Title: Integrating hydrological features and genetically validated occurrence data in occupancy modeling of an endemic and endangered semi-aquatic mammal species, *Galemys pyrenaicus*.

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Abstract
As freshwater habitats are one of the most endangered ecosystems, there is an urgent need to identify critical areas for conservation, especially for endangered species. The Pyrenean desman (*Galemys pyrenaicus*) is a semi-aquatic mammal for which basic ecological requirements are unknown, hindering the establishment of adequate conservation planning in spite of being considered as a threatened species. Species distribution modeling is a real challenge for freshwater species. Indeed, we must take into account the complexity of aquatic ecosystems (e.g., linearly and hierarchically ordered) as well as the false presence and absence of species, and also use high-quality and relevant descriptors of the hydrology. To understand the influence of environmental covariates on the occupancy and detection of the Pyrenean desman, we combine both a robust sign-survey data set (i.e. with genetic validation ensuring true presence information) and a hydrological model to simulate the flow regime all over a catchment. Markovian site-occupancy analyses, taking into account faeces detection and based on spatial adjacent replicates, indicated a positive influence of heterogeneity of substrate and shelters, and a negative influence of flow variability on the Pyrenean desman faeces detection. This valuable information would likely help the improvement of monitoring programs for this endangered species. Results also highlighted a spatially clustered distribution and a positive influence of the stream flow and number of tributaries on occupancy. Hence, modifications of flow regime (e.g. hydropower production, irrigation, climatic change) and habitat fragmentation appear to be major threats for this species, by altering the connectivity between tributaries and the mainstream river as well as between adjacent sub-catchments.

Keywords

Pyrenean desman, detection, Markovian site occupancy model, habitat use, Soil and Water Assessment Tool.

1. Introduction

Freshwater habitats hold a notable biodiversity with for example, one quarter of vertebrate species restricted to this ecosystem (Dudgeon et al., 2006). However, freshwater habitats are one of the most endangered ecosystems in the world (Vörösmarty et al., 2010) and human-induced alterations of the natural river conditions strongly affect aquatic biodiversity (Dudgeon et al., 2006; Vörösmarty et al., 2010). Extinction rates of freshwater fauna are currently extremely high (Allan et al., 2005). As a consequence, there is an urgent need to identify critical areas for conservation of freshwater biodiversity especially for rare, endemic and endangered species.

Among these freshwater ecosystems, the Pyrenean desman (*Galemys pyrenaicus*) is one of the less well-known European mammals. The distribution of this small semi-aquatic species is restricted to the Pyrenees (Andorra, France and Spain), as well as parts of northern and central Spain and northern Portugal. In the French Pyrenees, it lives in mountain brooks, cold and well oxygenated water courses from sea level to 2700 m (Némoz et al., 2011). The Pyrenean desman is becoming increasingly threatened, triggering several conservation regulations (Fernandes et al., 2008). Yet, even basic knowledge such as distribution range and habitat preferences that are essential for conservation planning are unknown for this species (Némoz et al., 2011).

Identification of environmental factors influencing spatial distribution of species can be achieved by the use of Species Distribution Models (SDMs). They model the statistical relationships between species presence and environmental variables, and may be used to predict habitat suitability for species in unsampled areas (Guisan and Zimmermann, 2000). Some studies have used SDMs for understanding ecological requirements of the Pyrenean desman and reported a positive influence of the elevation, and a strong but contrasted influence of climatic variables, depending on the study area (Barbosa et al., 2009; Morueta-Holme et al., 2010; Williams-Tripp et al., 2012). A negative effect of the density of urban areas was also identified (Barbosa et al., 2009). However, all these studies used atlas data and were applied at coarse resolutions (e.g., 10x10 km grid cells) and large scales (e.g., whole Iberian Peninsula), without taking into account the particular features of freshwater environments.

When SDMs are applied to aquatic species, models are still lacking enough data to fully describe links between the environment and the organisms (Jähnig et al., 2012). For example, it appears frequently that the linear configuration of the river network is not accounted for because SDMs are mostly built on grid cells covering the entire study area (both aquatic and terrestrial ecosystems confounded; e.g. Blank and Blaustein, 2012; Domisch et al., 2013). As aquatic species' movements are constrained by the spatial orientation of the watercourses and by the connectivity between streams and sub-catchments, these parameters should also be considered (Ottaviani et al., 2009).

The importance of hydrological variables on freshwater species ecology and distribution is well known (e.g. Kuemmerlen et al., 2014) even for river birds (Royan et al., 2014) or semi-aquatic mammals (Pedroso et al., 2014; Toner et al., 2010). Despite this, hydrological variables (e.g. stream flow) are often ignored in SDMs due to the lack of fine scale spatial data available for studies conducted in large areas. A solution to counterbalance this lack of data may be to simulate them using a hydrological model. One of the most applied, the Soil and Water Assessment Tool (SWAT), is a catchment-scale, physically based model (Arnold et al., 1998), running on daily time step and capable of continuous simulation over a long time period at different spatial scales (Gassman et al., 2007). By using spatial information (i.e. topography, climate, soil and land-use), SWAT simulates the hydrological cycle both in space and time (see Neitsch et al., 2005 for more details). To our knowledge, very few studies have coupled this tool with SDMs to understand the influence of hydrological parameters on the presence of aquatic species, and to predict habitat suitability (but see Kuemmerlen et al., 2014; Jähnig et al., 2012).

Another important challenge in SDMs is the quality of species presence-absence data. When surveys are based on the recording of indirect signs, such as faeces, ambiguous signs could lead to the risk of species misidentification, leading to false presence (i.e. wrongly attributed to the species of interest; Miller et al., 2011) or false absence (i.e. wrongly attributed to another species than the species of interest). To overcome this issue, techniques that identify species using DNA analyses from faecal samples have been increasingly used (Waits and Paetkau, 2005). Species detection is another major issue. It is well known that the absence of records in the field are a combination of undetected presence (i.e. false absence) and true absences (Gu and Swihart, 2004). Not accounting for the probability of species detection could thus have important consequences by inaccurately relating species records and environmental factors (Kéry et al., 2010) or underestimating species' distribution (Comte and Grenouillet, 2013). Semi-aquatic mammals are particularly sensitive to this detection issue as monitoring is usually based on faeces searches in heterogeneous environments. Site occupancy models have been developed to deal with species detection issues at large scale. They model the probability that a species occupies some sites even though it has not been detected with any certainty when the sites were visited (MacKenzie et al., 2002). This class of models requires replication of detection-non detection data at sampling sites. Usually based on temporal replication, recent developments of site occupancy models allow using spatial instead of temporal replicates. Among them, the Markovian occupancy model can be applied when spatial adjacent replicates are available at sites, to test for spatial correlation of occupancy probabilities between replicates (Charbonnel et al., *in press;* Hines et al., 2010). To date, this recent model has been rarely applied to investigate the influence of covariates on species distribution (see however Barber-Meyer et al., 2013; Karanth et al., 2011; Thorn et al., 2011).

