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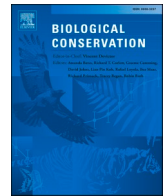
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## Intensive agriculture as the main limiting factor of the otter's return in southwest France

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### ABSTRACT

Rewilding has become a new paradigm to promote the natural recovery of many flagship species, including large carnivores. A better understanding of the factors that drive rewilding processes would allow predicting these in order to support them where desirable. Yet large-scale assessments of the factors that favor or limit mammal populations of conservation concern remain rare in Europe. This study sought to monitor changes in Eurasian otter (*Lutra lutra*) occupation over the years to identify the factors limiting its recolonization. To this end, we monitored otter signs and spraints over 1238 sampling sites in southwest France from 2003 to 2005 and then over 615 sites in 2011–2012. We modeled this dataset in a multi-season occupancy framework using biotic and abiotic covariates identified as potentially affecting otter detection, distribution and/or colonization rates. As otters are a cryptic and mobile mammal, we integrated detection probability and spatial autocorrelation (contagion) into the modeling design. Otter occurrence was detected at 31 % of the sites surveyed in 2003–2005 and 37 % of the sites surveyed in 2011–2012. Occupancy and colonization probabilities were strongly negatively correlated to the proportion of cultivated areas. Contagion covariates interacted strongly with other variables. These results suggest that, despite its recent colonization, the otter population in southwest France is still constrained in its expansion, notably by intensive agriculture. Natura 2000 schemes should incorporate rewilding approaches to further potentiate the colonization of this flagship species. Actions should focus on the conservation of natural riparian habitats and promote organic agriculture.

### 1. Introduction

Rewilding has recently been put forward as a new paradigm for nature conservation (Lorimer et al., 2015; Navarro and Pereira, 2015). It is notably illustrated by the recovery of large carnivores such as Brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*) and gray wolf (*Canis lupus*) which are recolonizing human-dominated landscapes of Europe (Chapron et al., 2014). This natural rewilding process relies on several convergent phenomena. First, most countries where it occurs have developed nature conservation policies such as coordinated legislation (Chapron et al., 2014) and developed extended protected areas. For instance, almost 18 % of the EU territory is now covered by Natura 2000 network which aims to maintain specific species and habitats in a

“favorable conservation status” (Ceaușu et al., 2015). Secondly, the abandonment of relatively large areas of marginal lands (Verburg and Overmars, 2009) has contributed to the recovery of original habitats, even in countries with intensive agricultural production (Navarro and Pereira, 2015). Habitat recovery promotes the recolonization of previously inhospitable areas, as habitat availability is one of the most critical limiting factors for many species, in particular for mammals (Schipper et al., 2008).

Understanding the factors that encourage ongoing rewilding processes is of paramount importance to predict how these will unfold and to support them (Fernández et al., 2017; Nogués-Bravo et al., 2016). A key consideration is that the recovery of large carnivores often results in conflicts with local farmers affected by predation on their livestock

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(Chapron et al., 2014). Anticipating where and when these species will eventually recolonize is thus crucial to allow stakeholders to implement management policies and actions such as herd protection or to work to improve social acceptability of recolonization (e.g. Louvrier et al., 2018). In parallel, understanding the limiting factors that can hinder or even prevent recolonization is also crucial so conservationists can try to remove these (Chapron et al., 2014; Ripple et al., 2014). Yet continuous large-scale assessments of the factors that favor or limit mammal species populations of conservation concern remain rare in Europe (Mortelliti et al., 2010).

The Eurasian otter (*Lutra lutra*) is a key example of a continent-scale recovery of a top predator in a general rewilding context. This species' distribution range has been in decline since the mid-20th century (or later in some European countries: see Hájková et al., 2007 and Fusillo et al., 2007). Due to this sharp, widespread decline, the species is listed by the IUCN as Near Threatened (Roos et al., 2015). However, it is now recovering in most European countries (Clavero et al., 2010; Marcelli and Fusillo, 2009; Roos et al., 2015).

Several factors operating at various scales explain the past decline or scarcity of the Eurasian otter that still threaten to limit its current recovery dynamics. These include:

- i. bioaccumulative toxic pollutants such as polychlorinated biphenyls (PCBs) that may contaminate otter body tissue and lead to reproductive disorders (Mason and Macdonald, 1994). Several studies (Delibes et al., 2009; Lafontaine et al., 2002) have shown the impacts of water pollution on otter distribution.
- ii. changes in prey species communities caused by habitat alteration may impact otter food availability. Several studies have shown that the primary productivity of an ecosystem, used as a proxy for food availability, was a major positive predictor of otter presence (Barbosa et al., 2003); or density (Ruiz-Olmo et al., 2011).
- iii. habitat degradation through agriculture (Marcelli et al., 2012; Carone et al., 2014) or its impact on water management, i.e. through drainage, artificial irrigation or canalization, which reduces wetland density and connectivity and affects otter distribution (Lafontaine et al., 2002; Van Looy et al., 2014).
- iv. urbanization impacts on landscape and river networks is also known to affect otter distribution dynamics by increasing road casualties, decreasing water quality, fish density and diversity, and more generally degrading hydrosystem quality downstream from urban areas (Clavero et al., 2010; Marcelli and Fusillo, 2009).

