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Integrated modelling of functional and structural connectivity of river corridors for European otter recovery

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Dendritic network– riparian corridor – dynamic occupancy modelling - Integral Index of Connectivity – colonisation – hydromorphology
Summary

Connectivity may be *structural*, based on adjacency of landscape features, or *functional*, based on how that adjacency translates to movement of organisms. We present a modelling approach that elucidates both aspects of connectivity to identify vital corridors and conservation priorities in a river network. For the dendritic network structure of river systems, at first a graph theoretic structure is developed to model the river network at the segment scale. To derive functional connectivity, a Bayesian hierarchical modelling of species dispersal is applied to infer the influence of riparian corridor characteristics to the species colonization.

The integration of the functional and structural component is realized with a graph-theoretic connectivity measure. With this approach, the European otter colonization of the Loire river basin over 25 years is modelled on the basis of large datasets on riparian corridor land use and hydromorphological characteristics of a 17 000 km river network. Channel straightening and riparian forest fragmentation are determined to be key elements to the functional connectivity. Road infrastructure is distinguished as a critical habitat factor, but not so much an obstacle for the species movement in the riparian corridor. Integration of the Bayesian model posterior colonization probability in the integrated connectivity analysis reveals the importance of the river network density to the otter colonization and locates conservation priorities mainly in the lower parts of the river basin.

*Synthesis and applications.* Both functional and structural connectivity are essential elements in the contexts of ecological network identification for species conservation and recovery. We successfully developed an integrated modelling of both components of connectivity that highlighted the importance of the downstream basin for a well-connected ecological network for the otter.
Introduction

The role of river corridors in providing connectivity is questioned in the context of defining ecological networks over large territories (Rouget et al., 2006; Grant et al., 2007). The assessment of connectivity in river networks generally poses specific methodological difficulties (Peterson and VerHoef, 2010), as does more generally the contribution of specific landscape features to the accommodation of biological processes (Simberloff et al., 1992).

Attempts to measure this interplay between landscape configuration and species movement, that we call functional connectivity, are still quite uncommon (Wainwright et al., 2011).

Structural connectivity is defined as the adjacency or proximity of patches within a landscape and is a measure of the degree to which patches are connected without regard to organism behaviour (Taylor et al., 1993). Alternatively, functional connectivity is conceptually defined as the degree to which a landscape impedes or facilitates movement of organisms among patches (Bélisle, 2005). Functional connectivity is mostly derived from species range or dispersal studies, at best with dynamic process-oriented population or distribution models (Marion et al., 2012; Schurr et al., 2012). Managing for structural connectivity is thought to increase functional connectivity, yet this implication is not so straightforward (Tischendorf and Fahrig, 2000). Ideally, functional and structural connectivity should be integrated when providing guidance for management. That is what we try to accomplish for dendritic river networks in this paper.

To demonstrate connectivity, biotic processes involving species movement have to be studied over extended spatial and temporal scales. To this purpose, we analyse the well-documented re-colonization of the French River Loire basin by the European otter. The European otter is an emblematic species for nature conservation in a broad societal context; therefore it is often advocated as a model species in studies for ecosystem services and ecological networks (Bifolchi and Lodé, 2005). Especially with respect to river corridor functioning the otter is
proposed as guiding and focal species (Barbosa et al., 2003) and indicator for the riparian landscape and its anthropogenic stressors (Robitaille and Laurance, 2002). To what extent anthropogenic disturbance of the riparian zone influences the corridor functioning is a central question in the understanding of ecological networks and the definition of restoration goals for river networks.

To determine connectivity in the river network based on the otter expansion, we use a graph theoretic method that integrates functional connectivity - derived from a colonization probability modelling - into a structural connectivity analysis. In this way we will highlight the separate functional and structural aspects of connectivity and ultimately create an integrated measure to both functional and structural connectivity in the river network. The overall objective of this integrated connectivity analysis is to identify priority conservation areas and effective corridors in the river network.