In this study, we applied the Markovian occupancy model to a genetically validated dataset for the Pyrenean desman, and used a hydrological model to simulate flow in the river network of a single catchment in the French Pyrenees. Our aim was to highlight the environmental factors, including hydrological variables, influencing detection and occupancy of this semi-aquatic threatened species for implementing better conservation plans.

2. <u>Methods</u>

2.1. Study area

The upper Salat river catchment (42-43°N, 0-1°S; 1156 km²) is a tributary of the Garonne river, located in the French Pyrenean Mountains (Fig. 1). It has 1413 km of stream length (CARTHAGE © DB). Elevation varies between 350 and 2870 m (mean elevation = 1200 m). Average annual rainfall, air temperature and stream flow at the outlet of the catchment are 1360 mm, 9.5°C (SAFRAN © DB) and 32.78 m^3/s (HYDRO © Bank), respectively. Land cover (Corine Land Cover © DB) is dominated by forests (50%) and herbaceous and shrubby vegetation (25%). We focused our study on this catchment because of (i) its representativeness of other French Pyrenean catchments, (ii) its conservation issues (this catchment is part of a Natura 2000 site) and (iii) the known presence of Pyrenean desman (Bertrand, 1994). The stream network (CARTHAGE © DB) was divided in 1388 1km-long sections (sections hereafter) for the extraction of covariates.

2.2. Field sampling

One hundred thirty one sites (i.e. river transects) were surveyed for this study (Fig. 1). They were selected using a spatially balanced, Generalized Random Tessellation Stratified sampling which is known to produce survey designs well adapted for aquatic systems (Stevens and Olsen, 2004). Searches for Pyrenean desman faeces were conducted along these river transects that were waded by pairs of skilled observers, meticulously inspecting each emergent rock, tree root or branch in the stream. The number of observers was limited as much as possible to minimize the observer bias for sign detection. All the faeces detected and suspected of being left by a Pyrenean desman based on their color, size, position, and smell. They were then harvested for genetic analyses. Surveys were conducted during summers 2011 to 2013, when faeces seem to persist longest, to maximize detection (Bertrand, 1994). We tried not to conduct surveys during or after a period of fluctuating water levels or heavy rainfall to minimize variations in sign detection probabilities (e.g., removal of faeces by water levels rises). Each site was a riverbed transect of 500m-long, which approximately matches the mean home range of the species (Melero et al., 2012). Each site was divided into five sub-units (i.e. segments) of equal length (i.e. 100m) that constituted adjacent spatial replicates, as this segment length appears appropriate for the Pyrenenan desman when analyzed with the Markovian occupancy model (Charbonnel et al., *in press*). For each segment, information of detection or non-detection of faeces was thus available.

2.3. Genetic validation of faeces identification

Genomic DNA from faeces samples were extracted using the Stool Mini Kit (Qiagen Inc., Hilden, Germany). DNA extractions were conducted in a separated room with an UV-sterilised platform where no Pyrenean desman tissue samples were previously treated. In order to identify the owner species of the sampled faeces, we amplified a small cytochrome b fragment of approximately 400bp using specific primers that were designed for this study (GPYRF1: 5'-TTGTAGAATGGAKCTGAGG-3', GPYRF2 : 5'-TTCCTTCACGAAACAGGATC-3' and GPYRR1: 5'-GTCGGCTGCTAAAAGTCAGAATA-3'). PCRs were carried out in 9µl volume containing 0.17µl of forward primer GPYRF1 and 0.17µl of reverse primer GPYRR1 (10µM), 2.89µl of sterile water, 0.58µl of dNTPs (10µM), 1.70µl of MgCl2 (25mM), 3.40µl of 5X GoTaq® buffer reaction (Promega Inc., Madison, USA), 0.09µl of GoTaq® DNA polymerase (Promega Inc., Madison, USA) and 8µl of DNA. Amplifications were performed in a thermal cycler VWR Unocycler using one activation step at 94°C for 5min followed by 40 cycles (denaturation at 94°C for 50s, annealing at 52°C for 45s, extension at 72°C for 45s) and final extension step at 72°C for 10 min. Three microlitres of the PCR product were amplified in a nested PCR with 14µl of the PCR mixture described above with additions of 5µl of sterile water and 0.17µl of forward primer GPYRF2 (10µM) in place of GPYRF1. PCR products were sequenced on an Applied Biosystems® 3730 DNA analyzer and were verified using CHROMASPRO v 1.5

(http://technelysium.com.au). Sequences were then submitted to the BLAST® functionality available on the NCBI website (http://blast.ncbi.nlm.nih.gov).

2.4. Simulation of stream flow using SWAT model

The combined use of hydraulic and distribution models involves hydrological information available at the same spatial resolution (here, 1km-long river sections). SWAT requires several input datasets using the ArcSWAT interface in ArcGIS 10.0 (Winchell et al., 2007). First, it uses a topography map to delineate the watershed that was divided into 1165 sub-basins (mean surface=100ha ±82; mean reaches length=873m ±704) with a discretization scale of 50ha (Fig. 2). In this study, we used (i) a 1:25 000 resolution Digital Elevation Model (ALTI © DB - IGN), (ii) a 1:5 000 000 Digital Soil Map of the World (FAO, 2007), and (iii) a 1:25 000 land cover map (BDOS ©, Regional Natural Parks of Midi-Pyrénées). Climatic variables used to calibrate SWAT models included daily rainfall, maximum and minimum air temperature, solar radiation, wind speed and relative humidity. They were derived from the SAFRAN © DB (1992-2011) which has a spatial resolution of 8 x 8km and account for the influence of the topography on atmospheric variables (Habets et al., 2007). As our study area is located in a mountainous region, we modified snow parameters to calibrate SWAT (Appendix A, Supplementary Materials). Observed monthly output flows of three hydropower reservoirs (Fig. 2; Electricity of France) were also included in simulations to increase their accuracy. After running SWAT, simulated stream flows were available in the 1165 sub-basins at monthly time step, between 1992 and 2011. For each of the 1388 1km long-sections, the flow value that was assigned was the one of the sub-basin it was included in. A simulation period of 20 years was chosen to reduce the influence of years with extreme hydrological events (e.g. flood, low water). Average monthly stream flow data recorded from 1992 to 2011 were available at five gauging stations (Fig. 2) and used to calibrate and evaluate the performance of the SWAT simulations using three different metrics: the Spearman correlation coefficient (rho), the coefficient of determination (R^2) and the Nash–Sutcliffe Efficiency (NSE) calculated between measured and simulated stream flow (e.g. Moriasi et al., 2007; Kiesel et al., 2010). The model was calibrated using the outlet gauging station (Saint-Lizier) and validated at the four other gauging stations (Fig. 2).

