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

3

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13

14 **Keywords**

15 Dendritic network– riparian corridor – dynamic occupancy modelling - Integral Index of

16 Connectivity – colonisation – hydromorphology

17

18

19

20 **Summary**

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

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

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

45 **Introduction**

46 The role of river corridors in providing connectivity is questioned in the context of defining
47 ecological networks over large territories (Rouget et al., 2006; Grant et al., 2007). The
48 assessment of connectivity in river networks generally poses specific methodological
49 difficulties (Peterson and VerHoef, 2010), as does more generally the contribution of specific
50 landscape features to the accommodation of biological processes (Simberloff et al., 1992).
51 Attempts to measure this interplay between landscape configuration and species movement,
52 that we call functional connectivity, are still quite uncommon (Wainwright et al., 2011).
53 Structural connectivity is defined as the adjacency or proximity of patches within a landscape
54 and is a measure of the degree to which patches are connected without regard to organism
55 behaviour (Taylor et al., 1993). Alternatively, functional connectivity is conceptually defined
56 as the degree to which a landscape impedes or facilitates movement of organisms among
57 patches (Bélisle, 2005). Functional connectivity is mostly derived from species range or
58 dispersal studies, at best with dynamic process-oriented population or distribution models
59 (Marion et al., 2012; Schurr et al., 2012). Managing for structural connectivity is thought to
60 increase functional connectivity, yet this implication is not so straightforward (Tischendorf
61 and Fahrig, 2000). Ideally, functional and structural connectivity should be integrated when
62 providing guidance for management. That is what we try to accomplish for dendritic river
63 networks in this paper.

64 To demonstrate connectivity, biotic processes involving species movement have to be studied
65 over extended spatial and temporal scales. To this purpose, we analyse the well-documented
66 re-colonization of the French River Loire basin by the European otter. The European otter is
67 an emblematic species for nature conservation in a broad societal context; therefore it is often
68 advocated as a model species in studies for ecosystem services and ecological networks
69 (Bifulchi and Lodé, 2005). Especially with respect to river corridor functioning the otter is

70 proposed as guiding and focal species (Barbosa et al., 2003) and indicator for the riparian
71 landscape and its anthropogenic stressors (Robitaille and Laurance, 2002). To what extent
72 anthropogenic disturbance of the riparian zone influences the corridor functioning is a central
73 question in the understanding of ecological networks and the definition of restoration goals
74 for river networks.

75

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

83

84 **Methods**

85 To determine key factors in the corridor functioning of riparian zones environmental gradients
86 and dispersal processes at different scales need to be addressed (Rouget et al., 2006). In this
87 context, connectivity is essentially used to address aspects of movement through the
88 landscape, for which the measurement can be at the landscape-level, but for the process-based
89 approach we also need to look to the more local context of habitat patches (Moilanen and
90 Hanski, 2001). The European otter, as semi-aquatic mammal with high dispersal capacity,
91 offers the opportunity to integrate these different scales. Where population expansion of the
92 otter plays out at the basin scale, individuals experience the local habitat and its connectivity
93 at the river segment scale. The otter is a highly mobile animal with home ranges of 2 - 100km
94 (Ruiz-Olmo et al., 2001). It is an opportunistic feeder, with a preference for fish but a broad

95 range of other possible prey (crayfish, amphibians, insects, small birds and mammals)(Kruuk
96 et al., 1997). A recovery of otter has been observed in the last decades for most of its Western
97 European distribution, recorded for Central Spain (Cortés et al., 1998), Southern Spain
98 (Clavero et al., 2010), Italy (Loy et al., 2009) and France (Lemarchand et al., 2007) after
99 many decades of decline (Lodé, 1993). The Loire river basin represents one of the few West-
100 European areas where a core of historical population persisted. A volunteer network gathered
101 5 surveys of otter distribution in the Loire River Basin over the last 25 years. Otter presence is
102 ascertained by spraint marks. As otter spraints cannot provide information on otter abundance,
103 only about presence, and furthermore the frequency of spraints may be very low when otters
104 are at low densities (Macdonald et al., 1978), we are limited to a species distribution
105 modelling capable of dealing with incomplete data. The consistent observation effort
106 nevertheless allows for a reconstruction in well-defined time-steps for the natural re-
107 colonization. The ascertained presence observations are attributed to the river segment in
108 question, which is from then considered as colonized/occupied. For the survey periods the
109 number of occupied segments raise gradually (1975-1985: 420 segments, 1985-1992: 585,
110 1992-1998: 923, 1998-2005: 1118, 2005-2011: 1790).

