a high specialisation 211 (S=1.17) that allows a discrimination of 6% of the river basin's segments as unfavourable in the niche 212 factor analysis due to urbanization pressure in the river corridor. The favourable river segments 213 represent for the otter in the Loire basin 82% of the 17 000km selected river length (Fig. 4). Where 214 favourable conditions can be found in all parts of the basin, the most unfavourable conditions are 215 concentrated in the downstream part of the river basin.

216

217 Network analysis

218 The network analysis based on local habitat, without connectivity integration, determined with ENFA

as favourable segments joined to ecological networks (Fig. 5a), results in 452 patches of linked

favourable segments over the basin with a mean length of 29.3km but high variability (sd = 62.1km)

and a dominance of smaller patches. The longest favourable patches (max= 590.2km) are mainly

situated along the middle sectors of the main rivers Loire and Allier.

223 The network connectivity analysis based on the dIIC-connection distance 5 (Fig. 5b) shows a different

224 picture. The favourable networks in the centre of the basin (for the main rivers of Loire and Allier and

the south-western sub-catchment of the Vienne-Creuse) are also highlighted, but in this analysis the

lower parts of the basin are identified as most important in the river network.

227

228 Scale-sensitivity of the method

229 Constraining the neighbourhood matrix up to the second neighbours (dIIC 2) allows identifying 230 networks based on local habitat availability (Fig. 6). This result shows a higher differentiation at the 231 local scale level. It differs from the network qualification based solely on the individual segment 232 quality (Fig. 5a) as it integrates the favourability of the local network. It differs also from the larger 233 scale connectivity analysis (Fig. 5b) as it reflects more strongly the local habitat availability, but not so 234 much the larger scale network structure of the dendritic river network. With a higher connectivity of 235 connection distance 10, the effect of local habitat availability gets completely lost for our studied 236 network structure and only the overall river basin connectivity is highlighted with dIIC values 237 gradually increasing from upstream to downstream.

238 Connectivity validation

239 The logistic regression model predicted the likelihood of colonization accurately in 35% of the cases.

240 Its modelled occurrence probability over the entire river basin showed a negative correlation with the

241 dIIC_5 (R -0.046, p<0.05) and a positive correlation with dIIC_2 (R 0.14, p<0.05). For the 1501

segments in the upstream PNRLF-region, the modelled occurrence probability showed a positive

correlation with both the dIIC_5 (R 0.2, p<0.001) and with the dIIC_2 (R 0.23, p<0.001). Still these

244 correlations are quite weak and so the question remains for otter occurrence being more explained by

245 local habitat factors than by connectivity.

For the PNRLF-region, colonization speed of the occupied segments was between 1 and 16, with an

average of 3. This colonization speed of the segments was marginally correlated to the results of the

static ENFA favourability (R 0.21, p<0.05) and of the dynamic logistic regression modelled

- 249 occurrence probability (R 0.19, p<0.05). Much stronger correlation was observed for the connectivity
- 250 measure of the dIIC_2 (R 0.52, p<0.001). The higher scale connectivity measure dIIC_5 on the
- 251 contrary shows a negative correlation (R -0.17, p<0.05).

252

253 Discussion

254 Integrated approach to network connectivity analysis

The presented approach adopts the recent developments in river ecology of graph based methods (Eros et al. 2011) and connectivity loss weighing (Moilanen et al. 2008; Hermoso et al. 2011). Yet, it differs 257 from existing connectivity analysis methods to prioritize conservation networks in its integrative 258 quantification of habitat availability and connections in the network. Furthermore, by integrating all 259 branches and connections in the neighborhood matrices we shifted from a linear to a branched river 260 network connectivity analysis (Fisher 1997; Grant et al. 2008). All neighbouring segments along the 261 branches of the dendritic network both in downstream as upstream direction are embedded in this 262 quantification. They are weighed by distance and constrained by a distance criterion to allow a scale-263 sensitive analysis. So, although it does not provide a method that weighs up specific trajectories and 264 connections (Carroll et al. 2012), we do accomplish the main objective for the analysis of networks, 265 that is to quantify connectivity in relationship with the ecological processes within the network. Most 266 recently developed connectivity measures - even those adjusted to river networks - only count for a 267 distance criterion of connections (Hermoso et al. 2011; Moilanen et al. 2008). In contrast to this strong 268 distance-based interpretation and the barrier emphasis of the least-cost path approaches (Pinto and 269 Keitt 2009; Morzillo et al. 2011), we incorporate the evaluation of the branch density of the dendritic 270 structure in the network analysis (Ganio et al. 2005), with the IIC that measures the density of 271 connectors, that is the 'branchiness' of the river network in our example. River segments are evaluated 272 at the same time as habitat and as connectors in our approach; which is a strong point in the 273 conservation context of ecological networks. In this way, the IIC is generally considered a habitat 274 availability index (Pascual-Hortal and Saura 2006) because it integrates topological properties 275 (network connectivity) with habitat quantity.