**Methods**

To determine key factors in the corridor functioning of riparian zones environmental gradients and dispersal processes at different scales need to be addressed (Rouget et al., 2006). In this context, connectivity is essentially used to address aspects of movement through the landscape, for which the measurement can be at the landscape-level, but for the process-based approach we also need to look to the more local context of habitat patches (Moilanen and Hanski, 2001). The European otter, as semi-aquatic mammal with high dispersal capacity, offers the opportunity to integrate these different scales. Where population expansion of the otter plays out at the basin scale, individuals experience the local habitat and its connectivity at the river segment scale. The otter is a highly mobile animal with home ranges of 2 - 100km (Ruiz-Olmo et al., 2001). It is an opportunistic feeder, with a preference for fish but a broad
range of other possible prey (crayfish, amphibians, insects, small birds and mammals) (Kruuk et al., 1997). A recovery of otter has been observed in the last decades for most of its Western European distribution, recorded for Central Spain (Cortés et al., 1998), Southern Spain (Clavero et al., 2010), Italy (Loy et al., 2009) and France (Lemarchand et al., 2007) after many decades of decline (Lodé, 1993). The Loire river basin represents one of the few West-European areas where a core of historical population persisted. A volunteer network gathered 5 surveys of otter distribution in the Loire River Basin over the last 25 years. Otter presence is ascertained by spraint marks. As otter spraints cannot provide information on otter abundance, only about presence, and furthermore the frequency of spraints may be very low when otters are at low densities (Macdonald et al., 1978), we are limited to a species distribution modelling capable of dealing with incomplete data. The consistent observation effort nevertheless allows for a reconstruction in well-defined time-steps for the natural re-colonization. The ascertained presence observations are attributed to the river segment in question, which is from then considered as colonized/occupied. For the survey periods the number of occupied segments raise gradually (1975-1985: 420 segments, 1985-1992: 585, 1992-1998: 923, 1998-2005: 1118, 2005-2011: 1790). This information can be synthesized in a spread rate of 180km annually over the river basin, from 1600km in 1985 to 6300 km in 2011 of occupied river length in the surveyed network. Translated to the river segments at the colonization front this reveals a propagation speed of 10km year\(^{-1}\). Although the re-colonization is surely not fully accomplished for the Loire basin - only 37% of the surveyed network is occupied –the different parts of the catchment are reached by now (Fig. 1). As dispersing individuals will preferentially choose the best available sites as a residence, this analysis of non-fully accomplished re-colonization of the river network allows discriminating the vital features in the riparian zone for dispersal and habitat selection (Ruiz-Olmo et al., 2001; Clavero et al., 2010).
In accordance to guidelines for otter survey and to avoid overestimating accidental visits of individuals to small water courses (Kruuk, 2006), only main streams in valley systems and rivers starting from a minimum catchment of >10km² are entered in the surveys. The surveyed river network consists of 17000km river length, divided into 4930 river segments homogeneous in hydromorphological characteristics. A systematic sectioning into river segments and assembling of environmental and hydro-morphological data for the riparian corridor in different buffer sizes (valley floor, floodplain, 100m, 30m, 10m) is realized for the entire French river network with the hydromorphology audit system SYRAH (Chandesris et al., 2008). For the river segments information is collated from two spatial scales; the catchment’s land cover information is gathered at regional sub-catchments (i.e. hydrological units delimited by water divides and river confluences) and local information on the riparian corridor is gathered for the individual river segments (Table 1). Temporal change of land cover is not considered in the analysis, as not all data sources could provide sufficient temporal coverage. Experiences with the data sources of catchment-scale land cover furthermore have evidenced it is rather stable for this period over the French territory (see http://www.eea.europa.eu/data-and-maps/data/corine-land-cover).

Graph theory application to connectivity analysis

Graphs are abstractions of landscapes, where patches are represented by nodes connected by links. Links stand for functional inter-patch connections, and in the landscape-ecological context they usually represent the dispersal potential or the number of dispersing individuals between patches (Urban et al., 2009). Integration of graph methods to structural connectivity measures are well-explored recently, and reviewed by Laita et al. (2011). From this review, the flux methods appear most promising to integrate functional connectivity. For the specific
graph structure of dendritic river networks, the Integral Index of Connectivity (Pascual-Hortal and Saura, 2006) offers the best perspectives as it implies a binary connection model. Here, at first the graph’s topological structure for the dendritic network structure of river systems is developed to model the riverscape at the segment scale (Erös et al., 2012). River segments are regarded as the nodes in the graph, whereas the confluences and segment junctions were considered as links in the network. Python scripts are developed to derive an adjacency matrix that depicts both network structure and numbers of connecting segments between all the nodes in the network. This structure enables collating observational and environmental data from different scales to linear entities, and afterwards interpreting the connections both in upstream and downstream direction. To this purpose an undirected graph model of the riverscape is built (Erös et al., 2010). We apply this graph structure first in the dynamic modelling of the species colonization to define functional connectivity over the network. The model results are then used in the integrated connectivity modelling by means of a weighted graph. Each node of the graph is weighted by the modelled colonization probability as a measure of functional connectivity.