To improve research on mammal conservation biology in Europe, Mortelliti et al. (2010) have put forward several methodological recommendation: (i) conduct studies over the long term; (ii) at a large scale, ideally at landscape scale; (iii) take spatial autocorrelation and detection probability into account; (iv) favor temporal (diachronic studies) rather than spatial replication (synchronic studies); (v) characterize habitat quality as comprehensively as possible; and (vi) assess colonization and extinction rates, demographic patterns and dispersal behavior. All of this information is valuable to strengthen inferences on spatial dynamics and the impact of habitat changes and plan conservation or rewilding strategy at the appropriate scale for species of conservation concern.

While the Eurasian otter has been the subject of several recent long-term and/or landscape-scale conservation studies across Europe (see e.g. Clavero et al., 2010; Marcelli et al., 2012; Marcelli and Fusillo, 2009; Carone et al., 2014), including France (Janssens et al., 2006; Kuhn, 2009; Pigneur et al., 2019), very few followed all of the above methodological recommendations. Notably, only Marcelli et al. (2012) explicitly accounted for both spatial autocorrelation and imperfect detection to model spatial dynamics. However, the Eurasian otter can be difficult to detect in the field (Fusillo et al., 2007; Janssens et al., 2006), and such detection issues can lead to biased inferences of population

dynamics (Parry et al., 2013).

The aim of this study was to assess the major drivers of otter occupancy and spatial dynamics in a context of rewilding in southwest France. By the 1980s, there were only remnant and isolated otter populations in the mountainous sectors of this area (Pigneur et al., 2019). Since the 1990s, the species has been recovering, from the edges of the study area (river headwaters) down to the cultivated lowland areas (Gomes, 2011). This extended region provides a remarkable natural laboratory to study the recolonization of otters, encompassing three sub-regions (the Pyrenees and Massif Central mountains and the Garonne plain) with contrasting geomorphological factors such as varying slopes and altitudes and different hydrographical network densities, all of which are known to affect otter occupancy and colonization rates (Marcelli et al., 2012; Carone et al., 2014; Ruiz-Olmo et al., 2011; Van Looy et al., 2014).

Human pressure also varies geographically in the region, from intensive human activities through transitional use to abandoned landscapes. Our study design incorporated all of the Mortelliti et al. (2010) methodological recommendations: it was conducted at a large scale (45,348 km<sup>2</sup>), over a long period (10 years), considered detection and autocorrelation issues, was based on diachronic monitoring to investigate colonization/extinction rates, and integrated a wide array of comprehensive habitat covariates at various scales.

## 2. Materials and methods

### 2.1. Study area

The study covered the whole Midi-Pyrénées region in southwest France (Fig. A.1, Appendix A). The area is composed of three morpho-structural units: In the central area, the Garonne valley consists of intensively cultivated plains and hills (cereal crops, vineyards, fruit trees, etc.), with many cornfields bordering the rivers. The region's main cities and conurbations (Toulouse, Auch, Montauban), as well as the main transport infrastructure are concentrated in this large lowland plain. South of this lie the Pyrenees, whose highest peaks reach an altitude over 3000 m. In this mountainous area, human settlement is scattered, and extensive husbandry is the main agricultural activity. North of the central lowlands lies the southern edge of the Massif Central, mainly composed of high plateaus cut by deep valleys and covered with dry grasslands and downy oak (*Quercus pubescens*) forests with a Mediterranean habitat. Aside from these plateaus, the region's landscapes have acidic soils with a mosaic of meadows, woods and small agricultural patches.

There is a remarkable diversity of river regimes and morphologies in the region. The Garonne River, one of the five biggest rivers in France, flows through the lowland valley. The rivers in the Pyrenees have a torrential regime. The river system of the Massif Central is a mix of dense small rivers with a torrential regime and a low-density hydrological network in a limestone context.

### 2.2. Field data collection

We conducted two separate surveys, one in 2003–2005 (hereafter 'survey 1') and one in 2011–2012 (hereafter 'survey 2'). As we were interested in tracking potential spatial colonization, the first did not target the center of the central lowlands, as otters were absent there at that time (Bertrand et al., 1993). We recorded otter presence at a small river catchment scale (Fig. A.2, Appendix A) as defined by the French National Geographic Institute (IGN) (BD Carthage). The average size of these catchments is 63 km<sup>2</sup>. We considered this spatial unit as relevant since hydrological network characteristics are the main drivers of otter movements and spatial structure of the populations (Clavero et al., 2010; Ottaviani et al., 2009). We selected the sampling sites to ensure homogenous sampling between water catchments.