111 This information can be synthesized in a spread rate of 180km annually over the river basin,
112 from 1600km in 1985 to 6300 km in 2011 of occupied river length in the surveyed network.
113 Translated to the river segments at the colonization front this reveals a propagation speed of
114 10km year⁻¹. Although the re-colonization is surely not fully accomplished for the Loire basin
115 - only 37% of the surveyed network is occupied –the different parts of the catchment are
116 reached by now (Fig. 1). As dispersing individuals will preferably choose the best available
117 sites as a residence, this analysis of non-fully accomplished re-colonization of the river
118 network allows discriminating the vital features in the riparian zone for dispersal and habitat
119 selection (Ruiz-Olmo et al., 2001; Clavero et al., 2010).

120

121 In accordance to guidelines for otter survey and to avoid overestimating accidental visits of
122 individuals to small water courses (Kruuk, 2006), only main streams in valley systems and
123 rivers starting from a minimum catchment of $>10\text{km}^2$ are entered in the surveys. The surveyed
124 river network consists of 17000km river length, divided into 4930 river segments
125 homogeneous in hydromorphological characteristics. A systematic sectioning into river
126 segments and assembling of environmental and hydro-morphological data for the riparian
127 corridor in different buffer sizes (valley floor, floodplain, 100m, 30m, 10m) is realized for the
128 entire French river network with the hydromorphology audit system SYRAH (Chandesris et
129 al., 2008). For the river segments information is collated from two spatial scales; the
130 catchment's land cover information is gathered at regional sub-catchments (i.e. hydrological
131 units delimited by water divides and river confluences) and local information on the riparian
132 corridor is gathered for the individual river segments (Table 1). Temporal change of land
133 cover is not considered in the analysis, as not all data sources could provide sufficient
134 temporal coverage. Experiences with the data sources of catchment-scale land cover
135 furthermore have evidenced it is rather stable for this period over the French territory (see
136 <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover>).

137

138 **Graph theory application to connectivity analysis**

139 Graphs are abstractions of landscapes, where patches are represented by nodes connected by
140 links. Links stand for functional inter-patch connections, and in the landscape-ecological
141 context they usually represent the dispersal potential or the number of dispersing individuals
142 between patches (Urban et al., 2009). Integration of graph methods to structural connectivity
143 measures are well-explored recently, and reviewed by Laita et al. (2011). From this review,
144 the flux methods appear most promising to integrate functional connectivity. For the specific

145 graph structure of dendritic river networks, the Integral Index of Connectivity (Pascual-Hortal
146 and Saura, 2006) offers the best perspectives as it implies a binary connection model.
147 Here, at first the graph's topological structure for the dendritic network structure of river
148 systems is developed to model the riverscape at the segment scale (Erös et al., 2012). River
149 segments are regarded as the nodes in the graph, whereas the confluences and segment
150 junctions were considered as links in the network. Python scripts are developed to derive an
151 adjacency matrix that depicts both network structure and numbers of connecting segments
152 between all the nodes in the network. This structure enables collating observational and
153 environmental data from different scales to linear entities, and afterwards interpreting the
154 connections both in upstream and downstream direction. To this purpose an undirected graph
155 model of the riverscape is built (Erös et al., 2010). We apply this graph structure first in the
156 dynamic modelling of the species colonization to define functional connectivity over the
157 network. The model results are then used in the integrated connectivity modelling by means
158 of a weighted graph. Each node of the graph is weighted by the modelled colonization
159 probability as a measure of functional connectivity.

160

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

170 species presences the logistic extension of the classic PLS in the package `plsRglm` is used
171 under the program R 2.12.0 (R Development Core Team 2008).