To allow comparison of the dynamic modelling of species colonization with static species distribution models (Guisan and Zimmermann, 2000), first a more classic species distribution analysis by Partial Least Square (PLS) regression is used to explore the determining habitat factors. For this analysis the presence in the most recent survey is retained (Fig. 1). The environmental variables associated with river corridor quality (Table 1) are selected as predictors for the PLS-R regression (Wold et al., 2001). In view of the spatial structuring of both the presences and the environmental conditions in the river network, the PLS technique limits the effects of co-linearity of the variables (Wold et al., 2001). Bootstrapping (n=1000) provides credible intervals for the standardized regression coefficients. For this analysis of
species presences the logistic extension of the classic PLS in the package plsRglm is used under the program R 2.12.0 (R Development Core Team 2008).

Bayesian inference of functional connectivity

Generating reliable colonization probabilities implies the construction of process-based habitat models (Hoffman et al., 2010), as indeed not accounting for species movement in habitat modelling may cause true patterns of corridor functioning to be masked (Kery et al., 2009). For a more dynamic modelling occupancy data can be used as a state variable (Hanski et al., 2000; MacKenzie et al., 2003; Royle and Kery, 2007) and incorporated in a spatially explicit modelling of occupied patches to derive estimates of colonization probabilities (Moilanen and Nieminen, 2002). We choose a Bayesian inference model as this enables the estimation of a large number of parameters (Zheng et al., 2007; Ovaskainen and Soininen, 2010). In surveys of most species it is not possible to observe occurrence without error. The estimation of colonization probability for species subject to imperfect detection has received considerable attention both for the spatial bias (MacKenzie et al., 2003; McCarthy et al., 2012) and for the temporal uncertainty (Honnay et al., 2009; Kery et al., 2009; Cianfrani et al., 2010) that arises with the inability to sample the complete population. Bayesian inference offers good perspectives to elucidate the functional component of connectivity, as it is renowned for dealing with spatially structured and incomplete data of species occurrence (Ellison, 2004; Minor and Urban, 2008; Ovaskainen and Soininen, 2010; McCarthy et al., 2012). Colonization rate depends on spatially varying environmental covariates. Random effects models employing Bayesian estimation via Markov Chain Monte Carlo simulations (MCMC) allow tackling this problem. This approach was already successfully applied in ecology for foraging behaviour and predator-prey interactions (see Ellison (2004) for an overview) and more recently for species distribution analysis based on mark-recapture data.
We estimate the colonization probability for river segments under influence of different potential limiting factors in the riparian corridor based on the observations in the different surveys for the river network of the Loire basin. Furthermore we take advantage of the iterative nature of Bayes’ Theorem, in integrating the time steps of observation (5 steps of 5 year) and spatial differentiation of the river network in the analysis (Ellison, 2004). In the comparison of the potential colonization and the observed, with a Monte Carlo Markov Chain type analysis, the environmental conditions of the riparian corridor can explain the observed variance in colonization speed. The environmental variables that are retained from the static regression are entered in this analysis to allow comparison. The model is constructed in a Markov chain with states $x_j = 0$ (absence), 1 (presence), with j corresponding to the different river segments ($j = 1, \ldots, J$) in which the species may occur. Under this model, if an individual is potentially observable at times $t=1,\ldots,5$ and its location $j$ at time $t$ is known, then the probability that the individual will propagate to the segments ($j +1$) in the network depends on the propagation speed and the environmental covariates. The modelling principle is based on a linear model, with a generalized extension of the linear model that allows embedding non-normal response variables (binomial in our case). The response can be adjusted according to the basic equation (Manly et al., 2002):

$$w(x) = (\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots \beta_p x_p)$$