We searched for signs of otters on emergent substrates of stream

sections following a technique similar to Reuther et al. (2000). Prospection starting points were chosen for their potential interest for otter sign detection (presence of potential marking sites such as bridges, water mills, confluences, etc.), and then 150 m of each bank upstream and downstream of these locations were carefully searched. Sites were considered positive if a spraint (otter scat) or a track was found on these

river banks. Field surveyors were selected from several local biodiversity conservation organizations. All of them were professionals working in public wildlife agencies or conservation NGOs. To minimize detection and identification issues (Andersen et al., 2021), we selected only experienced observers and provided them all with training in spraint detection/identification and in the survey methodology prior to field

**Table 1**

Description of the environmental covariates that were fitted for detection probability ( $p$ ), initial occupancy probability ( $psi$ ) and colonization probability ( $gamma$ ) of the otter surveys conducted in the Midi-Pyrénées region, France, in 2003–2005 (survey 1) and 2011–2012 (survey 2). The years mentioned for  $p$  and  $psi$  correspond to the periods of data collection.

Name	Description	Scale	Group	Type	$p$	$psi$	$gamma$	Source	Expected influence	References
fish	Fish richness: mean number of fish species	Stream	Stream characteristics	Linear	–	2000–05	2006–11	French Water Agency	$\nearrow psi/gamma$ with higher number of fish species; $\nearrow p$ due to higher spraint intensity	Clavero et al., 2003; Dettori et al., 2021
PSI	Polluo-Sensibility Index	Stream	Anthropogenic factor	Linear	–	2003	2011	French Water Agency	$\searrow psi/gamma$ with increasing pollution levels	Ruiz-Olmo et al., 2002; Delibes et al., 2009; Marcelli et al., 2012
connect	Proportion (%) of catchment's edge bordering otter-occupied catchments	Catchment	Contagion	Linear	–	2003	–	Field data	$\nearrow psi$ in highly connected to occupied-catchments	Clavero et al., 2010; Marcelli et al., 2012
distance	Distance to the nearest otter-occupied catchment in 2003–05	Sampled site	Contagion	Linear	–	–	2011	Field data	$\nearrow gamma$ in nearby previously occupied-catchments	Clavero et al., 2010; Marcelli et al., 2012
human	Human population density (inhabitants per km <sup>2</sup> )	200-m buffer	Anthropogenic factor	Linear	–	x	x	INSEE	$\searrow psi/gamma$ in densely populated areas; $\searrow p$ due to lower spraint intensity (disturbances...)	Clavero et al., 2010; Marcelli and Fusillo, 2009; Dettori et al., 2021
cultivated	Proportion (%) of cultivated area: CORINE code included between 211 and 244, except meadows (code 2.3)	200-m buffer	Anthropogenic factor	Linear	–	2006	2006	CORINE Landcover	$\searrow psi/gamma$ in intensively cultivated areas	Marcelli et al., 2012; Carone et al., 2014
irrigation	Mean water volume extracted from the streams for cultivation irrigation divided by the agricultural land surface area	Canton	Anthropogenic factor	Linear	–	2007–10	2007–10	Agreste, 2010	$\searrow psi/gamma$ in highly irrigated areas	Clavero et al., 2010
density	Length (km) of all the streams divided by the catchment area (km <sup>2</sup> )	Catchment	Stream characteristics	Linear	x	x	x	IGN 2013 / BD Carthage	$\nearrow psi/gamma$ with river network density; $\nearrow p$ due to higher spraint intensity	Van Looy et al., 2014
MSR	Minimum Stream Rank of the catchment: values ranging from 1 (large stream) to 4 (narrow stream)	Catchment	Stream characteristics	Linear/quadratic	x	x	x	IGN 2013 / BD Carthage	influence on $psi/gamma$ unknown; $\nearrow p$ in larger streams due to higher spraint intensity, accessibility or hydrolic agents	Ottino and Giller, 2004; Marcelli et al., 2012
hydrographical sector	18 hydrographical sectors defined over the three regions	Region	Location	Categorical	–	x	x	IGN 2013 / BD Carthage	–	–
year	Year of data collection: 2003 / 2011	–	Visit-related	Categorical	x	–	–	Field data	$\nearrow p$ due to higher otter densities (and spraints), to improvement of observers' skill etc.	Fusillo et al., 2007; Lanszki et al., 2008; Marcelli et al., 2012
obs	Observer organization	–	Visit-related	Categorical	x	–	–	Field data	Variation of $p$ depending of observers' organizations (i.e. skill differences)	Jeffress et al., 2011 on <i>Lontra canadensis</i>

sessions.

