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

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14 **Keywords**

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

16 Connectivity – colonisation – hydromorphology

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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.

44

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   (Bifolchi 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 >10km² 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

8

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 ($j = 1, \ldots, J$) in which the species may occur. Under this model, if an

209   individual is potentially observable at times t=1,...,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          $$w(\text{x}) = (\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \ldots \beta_p x_p)$$

216   Implemented with a link-functionlogit w(x) represents the colonization probability, the x_p are

217   the environmental variables and β_p the coefficients of the model:

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

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    $IIC = \Sigma_i \Sigma_j [P_i \times P_j / (1 + N_{ij})] / A_L^2$

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 forriver

259   segmentsi and j,N_{ij} is the number of segments in the shortest path between segments i and j,

260   for i = 1,...,n and j = 1,...,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   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 colonizationwith 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 considerbroad 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).

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

610   river segments.

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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 segmen
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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631   Fig. 1.
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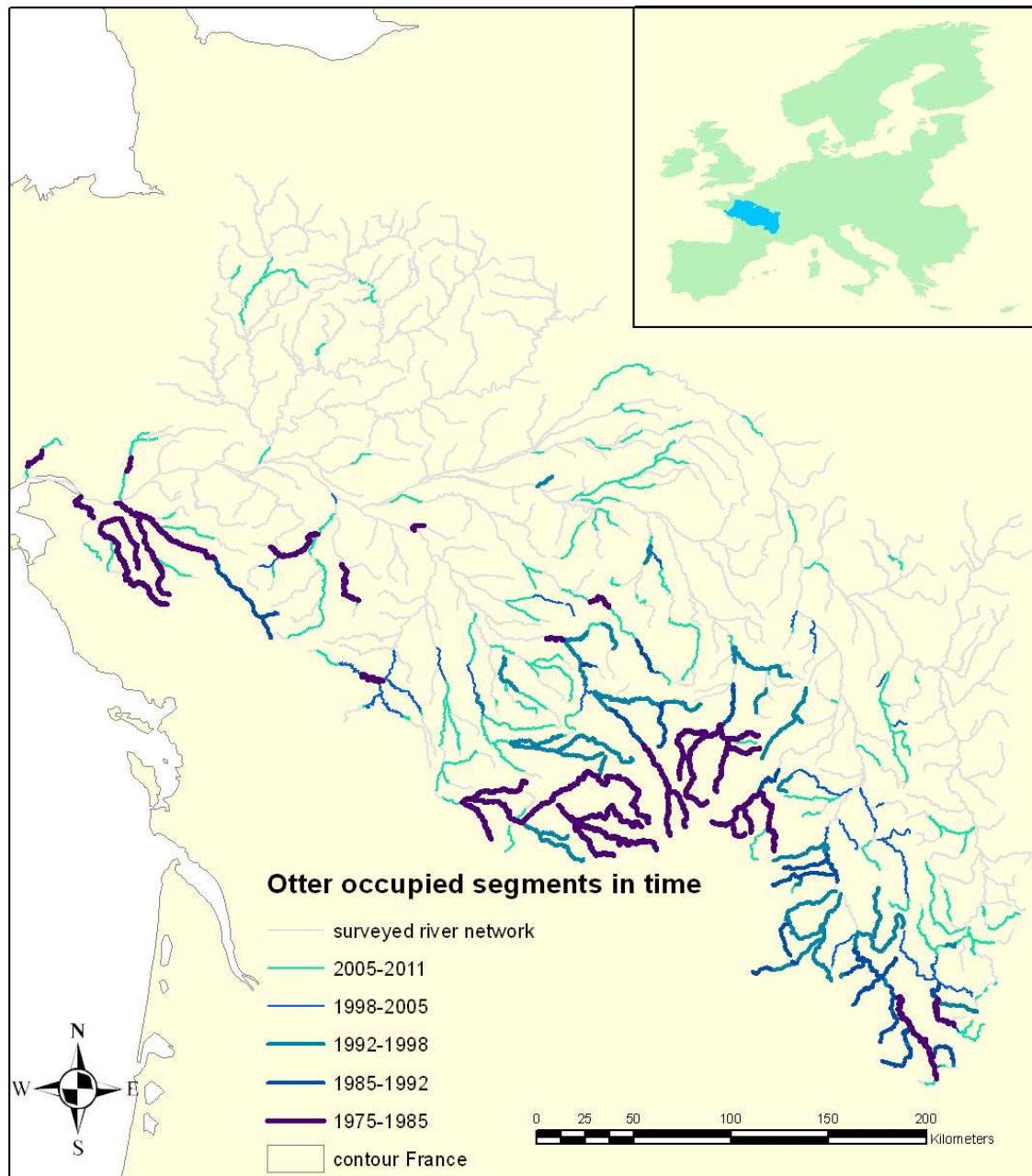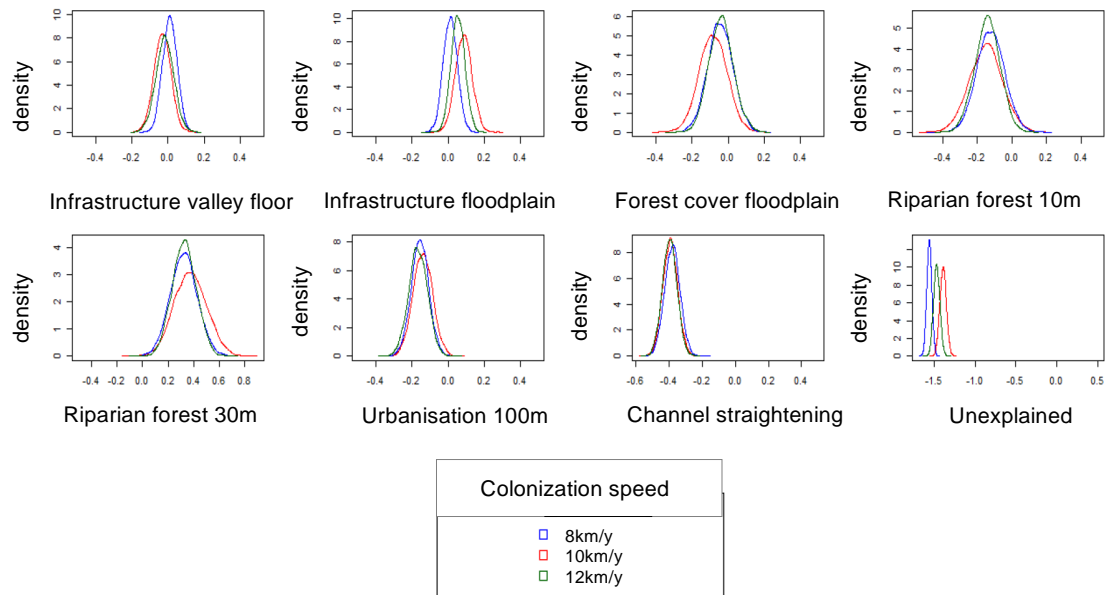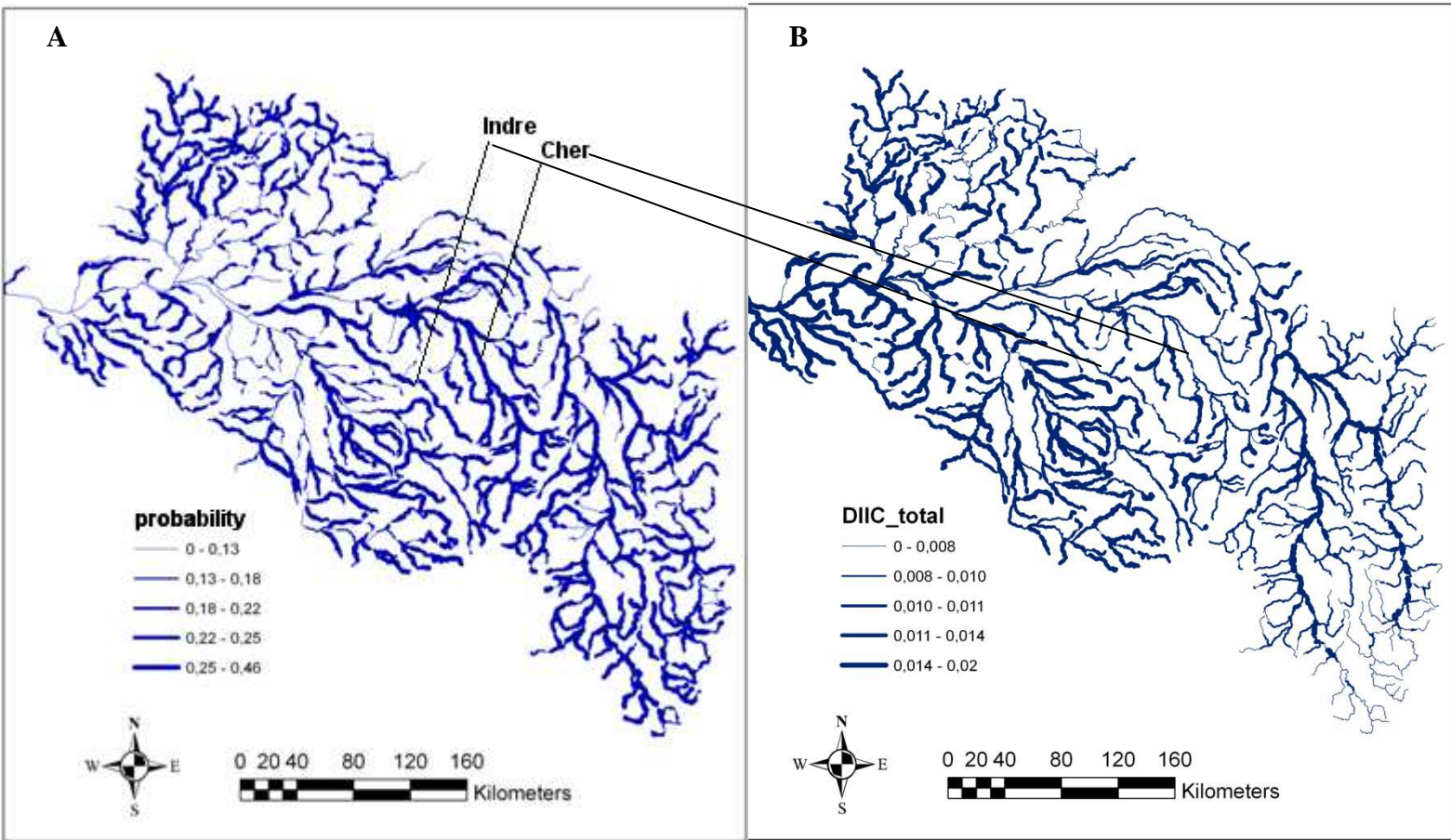
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