Implemented with a link-function logit $w(x)$ represents the colonization probability, the $x_p$ are the environmental variables and $\beta_p$ the coefficients of the model.
We fit the model in WinBUGS 1.4 (Spiegelhalter et al., 2003) by assuming conventional
diffuse prior distributions for all parameters. To check its proper functioning, the model is
first tested on a set of control data simulated under R. The lack of bibliographic data does not
allow introducing predefined informative priors into the model. In order to verify the
convergence of the model, three Markov chains are initialized for each run. After a burn-in
period of 1000 iterations, the following 4000 iterations are used to derive the parameter’s
posterior probability distribution.

The model is run simultaneously across all river segments, with information for each river
segment stored in a series of three matrices: first, the adjacency matrix of the dendritic river
network structure previously described; second, the environmental descriptors for each river
segment; and third, the otter presences for the river segments in the 5 time steps. For each time
step the theoretically reached neighbouring river segments are simulated and compared with
the observations. The models are run using different measures of propagation speed and then
validated by comparing predicted presence to observed data. For this pre-defined propagation
speed, three different rates of 8-10-12km year\(^{-1}\) are included, based on the observed 10km
year\(^{-1}\) expansion for the entire dataset for the Loire Basin, and a documented progress of
12km year\(^{-1}\) reported for a favourable central part of France (Janssens et al., 2008).

With the derived model we can calculate the posterior probability of colonization for every
segment in the river network. In the final step, we integrate these resulting posterior
probabilities into the graph-based structural connectivity measure to achieve an integrated connectivity assessment.

Graph-theoretic integrated model of connectivity

For the integrative step to the connectivity measurement, we apply the graph method of weighing network importance of nodes - river segments in our case (Urban, 2005), by integration of the dynamic model-derived colonization probability in the Integral Index of Connectivity (Pascual-Hortal and Saura, 2006, 2008). This index offers a measure that integrates a quality valuation of nodes with the structural connectivity of the river network.

Otter presence in the entirely colonized upstream part of the basin, proved better predicted by this IIC connectivity measure than by habitat quality (Van Looy et al., 2013). In this way the combination of the colonization probability and the structural connectivity, can provide a more reliable indication to the dispersal network and to critical migration routes that should have high conservation priority. The general formula of the integral index of connectivity is for our case defined as follows:

\[
IIC = \sum_i \sum_j \left[ \frac{P_i \times P_j}{(1 + N_{ij})} \right] / A_L^2
\]

With \(A_L\) the overall sum of posterior probabilities of colonization determined with the model for the entire river basin, \(P_i\) and \(P_j\) the posterior probabilities of colonization for river segments \(i\) and \(j\), \(N_{ij}\) is the number of segments in the shortest path between segments \(i\) and \(j\), for \(i = 1,\ldots,n\) and \(j = 1,\ldots,n\), where \(n\) is the total number of segments. The relative ranking of segments by their contribution to the overall index value is the most useful measure for the segment’s connectivity. To calculate this importance of individual segments, we systematically remove each particular segment and recalculate the IIC index. The percentage
of index value loss (delta value) measures the contribution of each segment to the overall
index value as follows:

\[ dIIC = 100 \frac{[(IIC - IIC')]}{IIC} \]

where IIC and IIC’ correspond to the IIC value before and after the loss of a certain segment,
respectively (Pascual-Hortal and Saura, 2006, 2008). We use the recently developed
ConeforSensinode 2.2 software (Saura and Torné, 2009) to calculate dIIC values for each
river segment.

Results

From the variables entered in the PLS-regression, seven variables of riparian corridor
attributes responded significantly, albeit that these only explained 12% of the otter
distribution. The geographic descriptors of altitude and slope, and the land use pressures of
urbanization and intensive agriculture in the upstream sub-catchment showed no relationship
with otter occurrence. The strongest response is observed for the channel straightening, which
shows the highest negative effect to otter occurrence. Positive factor is the forest cover in the
larger riparian corridor zones.