The survey 1 was conducted on 1238 sites distributed across 570 catchments, covering half of the study area (Fig. A.1, Appendix A), including most of the area believed to be occupied or potentially occupied by otters at that time in the Massif Central and Pyrenees. Each site was visited once ( $N = 68$ ), twice ( $N = 221$ ), three times ( $N = 826$ ) or four times ( $N = 123$ ) at the same period of the year (November to April) during two consecutive winters. The time interval of one year between consecutive winter is quite short considering the slow demographic traits and high site fidelity of the species, so that we can neglect colonization-extinction events during this interval and assume a closure assumption.

The survey 2 was conducted on 615 sites distributed across 831 catchments, covering the whole study area. In survey 2, sites in the area surveyed in survey 1 were randomly chosen among those previously sampled ( $N = 284$ ), while 331 sites were allocated homogeneously over the rest of the survey area. Each site was visited once ( $N = 4$ ), twice ( $N = 505$ ) or three times ( $N = 106$ ) during one winter season (between October 2011 and April 2012). Both surveys were conducted with the same methodology.

### 2.3. Environmental features

Otter colonization can be affected by habitat quality, characterized by levels of urbanization, agricultural practices, water quality and prey availability, so we defined three groups of covariates: stream characteristics, anthropogenic factors and contagion factors. For each sampling site, we collected data on 10 environmental features at several spatial scales from stream level to region. Further details on these features and predictions of their influence on otters, with associated references, are provided in Table 1.

#### 2.3.1. Hydromorphological covariates

We attributed several hydromorphological covariates to each sampling site operating at different scales. At the larger scale, we distinguished three biogeographical zones over the study area: the 'Massif Central' and 'Pyrenees' regions are mountainous, whereas the 'Garonne' region is relatively flat. The hydrographic basins of the French territory are divided into nested elements at several spatial scales (Institut Géographique National, 2013). For this study, we considered 'hydrographic sectors' ( $n = 18$  for the whole study area, Fig. A.2, Appendix A) and 'catchments' ( $n = 831$  for the whole study area, Fig. A.1, Appendix A), this latter being the thinnest level.

Within the catchments, each stream has a size level defined by a hierarchy of tributaries. This level ranges from 1 (large stream) to 4 (narrow stream) (source: Institut Géographique National, 2013). We assigned a 'Minimum stream rank' (MSR) to each catchment. It refers to the minimum size level obtained among the constituent streams of each of the catchments, thus reporting the widest stream inside a catchment. We also calculated the *density* of streams at the catchment level (total river length divided by catchment area). At the stream scale, we recorded the mean fish richness (*fish*) over the 2000–2005 and 2006–2011 periods. We obtained this data from a national monitoring scheme conducted since 1995 by the French National Agency for Water and Aquatic Environments and the Water Supply Agency (Poulet et al., 2011).

#### 2.3.2. Anthropogenic covariates

In a 200-m buffer area surrounding each stream, we recorded the human population density (*human*) calculated as the number of inhabitants per km<sup>2</sup> (Institut national de la statistique et des études économiques, 2010). We also recorded the proportion of cultivated areas (*cultivated*), defined as those habitats with a CORINE code ranging from 211 to 244, except meadows, which are code 2.3 (Project, 2006). At an intermediate scale (the 'canton', a French administrative division), we collected the mean water volume extracted from the streams for

irrigation over the 2007–2010 period (*irrigation*) and divided these values by the agricultural land surface area (Agreste, 2010). We also gathered an index of organic pollution, the Polluo-Sensibility Index (PSI) for survey 1 and survey 2 (Eau France, 2011).

#### 2.3.3. Contagion covariates

We computed stream's connectivity, i.e. the proportion (%) of each catchment's edge bordering catchments known to be occupied by otters in survey 1 (*connect*). For survey 2, we also calculated the linear distance (*distance*) from the sampled site to the nearest catchment known to be occupied by otters in survey 1.

### 2.4. Data analysis

We fitted dynamic site-occupancy models (MacKenzie et al., 2003) using R 4.0.2 (R Core Team, 2010) and the 'unmarked' package 0.10–3 (Fiske and Chandler, 2011). These models allowed the simultaneous estimation of the initial occupancy probability (*psi*) in survey 1, the colonization probability (*gamma*) of an unoccupied site between survey 1 and survey 2, the extinction probability (*epsilon*) of a previously occupied site, and the detection probability (*p*) of any sign of otter presence. Considering the high number of covariates tested and the high detection probability estimated (see results), we didn't consider hierarchical modeling approaches such as multistate or autologistic models (e.g. Bled et al., 2011). The otter was believed to be expanding over the whole Midi-Pyrénées region, making the number of extinction events (only 9 events in our raw dataset) of minor interest. We thus kept this parameter constant throughout the model selection procedure.

Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002). We fitted models combining the set of environmental covariates and some survey features potentially influencing *psi*, *gamma*, and *p* parameters. We scaled all the linear variables and log-transformed the most over-dispersed ones. We also checked for multicollinearity and did not include the more correlated variables ( $r_{\text{spearman}} > 0.60$ ) in the same model. Due to the large number of covariates, the number of model combinations was high, so we modeled *psi*, *gamma* and *p* parameters successively. We first fitted models including covariates on the *p* parameter while maintaining only the hydrographical sectors as predictors for *psi* and *gamma*, to capture a large part of the spatial occupancy heterogeneity. We fitted on *p* two design-related covariates (Table 1): the year of data collection (*year*: survey 1 or survey 2) and the observer organization as a categorical covariate (*obs*, seven levels). Stream size and density and human population density may impact otter density and otter marking behavior (Clavero et al., 2010; Lanszki et al., 2008; Barbosa et al., 2003; Van Looy et al., 2014) and consequently may affect its detection probability (Table 1). These three features were fitted as linear in the models, and as quadratic for the stream size (MSR). We used an automated model selection procedure (i.e. 'dredge function' from the 'MuMIn' package 1.43.17 in R) and tested all the possible combinations of covariates ( $n = 256$  competing models). We retained the covariates included in all of the models with  $\Delta\text{AICc} < 2$  with the best model.

Secondly, we assessed which covariates explained variation in *psi* while fixing the most influential covariates identified during the first step on *p*, and maintaining the hydrographical sector covariate for *gamma*. As few sites were initially occupied in the central lowland areas, corresponding to the Garonne region ( $n = 8$ ), we only fitted covariates for the two mountainous regions (Pyrenees and Massif Central) by fitting a specific interaction. We used the same dredging model selection procedure as for the previous step and fitted seven covariates corresponding to anthropogenic and environmental features (Table 1) and their interaction with the contagion covariate, leading to  $n = 9250$  competing models. We retained the covariates included in all of the models with  $\Delta\text{AICc} < 2$  with the best AICc score model.

Thirdly, we determined which covariates explained variation in



*gamma* while fixing covariates selected during the first and second step on  $p$  and  $psi$ . We used the same model selection procedure as for the previous step and fitted covariates on the overall data (including both mountainous and plain areas). We included the distance from an otter-occupied basin in survey 1 (distance) in interaction with the other covariates, totalising 1775 competing models.

### 3. Results

The model selection procedure is detailed in Table A.1, Appendix A.

The percentage of cultivated areas (*cultivated*) and irrigation volume (*irrigation*) were correlated ( $r_{\text{spearman}} = 0.62$ ). We thus retained the proportion of cultivated area for the model selection procedure as it showed the best fit for the data in the modeling of initial occupancy and colonization probabilities.

The best models for detection probability  $p$  ( $\Delta\text{AIC} < 2$ , minimum number of parameters) included year, observer organization, human population density and the quadratic effect of stream size defined by the MSR covariate (Table A.1, Appendix A).

Concerning the initial occupancy probability  $psi$  (step 2), the proportion of cultivated area and the human population density both in interaction with the contagion covariate (*connect*) were included in all the best models (Table A.1, Appendix A) and were thus retained for the last step of the modeling procedure.

Concerning the colonization probability  $gamma$  (step 3), the Polluo-Sensitivity Index and the proportion of cultivated area both in interaction with the contagion covariate (*distance*) were included in all the best models (Table A.1, Appendix A) and were thus retained in the final model.

Parameter estimates from the model including the covariates selected during the three steps modeling selection procedure (Table A.2, Appendix A) showed that detection probability  $p$  differed between the professional organization of the observer, ranging from 0.60 [CI 95 %: 0.33–0.82] to 0.94 [CI 95 %: 0.89–0.97] in optimal conditions of detection (*survey 2*, *MSR* = 2, *human* = 0). Detection probability  $p$  was higher in *survey 2* than in *survey 1*, with the difference reaching 0.28 for an organization of medium-detection performance (Fig. A.3, Appendix A). Detection probability was higher for larger streams, with the difference reaching 0.74 between MSR 2 and 4 (Fig. A.3, Appendix A).

Except for highly connected sites, initial otter occupancy probability

$psi$  and colonization probability  $gamma$  were negatively correlated to the proportion of cultivated area (Figs. 1A and 2A). This variable had varying effect strength depending on the contagion covariates.  $psi$  and  $gamma$  were higher in less cultivated areas, ranging from 0.57 to 0.80 and from 0.54 to 0.71 respectively. They strongly decreased with an increasing proportion of cultivated area for streams less connected to otter-occupied streams (for  $psi$ ) and more distant from initially occupied streams (for  $gamma$ ) (Figs. 1A and 2A respectively). They decreased less for streams more connected to occupied streams (for  $psi$ ) or adjacent to an initially occupied stream (for  $gamma$ ).

