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Are generalist and specialist species influenced differently by anthropogenic stressors and physical environment of riparian corridors?

Abstract

The well-documented re-colonisation of the French large river basins of Loire and Rhone by European otter and beaver allowed the analysis of explanatory factors and threats to species movement in the river corridor. 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. The generalist or specialist nature of target species might be determining for the responses to habitat quality and barriers in the riparian corridor.

Detailed datasets of land use, human stressors and hydro-morphological characteristics of river segments for the entire river basins allowed identifying the habitat requirements of the two species for the riparian zone. The identified critical factors were entered in a network analysis based on the ecological niche factor approach. Significant responses to riparian corridor quality for forest cover, alterations of channel straightening and urbanisation and infrastructure in the riparian zone are observed for both species, so they may well serve as indicators for corridor functioning. The hypothesis for generalists being less sensitive to human disturbance was withdrawn, since the otter as generalist species responded strongest to hydro-morphological alterations and human presence in general. The beaver responded the strongest to the physical environment as expected for this specialist species. The difference in responses for generalist and specialist species is clearly present and the two species have a strong complementary indicator value. The interpretation of the network analysis outcomes stresses the need for an estimation of ecological requirements of more species in the evaluation of riparian corridor functioning and in conservation planning.

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Introduction

The choice of target species for the conservation and design of riparian corridors is challenging, both with regard to resource selection and mobility [1], as to potential biotic interactions [2]. To identify effective movement corridors, the specification of the objectives for a corridor and empirically based evidence for corridor use by target species is crucial [3,4]. Corridor design needs to be species-specific, despite a desire by managers to provide corridors to suit a wide range of species [5]. In this respect, concepts as umbrella species and flagships are introduced to deal with the restriction in target species selection for modelling and design purposes. The European otter *Lutra lutra* and the European beaver *Castor fiber* are often presented as umbrella species [6] respectively keystone or engineering species (Naiman et al., 1986) and indicators for the riparian landscape and its anthropogenic stressors [7,8]. To evaluate the quality of the riparian corridor, both large-scale and local corridor functioning need to be addressed in enabling species movement between populations and locally between habitat components, integrating elements of environmental gradients and dispersal processes at different scales [9]. Larger mammals offer the opportunity to integrate these different scales; as population dynamics of riparian species like otter and beaver play at the river basin scale, whereas local individuals experience the habitat and its connectivity at the river stretch scale. These two scale levels are the relevant scales to gather data for the assessment of river corridor quality and functions [10,11].

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The potential for restoration and colonization of habitat is regarded as dependent on the generalist or specialist nature of the target species [12]. Generalist species with high dispersal capacities and a wide range of food resources are expected to be less constrained by barriers and unfavourable habitat in ecological networks [13] and so anthropogenic alterations to the riparian corridor are assumed to be more decisive in corridor functioning for specialist species with low dispersal capacity than for more mobile species with broad niche and food resources. Here, we test this hypothesis for the beaver as specialist and the otter as generalist species with an analysis of habitat preference and human disturbance to the river corridor for two large river basins of the rivers Rhone and Loire in France. To identify the determining environmental variables for riparian corridor functioning in terms of connectivity, both the integration of information from multiple scale levels as a specific approach to the dendritic network structure is required [14,15]. For this purpose, we cross-examine the spatial distribution of species with land use and environmental variables both at the river stretch and the catchment scale, to identify functional riparian corridors for the movement of species and ecological networks based on graph theory and network analysis [14,16,17]. Ecological network analysis shows a remarkable expansion on the methodological side of modelling techniques [18] and concepts (for instance integration of graph methods [17]), but little progress is made in bridging the gap between these models and their applicability for the identification of conservation corridors (but see [19,20]. To what extent anthropogenic disturbance of the riparian zone influences the corridor functioning is a central question in the realisation of ecological networks and the definition of restoration goals for river networks [10,17]. Our analysis proposes an integrated yet straightforward approach to conservation network design based on multiple species and gives insights in the importance of choices of target species in both modelling and designing conservation corridors.

Method

Observational data for otter and beaver

In the last 2 decades a recovery of otter is observed for most of its West-European distribution, recorded for Spain [21], Italy [22] and France [23] after many decades of decline [24,25]. For beaver most recorded re-colonisations are accommodated by reintroduction programmes, but often show remarkable expansions consequently, as in Sweden and Germany [26]. In the Rhone basin a more exceptional natural re-colonisation over the last two decades took place. Data from the Loire river basin for the otter and the Rhone for the beaver were selected as for these river basins a core of historical population persisted and a strong re-colonisation is observed. Furthermore, the inventory for the colonisation of these river basins was done very consistently over a period of 25 years; allowing for a reconstruction of the natural re-colonisation for the beaver in the Rhone basin and the otter in the Loire basin.

The otter is a highly mobile animal with home ranges of 2 - 100km [27]. 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)[28]. Although the European otter is often depicted as a highly selective and sensible species, it appears as much more flexible and generalist in its recovery nowadays. The image of a specialised species arose from its very restricted high quality relict ranges in West-Europe and from interpretation of behaviour and feeding habits of localised studies [29]. An often documented narrow range of fish resources for the otter may be the result of the local abundance, or because there are no alternative resources available. Where on a local scale some species may appear to be functioning as specialists, across their entire geographic range they often have generalised ecologies [30]. The beaver is much more restricted in mobility (home range 0.5 – 2km) and reliant on the presence of softwood riparian forests for foraging. For this reason, human stressors to the riparian corridor are expected to play a more important role in its colonization.