276

277 Scale-sensitive ecological network analysis

The scale-sensitive integration of river segment length and resolution of the network under study is in accordance to species behaviour (Baguette and Vandyck 2007) and is the basis for the aggregation of the local habitat with the connectivity over the drainage basin, a necessary step in ecological network analyses for the otter (Ottaviani et al. 2009). This scale-sensitive approach demands the acquisition of environmental variables from different scales according to the network structure. Most species distribution studies at large scale start from raster-based landscape representations and metrics (Barbosa et al. 2001, 2003; Loy et al. 2009; Clavero et al. 2010) that do not allow interpretation of

285 data gathered at multiple scales to the dendritic network. Only recently the geometric network 286 analysis has been developed with the graph methods (Urban and Keitt 2001; Jordán et al. 2003). The 287 presented integration of scale-sensitivity by confining the extent of connections allows the 288 prioritization of conservation networks based on specific objectives, like sets of target species or 289 ecosystem processes and functions with specific spatial demands. 290 The presented case study shows some restrictions for the attribution of habitat quality to the 291 observations as the data of otter occurrence only allowed for a presence-only approach with its 292 weaknesses (Tsoar et al. 2007). Still we believe this dataset for the Loire basin is one of the best 293 documented examples of otter colonization globally, especially in view of its time span and the size of 294 the basin. The unique large scale dataset on environmental quality of the riparian zones proved 295 appropriate to infer the relevant ecological factors in the colonization process. Restrictions of this 296 environmental dataset concern aspects of water quality, food resources and the height of dams and 297 dikes. Yet, from earlier analyses in the Loire basin no relationship between otter expansion and water 298 quality, prey abundance or fish community could be inferred (Lemarchand et al. 2007; Janssens et al. 299 2008), neither proved the height of dams a significant obstacle to the species' progress (Varray 2011). 300 Therefore and also based on the limited data at hand for these variables, we did not include them in the 301 analysis. 302 The ecological potentials and targets for the river system in question will determine the scale of 303 connectivity to incorporate in the designation of conservation priorities. In our case for the Loire River 304 basin, a well-preserved aquatic biodiversity together with a high potential for conservation and 305 restoration of mobile riverine species like otter, beaver, salmon, sturgeon, osprey and river terns, calls 306 for the larger scale connectivity approach and identifies priorities principally in the downstream 307 reaches.

308

309 Connectivity in river networks

310 Our results confirm the conclusions of Moilanen and colleagues that realistic modelling of

311 connectivity has a major influence on the areas proposed for conservation, pointing out different parts

312 of river basins as high priority conservation targets (Moilanen et al. 2008). Same as several other

313 recent publications (Carranza et al. 2012; Hermoso et al. 2012), we supply evidence and methods to 314 integrate different scales and dimensions in connectivity measures, although not focussed on inter-315 basin connectivity as these authors. The proposed method for the integrated connectivity measure 316 proves even more accurate in predicting species occurrence than the dynamic probability modelling 317 that sorted as best available method from earlier comparisons (Van Teeffelen, 2006).