2.5. Covariates influencing detection and occupancy

Covariates related to detection probability.
Bias in sign detection may arise due to a variety of factors including weather, habitat structure or observer. First, species detection is known to be influenced by the experience of the observer (MacKenzie et al., 2006). Hence, we used the pairs of observers which inspected each transect as a first covariate (OBS; 3 categories). For the Pyrenean desman, we then hypothesize that substrate heterogeneity may influence faeces detection as emergent items are supports for faeces deposit. We could expect that the higher the heterogeneity, the higher the detection. Hence, during sampling, observers estimated the percentage of heterogeneity of substrate and shelters (e.g. rocks, tree roots or branches) in the riverbed (SUBSTRATE). Rainfall may negatively influence the faeces detection by washing out emergent items, as already shown for the European otter (*Lutra lutra*; Reid et al., 2013). It could thus be more difficult to find faeces in areas with high annual rainfall as items are regularly washed out. Flow variability might also influence detection with higher variation in stream flow resulting in faeces regularly removed by the fluctuating water level. Consequently, we used the mean annual rainfall (RAIN, mean of the annual rainfall from 1992 to 2011, SAFRAN © DB) and the inter-monthly flow variability (FLOW VAR, variance of the twelve monthly flows simulated from SWAT, averaged from 1992 to 2011). All these covariates were calculated for each 1 km-long section.

Covariates related to occupancy probability.
To limit convergence issues in statistical modelling, we retained only four covariates. First, we used the mean monthly flow (FLOW, mean of the twelve monthly flows, averaged from 1992 to 2011, simulation of SWAT models). Second, as all climatic covariates were strongly correlated ($|r| \geq 0.72$,

$p<0.05$), we used the first axis of a principal component analysis (PCA) which explained 93.80 % of the variation of the climatic covariates derived from the SAFRAN © DB (1992-2011). The values of this synthetic covariate (CLIMATE) increased while mean annual rainfall increased but mean annual temperature decreased. For both FLOW and CLIMATE, linear and quadratic terms were included in occupancy models. Third, we calculated the number of tributaries (TRIBUTARIES, derived from CARTHAGE © DB) for each 1-km section and its proximal upstream and downstream sections. Finally, the influence of the three main hydrographic sub-sectors was also tested (SUB-SECTOR; 3 categories; Fig. 1). To improve the convergence of occupancy models, all non-categorical covariates were log-transformed and normalized.

2.6. Data analyses

We applied to our dataset the Markovian occupancy model recently developed by Hines et al. (2010) which estimated four parameters: p, the probability of detecting the species conditional on the presence of the species on the site (i.e. probability of detection); ψ, the probability that a site is occupied or used by a species (i.e. probability of site occupancy); θ_0, the probability that a species is present on a segment given the site is occupied but the species was absent on the previous adjacent segment; and θ_1, the probability that a species is present on the segment given the site is occupied and the species was present on the previous adjacent segment (see Charbonnel et al., *in press*, and Hines et al., 2010 for more details).

Our model selection process initially focused on determining a suitable covariates model structure for detection (p) and subsequently used this model structure to estimate the most important covariates influencing occupancy. We first defined a full occupancy model (i.e. including all occupancy covariates) based on the recommendations of Burnham and Anderson (2002) and MacKenzie et al. (2006). Then, we formulated covariates for detection, either without any covariates, or individually or in additive combination, restricting models to a maximum of two covariates to reduce convergence problems (Burnham and Anderson, 2002). This resulted in eleven different models. All model comparisons were based on Akaike Information Criterion (AIC) values (Burnham and Anderson, 2002). The Akaike weights (ωi) were also calculated. To assess the relative importance of each detection covariate, the sum of ωi of models ($\Sigma \omega i$) that included each covariate was calculated. As this process was repeated 131 times to assess the predictive performance of models (jackknife iteration), we then summed the Akaike weights obtained for the 131 iterations. Based on this global Akaike weight, the detection covariates were ranked and the ones with the highest rank were selected to fix the model structure for p. Thereafter, we kept this model structure component unchanged and ran further occupancy analyses for comparing models involving either none covariates or all combinations of covariates for ψ or none covariates, resulting in sixteen models. No covariates were included for local occupancy parameters θ_0 and θ_1 to reduce the number of parameters to estimate. As for detection covariates, the global Akaike weight of each occupancy covariate was calculated. For each iteration, model averaging was used to determine the effect size (β regression coefficient) of each covariate across the top set of models ($\Delta AIC \leq 2$; Burnham and Anderson, 2002). Finally, a global average coefficient was computed for each covariate from the 131 iterations, and used to build covariate response curves for occupancy and detection. Ninety-five percent confidence intervals were calculated through the jackknife procedure. Estimates obtained through model averaging for each iteration were then used to predict occupancy probabilities over the whole Salat catchment. A final prediction map was thus produced through the computation of average probabilities across the 131 iterations. The predictive accuracy was evaluated using the area under the ROC curve (AUC) which is an index of classification accuracy independent of species prevalence and arbitrary threshold effects (Manel et al., 2001). We fitted all the models using the freeware PRESENCE v. 6.2 (Hines, 2006) and R.2.14.1.

3. Results

3.1. Desman detection

A total of 579 faeces were collected from 94 out of the 131 sampled sites. Only 69% of these faeces were genetically confirmed to be Pyrenean desman, sampled in 54 sites (naïve occupancy of 0.41). Among these 54 sites, 13 had only one 100m segment with detection, 11 had two segments with detection, 9 had three segments with detection, 12 had four segments with detection and 9 had all the five segments with detection. Eighty-seven percent of sites with detection were located in the Salat sub-sector, 13% in the Lez but none presence was recorded in the Baup sub-sector (Fig. 1).

3.2. SWAT flow simulation

SWAT simulations of stream flow were accurate, as indicated by the model evaluation statistics (rho= 0.89; R^2= 0.78; NSE= 0.73) computed between measured and simulated monthly stream flow at the gauging station used for calibration (Saint Lizier; Fig. 2 & 3a). Evaluation statistics were also high good at the gauging stations used for the validation step (0.81≤ rho≤ 0.91; 0.50≤ R^2≤ 0.85; 0.33≤ NSE≤ 0.8; Fig. 3b,c,d,e). Simulated mean monthly flow over the 1992-2011 period ranges spatially from 0.01 to 35.39 m^3/s, with a mean of 0.92 m^3/s (Fig. 2).