The initial otter occupancy probability  $psi$  was also correlated to human population density in interaction with connectivity to otter-occupied streams (Fig. 1B). When streams were barely connected (*connect*  $\leq 40$  %) to an occupied stream,  $psi$  increased with human population density, with a stronger increase in the least connected, i.e. the more isolated occupied sites. Conversely, otter occupancy probability decreased with increasing human population density for streams fully connected (*connect* = 100 %) to occupied streams.

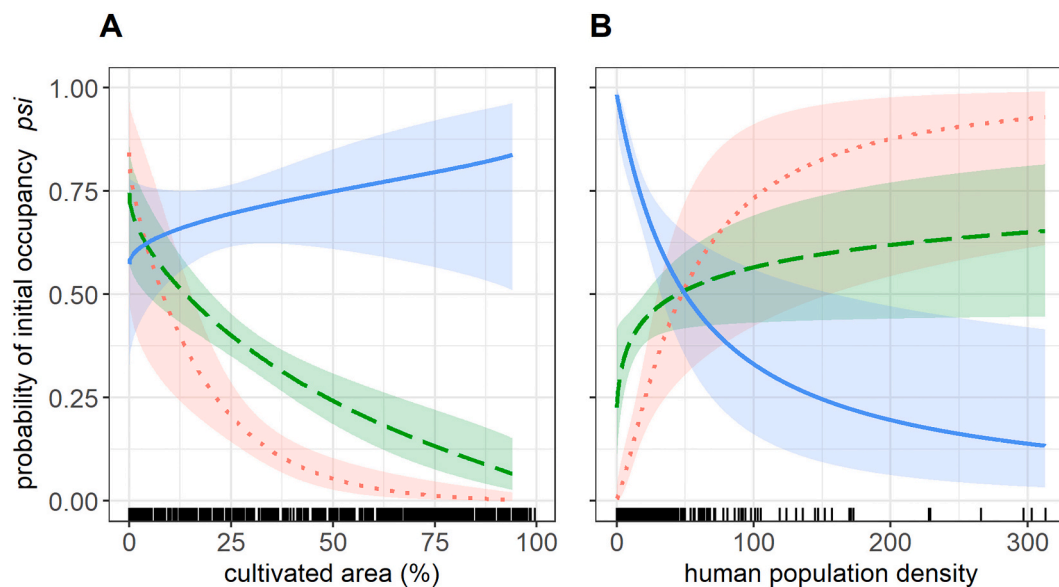
Colonization probability  $gamma$  increased with the Polluo-Sensitivity Index for streams close (*distance* < 50 km) to otter-occupied streams in survey 1 (Fig. 2B). The opposite trend was observed at a greater distance from occupied sites, but with large confidence intervals, suggesting a non-significant effect at this scale.

### 4. Discussion

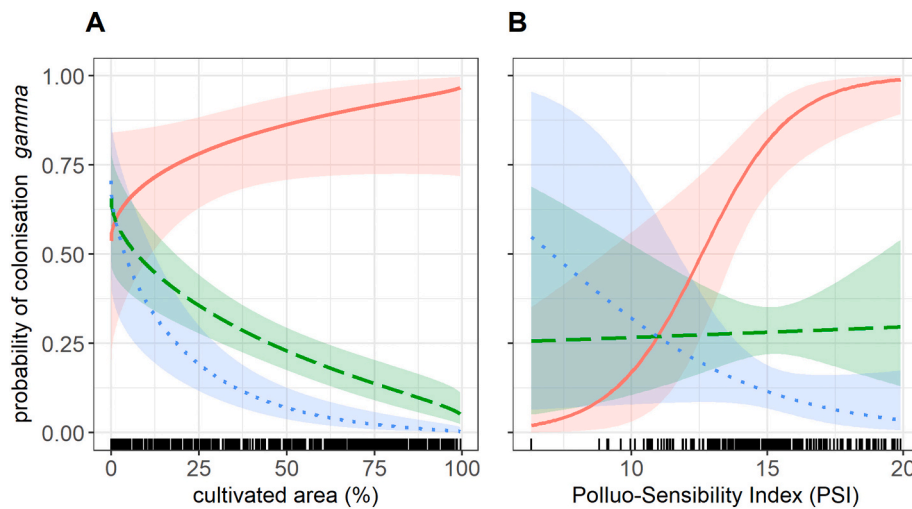
The current range dynamics of the European otter as observed overall in Europe are a good example of the ongoing process of natural rewilding (i.e. without translocation programs) (Carey, 2016). By studying this process at a large scale, we found that otter distribution dynamics in this region are primarily affected by intensive agriculture. We also revealed that covariates describing contagion processes were of high importance to understand initial occupancy and colonization, as they strongly interact with agriculture, human population density and pollution covariates.