Data of presences were gathered for the otter in the Loire Basin by a network of associations' volunteers gathered under the Loire Basin Mammal Network, and for beaver in the Rhone basin by the field workers of the National Wildlife Office (ONCFS). Harmonised protocols in data collection were adopted following the internationally agreed otter census protocol [24] and for the beaver a similar standardised protocol was developed. For the otter, presence is confirmed from the observation of spraints, whereas for the beaver traces of recent cuttings are used to determine the species' presence. The density of the river network entered in the analysis differs for the two species. In accordance to guidelines for the confirmation of otter presence and to avoid overestimating accidental visits of individuals to small water courses [28], only main water courses in valley systems and rivers starting from a minimum catchment of >10km² are entered in the otter analysis. For the beaver who occupies a much more restricted stretch of river, a much higher resolution of the river network is integrated in the analysis, up to small brooks. In this way our approach adopts the species specific choice of a suitable scale for the ecological niche analysis [31]. So, for the otter with its large home ranges a coarser network in the Loire basin is selected than for the beaver in the Rhone basin, also complying with guidelines for reliability and interpretation of observations for the species [28]. This difference in spatial resolution is also necessary for the testing of our hypothesis concerning vulnerability of specialist versus generalist species in the light of the different mobility of the two species.

As Otter spraints cannot provide information on otter abundance, only about presence [32], and furthermore the frequency of spraints may be very low when otters are at low densities [33], the species distribution analysis is limited to a presence only approach. The same remarks counts for the beaver traces, for which both the period of survey and the local variety of food resources would make interpretation of abundance based on cut trees unreliable. Further difficulty is the unreliability of the absence of traces, in assuring the absence

of the species. But this lack of confidence on absences can be solved in the choice of analysis methods.

For the analysis of habitat preference, the presence in the most recent surveys is retained (Figure 1). For the presence of the beaver in Rhone basin, only 777 (5.5%) of the nearly 14 000 segments (41 740km) in the basin are occupied in 2011, and 54 segments (0.4%) showed a temporary occupation during the re-colonisation process. This allowed an additional screening for the abandoned river segments to the detected habitat variables.

For the otter 6300km (37%) of the surveyed 17 000km (4930 segments) in the Loire basin are occupied in 2011. Both for the otter and the beaver a series of surveys between 1985 and 2011, allowed the control of the results for different time steps. This observation period spans the entire period of the re-colonisation of the river basins up to date. Although the species have reached the outer bounds of the basins, still a strong increase in the populations and expansion of occupied river segments is expected.

Environmental and anthropogenic stressor data of the riparian corridor

A systematic splitting into river segments and assembling of hydro-morphological data for the riparian corridor in different buffer sizes (valley floor, floodplain, 100m, 30m, 10m) was realised for the entire French river network with the hydro-morphology audit system SYRAH [34]. Rivers were subdivided
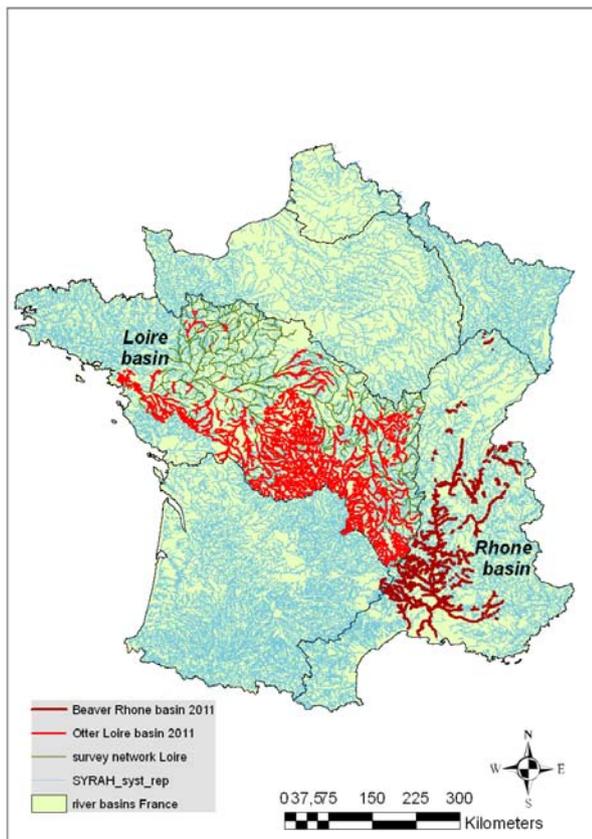

Figure 1. *Presence of otter in the Loire river basin and beaver in the Rhone basin.*

in hydro-morphological entities based on a splitting that distinguished changes in channel and valley form based on variation in valley floor width and lithography derived from geological maps. Resulting river segments range from 1km on average for small rivers (Strahler order 1) up to 20km on average for large rivers of Strahler order 7-8. For each of these 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) level and locally for the individual river stretch. Land use in the sub-catchments was interpreted from the CORINE land cover map of 2000 (http://terrestrial.eionet.europa.eu/CLC2000). CORINE land cover data is classified in 5 broad land cover categories (1: artificial surfaces, 2: agricultural areas, 3: forests and semi-natural areas, 4: wetlands and 5: waterbodies). For the otter and beaver presence analysis, only the categories of agricultural use, urbanisation and near-natural classes as percentage cover of the sub-catchments were retained.