3.3. Covariates influence on detection and occupancy

The covariate influencing the most the desman detection was FLOW VAR (global Akaike weight = 130.56) followed by SUBSTRATE (global Akaike weight = 70.26). OBS had a moderate influence (global Akaike weight = 44.83) while RAIN (global Akaike weight = 0.60) did not explain desman detection at all. To avoid statistical convergence issues only the first two covariates, FLOW VAR and SUBSTRATE, were selected to build the occupancy models.

The probability of detecting Pyrenean desman faeces decreased with increasing flow variability (Fig. 4a) and was higher in streams dominated by heterogeneous substrates and shelters in spite of a large variability in detection probabilities for stream reaches with low heterogeneity (Fig. 4b).

For desman occupancy, the covariate SUB-SECTOR exerted the strongest influence (global Akaike weight = 131.00). FLOW was also important (global Akaike weight = 88.99) followed by TRIBUTARIES (global Akaike weight = 76.20) and then CLIMATE (global Akaike weight = 57.07). The Pyrenean desman occupancy was very different between sub-sectors with the highest occupancy probabilities for stream sections located in the Salat sub-sector (Fig. 1 & 4c). As no detection events have been reported in the Baup sub-sector (Fig. 1), occupancy probability in this area was estimated to be null. Both covariates FLOW and TRIBUTARIES had a positive influence on occupancy probability (Fig. 4d & e) suggesting that the Pyrenean desman has a higher occupancy probability in stream sections with high mean monthly flow and several tributaries. Finally, it appears that the Pyrenean desman occupancy was higher in areas with more abundant annual rainfall and colder annual temperature (i.e. high values of CLIMATE; Fig. 4f), although this covariate was the least influencing.

Expected spatial dependence was highlighted by the average model estimates that showed that the probability of Pyrenean desman sign presence on a segment, given absence on the previous segment (θ_0= 0.48, 95% IC = 0.46-0.49) was lower than the probability of Pyrenean desman sign presence on a segment given presence on the previous segment (θ_1= 0.72, 95% IC = 0.71-0.73).

3.4. Predictive occupancy map

The average predicted occupancy probability for the Pyrenean desman across the study area had a moderate accuracy compared to observations given that AUC value was 0.74. Occupancy probability estimates ranged from 0 to 0.97 suggesting that some streams are very suitable for the Pyrenean desman while some others are not suitable at all in the upper Salat catchment. There was a large contrast among occupancy probabilities predicted on sections of the three sub-sectors, with a mean occupancy of 0.63±0.18 in the Salat, 0.15±0.12 in the Lez and 0.00±0.00 in the Baup (Fig. 1, 4c & 5a). Higher occupancy probabilities were predicted for major rivers of the Lez and Salat sub-sectors while lower occupancy probabilities were predicted for small tributaries (Fig. 5a), underlining the positive relationship with stream flow. These predictions indicate a potential linear distribution of 176 km (12.5 %) with predicted occupancy probability ≥ 0.80, and 462 km (32.7 %) with predicted probabilities ≥ 0.60 in the whole upper Salat river catchment. Last, the area with the highest variability in predicted occupancy across the 131 iterations was located on the Lez river, upstream of the Lez and the Salat confluence, and also in headwaters of the Lez sub-sector (Fig. 5b).

4. Discussion

4.1. Genetic validation of presence records

Whereas the importance of accounting for false negative errors is frequently recognized, much less attention has been given to false positive errors (Miller et al., 2011). In this study, without genetic analyses, false positives would have occurred by misidentifying the faeces of other species (e.g. *Neomys* spp., *Glis* spp., *Myotis* spp, *Turdus* spp. or *Pordarcis* spp.) as being Pyrenean desman. For species with shrinking ranges such as the Pyrenean desman, false-positive observations may indeed result in a dangerous underestimation of the population decline. However, the use of modern DNA techniques enabled us to make sure that collected faeces belonged to Pyrenean desman individuals, thus resulting in a reduced risk of overestimating occupancy probabilities. Given the serious consequences of inaccurate estimates of the status of rare species for conservation and management decisions, accounting for false-positive detections should be an important component when designing and analyzing monitoring programs for rare species (Miller et al., 2011). Hence, genetic analyses seem to be an efficient tool to tackle this crucial issue. Moreover, false positives can also be accounted for with a specific occupancy model developed by Royle and Link (2006) when genetic analyses are too expensive and not appropriate for some survey techniques (e.g. visual observations, listening points).

4.2. *Influence of covariates on detection probability of the Pyrenean desman*

A major issue in monitoring wild animal populations is the difficulty in detecting individuals visually and the logistics constraints of surveying species in rough terrain (Aing et al., 2011). Consequently, survey methods based on the recording of indirect cues of species presence have become standard practices for many species (Heinemeyer et al., 2008). Depending on the species ecology, if data are based on sign surveys and present spatial replicates, they could be analyzed with the Markovian occupancy model to account for imperfect detection and avoid false absence data (e.g. Charbonnel et al., *in press*; Hines et al., 2010). We applied this model to the Pyrenean desman for which variability in detection across the diversity of its habitats is expected (Agirre-Mendi, 2004; Gonzalez-Esteban et al., 2003), but has never been quantified to date. As predicted, we have emphasized that the probability of detecting desman faeces decreases in areas with high flow variability, which may regularly submerge emergent items where desman usually leaves its faeces and then limit the accumulation of signs. We also showed that the detection probability rises in streams with a larger diversity of substrate and shelters as expected by field observers who found more signs when many rocks, tree roots or branches were present in the riverbed. The lack of relationship with the annual amount of rainfall is not surprising because the sampling was not conducted after heavy rainfall. Further researches are needed to identify other factors that may impact the detection probability of the desman. For instance, as found for the European otter, the marking behavior of the Pyrenean desman may vary with population density (Hutchings and White, 2000), food resources (Almeida et al., 2012) or season (Yoxon and Yoxon, 2014) and may thus affect the conclusion regarding occupancy probability. Riverine vegetation may also influence detection as faeces should be more preserved on wet emergent items hidden often shadowed, as already known for European otter tracks (Reid et al., 2013).