Colonization model outcome

The three chains launched in the WINBUGS program blended together well before 1000
iterations in the calibration runs, assuring reliability in the answer for the model. This
reliability is reflected in the well-balanced estimates for the regression coefficients for the
different predictor variables (Fig. 2). The density distributions are all quite narrow and
conform for the three different propagation speeds. The 8km year\(^{-1}\) model showed an explained variance of 23% of the observed propagation with the selected descriptors, whereas for the 10km year\(^{-1}\) and 12km year\(^{-1}\) models the descriptors predicted correctly 36% and 35% respectively of the observed species propagation.

The hydromorphological stressor of channel straightening shows the narrowest posterior density distribution and takes the largest part of the explained variance for the otter colonization. Second discriminator is the forest cover in the 30m buffer; both a habitat element as a stressor descriptor for fragmentation of the riparian corridor. Remarkable is that the cover of forest in the 10m buffer and in the larger valley floor didn’t respond significantly. The human presence, observed in urbanization of the 100m buffer, is the third significant variable for the otter colonization with inferred model parameter significantly differing from zero. The variables of infrastructure in the riparian corridor showed no influence as no significant deviation from zero was inferred.

**Integrated connectivity**

The posterior probabilities of colonization for the entire river network are presented in figure 3A. Integrating these colonization probabilities for the river segments in the Integral Index of Connectivity, results in the proposed integrated measure of connectivity for each segment (Fig. 3B). Explained variance for the species propagation is raised up to 60% for the observations with this integrated model. Presented on the map, this integrated connectivity index clearly brings in additional elements to the colonization process. Certain reaches that show high probability of colonization based on the absence of obstacles in the corridor, show in the observations little progress. This can be explained with this connectivity index that integrates the branchiness and density of the dendritic network structure. The observed slow
progress of colonization counts for some rivers in the centre of the basin (Cher and Indre, Fig. 3A-B), that show lower integrated connectivity values as the local river network is less branched and dense, resulting in lower network attractiveness.

Discussion

The presented approach is novel in its integration of structural and functional connectivity in a single measure. A modified version of the Integral Index of Connectivity (Pascual-Hortal and Saura, 2006) is developed for a graph-based dendritic network application with river segments as nodes. So, the ‘integral’ part of the IIC is extended with a notion of permeability of the corridors in combination with the network distance between nodes to fully evaluate the dendritic network connectivity. Weighted graphs are constructed to integrate the functional connectivity valuation of the network nodes, allowing the calculation of an integrated connectivity measure based on the adjacency matrices for all connections in the river network. The applied method is a significant advance compared to existing graph-based methods in connectivity analysis that are restricted to qualification of habitat patches as nodes (Urban, 2005), and the notion of functional connectivity to a species-specific distance or barrier criterion (Laita et al., 2012; Perkin, Gido, Al-Ta’ani et al., 2013). Most analysis methods of connectivity are still based on the uniform percolation theory (Gardner et al., 1989) and in this way do not integrate information on functional corridor quality. Here we use the weighted graphs to integrate not only distances but also the functional corridor quality to the connectivity analysis. Challenges for this integrative approach to functional and structural connectivity for riparian corridors arose at two fronts: both the dendritic structure of the river network that we fully integrate with the graph method, and the functional connectivity inference for the species
movement based on spatially structured data (Grant et al., 2007, Peterson et al., 2013), in our
case questioned for otter colonization probability. To infer the functional connectivity, we propose a Bayesian hierarchical modelling approach
that allows dealing with the graph structure and the temporal observational and incomplete
data. For other cases a metapopulation model or even a classic distribution model – for
instance for more exhaustive population surveys with less temporal spread - might reveal the
functional connectivity component, and enable an integrated connectivity analysis in the same
way. Our otter observational data does not offer the necessary information to apply the
attractive metapopulation models and metrics for identifying network connectivity (Hanski
and Ovaskainen, 2003). The proposed approach might furthermore be extended to aquatic
species modelling with integration into the graph structure of elements of stream network
models (Peterson and Ver Hoef, 2010).