At the basis of the metrics for the river segment is finer scaled information on the land use of the riparian corridor that was gathered from the national geographical database of BDTOPO IGN®. Riparian forest cover in different buffers is derived from national aerial sensed data (BDORTHO IGN®). From the SYRAH database, a set of 22 metrics at the river segment scale (Table 1), potentially influencing species presence, was selected: altitude, river slope, valley slope perpendicular to the river, mean annual discharge, channel straightening and sinuosity, density of bars and weirs/dams on the river segment, connected and disconnected waters in the floodplain, forest cover, density of infrastructure, bridges, dikes, agricultural land use and urbanisation in different buffer widths.

Analysis of distribution in relation to environmental data

To assess the contribution of the different aspects of the riparian corridor functioning and compare them for the otter and beaver datasets, a similar approach for the two investigated river basins is followed. A habitat qualification approach for species distribution by PCA and PLS-R regression [35] is used to explore the determining 'habitat' factors, followed by a network analysis integrating the 'ecological niche factor analysis' framework [36].

The first step is the analysis of the species presences in relationship to the environmental data for the river segments. After a first exploratory PCA analysis, to retain only the relevant variables for the habitat and stressors, a Partial Least Square (PLS) regression is carried out on the selected set of variables. In view of the spatial structuring of both the presences as the environmental conditions of the river network, this technique limits the effects of co-linearity of the variables. In PLS regression, the coefficients of the predictors can be interpreted as degrees of correlation between each predictor and the dependent variable, even when there is a strong correlation between the predictors (Wold et al., 2001). These standardised coefficients are presented as beta regression coefficients. For the analysis of species presences the logistic extension of the

Table 1. Environmental predictors with potential relevance for the riparian species.

Watershed	
urbanisation	percentage cover of urban land use class in CORINE land cover data of the sub-catchments
intensive agriculture	percentage cover of intensive agricultural CORINE land cover classes of the sub-catchments
natural	percentage cover of near-natural CORINE land cover classes data of the sub-catchments
River segment	
altitude	elevation at downstream point of river segments
river slope	slope of the river bed over the segment
valley slope	valley slope perpendicular to the river
discharge	mean annual discharge for gauging station or model prediction at river segment level
sinuosity	sinuosity of the river bed over the segment
channel straightening	percentage of straight reaches over the segment, weighted by river type
density of bars	number of lateral bars over the segment, divided by river length
density of weirs/dams	number of weirs/dams per segment, divided by river length
density of bridges	number of river crossing bridges per segment, divided by river length
Alluvial plain	
alluvial forest cover	percentage cover of forest patches over the alluvial plain of the river segment
infrastructure	percentage cover of infrastructure over the alluvial plain of the river segment
urbanisation	percentage cover of urbanisation over the alluvial plain of the river segment
density of dikes	length of flood protection levees per segment, divided by river length
connected waters	percentage cover of connected standing waters over the alluvial plain of the river segment
disconnected waters	percentage cover of disconnected standing waters over the alluvial plain of the river segment
River bank	
riparian forest cover	percentage cover of forest patches for the 30m riparian buffer of the river segment
riparian forest canopy	percentage cover of forest patches for the 10m riparian buffer of the river segment
infrastructure	percentage cover of infrastructure over riparian buffer of three river widths of the segment
urbanisation	percentage cover of urbanisation for the 100m riparian buffer of the river segment

classic PLS in the package plsRglm is used under the program R 2.12.0 (R Development Core Team, 2008). The significance of the standardised regression coefficients is estimated with a bootstrap (n=1000).

Network Approach

The dendritic river network structure needs an adequate topological definition for the analysis of its potential as ecological network for the species [15]. For this purpose and in agreement with terrestrial network frameworks, the river segments are regarded as habitat nodes whereas the true river network nodes (confluences and segment junctions) are regarded as connectors in the network [16]. As we regard corridor functioning and species movement both in up- and downstream direction, the full complexity of dendritic networks comes in the picture.

Scripts were developed to derive neighbourhood matrices that depict both network structure and distances between the nodes in the network. These matrices allow the calculation of the ecological networks, based on euclidean distance criteria between the endpoints of the segments (upstream point for upstream connection and downstream point for downstream connection).