172

173 **Bayesian inference of functional connectivity**

174 Generating reliable colonization probabilities implies the construction of process-based
175 habitat models (Hoffman et al., 2010), as indeed not accounting for species movement in
176 habitat modelling may cause true patterns of corridor functioning to be masked (Kery et al.,
177 2009). For a more dynamic modelling occupancy data can be used as a state variable (Hanski
178 et al., 2000; MacKenzie et al., 2003; Royle and Kery, 2007) and incorporated in a spatially
179 explicit modelling of occupied patches to derive estimates of colonization
180 probabilities (Moilanen and Nieminen, 2002). We choose a Bayesian inference model as this
181 enables the estimation of a large number of parameters (Zheng et al., 2007; Ovaskainen and
182 Soininen, 2010). In surveys of most species it is not possible to observe occurrence without
183 error. The estimation of colonization probability for species subject to imperfect detection has
184 received considerable attention both for the spatial bias (MacKenzie et al., 2003; McCarthy et
185 al., 2012) and for the temporal uncertainty (Honnay et al., 2009; Kery et al., 2009; Cianfrani
186 et al., 2010) that arises with the inability to sample the complete population. Bayesian
187 inference offers good perspectives to elucidate the functional component of connectivity, as it
188 is renowned for dealing with spatially structured and incomplete data of species occurrence
189 (Ellison, 2004; Minor and Urban, 2008; Ovaskainen and Soininen, 2010; McCarthy et al.,
190 2012). Colonization rate depends on spatially varying environmental covariates. Random
191 effects models employing Bayesian estimation via Markov Chain Monte Carlo simulations
192 (MCMC) allow tackling this problem. This approach was already successfully applied in
193 ecology for foraging behaviour and predator-prey interactions (see Ellison (2004) for an
194 overview) and more recently for species distribution analysis based on mark-recapture data

195 (Zheng et al., 2007), metapopulation models (O'Hara et al., 2002) and dynamic community
196 models (Kery et al., 2009; Bled et al., 2011).

197

198 We estimate the colonization probability for river segments under influence of different
199 potential limiting factors in the riparian corridor based on the observations in the different
200 surveys for the river network of the Loire basin. Furthermore we take advantage of the
201 iterative nature of Bayes' Theorem, in integrating the time steps of observation (5 steps of 5
202 year) and spatial differentiation of the river network in the analysis (Ellison, 2004). In the
203 comparison of the potential colonization and the observed, with a Monte Carlo Markov Chain
204 type analysis, the environmental conditions of the riparian corridor can explain the observed
205 variance in colonization speed. The environmental variables that are retained from the static
206 regression are entered in this analysis to allow comparison. The model is constructed in a
207 Markov chain with states $x_j = 0$ (absence), 1 (presence), with j corresponding to the different
208 river segments ($j = 1, \dots, J$) in which the species may occur. Under this model, if an
209 individual is potentially observable at times $t=1, \dots, 5$ and its location j at time t is known, then
210 the probability that the individual will propagate to the segments ($j + 1$) in the network
211 depends on the propagation speed and the environmental covariates. The modelling principle
212 is based on a linear model, with a generalized extension of the linear model that allows
213 embedding non-normal response variables (binomial in our case). The response can be
214 adjusted according to the basic equation (Manly *et al.*, 2002);

215
$$w(x) = (\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \dots \beta_p x_p)$$

216 Implemented with a link-function $\text{logit } w(x)$ represents the colonization probability, the x_p are
217 the environmental variables and β_p the coefficients of the model:

$$w(\mathbf{x}) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \dots \beta_p x_p)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \dots \beta_p x_p)}$$

218

219

220 We fit the model in WinBUGS 1.4 (Spiegelhalter et al., 2003) by assuming conventional
221 diffuse prior distributions for all parameters. To check its proper functioning, the model is
222 first tested on a set of control data simulated under R. The lack of bibliographic data does not
223 allow introducing predefined informative priors into the model. In order to verify the
224 convergence of the model, three Markov chains are initialized for each run. After a burn-in
225 period of 1000 iterations, the following 4000 iterations are used to derive the parameter's
226 posterior probability distribution.

227 The model is run simultaneously across all river segments, with information for each river
228 segment stored in a series of three matrices: first, the adjacency matrix of the dendritic river
229 network structure previously described; second, the environmental descriptors for each river
230 segment; and third, the otter presences for the river segments in the 5 time steps. For each time
231 step the theoretically reached neighbouring river segments are simulated and compared with
232 the observations. The models are run using different measures of propagation speed and then
233 validated by comparing predicted presence to observed data. For this pre-defined propagation
234 speed, three different rates of 8-10-12km year⁻¹ are included, based on the observed 10km
235 year⁻¹ expansion for the entire dataset for the Loire Basin, and a documented progress of
236 12km year⁻¹ reported for a favourable central part of France (Janssens et al., 2008).

237

238 With the derived model we can calculate the posterior probability of colonization for every
239 segment in the river network. In the final step, we integrate these resulting posterior

240 probabilities into the graph-based structural connectivity measure to achieve an integrated
241 connectivity assessment.