4.3. Influence of environmental covariates on occupancy probability of the Pyrenean desman

This study gives first insights into the environmental factors influencing the Pyrenean desman distribution at the scale of a single catchment. To date, few studies have investigated ecological requirements of this cryptic and elusive species, and only at large scale (see Barbosa et al., 2009; Morueta-Holme et al., 2010; Williams-Tripp et al., 2012). It has been shown that air temperature has a positive influence whereas solar radiation and precipitation a negative influence in France (Williams-Tripp et al., 2012). By contrast, in Spain and Portugal, there is a positive relationship between precipitation, water balance and the Pyrenean desman presence, and a negative relationship with air temperature (Barbosa et al., 2009; Morueta-Holme et al., 2010). At a finer scale (i.e. catchment scale), our results suggest that climatic variables appear to be less influential and highlight the importance of taking into account hydrological factors, such as mean flow or flow variation, to better understand the distribution of aquatic species. However, in species distribution modelling, relevant data to explain aquatic species ecology and distribution such as water flow are rarely available at large scale resulting in an incomplete description of species ecological niche (Ottaviani et al., 2009). Moreover, very few studies have coupled hydrological models with SDMs to date (but see Kuemmerlen et al., 2014; Jähnig et al., 2012). The SWAT model made it possible to simulate stream flow across all the stream network of the study area with an acceptable accuracy. We found that stream flow was an important covariate to explain the Pyrenean desman distribution, as its probability of occupancy increases as flow increases. Some authors suggested a preference of the Pyrenean desman for fast flowing waters (Queiroz et al., 1993; Ramalhinho and Boa Vida, 1993), but the effect of flow was never quantitatively tested. Our result is consistent with the fact that the action of flowing water is a dominant feature of freshwater ecosystems, determining the distribution and diversity of river organisms (Poff et al., 1997). Invertebrates abundance and richness, which constitute the main prey of the Pyrenean desman (Bertrand, 1994), are known to decrease when the flow decreases (Dewson et al., 2007), maybe explaining why the Pyrenean desman tends to favor streams with high annual water flow in mountainous region.

Our results also revealed the positive influence of the number of tributaries on the Pyrenean desman presence. This finding is in agreement with many studies that showed that more species were likely to be present in stream reaches with higher connectivity (see Fullerton et al., 2010 for a review). Filipe et al. (2009) found that the influence of hydrological connectivity was important for species strictly restricted to freshwater and that might only disperse through aquatic environments. Moreover, a high number of tributaries may act as refuge areas for the Pyrenean desman in case of natural or artificial flooding (Magoulick and Kobza, 2003).

The strong influence of the geographic area that we found may indicate that the Pyrenean desman occurrences show a spatial clustering, with an influence of terrestrial barriers, and a mobility mainly constrained by aquatic environments. This spatial pattern is well known for species restricted to aquatic ecosystems (Filipe et al., 2009). For instance, some authors have emphasized that different pools of fish and amphibian species occur in different river basins at the scale of the Iberian Peninsula, highlighting the relevance of basin delineation to dispersal (Filipe et al., 2009; Vargas et al., 1998). We never collected Pyrenean desman faeces in the Baup catchment, suggesting extremely low sign detection or possible extirpation of desman from this area due to unsuitable environmental conditions within this catchment (i.e. agricultural lands, drier and warmer climate).

Last, other abiotic and biotic covariates potentially affecting the distribution of the Pyrenean desman could have been included in this study. However, the lack of direct data on food resources or predation prevented us to conduct further investigations about the effects of such biological interactions given that they were not available in a spatially explicit way along streams for the entire upper Salat catchment. In addition, although our results support that the Pyrenean desman may be strongly dependent to the aquatic environment, local factors related to the riverbed and bank characteristics may also have been important to explain its spatial distribution. However, we had to reduce the number of environmental covariates to the minimum number given small sample size and statistical convergence issues.

4.4. Concluding remarks : Implication for conservation

Our finding concerning the influence of both flow variability and heterogeneity of substrate on the Pyrenean desman detection constitutes valuable information to improve monitoring programs of this endangered species. We indeed suggest that periods of heavy rain or high water flow as well as the period shortly following flood events should be avoided when survey involves faeces detection. When streams with homogeneous substrate and shelter or high flow variability (natural or artificial) have to be monitored, more efforts should be allocated to compensate the low detection, or other survey methods should be applied such as direct captures.

As the Pyrenean desman appears to favor moderate to high stream flow, artificial reduction of flow regime (induced, for example, by hydropower production or irrigation) may likely have a negative impact on the species (e.g. Murchie et al., 2008 for fish examples), especially in mountain rivers which are more sensitive to the reduction of flow. The spatial clustering of Pyrenean desman occurrences and the high probability of suitable habitats in the Salat sub-sector both suggest that this area may represent one large population connected by movement and gene flow. If true, the demography of tributary populations might not be independent from the mainstream river. Stream connectivity should thus be favored and dams, plants or weirs should be built cautiously as habitat fragmentation could potentially decrease demographic support for tributaries and lead to isolation of populations. Until more data on movement and dispersal of the Pyrenean desman are available, the most cautious conservation strategy is thus to protect habitat quality and connectivity throughout the entire sub-sector. Last, the scale of catchment seems to be the most appropriate spatial unit to plan conservation strategies for semi-aquatic vertebrates (Ottaviani et al., 2009). The predicted occupancy map would therefore be useful as a decision-making instrument for future developments within this catchment, such as the building of new hydroelectricity plants or future conservation actions. Identifying the areas the most suitable with the highest certainty for the Pyrenean desman will help to prioritize the protection of these streams.

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Appendix A. Supplementary material.

