Shrinking of the endangered brown bear *Ursus arctos* distribution in the French Pyrenees revealed by dynamic occupancy modeling

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Abstract

The Pyrenean brown bear (*Ursus arctos*) in the mountainous border between France and Spain is one of the smallest and most endangered populations of large carnivores in Europe. Here, we aimed at assessing trends in brown bear distribution in the Pyrenees and determining the underlying environmental and anthropogenic drivers. Using detection/non-detection data collected between 2008 and 2014 through non-invasive methods, we developed occupancy models to investigate the dynamic of brown bear distribution in the Pyrenees through local colonization and extinction processes. Our results showed a negative correlation between human density and bear occupancy in agreement with previous studies on brown bear habitat suitability. We found two non-connected occupancy cores, one located in the West and another in the Center of the Pyrenees. Importantly, we showed that the population distribution significantly decreased between 2008 and 2014, and that while bear went locally extinct in some areas, there was no sign of colonization of new ones.

Keywords: dynamic occupancy model, extinction, imperfect species detection, large carnivores, local extinction, species distribution, *Ursus arctos*

Introduction

Over the last decades, large carnivore populations have been recovering in Europe following the implementation of conservation policies (Chapron *et al.*, 2014). Among the four species in continental Europe is the brown bear *Ursus arctos*, which is widely distributed all over the continent and split in numerous populations of varying sizes and ranges (Swenson, Taberlet and Bellemain, 2011), including the large Swedish population (Kindberg *et al.*, 2011) or the much smaller one living in the Italian Apennines (Gervasi *et al.*, 2012). One of the smallest and most endangered of these populations resides in the Pyrenees mountains between Southwestern France and Northeastern Spain and is considered to be critically endangered by the IUCN (Huber, 2007). Its survival required the translocation of Slovenian individuals in 1996-97 and 2006 after only five individuals were detected in 1995, and it remains to this day small and threatened by demographic stochasticity and inbreeding (Chapron *et al.*, 2009, Swenson *et al.*, 2011).

Despite the recovery of European large carnivores, conflicts surrounding the animals' presence subsist (Treves and Karanth, 2003). More than the direct danger caused by carnivore presence, the main sources of conflicts are the damage on livestock and the competition with local hunters (Ericsson and Heberlein, 2003, Gunther *et al.*, 2004, Piédallu *et al.*, 2016a). For these conflicts to be solved or at least mitigated - a necessary step in the conservation of wild populations - the expectations of all stakeholders should be considered and the management decisions rely on solid ecological data (Redpath *et al.*, 2013).

The distribution of a wild population is a key element on which the IUCN relies to determine its conservation status (IUCN, 2012). However, this state variable is difficult to assess in the case of elusive species with large home ranges (Gittleman and Harvey, 1982), brown bear making no exception, and requires their monitoring to rely on tracks and indirect observations coupled with DNA analyses to identify the individuals (e.g., Bellemain *et al.*, 2005, McDonald, 2004, Taberlet *et al.*, 1997). In the case of the French brown bear, its actual distribution remains poorly studied. Martin *et al.* (2012) conducted a habitat suitability analysis on the Cantabrian brown bear population in Spain and transferred their results using presence data in the Pyrenees. Here, we intend to build on these results to address two main issues in standard species distribution models.

