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► To cite this version:

K. van Looy, C. Cavillon, T. Tormos, Jeremy Piffady, P. Landry, et al.. A scale-sensitive connectivity analysis to identify ecological networks and conservation value in river networks. *Landscape Ecology*, 2013, 28 (7), p. 1239 - p. 1249. 10.1007/s10980-013-9869-x . hal-01073015

HAL Id: hal-01073015

<https://hal.science/hal-01073015>

Submitted on 8 Oct 2014

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

Connectivity analysis in river networks

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Keywords: Ecological Niche Factor Analysis, Integral Index Connectivity, network analysis, hydro-morphological quality, otter

Abstract

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

Introduction

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

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

different scales (Rouget et al. 2006). The choice of target species for prioritizing conservation determines the resolution of environmental data needed and the connectivity required (Arponen et al. 2012), both with regard to resource selection and mobility (Moilanen and Hanski 2001), as to potential biotic interactions (Godsoe et al. 2012). The otter is often presented as target species and indicator for the connectivity and quality of the river ecosystem (Robitaille and Laurance 2002). Population dynamics of the otter plays at the river basin scale, while individuals experience the local habitat and its connectivity at the river segment scale. These two scale levels are the relevant scales to gather data for the assessment of river corridor quality and functions (Allan 2004; Wiens 2002).

In this contribution we describe the proposed method of integrated network connectivity and habitat availability assessment and compare it to more commonly used distribution model approaches both in its power to predict species occurrence in the river network, and to its ability to highlight the contribution of connectivity in relationship to the observed ecological pattern of the otter re-colonization over the river network. For this validation the importance of connectivity for otter was tested in a part of the river basin where the re-colonization was fully accomplished.

Methods

Observational data for otter

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

Environmental and anthropogenic stressor data of the riparian corridor

A systematic sectioning into river segments and assembling of hydromorphological and land cover data for the riparian corridor in different buffer sizes (valley floor, floodplain, 100m, 30m, 10m) was realised for the entire river network (Chandesris et al. 2008). Rivers were subdivided into hydro-morphological units based on a semi-automatic sectioning that distinguished changes in geological

entities, channel form, sinuosity and valley floor width. Resulting river segments range from 1km on average for small streams and up to 20km on average for large rivers. For each of these river segments, information was collected from two spatial scales: the catchment's land cover information was gathered for regional sub-catchments (i.e. hydrological units delimited by water divides and river confluences) and locally information on land cover and hydromorphology was extracted for the individual river segment in different dimensions for the riparian corridor (Table 1).

Ecological niche factor network analysis

The restriction to presence only data was the reason to apply the ecological niche factor analysis (ENFA) in the definition of ecological networks for the species (Hirzel et al. 2001). This method also allowed inferring key habitat factors from incomplete distribution data as was obviously the case for this colonizing species' distribution (Clavero et al. 2010). ENFA allowed integrating the inferred habitat factors in a network analysis to mark the potential network occupied by the species (Basilie et al. 2009). The marginality and specialisation of the species' presences was determined for the environmental variables over the river segments to describe the ecological niche of the species. The 95% confidence intervals of the variables with significant marginality and specialisation for occupied segments were selected as boundary values to consider segments as favourable. An extrapolation of this ecological niche over the entire river basin was carried out. Distance criteria were applied to join favourable segments based on the minimum home range values of 2km for otter, and this resulted in networks of non-fragmented habitat patches over the river basin.

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.

We adopted the graph method of weighing network importance of nodes (Urban 2005), defined as river segments in our case, by a specified application of the Integral Index of Connectivity (Pascual-Hortal and Saura 2006). This index offered a measure that integrates the habitat quality of nodes with the complexity and connectivity of the landscape. For our specific river network implementation, integrating the habitat suitability output of the ENFA, the general formula of the Integral Index of Connectivity was defined as follows:

$$IIC = \frac{\sum_i \sum_j [favourability_i \times favourability_j / (1 + nl_{ij})]}{A_L^2}$$

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

Constraining the connection distance nl_{ij} of number of segments, and thus the extent of the neighbourhood matrix, allowed a scale-sensitive calculation of the index. With connection distance 0, no integration took place of connectivity and habitat quality of the surrounding segments. In this way, the classical habitat network analysis was performed as described above, based on local habitat

quality. For a connection distance of 2 and 5, local network structure integrating the habitat quality of the segments was considered. With regard to the otter's home range this measure of 2 to 5 neighbouring segments corresponded to a relevant ecological network scale level covering river lengths from 5 up to 100km, which was in agreement with the species' home range. To infer the scale-sensitivity of this network qualification approach, the calculation was also performed with constraining connection distances to 10.

Validation importance of connectivity

To evaluate the merits of the proposed connectivity analysis, its outcome was compared to both the ENFA approach described above and more dynamic distribution modelling approaches. We generated five different data sets for this comparison. One set consisted of the presence-absence data directly. Four other sets are probabilities of occurrence, generated with respectively the ENFA, a logistic regression and the IIC with connection distances 2 and 5.