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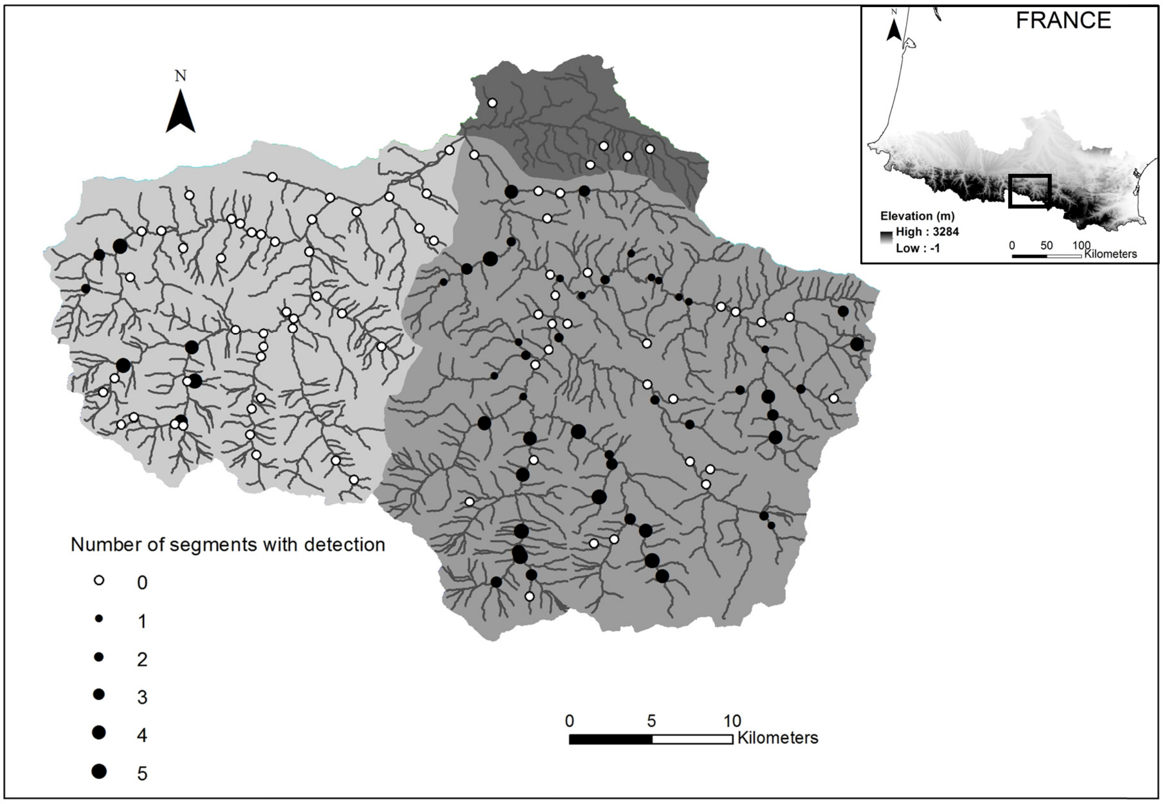
Fig. 1: Map of the upper Salat river catchment (study area). Hydrographic sub-sectors (light grey: Lez, medium grey: Salat and dark grey: Baup) and sampling sites location (dots, N=131). The size of circles indicates the number of segments with detection for each site.

Fig. 2: Map of SWAT sub-basins distribution, hydropower reservoirs (black squares) and gauging stations (red triangles) used to calibrate and validate SWAT modelling. The average simulated stream flow (1992-2011) is also shown.

Fig. 3: Measured (grey) and simulated (black) Soil and Water Assessment Tool (SWAT) stream flow at the downstream gauging station used for the calibration step (a) and at gauging stations used for the validation step (b ,c, d, e; see Fig.1 for the location). Model simulations were evaluated with the Spearman coefficient correlations (rho), coefficient of determination (R^2), and Nash–Sutcliffe efficiency (NSE) between measured and simulated stream flow.

Figure 4: Relationship between detection (a, b) and occupancy probability (c, d, e, f) and covariates for the Pyrenean desman in the upper Salat river catchment. For occupancy, solid black lines show covariates relationships for the Salat sub-sector, solid grey lines for the Lez sub-sector and dashed black lines for the Baup sub-sector. 95% confidence intervals are shown with dotted lines. Predictions were computed with the other covariates at their mean values.

Figure 5: Maps of (a) the average predicted occupancy probability of the Pyrenean desman in the upper Salat river catchment across the 131 iterations and (b) the prediction variability (i.e. coefficient of variation) across the iterative jackknife procedure.


N
FRANCE
Elevation (m)
High : 3284
Low : -1
0
50
100
Kilometers
Number of segments with detection
0
1
2
3
4
5
0
5
10
Kilometers