Recently a range of distribution model types are explored for the European otter. It concerns
mostly classic species distribution models (Barbosa et al., 2003; Cianfrani et al., 2011), but
also some more specific models emphasizing the riparian corridor functioning (Ottaviani et
al., 2009) or re-colonization patterns through land use changes over time (Marcelli and
Fusillo, 2009; Clavero et al., 2010). In contrast to all these models, we adopt a more dynamic
modelling of the spatial and temporal sequences of site occupancy to identify functional
connectivity (Kery et al., 2009). With the Bayesian model we revealed different determining
factors for the colonization process than the habitat factors revealed by the static PLS
regression of otter presence in the basin. The significant responses to infrastructure density
observed in the otter distribution model were not present in the colonization analysis. For the
colonization process the presence of infrastructure did not seem an obstacle. Roads are
obviously a major threat to the species (Philcox et al., 1999), which is confirmed here in the
distribution model confirming the negative association of infrastructure with habitat quality. On the other hand, infrastructure density does not appear as a factor hampering colonization. So, where the fitted model lacks predictive power to population dynamics as no abundance data was available, it nevertheless clearly identifies the determining corridor aspects. The detailed information for the riparian zone proves appropriate to infer the relevant factors in the colonization process. Still, the absence of multi-temporal land cover data in the analysis might contribute to the rather low explained fractions in the model. But in the same way we didn’t include climatological or population dynamic elements to this analysis. Nevertheless, the model shows its merits for the highly mobile otter with its remarkable recovery. Most of the recently developed otter distribution models (Robitaille and Laurance, 2002; Barbosa et al., 2003; Cianfrani et al., 2011) only consider broad scale factors of climate, geography and anthropogenic stressors of urbanization and infrastructure density. These models all have the disadvantage of a coarse grid-based landscape representation that is inappropriate to describe accurately the land use in the riparian corridor (Tormos et al., 2011). In our analysis no geographic or land cover elements at large scale explain otter distribution. And for the colonization even the landscape features in the larger buffers of the valley floor and the floodplain appear as non-significant. The integrated connectivity analysis reveals the importance of the density of the local hydrographical network for the otter colonization. This conclusion corresponds to other large scale studies that relate otter occurrence to the abundance of rivers and lakes (Barbosa et al., 2003). The integrated connectivity analysis (fig 4B) reveals that the vital corridors and conservation networks for otter are more concentrated in the lower parts of the river basin. Partly, this can be due to the fact that we take into account only longitudinal connectivity describing the species movement within one river system (Cote et al., 2009). Instead, for the
dispersal of semi-aquatic species the use of the surrounding matrix to colonize neighbouring river catchments could also be important (Grant et al., 2007). In other words the lateral connectivity explaining the dispersal movements toward neighbouring basins could be important on developing the network model and subsequent connectivity analyses (Wiens, 2002; Carranza et al., 2013).

The conclusion for vital networks in the downstream part contrasts to the actual occurrence of the species in the Loire basin and also to data from Spain (Prenda and GranadoLorencio, 1996; Barbosa et al., 2003) and Italy (Marcelli and Fusillo, 2009; Ottaviani et al., 2009), where better otter habitat is documented upstream than downstream due to lower human-related landscape degradation. Yet, some studies of otter populations conclude that the preferred otter habitat comprises the slower and more productive middle and lower reaches of rivers (Madsen and Prang, 2001). Here, the modelled habitat and functional connectivity is more guaranteed upstream in the river basin, whereas the integrated connectivity points at the importance and opportunities for the downstream reaches to establish a well-connected ecological network. The marked difference in the modelled connectivity values between headwaters at top left and bottom of the figure 3B is due to the high density of the network, where the both regions have high colonization probabilities. The branchiness is higher in this lowland region than in the upstream mountainous headwaters, and furthermore is this plains region more productive. Same observation was made for the rivers Cher and Indre: these rivers present in their central part some 100km of river with only a few for otter relevant tributaries arriving.

So, the lower reaches of the river basin emerge from this integrated analysis as more important to the overall river network connectivity than the upstream basin, even though their corridor quality is in general weaker. The lower reaches allow more contact between the different parts of the river basin and mostly present more densely branched structures which
explains the higher importance with respect to connectivity. Also in the other parts of the river basin this integrated connectivity analysis points out the relative contribution of the different segments in the ecological network for the species, and in the overall river network connectivity. In this way, the analysis emphasizes uniquely portions of the river system which may not be important as prime otter habitat, yet are important to enable colonization by allowing the otters to pass through to better habitat. To provide information about restoration opportunities the analysis can also be turned to tackle the opposite question - which segments have high structural connectivity, but poor functional connectivity; essentially where should restoration dollars be spent to increase otter colonization. In conclusion, this integrated analysis to identify vital segments for network connectivity improves our knowledge of effective corridors for conservation and restoration and it gains in weight thanks to the emblematic and economic value of the chosen species (White et al., 1997).