242

243 **Graph-theoretic integrated model of connectivity**

244 For the integrative step to the connectivity measurement, we apply the graph method of
245 weighing network importance of nodes - river segments in our case (Urban, 2005), by
246 integration of the dynamic model-derived colonization probability in the Integral Index of
247 Connectivity (Pascual-Hortal and Saura, 2006, 2008). This index offers a measure that
248 integrates a quality valuation of nodes with the structural connectivity of the river network.
249 Otter presence in the entirely colonized upstream part of the basin, proved better predicted by
250 this IIC connectivity measure than by habitat quality (Van Looy et al., 2013). In this way the
251 combination of the colonization probability and the structural connectivity, can provide a
252 more reliable indication to the dispersal network and to critical migration routes that should
253 have high conservation priority. The general formula of the integral index of connectivity is
254 for our case defined as follows:

$$255 \text{ IIC} = \frac{\sum_i \sum_j [P_i \times P_j / (1 + N_{ij})]}{A_L^2}$$

256

257 With A_L the overall sum of posterior probabilities of colonization determined with the model
258 for the entire river basin, P_i and P_j the posterior probabilities of colonization for river
259 segments i and j , N_{ij} is the number of segments in the shortest path between segments i and j ,
260 for $i = 1, \dots, n$ and $j = 1, \dots, n$, where n is the total number of segments. The relative ranking of
261 segments by their contribution to the overall index value is the most useful measure for the
262 segment's connectivity. To calculate this importance of individual segments, we
263 systematically remove each particular segment and recalculate the IIC index. The percentage

264 of index value loss (delta value) measures the contribution of each segment to the overall
265 index value as follows:

266

$$267 \quad dIIC = 100 [(IIC - IIC') / IIC]$$

268

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

273

274

275 **Results**

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

283

284 **Colonization model outcome**

285 The three chains launched in the WINBUGS program blended together well before 1000
286 iterations in the calibration runs, assuring reliability in the answer for the model. This
287 reliability is reflected in the well-balanced estimates for the regression coefficients for the
288 different predictor variables (Fig. 2). The density distributions are all quite narrow and

289 conform for the three different propagation speeds. The 8km year⁻¹ model showed an
290 explained variance of 23% of the observed propagation with the selected descriptors, whereas
291 for the 10km year⁻¹ and 12km year⁻¹ models the descriptors predicted correctly 36% and 35%
292 respectively of the observed species propagation.

293

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

303

304 **Integrated connectivity**

305 The posterior probabilities of colonization for the entire river network are presented in figure
306 3A. Integrating these colonization probabilities for the river segments in the Integral Index of
307 Connectivity, results in the proposed integrated measure of connectivity for each segment
308 (Fig. 3B). Explained variance for the species propagation is raised up to 60% for the
309 observations with this integrated model. Presented on the map, this integrated connectivity
310 index clearly brings in additional elements to the colonization process. Certain reaches that
311 show high probability of colonization based on the absence of obstacles in the corridor, show
312 in the observations little progress. This can be explained with this connectivity index that
313 integrates the branchiness and density of the dendritic network structure. The observed slow

314 progress of colonization counts for some rivers in the centre of the basin (Cher and Indre, Fig.
315 3A-B), that show lower integrated connectivity values as the local river network is less
316 branched and dense, resulting in lower network attractiveness.

317

318 **Discussion**

319 The presented approach is novel in its integration of structural and functional connectivity in a
320 single measure. A modified version of the Integral Index of Connectivity (Pascual-Hortal and
321 Saura, 2006) is developed for a graph-based dendritic network application with river segments
322 as nodes. So, the ‘integral’ part of the IIC is extended with a notion of permeability of the
323 corridors in combination with the network distance between nodes to fully evaluate the
324 dendritic network connectivity. Weighted graphs are constructed to integrate the functional
325 connectivity valuation of the network nodes, allowing the calculation of an integrated
326 connectivity measure based on the adjacency matrices for all connections in the river network.
327 The applied method is a significant advance compared to existing graph-based methods in
328 connectivity analysis that are restricted to qualification of habitat patches as nodes (Urban,
329 2005), and the notion of functional connectivity to a species-specific distance or barrier
330 criterion (Laita et al., 2012; Perkin, Gido, Al-Ta’ani *et al.*, 2013). Most analysis methods of
331 connectivity are still based on the uniform percolation theory (Gardner et al., 1989) and in this
332 way do not integrate information on functional corridor quality. Here we use the weighted
333 graphs to integrate not only distances but also the functional corridor quality to the
334 connectivity analysis.