318

319 The more classical habitat-based network analysis corresponds to the result without node network 320 connections $(n_{ii} = 0)$ in our approach. This result clearly deviates from the results with integration of 321 functional connections. For the analysis of ecological networks for the otter the local network-322 focussed dIIC_2 provides the most accurate predictor for otter occurrence probability. Still, for the 323 long time population expansion and survival, as well as for the conservation prioritization, the dIIC_5 324 surely brings important additional information as well. The comparison to the observed colonisation 325 speed in the upstream part of the basin shows that the dIIC 5 measure is probably not the best 326 predictor for otter colonisation, but it might well be the best prospection for an ecological network to 327 assure otter survival in the long run. This assumption of course needs another type of analysis, or a 328 repeated analysis by the time the colonisation process is fully accomplished over the river basin. The 329 validation of the connectivity analysis with the comparison to the static and dynamic distribution 330 modelling approaches, showed the strength of our approach as it predicted better the otter 331 colonization. Where our approach starts from a static distribution modelling approach, this result 332 proves the strength of the proposed approach, as it even gives a better result than the dynamic habitat-333 based colonization model that is based on the extended dataset on otter presence over time in the river 334 basin. We didn't integrate this more dynamic distribution model in the proposed method for 335 connectivity analysis, as obviously such a dynamic model needs to be based on temporally explicit 336 data and an exceptionally rich dataset as presented here is mostly not available.

337

338 In conclusion we can say that the presented method meets our goal to quantify connectivity in the river 339 network, considering both the complexity of the dendritic network structure and the scale-sensitivity 340 of relationships between network structure and ecological patterns in rivers. It even showed more

341 reliable results in predicting species colonization in the network than distribution modelling 342 techniques. The outcome proves the importance of connectivity for the otter, as the movement and 343 occurrence in the river network was more explained by connectivity measures than just with habitat 344 quality aspects. In this way it confirms the otter as a guiding species for connectivity and not solely 345 for habitat quality. 346 With the presented method insight can be gained into the choices for river restoration and conservation 347 prioritization. Allocation of financial resources for conservation and restoration can be based on this 348 kind of analyses with the integration of multi-species approaches (Schwenk and Donovan 2011). 349 Cross-examining resulting ecological networks for multiple species with multiple relevant scales for 350 connectivity can reveal priorities for conservation (Williams et al. 2005). The here presented approach 351 can also be used for fully aquatic species in river systems with integration of flow-directed 352 connectivity. 353 354 Acknowledgments 355 This work was only possible thanks to the strong observation effort of the volunteers of the Loire 356 Basin Mammal Network and the agents of the National Wildlife Office (ONCFS) since 1985. Nadine 357 Nogaret of the Regional Nature Parc of the Livradois-Forez provided detailed information on the 358 species' re-colonization. The river data collection in the hydro-morphology audit system SYRAH is 359 financed by the French Ministry of Research and the Ministry of Environment and Sustainable 360 Development. We are indebted to Sandrine Ruette (ONCFS) and Charles Lemarchand (University 361 Clermond-Ferrand) for their constructive comments on the analysis approach and interpretation of the 362 species' inventories. The editor and two anonymous reviewers offered useful suggestions to improve 363 the manuscript. 364 365 References 366 Allan JD (2004) Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. Ann

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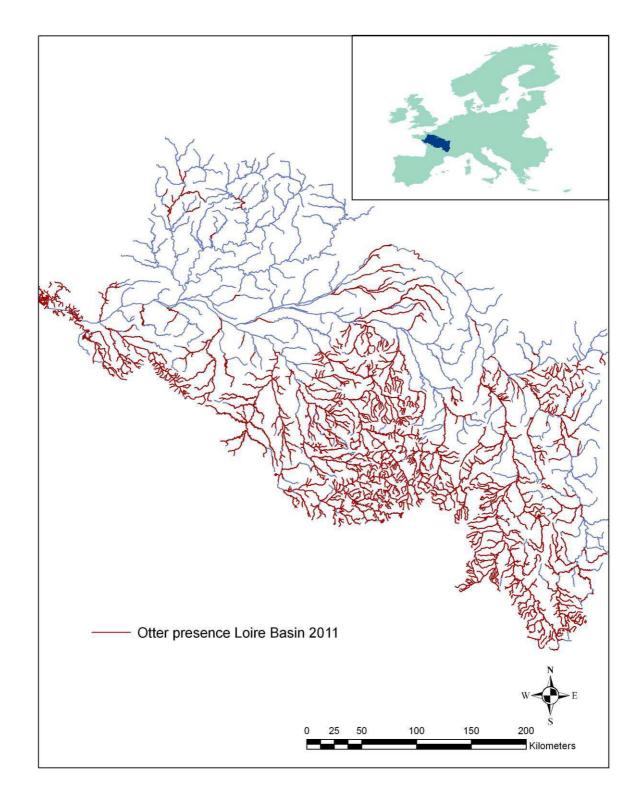
- 501 Table 1. Environmental variables from the different spatial scales that were attributed to the river
- 502 segments.
- 503