Acknowledgments

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Literature cited


Table 1. Environmental variables from the different spatial scales that were collated to the river segments.

<table>
<thead>
<tr>
<th><strong>Catchment landcover</strong></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>urbanisation</td>
<td>percentage cover of urban land use class in CORINE land cover data of the sub-catchments</td>
</tr>
<tr>
<td>intensive agriculture</td>
<td>percentage cover of intensive agricultural CORINE land cover classes of the sub-catchments</td>
</tr>
<tr>
<td>natural</td>
<td>percentage cover of near-natural CORINE land cover classes data of the sub-catchments</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>River segment</strong></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude</td>
<td>elevation at downstream point of river segments</td>
</tr>
<tr>
<td>river slope</td>
<td>slope of the river bed over the segment</td>
</tr>
<tr>
<td>valleyslope</td>
<td>valley slope perpendicular to the river</td>
</tr>
<tr>
<td>discharge</td>
<td>mean annual discharge for gauging station or model prediction at river segment level</td>
</tr>
<tr>
<td>sinuosity</td>
<td>sinuosity of the river bed over the segment</td>
</tr>
<tr>
<td>channelstraightening</td>
<td>percentage of straight reaches over the segment, weighted by river type</td>
</tr>
<tr>
<td>density of bars</td>
<td>number of lateral bars over the segment, divided by river length</td>
</tr>
<tr>
<td>density of weirs/dams</td>
<td>number of weirs/dams per segment, divided by river length</td>
</tr>
<tr>
<td>density of bridges</td>
<td>number of river crossing bridges per segment, divided by river length</td>
</tr>
<tr>
<td>alluvial forestcover</td>
<td>percentage cover of forest patches over the alluvial plain of the river segment</td>
</tr>
<tr>
<td>alluvial plain infrastructure</td>
<td>percentage cover of infrastructure over the alluvial plain of the river segment</td>
</tr>
<tr>
<td>alluvial plain urbanisation</td>
<td>percentage cover of urbanisation over the alluvial plain of the river segment</td>
</tr>
<tr>
<td>density of dikes</td>
<td>length of flood protection levees per segment, divided by river length</td>
</tr>
<tr>
<td>connected waters</td>
<td>percentage cover of connected standing waters over the alluvial plain of the river segment</td>
</tr>
<tr>
<td>disconnected waters</td>
<td>percentage cover of disconnected standing waters over the alluvial plain of the river segment</td>
</tr>
<tr>
<td>riparianforestcover</td>
<td>percentage cover of forest patches for the 30m riparian buffer of the river segment</td>
</tr>
<tr>
<td>riparianforestcanopy</td>
<td>percentage cover of forest patches for the 10m riparian buffer of the river segment</td>
</tr>
<tr>
<td>riparian infrastructure</td>
<td>percentage cover of infrastructure over riparian buffer of three river widths of the segment</td>
</tr>
</tbody>
</table>
Fig. 1. River segments with confirmed presence of the European otter in the Loire river basin in the consecutive time steps.

Fig. 2. Density distributions of the posterior regression coefficient estimates for the different predictor variables in the model for the three propagation speed calibrations.

Fig. 3.(A) Modelled colonization probability and (B) Integral Index of Connectivity (dIIC) values for the river segments of the Loire basin. The probability values are calculated for each river segment corresponding to the inference model result, with equal class distribution of modelled values for the probability of colonization at the colonization front based on the 12km/y propagation speed run. These values identify the functional corridor quality of the individual segments. Based on this corridor quality, the dIIC gives the integrated measure of functional and structural connectivity, that allows to identify the effective corridors and priority areas for the network connectivity. The dIIC-values indicate the relative contribution of the individual river segments to the overall connectivity.
Fig. 1. Otter occupied segments in time

surveyed river network
2005-2011
1998-2005
1992-1998
1985-1992
1975-1985
contour France
Fig. 2.
Fig. 3.