335 Challenges for this integrative approach to functional and structural connectivity for riparian
336 corridors arose at two fronts: both the dendritic structure of the river network that we fully
337 integrate with the graph method, and the functional connectivity inference for the species

338 movement based on spatially structured data(Grant et al., 2007, Peterson et al., 2013), in our
339 case questioned for otter colonization probability.
340 To infer the functional connectivity, we propose a Bayesian hierarchical modelling approach
341 that allows dealing with the graph structure and the temporal observational and incomplete
342 data. For other cases a metapopulation model or even a classic distribution model – for
343 instance for more exhaustive population surveys with less temporal spread - might reveal the
344 functional connectivity component, and enable an integrated connectivity analysis in the same
345 way. Our otter observational data does not offer the necessary information to apply the
346 attractive metapopulation models and metrics for identifying network connectivity (Hanski
347 and Ovaskainen, 2003). The proposed approach might furthermore be extended to aquatic
348 species modelling with integration into the graph structure of elements of stream network
349 models (Peterson and Ver Hoef, 2010).

350

351 Recently a range of distribution model types are explored for the European otter. It concerns
352 mostly classic species distribution models (Barbosa et al., 2003; Cianfrani et al., 2011), but
353 also some more specific models emphasizing the riparian corridor functioning (Ottaviani et
354 al., 2009) or re-colonization patterns through land use changes over time (Marcelli and
355 Fusillo, 2009; Clavero et al., 2010). In contrast to all these models, we adopt a more dynamic
356 modelling of the spatial and temporal sequences of site occupancy to identify functional
357 connectivity (Kery et al., 2009). With the Bayesian model we revealed different determining
358 factors for the colonization process than the habitat factors revealed by the static PLS
359 regression of otter presence in the basin. The significant responses to infrastructure density
360 observed in the otter distribution model were not present in the colonization analysis. For the
361 colonization process the presence of infrastructure did not seem an obstacle. Roads are
362 obviously a major threat to the species (Philcox et al., 1999), which is confirmed here in the

363 distribution model confirming the negative association of infrastructure with habitat quality.
364 On the other hand, infrastructure density does not appear as a factor hampering colonization.
365 So, where the fitted model lacks predictive power to population dynamics as no abundance
366 data was available, it nevertheless clearly identifies the determining corridor aspects. The
367 detailed information for the riparian zone proves appropriate to infer the relevant factors in
368 the colonization process. Still, the absence of multi-temporal land cover data in the analysis
369 might contribute to the rather low explained fractions in the model. But in the same way we
370 didn't include climatological or population dynamic elements to this analysis. Nevertheless,
371 the model shows its merits for the highly mobile otter with its remarkable recovery.
372 Most of the recently developed otter distribution models (Robitaille and Laurance, 2002;
373 Barbosa et al., 2003; Cianfrani et al., 2011) only consider broad scale factors of climate,
374 geography and anthropogenic stressors of urbanization and infrastructure density. These
375 models all have the disadvantage of a coarse grid-based landscape representation that is
376 inappropriate to describe accurately the land use in the riparian corridor (Tormos et al., 2011).
377 In our analysis no geographic or land cover elements at large scale explain otter distribution.
378 And for the colonization even the landscape features in the larger buffers of the valley floor
379 and the floodplain appear as non-significant.

380

381 The integrated connectivity analysis reveals the importance of the density of the local
382 hydrographical network for the otter colonization. This conclusion corresponds to other large
383 scale studies that relate otter occurrence to the abundance of rivers and lakes (Barbosa et al.,
384 2003). The integrated connectivity analysis (fig 4B) reveals that the vital corridors and
385 conservation networks for otter are more concentrated in the lower parts of the river basin.
386 Partly, this can be due to the fact that we take into account only longitudinal connectivity
387 describing the species movement within one river system (Cote et al., 2009). Instead, for the

388 dispersal of semi-aquatic species the use of the surrounding matrix to colonize neighbouring
389 river catchments could also be important (Grant et al., 2007). In other words the lateral
390 connectivity explaining the dispersal movements toward neighbouring basins could be
391 important on developing the network model and subsequent connectivity analyses (Wiens,
392 2002; Carranza et al., 2013).