Watershed

urbanisation

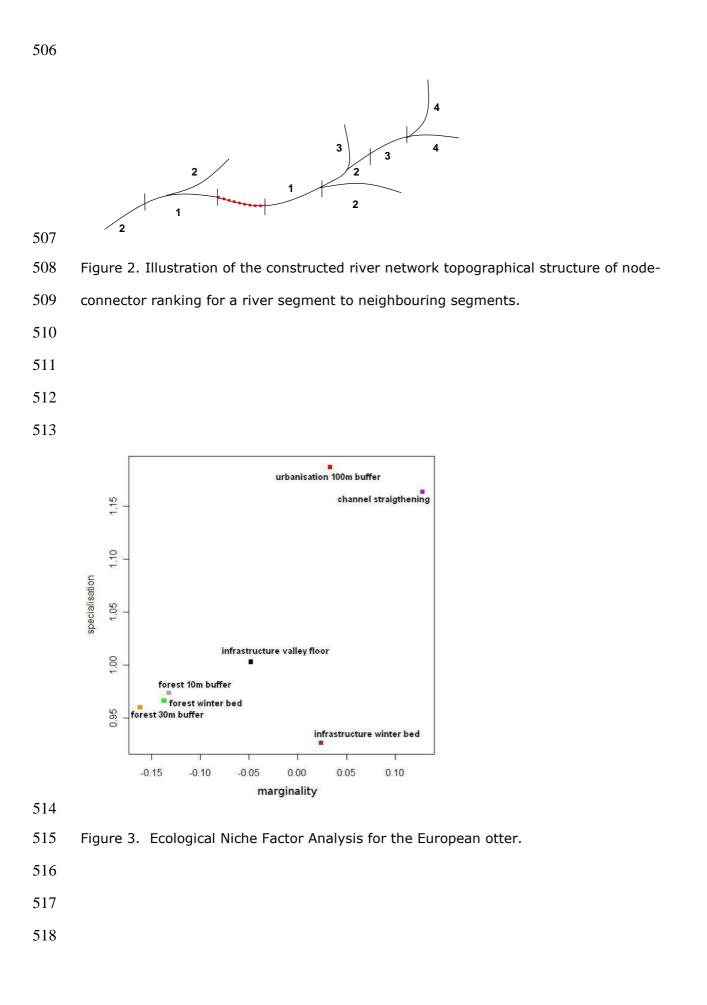
urbanisation	percentage cover of urban land use class in CORINE land cover data of the sub-catchments			
intensive agriculture	percentage cover of intensive agricultural CORINE land cover classes of the sub-catchments			
Natural	percentage cover of near-natural CORINE land cover classes data of the sub-catchments			
River segment				
Altitude	elevation at downstream point of river segments			
river slope	slope of the river bed over the segment			
valley slope	valley slope perpendicular to the river			
Discharge	mean annual discharge for gauging station or model prediction at river segment level			
Sinuosity	sinuosity of the river bed over the segment			
channel straightening	percentage of straight reaches over the segment, weighted by river type			
density of bars	number of lateral bars over the segment, divided by river length			
density of weirs/dams	number of weirs/dams per segment, divided by river length			
density of bridges	number of river crossing bridges per segment, divided by river length			
Alluvial plain				
alluvial forest cover	percentage cover of forest patches over the alluvial plain of the river segment			
Infrastructure	percentage cover of infrastructure over the alluvial plain of the river segment			
urbanisation	percentage cover of urbanisation over the alluvial plain of the river segment			
density of dikes	length of flood protection levees per segment, divided by river length			
connected waters	percentage cover of connected standing waters over the alluvial plain of the river segment			
Disconnected waters	percentage cover of disconnected standing waters over the alluvial plain of the river segment			
River bank				
riparian forest cover	percentage cover of forest patches for the 30m riparian buffer of the river segment			
riparian forest canopy	percentage cover of forest patches for the 10m riparian buffer of the river segment			
Infrastructure	percentage cover of infrastructure over riparian buffer of three river widths of the segment			