The analysis of presence only data is the reason to apply the ecological niche factor analysis (ENFA) [37]. This technique fits well our objectives, as we are not so much interested in the probability of presence of the species, but more in the understanding of the habitat factors [38]; the ENFA allows to analyse the variables that explain the favourability of the habitat without reference to their predictive power. Starting from the observed responses in the regression, ENFA allows

to integrate the inferred habitat factors in a network analysis to draw the potential network occupied by the species [39]. Based on the distinction of the marginality and specialization of the ecological niches of the species, an extrapolation of favourable habitat (95% confidence intervals based on marginality and specialization) in the entire river basin is carried out. The marginality measures the position of the habitat within the environment (i.e. deviation of the average conditions in the habitat used from the average conditions available in the environment). The specialization measures the dispersion of the habitat within the available environment (i.e. tolerance of the species according to characteristics of its environment). Calculation is based on the occupied and entire set of data for the river segments, with the following formulas for marginality: M= *mean((Var[Niche_glob])-mean(Var[niche_occup]))/1.96*sd(Var[Niche_glob])* and specialization: S = *sd(Var[Niche_glob] / sd Var[niche_occup])* .

Integration of distance criteria to join favourable segments based on the minimum home range values of 0,5km for beaver and 2km for otter, results in non-fragmented habitat patch networks over the river basins. For the Rhone basin with its dense inventoried river network the resulting favourable habitat is presented agglomerated per sub-catchment.

Results

Species niches

For the beaver 11 environmental and anthropogenic stressor variables responded significantly in the PCA and were entered in the regression analysis. Three groups of response variables were distinguished with the first two PCA-axes that explained 44% of the variance (Figure 2). At first a group of physical-geographical variables: altitude, river slope, valley slope and discharge, explained significantly the geographical preference
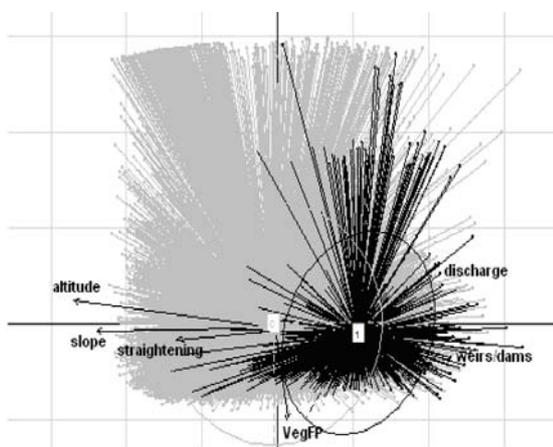
of the species for the downstream low slope rivers. Analysis of the abandoned river segments further informed on these factors. For abandonment, the valley slope proved most significant and strongly V-shaped valleys seem less hospitable for the beaver (Figure 3) especially in combination with higher stream power. For the anthropogenic stressor variables, grouped at the right hand of the PCA, density of infrastructure and urbanisation in the floodplain responded the strongest, followed by the density of bridges and weirs/dams on the river stretch, and finally the channel straightening as indicator for strong morphological alteration of channel form. At the bottom end of the PCA are grouped the riparian corridor habitat factors of forest cover in the floodplain. These vegetation cover variables responded significantly for the different buffer widths. After omitting the redundant variables (discharge and valley slope, density of bridges), the resulting PLS-regression (n components=3, R^2=0.22) showed a strong response for four variables: forest cover and infrastructure in the floodplain and altitude and river slope (Table 2). The ENFA analysis of the specialization and marginality of the occupied segments also shows the distinction of these four discriminating factors (Figure 4A). The hydro-morphological control variables are the most distinguishing factors. For the river slope (beta = -0.14) the marginality and specialization are very high (M=0.44, S=2.32). The beaver exploits only a minor part of the basin with a preference for the lowest slopes (max 0.95 = 4.61%). Altitude also presents a strong marginality towards the lower values but this response is less pronounced than for river slope (beta = -0.12, M = 0.47). A minor significant hydro-morphological factor is the channel straightening with a strong marginality (beta = -0.07, M = 0.26), but little specialization (S = 0.82) for this factor. Using this factor in the ecological niche factor analysis only discriminates 11% of the river segments as unfavourable, compared to 36 and 39% for altitude and river slope.
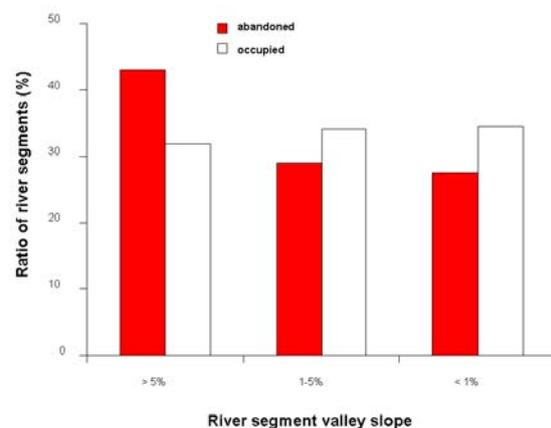

Figure 2. *PCA's first two explanatory axes showing in grey (and centred around the origin of the axes) the segments without beaver and in black the presences for the analysis of the environmental factors.*

Figure 3. *Percentage of beaver occupied and abandoned river segments over categories of valley slope for the beaver distribution in the Rhone basin. The predominance of unfavourable steep valley slopes for the abandoned river segments illustrates that the majority of temporarily occupied stretches are characterised by non-optimal habitat.*

Table 2. Hierarchy in factor contribution for PLS regression results for beaver and otter.

beaver	beta
floodplain infrastructure	0,19
river slope	0,14
altitude	0,12
floodplain forest	0,11
riparian forest 30m	0,07
channel straightening	0,06
infrastructure valley floor	0,03
riparian forest 10m	0,03
urbanisation 100m	0,01
otter	
channel straightening	0,19
infrastructure valley floor	0,14
infrastructure floodplain	0,13
riparian forest 30m	0,13
floodplain forest	0,1
urbanisation 100m	0,07
riparian forest 10m	0,03

A

B

Figure 4. Ecological Niche Factor Analysis for the European beaver (A) and otter (B).