First, when dealing with free-ranging populations, species detectability is most likely less than 1, which can lead to false negatives where animals are present but not seen during the survey (Kéry, 2011). Falsely assuming perfect detection can lead to an underestimation of the actual species distribution (Lahoz-Monfort, Guillera-Arroita and Wintle, 2014), which in turn can have negative effects on the resolution of a conflict by generating distrust among stakeholders (Redpath *et al.*, 2013). Site-occupancy models were specifically developed to explicitly disentangle a non-detection from an actual absence through the modeling of the imperfect, possibly heterogeneous, observation process (MacKenzie *et al.*, 2002). Second, another limit of standard species distribution models is the assumption that the species always occupy the most favorable area, and that dispersal allows reaching these ideal territories - both statements originating from the ecological niche concept (Leibold, 1995). However, natural barriers or dispersal limitations (such as being an extremely small population) may prevent a species from reaching a favorable area (Araújo and Guisan, 2006). To address this issue, static occupancy models were extended to account for colonization and extinction processes – so-called dynamic or multi-season occupancy models (MacKenzie *et al.*, 2003). Although static occupancy models have often been used on large carnivores (e.g., Bayne, Boutin and Moses, 2008, Carroll and Miquelle, 2006, Carroll *et al.*, 2003, Hines *et al.*, 2010), there are only few applications of dynamic occupancy models (Miller *et al.*, 2013, Molinari-Jobin *et al.*, 2012).

In this study, besides identifying environmental or anthropogenic drivers of brown bear distribution in the French Pyrenees, we aimed at assessing trends in its range dynamics. To do so, we fitted a dynamic occupancy model on detection/non-detection data obtained through a multi-source systematic monitoring protocol between 2008 and 2014.

Material & Methods

1. Study area and bear population

This study was performed on the French side of the Pyrenees at the border between Northeastern Spain and Southwestern France (Figure 1). The bears that live here mostly descend from individuals that were translocated from Slovenia to the Pyrenees in 1996-1997 (2 females and 1 male) and 2006 (4 females and 1 male), even though one bear's mother belonged to the remnant of the original Pyrenean bear population which was thought to include 5 individuals in 1995. Field observations suggest that two population cores exist on the French side of the Pyrenees: the Western one is made of two male bears, and the Central one accounts for the rest of the population. The Western core is located on two French counties: the Southeast of the Pyrénées-Atlantiques, and the Southwest of the Hautes-Pyrénées. The Central core, meanwhile, is currently located on the Southeast of the Haute-Garonne county and the Southwest of the Ariège county, but until 2011 also extended on the Southeast of Ariège and the Southwest of the Aude and Pyrénées-Orientales counties (Figure 1).

2. Bear data collection and monitoring

The data used for this analysis was gathered between 2008 and 2014 by members of the national Brown Bear Network (135 professional members from government agencies and 228 unaffiliated amateur members) under the supervision of the French Game and Wildlife Agency (ONCFS). A systematic monitoring protocol was followed using fixed itineraries along which the agents looked for bear tracks such as hair, scats, claw marks or paw prints. The Pyrenees were broken down in mountain massif subsections using ridge lines and the bottom of valleys. Each one of the 84 investigated subsections of the mountain massif included one itinerary, which could either be active or inactive each year. An itinerary was assigned the inactive status after three years without any track discovered in the corresponding subsection. Active itineraries were visited at least once every month from July to November. Tracks and observations were validated by ONCFS experts, therefore minimizing the risk of false positives due to species misidentification (Molinari-Jobin *et al.*, 2012).

3. Model building and selection

To estimate the probability of bear presence in all the mountain massif subsections, we built a dynamic occupancy model (MacKenzie *et al.*, 2003) that was parameterized with the probabilities of colonization γ (the probability for a subsection to become occupied while it was unoccupied the year before), extinction ε (the probability for a subsection to become unoccupied while it was occupied the year before) and initial occupancy ψ (the probability for a subsection to be occupied the first year of the study), along with the species detection probability p (the probability for a subsection to be seen as occupied when bears are present). The subsections itineraries were visited every month between July and November. We used years as primary occasions, between which colonization and extinction probabilities could be estimated, and the months of July to November as secondary occasions during which we considered the subsections’ occupancy status to remain unchanged (the so-called closure assumption). By focusing on the July-November period, we excluded the reproduction season (April to June) during which male bears in particular are known to increase their movement range while they look for females (Clevenger, Purroy and Pelton, 1990). Despite this precaution, movements may still occur, and occupancy should be interpreted as use of the subsections rather than the proportion of area occupied by the species (MacKenzie and Nichols, 2004).