#### 4.1. Detection issues

We controlled the different sources of variability in detectability by constraining the survey protocol: dedicated training to observers, all



**Fig. 1.** Initial occupancy probability  $psi$  of the European otter as a function of % of cultivated areas (A) and human population density (B) in interaction with % of connection with otter-occupied catchment as estimated from the best dynamic occupancy model for European otters in the Midi-Pyrénées (southwest France). Solid lines: connection = 100; dashed lines: connection = 40; dotted lines: connection = 0; vertical lines: raw data.



**Fig. 2.** Colonization probability gamma of the European otter as a function of % of cultivated areas (A) and the Polluo-Sensibility Index (B) in interaction with the distance to the nearest otter-occupied catchment as estimated from the best dynamic occupancy model for the European otter in the Midi-Pyrénées (southwest France) between 2003 and 2005 (survey 1) and 2011–2012 (survey 2). Solid lines: distance = 0 km; dashed lines: distance = 50 km; dotted lines: distance = 300 km; vertical lines: raw data.

sampling sites were surveyed by a single person, surveyed transect lengths were standardized, and field prospections were carried out in the appropriate season.

Despite these precautions, detection probability was below one (mean value of  $p$  (survey 1) = 0.58, mean value of  $p$  (survey 2) = 0.75) and quite similar to detection probabilities recorded in other otter studies (Jeffress et al., 2011; Marcelli et al., 2012). These high detection probability values suggest that otter signs are easily detectable and/or field techniques used are pretty efficient. However, our results also show that detection was heterogeneous in time and space. It varied between observer groups, probably because some were more experienced than others (Jeffress et al., 2011), but also because some observers surveyed sites where prospection was more difficult (due to slopes, vegetation, etc.) or where otter density was lower, leading to a lower number of signs available for detection (Fusillo et al., 2007; Marcelli et al., 2012). Detection probability increased between survey 1 and survey 2 while the observers and training remained generally the same. This could be due to an overall improvement in the observers' skill or to a general increase in otter density, intensifying intra-specific competition and thus marking behavior (see e.g. Lanszki et al., 2008). We also found an effect of river width on detection probability, with a lower detection rate recorded in narrower streams, as has also been found in Ireland (Ottino and Giller, 2004) contrarily to results obtained in Czech Republic (Marcelli et al., 2012). Wider rivers may be more easily surveyed in our study area, and have more regular flows, thus reducing the risks of decay or washing of spraints. Finally, we showed that human population density negatively affected the detection probability of otters. This may be due to lower spraint densities in urban areas than in natural areas (Dettori et al., 2021), thus impacting the chances of finding clues of presence of otters while present.

#### 4.2. Factors affecting otter distribution and colonization dynamics

Two of the environmental covariates we studied showed no impact on otter distribution or colonization. The first was the mean fish richness, which was considered a proxy of prey availability. While this could mean that the fish richness may not be a limiting factor for otters in southwest France, it is also possible that the proxy we used is not representative enough of overall food availability. Fish biomass may be a better predictor of otter's abundance (Ruiz-Olmo et al., 2011; Dettori et al., 2021) and we suspect it could also be the case for occupancy. Moreover, although fish are by far the most frequent food in the otter diet, they are not its only prey. Diet composition may vary spatially (Clavero et al., 2003) and temporally (Britton et al., 2017). For instance, some otter populations behave as more generalist predators, relying less

on fish, and more on alternative preys such as aquatic invertebrates and amphibians (e.g. Clavero et al., 2003) or invasive crayfish (Ruiz-Olmo et al., 2011; Dettori et al., 2021; Britton et al., 2017).

Secondly, we found no significant effect of the density of the stream network either on initial otter occupancy or colonization while otter colonization in the Loire basin in Western France was influenced by the density of streams, probably because this improves landscape connectivity, including lateral connectivity (Van Looy et al., 2014). The absence of this effect in our study may be due to the fact that stream density is relatively high in our study area and not a constraining factor. On the other hand, its impact may be masked by stronger constraints such as intensive agriculture that may be detrimental to colonization whatever the connectivity between streams (see below).

Our results showed that the proportion of cultivated area has a strong negative impact on both initial otter occupancy and colonization for areas that lack connectivity. In our study area, cultivated areas mainly consist of highly productive field crops (e.g. cereals, oilseeds) and to a lesser extent orchards and vineyards. These crops are locally managed with a high level of intensity (Rega et al., 2020). We thus assume that the proportion of cultivated area is a good proxy of intensification of land management in our study area. It is known that habitat quality is an important driver of otter range dynamics (Fusillo et al., 2007; Marcelli and Fusillo, 2009). The otter colonization was more likely to occur where a reduction in agricultural land was larger in the Czech Republic (Marcelli et al., 2012). Likewise, the replacement of agricultural areas with forests along the riverbanks probably explained the otter expansion in some regions of Italy (Carone et al., 2014). This impact was explained by the decrease in riparian habitats and freshwater biodiversity in intensively cultivated areas, leading to a decrease in food resources and availability of shelter for resting and reproduction.