The infrastructure in the floodplain presents the strongest response in the regression (beta = 0.19) with a strong marginality (M = -0.43). Nevertheless, the absence of a specialization hampers its use in the ecological niche approach. The forest cover in the floodplain responded significantly (beta = 0.11) with a strong specialization (S = 1.56) for high forest cover. This factor allowed the discrimination of 20% of the river basin as unfavourable.

For the otter presence, the pls-glm regression with the hydro-morphological and land cover metrics is less explicative (n components=3, R²=0.12). For the seven metrics significantly responding in the regression, five were retained after analysis of marginality and specialization (Figure 4B). Only 20 % of the river segments in the Loire basin were determined as unfavourable from the resulting ecological niche factor analysis.

The strongest response in the regression was for the channel straightening (beta = -0.19), with significant marginality and specialization (M = 0.12, S = 1.16). This factor showed in the modelling the highest discriminating power on the river network (Discrim=12%). The forest cover in the floodplain (beta = 0.10, M = -0.13, S = 0.97) and in the 30m buffer (beta = 0.14, M = -0.16, S = 0.96) present similar responses and marginality scores with little specialization though. Infrastructure and urbanisation in the floodplain also responded significantly in the regression (beta =-0.13 and -0.07 respectively), with a high specialization for urbanisation (S=1.17) that allows a discrimination of 6% of the river basin's segments as unfavourable in the niche factor analysis due to urbanisation pressure in the river corridor.
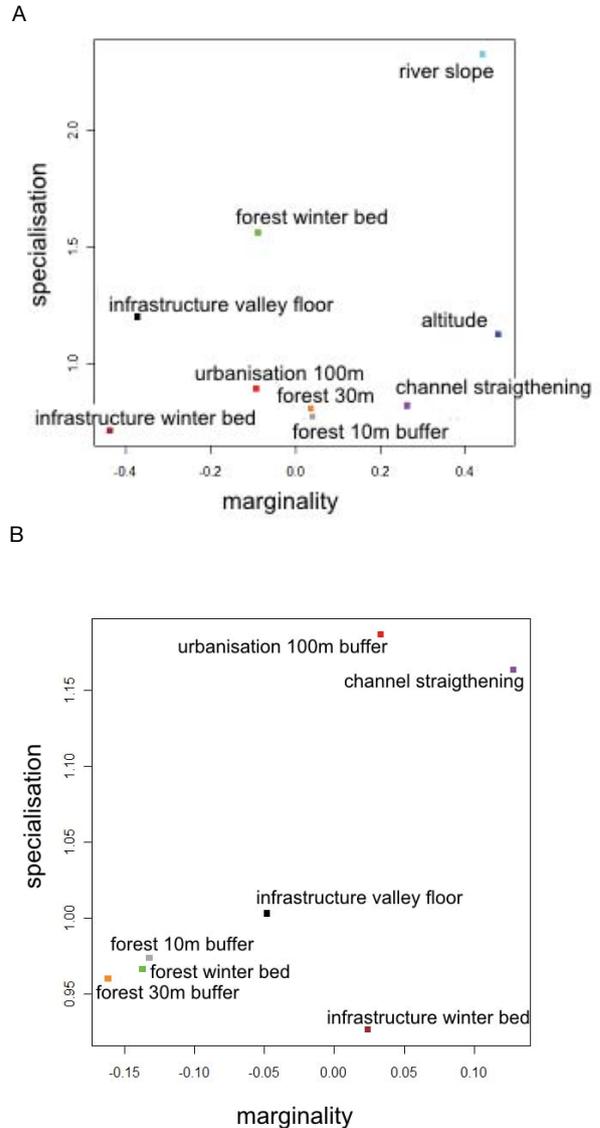
Extrapolation and network analysis