676 Fig. 1
677

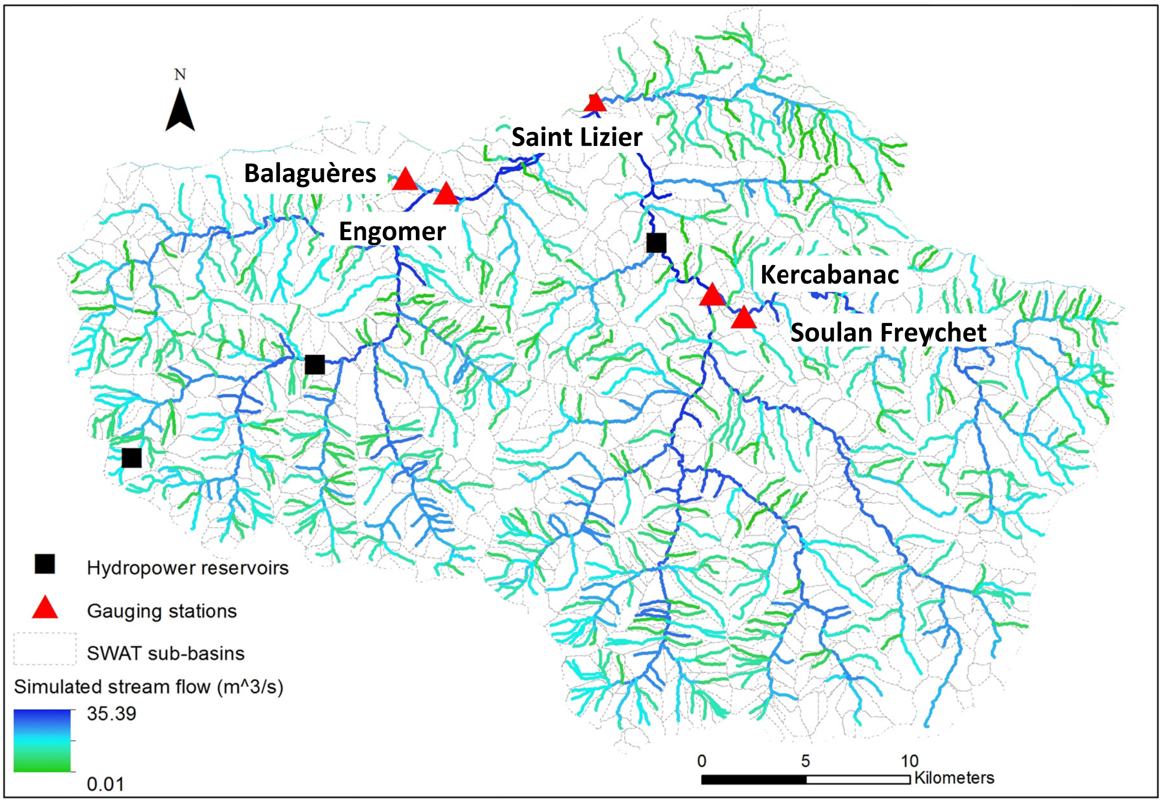
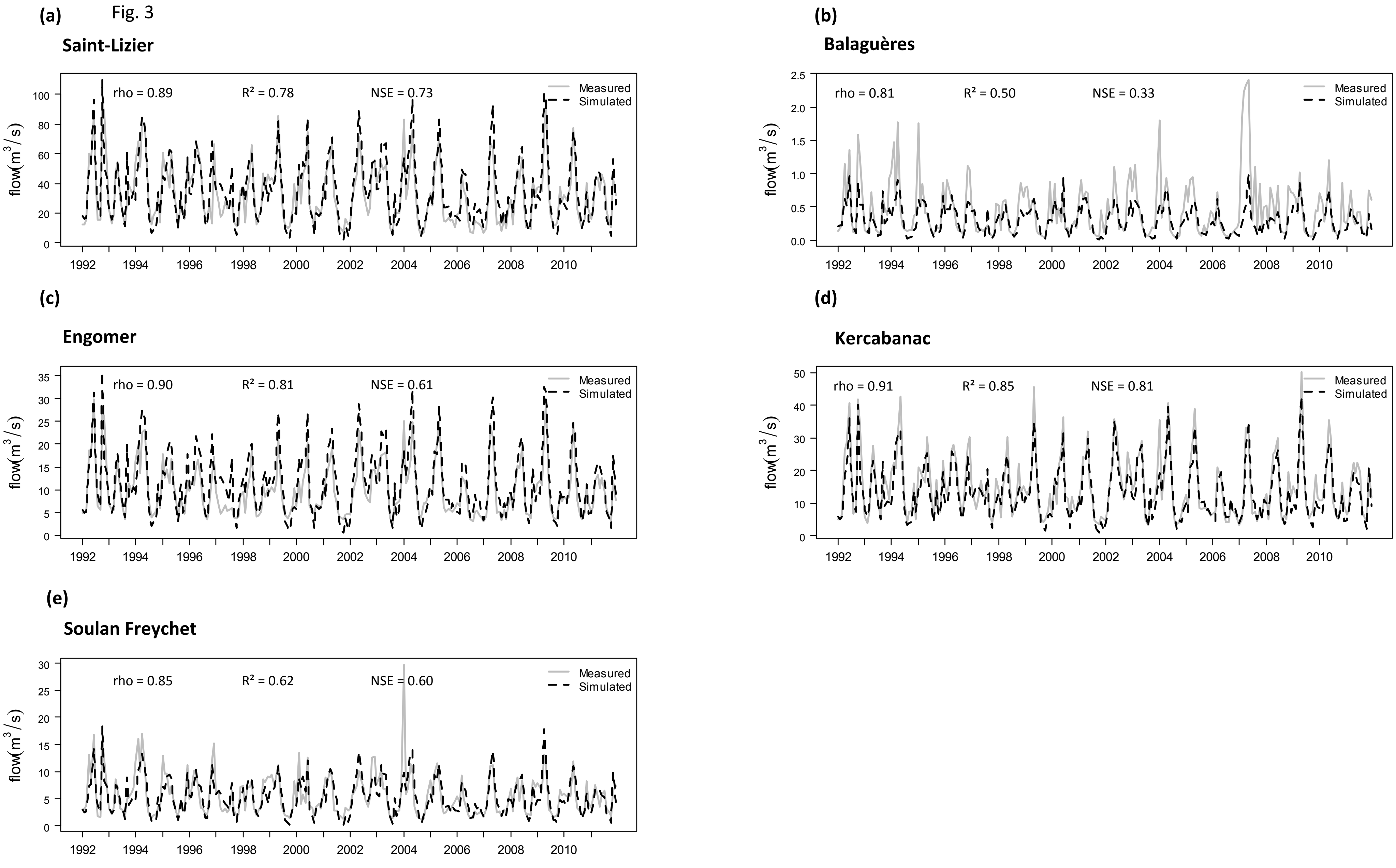

N
Saint Lizier
Balaguères
Engomer
Kercabanac
Soulan Freychet
Hydropower reservoirs
Gauging stations
SWAT sub-basins
Simulated stream flow (m^3/s)
35.39
0.01
0
5
10
Kilometers

Fig. 2

Fig. 3


(a)
Saint-Lizier
rho = 0.89
R² = 0.78
NSE = 0.73
Measured
Simulated
flow(m3/s)
(b)
Balaguères
rho = 0.81
R² = 0.50
NSE = 0.33
(c)
Engomer
rho = 0.90
R² = 0.81
NSE = 0.61
(d)
Kercabanac
rho = 0.91
R² = 0.85
NSE = 0.81
(e)
Soulan Freychet
rho = 0.85
R² = 0.62
NSE = 0.60
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010