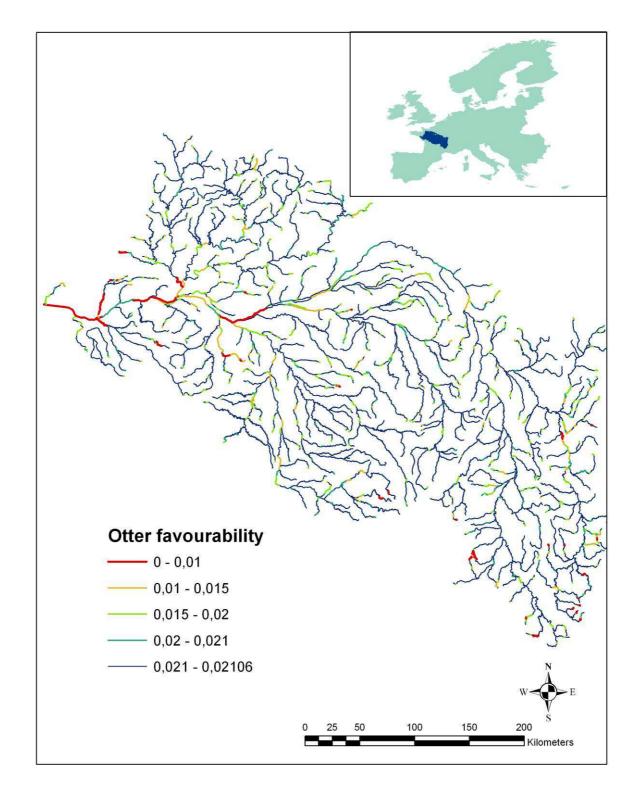
percentage cover of urbanisation for the 100m riparian buffer of the river segment





505 Figure 1. Presence of the European otter in the Loire river basin in 2011

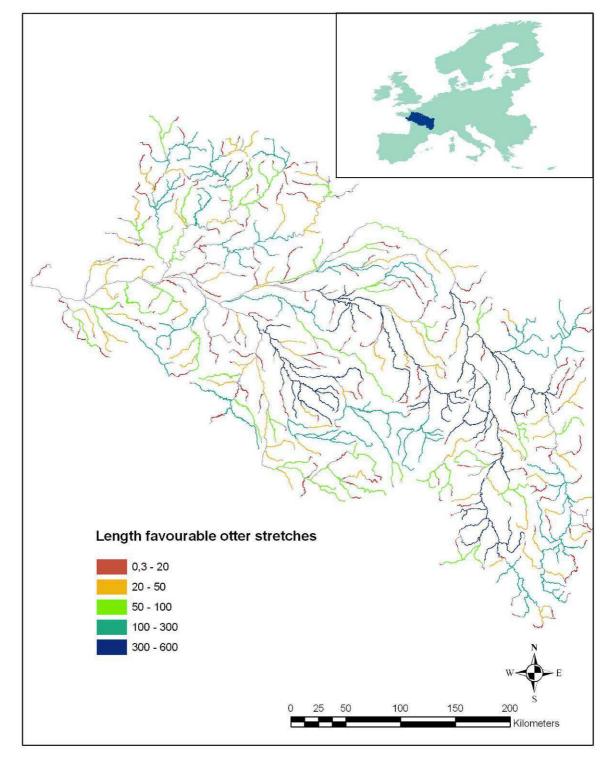




- 520
- 521 Figure 4. Otter favourability of river segments in the network of the Loire basin