The dynamic logistic regression model was obtained from the otter presences over the five surveys. The determining habitat factors detected with ENFA were entered in a logistic regression model to derive a colonization likelihood estimate. For each time step (5 steps of 5 year) the neighbouring river segments at the colonization front were simulated and confronted with the observed progression. With this model probability of occurrence was inferred over the entire river network, and confronted with the results of the other analyses for occurrence probability. For this comparison correlations were tested for the river segments of the entire river network between the modelled ENFA habitat favourability, the regression model occurrence probability and the integrated connectivity measures. Afterwards, the model results were confronted with the recorded colonization process for the fully-colonized upstream part of the basin, based on the detailed dataset of the regional nature park of the Livradois-Forez (PNRLF). A measure of colonization speed for the PNRLF river network was calculated over the three recent time steps in which the re-colonization took place: 1995-1999, 2000-2004, and 2005-2009. Each newly occupied river segment was attributed a value of colonization 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.
201

Results

Species niche

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

Network analysis

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.

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

Scale-sensitivity of the method

Constraining the neighbourhood matrix up to the second neighbours (dIIC_2) allows identifying networks based on local habitat availability (Fig. 6). This result shows a higher differentiation at the local scale level. It differs from the network qualification based solely on the individual segment quality (Fig. 5a) as it integrates the favourability of the local network. It differs also from the larger scale connectivity analysis (Fig. 5b) as it reflects more strongly the local habitat availability, but not so much the larger scale network structure of the dendritic river network. With a higher connectivity of connection distance 10, the effect of local habitat availability gets completely lost for our studied network structure and only the overall river basin connectivity is highlighted with dIIC values gradually increasing from upstream to downstream.

Connectivity validation

The logistic regression model predicted the likelihood of colonization accurately in 35% of the cases. Its modelled occurrence probability over the entire river basin showed a negative correlation with the 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 correlations are quite weak and so the question remains for otter occurrence being more explained by 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 occurrence probability ($R = 0.19$, $p < 0.05$). Much stronger correlation was observed for the connectivity measure of the dIIC_2 ($R = 0.52$, $p < 0.001$). The higher scale connectivity measure dIIC_5 on the contrary shows a negative correlation ($R = -0.17$, $p < 0.05$).

Discussion

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

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

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

data gathered at multiple scales to the dendritic network. Only recently the geometric network analysis has been developed with the graph methods (Urban and Keitt 2001; Jordán et al. 2003). The presented integration of scale-sensitivity by confining the extent of connections allows the prioritization of conservation networks based on specific objectives, like sets of target species or ecosystem processes and functions with specific spatial demands.

The presented case study shows some restrictions for the attribution of habitat quality to the observations as the data of otter occurrence only allowed for a presence-only approach with its weaknesses (Tsoar et al. 2007). Still we believe this dataset for the Loire basin is one of the best documented examples of otter colonization globally, especially in view of its time span and the size of the basin. The unique large scale dataset on environmental quality of the riparian zones proved appropriate to infer the relevant ecological factors in the colonization process. Restrictions of this environmental dataset concern aspects of water quality, food resources and the height of dams and dikes. Yet, from earlier analyses in the Loire basin no relationship between otter expansion and water quality, prey abundance or fish community could be inferred (Lemarchand et al. 2007; Janssens et al. 2008), neither proved the height of dams a significant obstacle to the species' progress (Varray 2011). Therefore and also based on the limited data at hand for these variables, we did not include them in the analysis.

The ecological potentials and targets for the river system in question will determine the scale of connectivity to incorporate in the designation of conservation priorities. In our case for the Loire River basin, a well-preserved aquatic biodiversity together with a high potential for conservation and restoration of mobile riverine species like otter, beaver, salmon, sturgeon, osprey and river terns, calls for the larger scale connectivity approach and identifies priorities principally in the downstream reaches.

Connectivity in river networks

Our results confirm the conclusions of Moilanen and colleagues that realistic modelling of connectivity has a major influence on the areas proposed for conservation, pointing out different parts of river basins as high priority conservation targets (Moilanen et al. 2008). Same as several other

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

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

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

reliable results in predicting species colonization in the network than distribution modelling techniques. The outcome proves the importance of connectivity for the otter, as the movement and occurrence in the river network was more explained by connectivity measures than just with habitat quality aspects. In this way it confirms the otter as a guiding species for connectivity and not solely for habitat quality.

With the presented method insight can be gained into the choices for river restoration and conservation prioritization. Allocation of financial resources for conservation and restoration can be based on this kind of analyses with the integration of multi-species approaches (Schwenk and Donovan 2011). Cross-examining resulting ecological networks for multiple species with multiple relevant scales for connectivity can reveal priorities for conservation (Williams et al. 2005). The here presented approach can also be used for fully aquatic species in river systems with integration of flow-directed connectivity.

Acknowledgments

This work was only possible thanks to the strong observation effort of the volunteers of the Loire Basin Mammal Network and the agents of the National Wildlife Office (ONCFS) since 1985. Nadine Nogaret of the Regional Nature Parc of the Livradois-Forez provided detailed information on the species' re-colonization. The river data collection in the hydro-morphology audit system SYRAH is financed by the French Ministry of Research and the Ministry of Environment and Sustainable Development. We are indebted to Sandrine Ruelle (ONCFS) and Charles Lemarchand (University Clermont-Ferrand) for their constructive comments on the analysis approach and interpretation of the species' inventories. The editor and two anonymous reviewers offered useful suggestions to improve the manuscript.

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

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

Figure 2. Illustration of the constructed river network topographical structure of node-connector ranking for a river segment to neighbouring segments.

Figure 3. Ecological Niche Factor Analysis for the European otter.

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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).

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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.
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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.

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