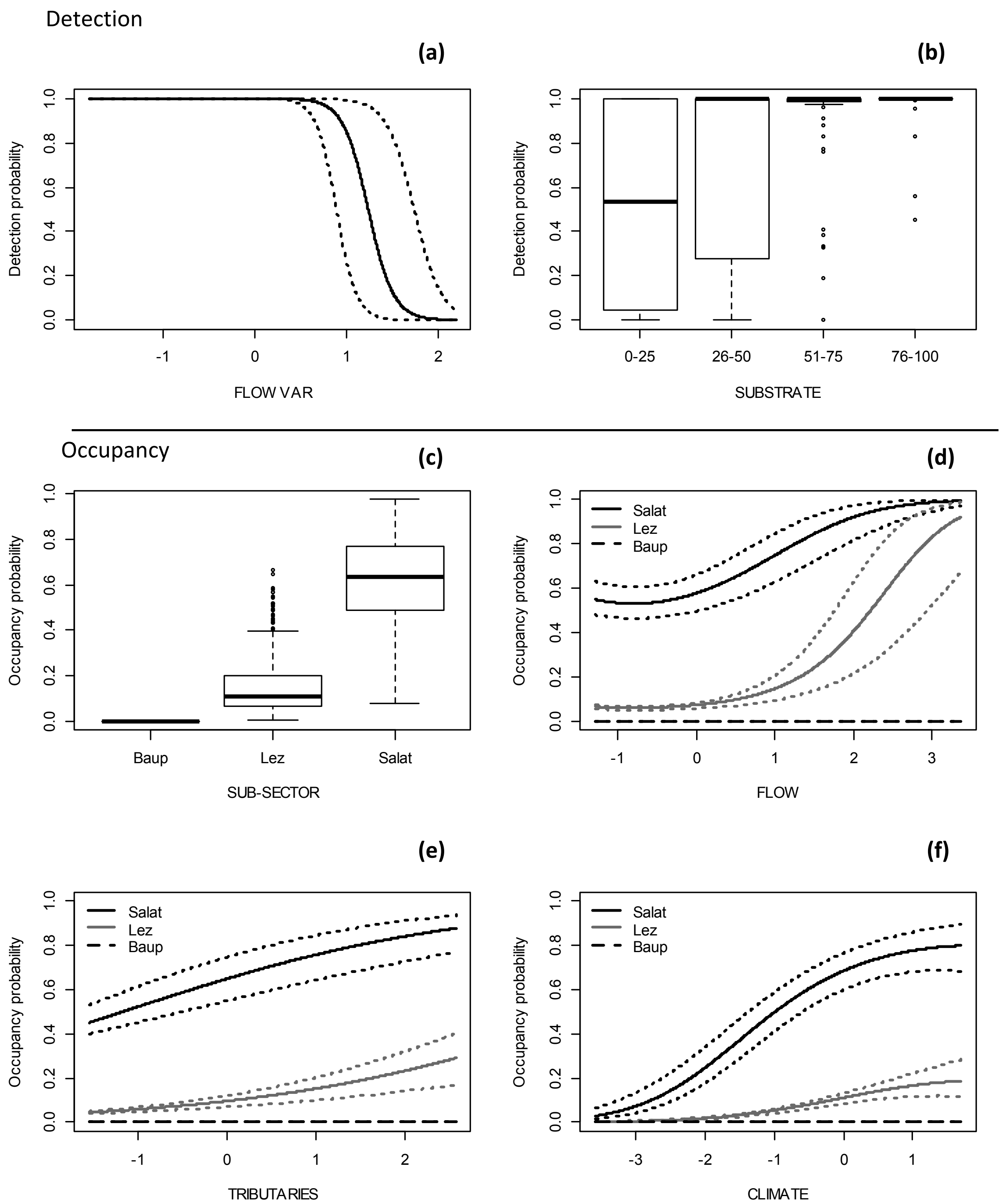

Detection
(a)
(b)
Detection probability
FLOW VAR
0-25
26-50
51-75
76-100
SUBSTRATE
Occupancy
(c)
(d)
Occupancy probability
Baup
Lez
Salat
SUB-SECTOR
FLOW
(e)
(f)
TRIBUTARIES
CLIMATE

Fig. 4

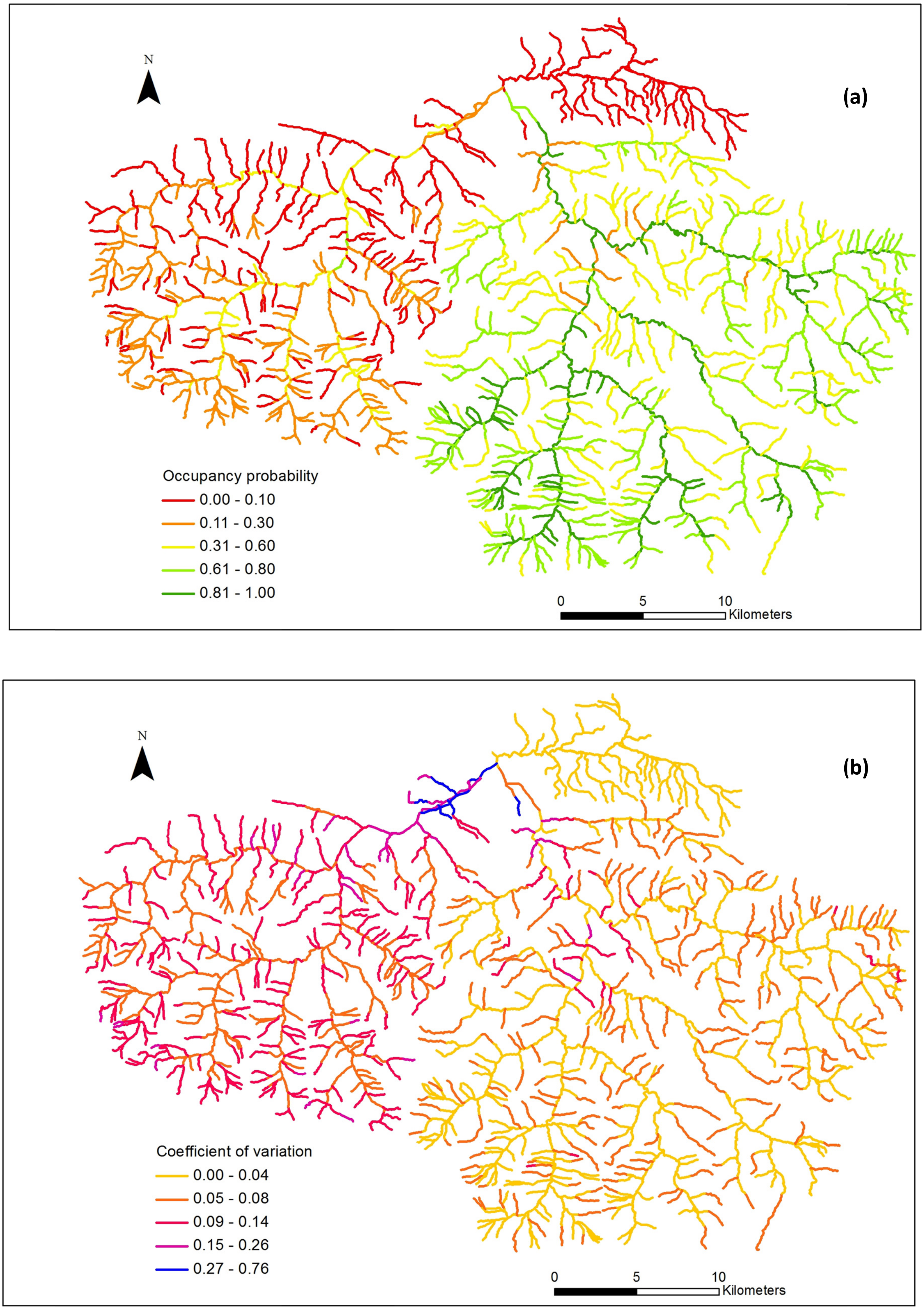

N
(a)
Occupancy probability
0.00 - 0.10
0.11 - 0.30
0.31 - 0.60
0.61 - 0.80
0.81 - 1.00
0
5
10
Kilometers
N
(b)
Coefficient of variation
0.00 - 0.04
0.05 - 0.08
0.09 - 0.14
0.15 - 0.26
0.27 - 0.76
0
5
10
Kilometers

Fig. 5