The available favourable river segments represent for the beaver in the Rhone basin some 14 192km of river length or 34 % of the river network. The largest part of favourable segments is present in the western part of the basin, although the highest densities of favourable segments per hydrographical unit are present in the downstream and central part of the Rhone valley (Figure 5A). The same pattern arises in the result of the network analysis, when connected favourable segments are assembled in an ecological network for the Rhone basin. The longest networks of favourable segments are present in the downstream and central part of the Rhone basin (Figure 5B). Clearly, the Alpine and Lower Alpine sectors of the basin present the least favourable conditions for the beaver. Over the entire basin 776 favourable patches are present with a mean length of 18.4km but high variability (sd = 111.6km) and a dominance of smaller patches. The longest
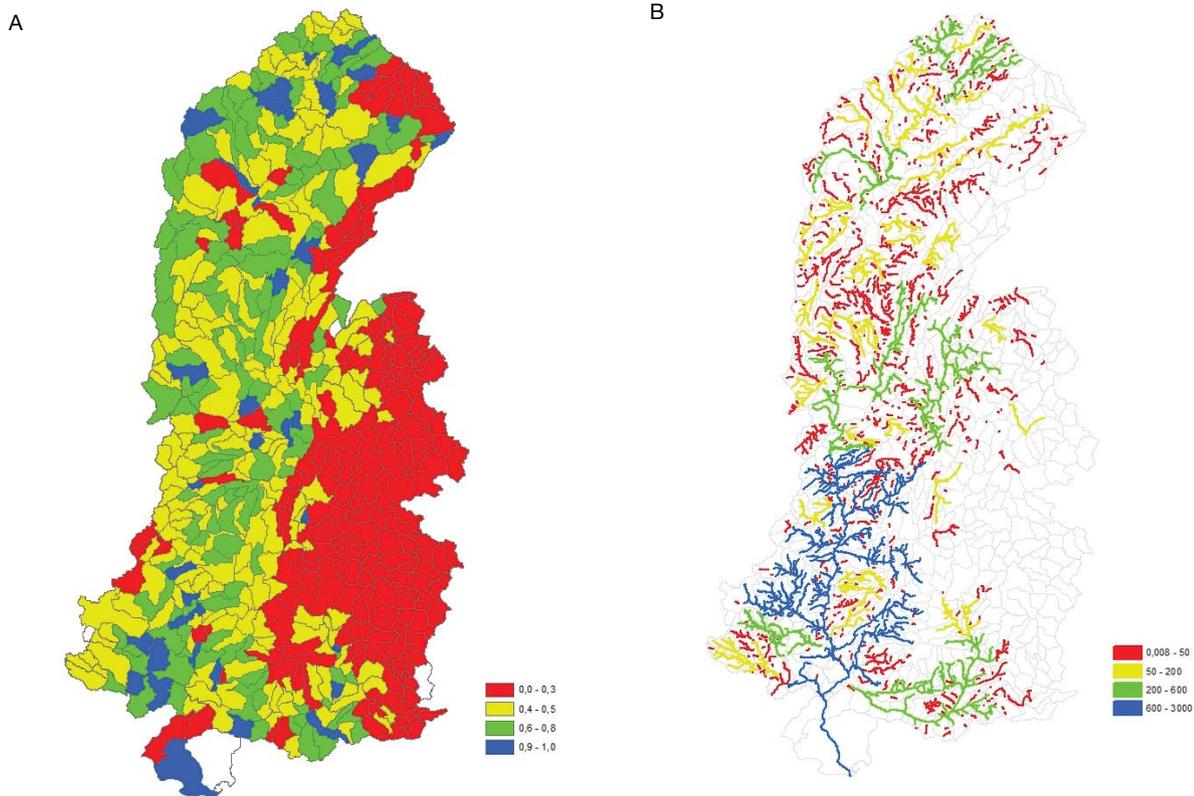
A

B

Figure 5. (A) Beaver favourability of river segments in the Rhone basin, gathered by hydrological unit, with indices representing favourable length on total river length per unit. (B) Favourable segments gathered (barrier threshold distance 500m) in non-fragmented patches of river corridor for the beaver in the Rhone basin. The colours indicate km of linear in classes.

favourable patch that unites the downstream part of the river Rhone with a series of tributaries up to its mouth ranges over 2 847km. On the other hand, in the northern part of the basin most patches do not reach 50km length.

For the otter in the Loire basin 82% of the 17 000km selected river length showed favourable habitat conditions in the river corridor (Figure 6A). Where highly favourable conditions can be found in all parts of the basin, the most unfavourable conditions are concentrated along the downstream part of the main river. 452 patches of favourable segments are present over the basin with a comparable distribution of lengths as for the beaver in the Rhone basin, with high variability and abundance of small patches (mean= 29.3km; sd= 62.1; Figure 6B). The longest favourable corridors (max= 590.2km) are mainly situated along the middle sectors of the main rivers Loire and Allier.

Discussion

River corridor network analysis

Spatial contagion is surely the principal element in the distribution of these colonising species [40]. For this reason a detailed and sophisticated approach is needed to determine factors explaining corridor functioning and its impairment by anthropogenic disturbances. The strength of our approach is the combination of a classic habitat suitability inference with the ENFA integrated in a network analysis. Instead of limiting as much

as possible the number of predictors to improve AUC values as advocated by "ensemble modelling" [18,41], in our approach we try to conserve as many as possible predictors, to increase the mechanistic understanding of the complex interaction between the corridor's habitat quality and connectivity in relation to the network structure and anthropogenic stressors present.