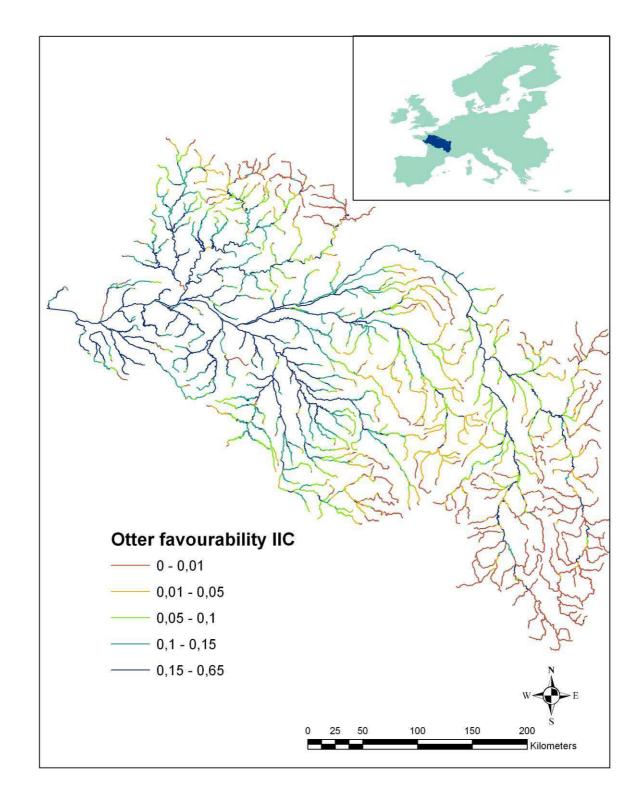
522 (favourability values present contribution of individual segments in percentage to total

523 network).



529 (a).

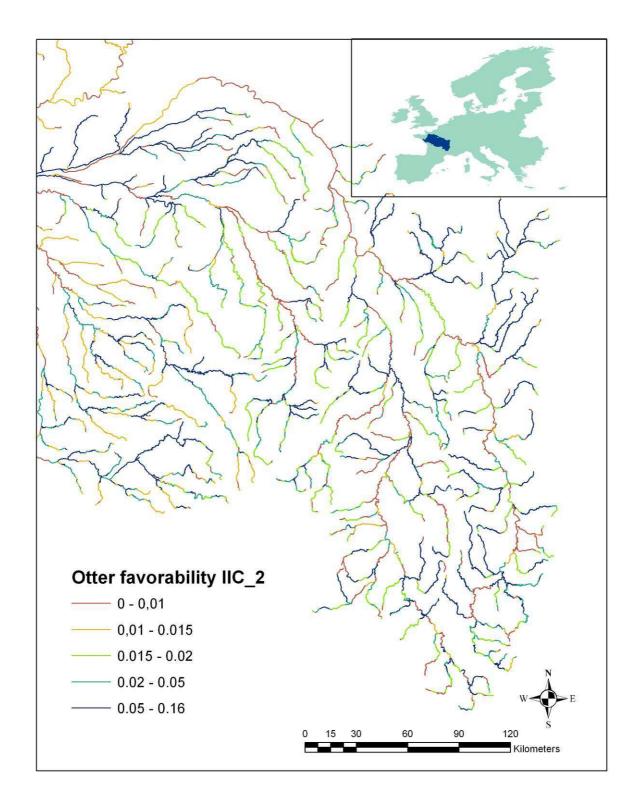
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532 (b).

- 533 Figure 5. The ecological networks based on local habitat quality with connection
- 534 distance 0 (a), and based on the Integral Index of Connectivity calculation for
- 535 connection distance 5 (b). The figure 5a presents length (km) of continuous favourable

- 536 habitat for otter (favourable segments gathered with barrier threshold 2km) in the Loire
- 537 basin (colours indicate km of linear in classes). Figure 5b presents the Integral Index of
- 538 Connectivity calculated dIIC network values. The dIIC values give an immediate
- 539 ecological network qualification (the values present contribution of individual segments in
- 540 percentage to total network) and representation.
- 541



543

544 Figure 6. The ecological network qualification based on the Integral Index of

545 Connectivity calculation for connection distance 2 for the central and upstream part of

546 the Loire River basin.