393 The conclusion for vital networks in the downstream part contrasts to the actual occurrence of
394 the species in the Loire basin and also to data from Spain (Prenda and GranadoLorencio,
395 1996; Barbosa et al., 2003) and Italy (Marcelli and Fusillo, 2009; Ottaviani et al., 2009),
396 where better otter habitat is documented upstream than downstream due to lower human-
397 related landscape degradation. Yet, some studies of otter populations conclude that the
398 preferred otter habitat comprises the slower and more productive middle and lower reaches of
399 rivers (Madsen and Prang, 2001). Here, the modelled habitat and functional connectivity is
400 more guaranteed upstream in the river basin, whereas the integrated connectivity points at the
401 importance and opportunities for the downstream reaches to establish a well-connected
402 ecological network. The marked difference in the modelled connectivity values between
403 headwaters at top left and bottom of the figure 3B is due to the high density of the network,
404 where the both regions have high colonization probabilities. The branchiness is higher in this
405 lowland region than in the upstream mountainous headwaters, and furthermore is this plains
406 region more productive. Same observation was made for the rivers Cher and Indre: these
407 rivers present in their central part some 100km of river with only a few for otter relevant
408 tributaries arriving.

409 So, the lower reaches of the river basin emerge from this integrated analysis as more
410 important to the overall river network connectivity than the upstream basin, even though their
411 corridor quality is in general weaker. The lower reaches allow more contact between the
412 different parts of the river basin and mostly present more densely branched structures which

413 explains the higher importance with respect to connectivity. Also in the other parts of the river
414 basin this integrated connectivity analysis points out the relative contribution of the different
415 segments in the ecological network for the species, and in the overall river network
416 connectivity. In this way, the analysis emphasizes uniquely portions of the river system which
417 may not be important as prime otter habitat, yet are important to enable colonization by
418 allowing the otters to pass through to better habitat. To provide information about restoration
419 opportunities the analysis can also be turned to tackle the opposite question - which segments
420 have high structural connectivity, but poor functional connectivity; essentially where should
421 restoration dollars be spent to increase otter colonization. In conclusion, this integrated
422 analysis to identify vital segments for network connectivity improves our knowledge of
423 effective corridors for conservation and restoration and it gains in weight thanks to the
424 emblematic and economic value of the chosen species (White et al., 1997).

425

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

610 river segments.

611

Catchment landcover

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-catchment
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
valleyslope	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
channelstraightening	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 forestcover	percentage cover of forest patches over the alluvial plain of the river segment
alluvial plain infrastructure	percentage cover of infrastructure over the alluvial plain of the river segment
alluvial plain 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
riparianforestcover	percentage cover of forest patches for the 30m riparian buffer of the river segment
riparianforestcanopy	percentage cover of forest patches for the 10m riparian buffer of the river segment
riparian infrastructure	percentage cover of infrastructure over riparian buffer of three river widths of the segment

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

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613 Fig. 1. River segments with confirmed presence of the European otter in the Loire river basin
614 in the consecutive time steps.