The integration of environmental data from different scale levels, collated to the river segment and to a fine-scale level of land use in different buffer widths offers a unique and pertinent dataset to the analysis of riparian corridor functioning. The long year colonization observations for the two species over the entire river basins strengthen this large geographic scale network analysis. Most studies interpreting semi-aquatic species distribution start from a landscape pixel approach [22,29,40]. Only recently the geometric network approach to connectivity has been developed in landscape ecology with the graph methods [42,43]. This graph-based concept has the advantage of its simplicity to unify and evaluate the connectivity of habitats, as well as to quantify the structural or functional connectivity [17]. To assess the corridor functioning of the riparian zone this graph-based approach integrates both the dendritic structure of the river network [15] as the evaluation of both habitat quality and connectivity [14]. With the applied network analysis we complement the information gathered for the local habitat with the connectivity of the drainage basin network, a necessary step in the utilization of
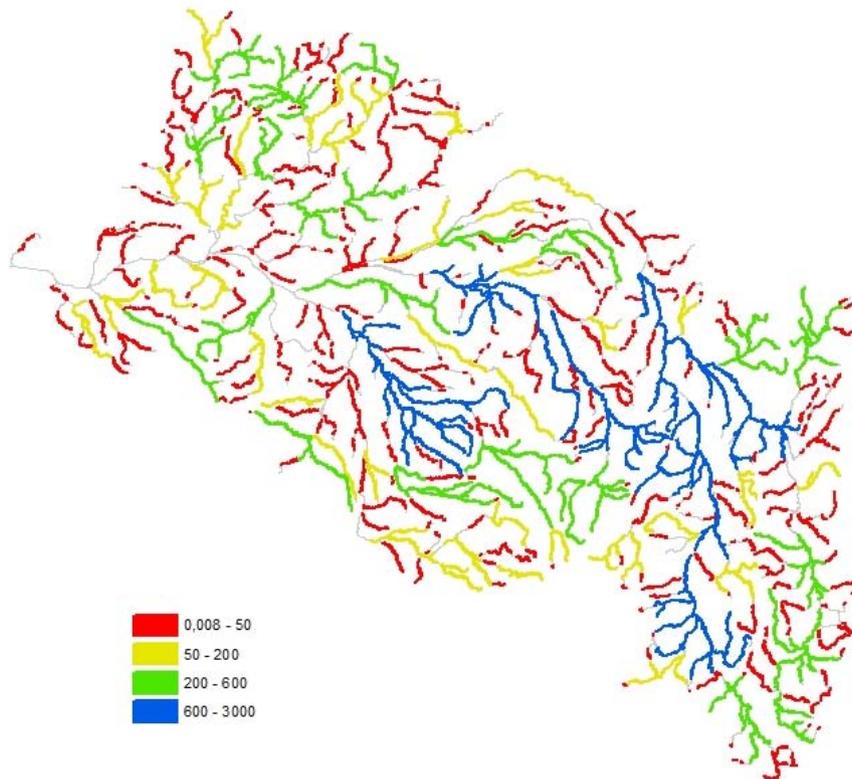
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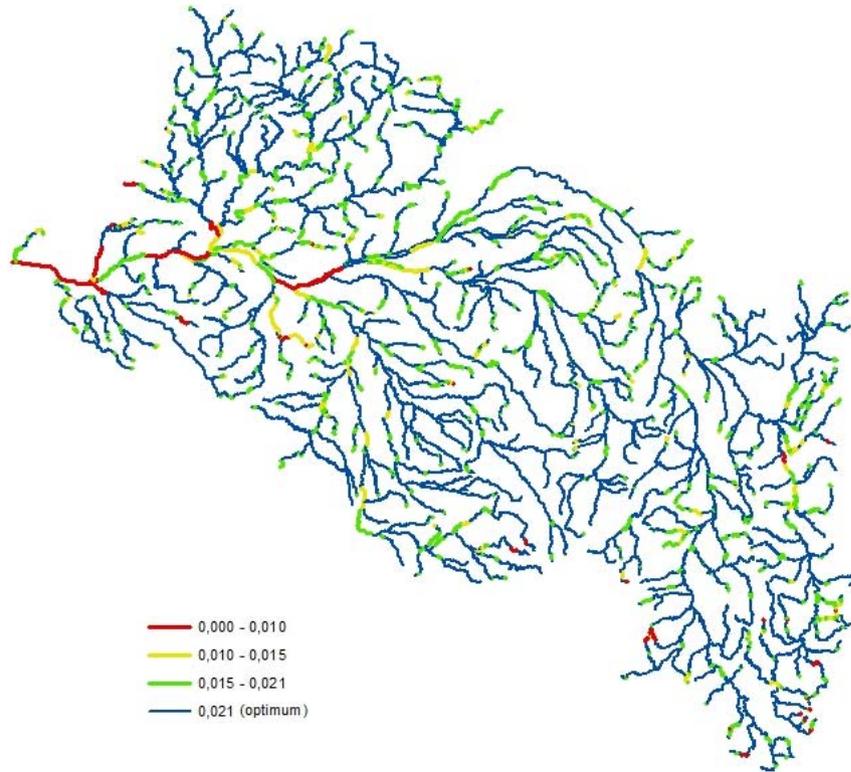
B

Figure 6. (A) Otter favourability of river segments in the network of the Loire basin (indices present contribution of individual segments in percentage to total for the basin). (B) Favourable segments gathered (barrier threshold 2km) in non-fragmented patches of river corridor for the otter in the Loire basin (colours indicate km of linear in classes).

habitat suitability analyses [44]. This allows to visualize the barrier effects of human stressors to the species colonization [29,45] and of natural causes like steep watersheds [23]. The integration of the information for the riparian landscape from multiple scales into a graph-based network analysis for riparian corridor functioning offers a new conservation ecology approach to river systems. Mostly, connectivity analyses for river systems are either based on barriers for fish migration, or on species habitat models that start from grid cell land use and climatic data. Here a dendritic network analysis of riparian corridor functioning is presented that allows conclusions for connectivity over the river network.