We also found a negative effect of human density on initial occupancy probability in areas highly connected to otter-occupied catchments, suggesting that in the core area of their distribution, otter populations are negatively impacted by human disturbance. The impact of human disturbance on otter populations has also been shown in several European areas (Calzada et al., 2010; Clavero et al., 2010; Baltrūnaitė et al., 2009; Marcelli et al., 2012; Dettori et al., 2021). Human density can lead to direct disturbance of otters, as well as indirect disturbance through simplification of riparian vegetation, habitat reclamation for urbanized areas, roadkilling etc. (Ottaviani et al., 2009; Dettori et al., 2021). More unexpectedly, we found a positive relationship (but with high confidence intervals) between human density and initial occupancy probability where occupied sites were isolated. Instead of ecological reasons, we suspect this result to be linked to spurious correlations or other methodological artefacts.

Finally, we found a positive effect of organic pollution on colonization probability for sites close to source populations. This result is counterintuitive, considering that pollution, notably due to organochlorine compounds (from industrial sources and agriculture) and heavy metals, has been recognized as detrimental to otter population (Delibes et al., 2009; Marcelli et al., 2012; Carone et al., 2014). However, in our case, the pollution-sensitivity index we used is based on diatoms, which are indicators of pH levels, nutrients (nitrogen and phosphorus), organic matter and water oxygenation. We suspect that this indicator may be a proxy of some other factors such as higher ecosystem productivity or food availability for otters.

#### 4.3. Contagion, a major factor in recolonization

Previous studies on otter populations emphasize the importance of connectivity to understand spatial distribution as it is a major mechanism in the temporal dynamics of otter distribution (Clavero et al., 2010; Marcelli et al., 2012). Our results showed that connection to occupied catchments and proximity to previously occupied catchments strongly influence effects of habitat or anthropogenic covariates on occupancy and colonization of a site. For instance, the negative impact of cultivated areas on colonization probability was much stronger on sites far from the core population than on sites close to initially occupied sites.

Several mechanisms may underline this contagion process. First, due to spatial constraints, otters might colonize sub-optimal or even poor-quality habitats (polluted, with a high level of agriculture) near saturated populations, while being unable to reach remote suitable sites (Clavero et al., 2010). This could be interpreted as a buffer-effect process (sites of lower quality become occupied as density increases). Conversely, when colonizing an area relatively free of conspecifics (far from core populations), otters may select for optimal sites (unpolluted, with a low level of agriculture). An alternative mechanism explaining this contagion process would be that proximate and distant otter colonizers select the same habitats; however, the higher colonization rate in areas close to occupied areas increases the persistence of populations (e.g. via 'rescue effect', Brown and Kodric-Brown, 1977) in these sub-optimal areas, so that the avoidance is detectable only in isolated areas. Whatever the mechanisms underlying this contagion process, our results highlight the need to improve connectivity between the core population and isolated high-quality habitats.

#### 4.4. Conclusions

Our results show an increase in otter occupancy in our study area between 2003 and 2012, despite the fact that during this period there was no specific action targeted at otter conservation. Despite this positive trend, otter colonization in southwest France still faces large-scale structural constraints, especially in the lowland streams. Intensive agriculture appears the main limitation to otter colonization through its responsibility for biodiversity loss and degradation of habitat quality. These findings largely echo those obtained by Clavero et al. (2010) and Marcelli et al. (2012) in southern Spain and the Czech Republic, suggesting this pattern may be general at the European scale. The negative impact of intensive agriculture on biodiversity is now well known (Emmerson et al., 2016). Our study shows that this impact is also detectable on recolonizing processes despite a species plasticity. We recommend Natura 2000 schemes to incorporate rewilding approaches to further potentiate the large-scale colonization of this flagship species. Contrarily to large carnivores taking advantage of the spaces and resources made available by land abandonment (Ceașu et al., 2015), rewilding approaches for otters should focus on the conservation and restoration of natural riparian habitats (Marcelli et al., 2012) and promote organic agriculture. More generally, a radical change in agricultural practices at a European scale is needed in order to halt biodiversity loss and favor its recovery (Pe'er et al., 2020).

#### CRediT authorship contribution statement

Thibaut Couturier: Formal analysis, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing.

Julien Steinmetz: Conceptualization, Methodology, Data curation, Writing – original draft, Project administration, Writing – review & editing.

Pierre Defos Du Rau: Conceptualization, Methodology, Data curation, Writing – original draft, Funding acquisition, Writing – review & editing.

Daniel Marc: Conceptualization, Methodology, Funding acquisition, Writing – review & editing.

Emma Trichet: Software (GIS analysis), Ressources.

Régis Gomes: Ressources, Methodology, Investigation.

Aurélien Besnard: Formal analysis, Methodology, Software, Validation, Writing – original draft, Writing – review & editing.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

The authors do not have permission to share data.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.109927>.

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