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

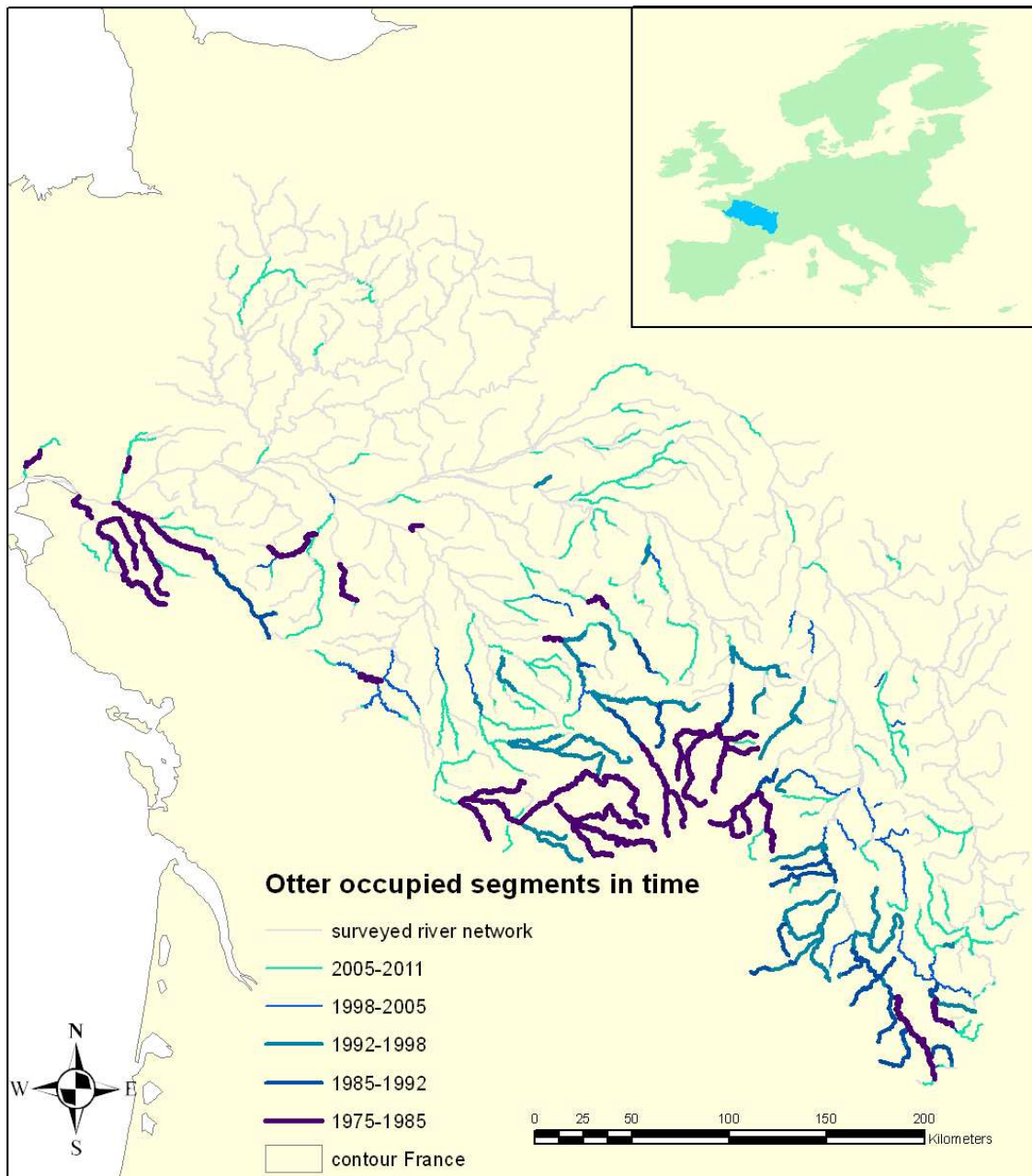
617 Fig. 3.(A) Modelled colonization probability and (B) Integral Index of Connectivity (dIIC)
618 values for the river segments of the Loire basin. The probability values are calculated for each
619 river segment corresponding to the inference model result, with equal class distribution of
620 modelled values for the probability of colonization at the colonization front based on the
621 12km/y propagation speed run. These values identify the functional corridor quality of the
622 individual segments. Based on this corridor quality, the dIIC gives the integrated measure of
623 functional and structural connectivity, that allows to identify the effective corridors and
624 priority areas for the network connectivity. The dIIC-values indicate the relative contribution
625 of the individual river segments to the overall connectivity.

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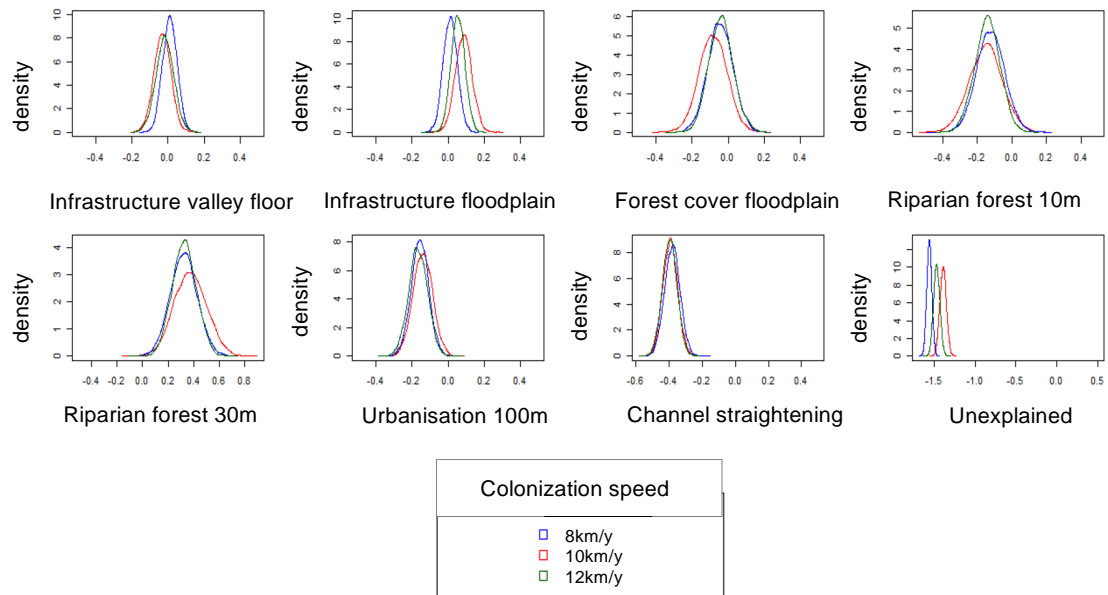
Fig. 1.