With the complementary otter and beaver evaluation of anthropogenic disturbance the entire river basin can be assessed in an integrated riparian corridor evaluation. For the Rhône basin the downstream parts are well connected (least fragmented). For the Loire basin difficulties of anthropogenic disturbance to the riparian corridor arise mostly in the downstream sectors. This conclusion holds notwithstanding the different basins investigated for the two species; the otter's re-colonisation in the downstream parts of the Loire basin and the Atlantic front in general is much retarded compared to the expansion of the population in central France [23,24].

Consistency of responses

None of the metrics at the catchment' scale level (land cover categories) responded significantly. This contrasts to the observations for aquatic biota in river networks, for which urbanisation and agricultural land use at the catchment scale are mostly the main predictors [46], due to their impact on water quality. In our analysis only variables defined at the river stretch scale proved significant, although some local variables like slope and altitude also reflect regional geography. The observed significant responses for the hydro-morphological quality of the riparian corridor in the regression analysis are generally weak due to two factors. At first, the incomplete re-colonisation of the river network results in a strong spatial autocorrelation in the distribution [7,40]. Including spatial and climatic parameters would significantly improve the predictive power of the regression function, but as these variables would be significantly biased by the spatial autocorrelation [40,47], and furthermore fall out of the scope of our study, we did not integrate them. Secondly, the lack of abundance data deters strong responses to habitat factors. The use of presence observations of these mobile species in this large dataset poses risks in discriminating habitat factors, as also in marginal or even unfavourable habitat individuals can be detected during dispersal events or in the vicinity of highly occupied sites according to the source-sink dynamics [32]. Furthermore expansion in range is much faster than expansion in population [26], increasing the risk of over-representing the observations of migrating individuals [23]. Nevertheless, the verification of regression results in the ENFA allowed identifying significantly the environmental factors that determine the quality of the species' specific habitats [39].

Determining factors for generalists and specialists in the river corridor

From the set of physical geographic and hydro-morphological parameters and human occupation in different buffers describing the riparian corridor, for the specialist species the natural environmental factors were most determining as expected. For the otter as generalist species in contrast only stressor factors explained its colonisation pattern. This conflicts to our hypothesis that specialists would be more influenced by anthropogenic alterations. For the beaver indeed important geographic limits are detected and furthermore the preference for substantial areas of forest in the floodplain. For the otter in the first place alteration of the river channel was identified as the strongest determining factor to its presence. Furthermore for the forest cover, the buffer width of 30m proved most significant. This measure indicates strongest the fragmentation of the riparian corridor, therefore it is more a stressor indication than a forest habitat preference. This effect of fragmentation is further confirmed by the significance of the urbanisation in the 100m buffer as strongest indicator for the pressure of human presence. No metrics at basin scale (land cover of intensive agriculture, urbanisation or natural classes in the catchment) came in the picture, so the species truly qualifies the river corridor functioning. Most of the recent studies for this semi-aquatic species [7,29,41,48] only account for distribution limitations to anthropogenic stressors of urbanisation and infrastructure. These studies all have the disadvantage of a large-scale approach based on land cover data (CORINE) that is inappropriate to describe accurately the land use and features in the riparian corridor [49]. Older publications on these species' preferences all stressed the importance of forest cover for maintaining their populations [24,33]. In our detailed analysis of corridor attributes, the three measures for forest cover in the different buffer widths are well distinguished in the PLS regression and the ENFA for the two species, although they are highly correlated and grouped together in the PCA. This indicates the strong preference of the beaver as specialist for well-developed riparian forests providing shelter and food, whereas for the otter the fragmentation of the corridor is at stake.

As a result of the diverse habitat preferences, the ecological networks for beaver and otter differ basically. For the beaver these are concentrated in larger downstream river segments with extensive floodplain forests, as this species is most restricted by the geographic setting (headwater streams less suitable) and local resources and less influenced by alterations to the physical environment of the river corridor or human presence. In contrast, the otter is more headwater-oriented, due to its sensitivity to human disturbance, alterations to the hydro-morphology and habitat fragmentation. This allows us to conclude that beaver and otter can be regarded as complementary indicator species for the evaluation of the riparian corridor functioning. Not so much the observed geographic distinction between the preferences – upstream for otter and downstream for beaver -, but mostly the difference in response to riparian corridor habitat and stressor elements, is an argument for their complementarities as indicators for the riparian corridor quality. Coupling different

species requirements to the analysis of corridors over different landscape gradients and habitat components already proved successful for terrestrial species [9]. The complementary approach for different species integrating both habitat aspects and ecological networks offers perspectives to address more exhaustively ecological requirements for riparian corridor functioning, and challenges restoration by the diverse needs of different species [50]. In this way our results underpin the need for the use of multi-species approaches to design corridors, with focal species differing in mobility, resource selection and resistance [20]. In addition the applied network analysis provides a tool to evaluate and prioritize conservation and restoration efforts for the riparian corridor both within individual river systems and across catchments [19,51]. The presented analysis enables the identification of priority segments and for the individual

segments it informs about the stressors to tackle and the habitat elements that need improvement.

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