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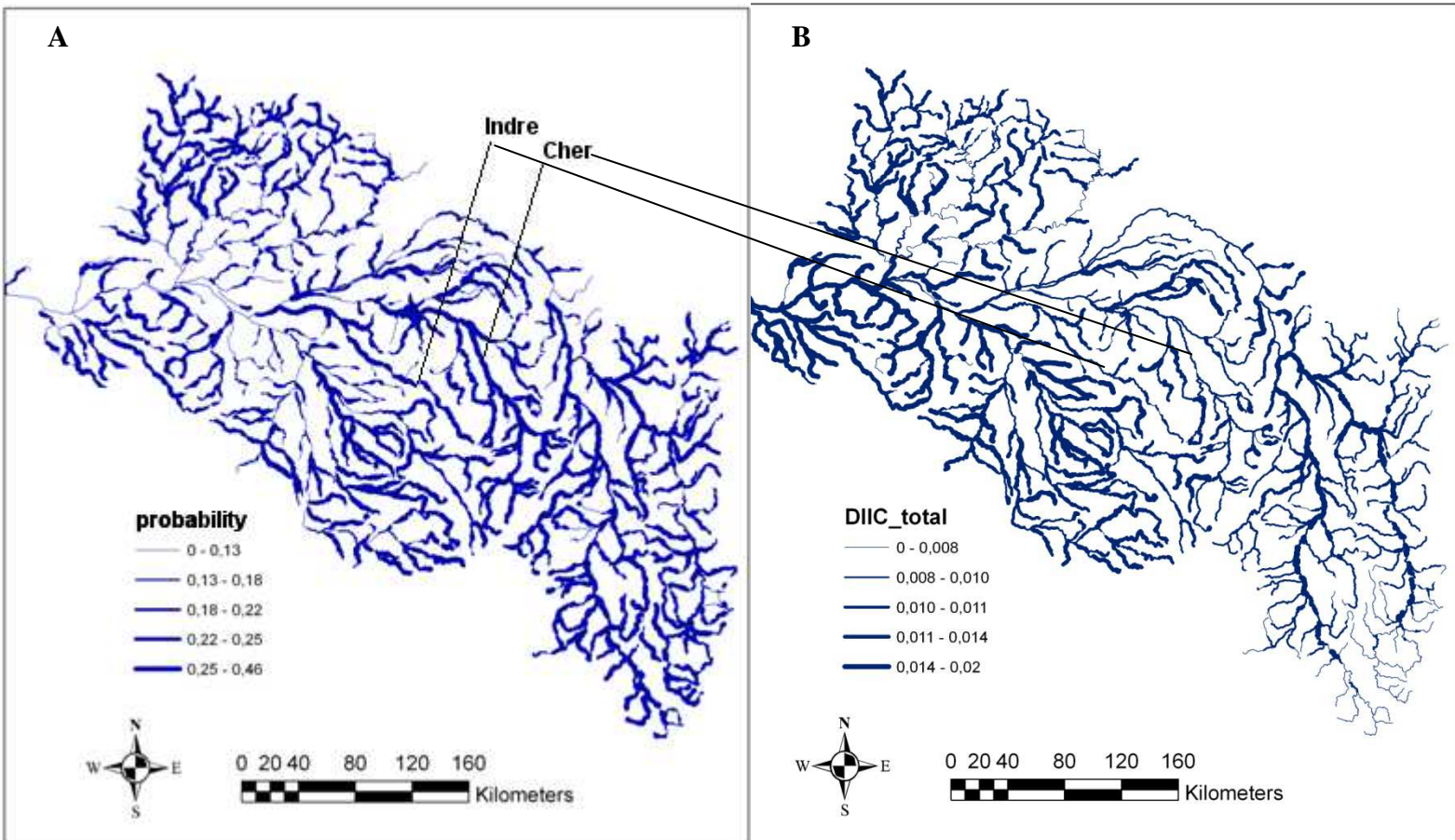
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640 Fig. 2.

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645 Fig. 3.

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