We relied on previous habitat suitability studies on brown bears in Europe to select candidate environmental and anthropogenic covariates for our analysis (Martin *et al.*, 2010, Martin *et al.*, 2012, Mertzanis *et al.*, 2008). We considered eight environmental and anthropogenic covariates for each mountain massif subsection (Table 1). We used the IGN BD_ALTI® database (250m resolution) to calculate the mean altitude of each massif subsection (ALT). Roughness was obtained as the mean of the absolute differences between the altitude of a massif subsection and the value of its contiguous mountain subsections (Wilson *et al.*, 2007). Forest cover and shrub cover covariates were extracted from the CORINE Land Cover® database (U.E – SoeS. Corine Land Cover 2012). Road length was built using the IGN ROUTE 500® database. Human density was obtained from the NASA Socioeconomic data and applications center (http://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-count/data-download). Lastly, we followed Martin *et al.* (2012) and included an index of forest connectivity that was built for each massif subsection as the average proportion of forest cover in the contiguous massif subsections. We also considered an index of human diffusion calculated for each massif subsection as the average human population in the contiguous massif subsections.

Due to the large number of covariate combinations, we used a multi-stage approach to model selection (Dugger, Anthony and Andrews, 2011, Lee and Bond, 2015, MacKenzie *et al.*, 2012). We used Akaike's Information Criterion corrected for sample size (AICc, Burnham and Anderson (2002)) to rank models at each stage. The covariates were standardized prior to the analyses. Model selection proceeded as follows:

(1) We started by selecting the best model structure by focusing on time-varying covariates only, namely *year* and *survey*. We considered 8 different models in total, with either no effect (.) or a *year* effect on colonization γ and extinction ε, and either no effect (.) or a *survey* effect on detection probability p (Table 2). Because the sampling effort was homogeneous over the study period, we did not consider a *year* effect on detection.

(2) Based on previous bear occupancy studies (Martin *et al.*, 2010, Martin *et al.*, 2012, Mertzanis *et al.*, 2011, Nielsen *et al.*, 2010, Nielsen, Stenhouse and Boyce, 2006) and bear biology, we considered specific combinations of the environmental or anthropogenic effects on each of the parameters (ψ, γ, ε and p, Table 1). We investigated possible negative effects of covariates human density and road length on initial occupancy ψ as a previous study showed that bears avoided human-caused disturbances (Martin *et al.*, 2010, Mertzanis *et al.*, 2011, Naves *et al.*, 2003). Altitude, roughness, shrub cover and forest cover were all positively associated with bear presence albeit performed at different scales in previous studies (Apps *et al.*, 2004, Martin *et al.*, 2010, Martin *et al.*, 2012, Naves *et al.*, 2003, Nellemann *et al.*, 2007). For colonization γ, we studied a possible effect of forest connectivity, using it as a possible indicator of landscape fragmentation which was shown to influence mammal distribution (Crooks, 2002), along with possible effects of roughness and human density, which were the most commonly significant covariates in previous bear distribution studies (Martin *et al.*, 2010). We considered for extinction ε the possible effect of the three anthropogenic covariates human density, road length and human diffusion. Finally, we tested the possible effect of roughness and forest cover on detection p as both could potentially influence the accessibility of bear tracks to observers.

(3) We sequentially fitted a set of models, using a focal parameter for which we selected the best model among all different covariates combinations while the other parameters were held constant. Once the main effect was determined for a parameter, we fitted the best model for the next focal parameter. We repeated those steps until no better model was selected on all four parameters. Focal parameters were selected in the following order: detection p, colonization γ, extinction ε then initial occupancy ψ.

To assess a trend over the years in occupancy, we first estimated the posterior mean of occurrence at each subsection and for each year. We then tested a linear effect of year on occurrence using a conditional autoregressive correlation model and an adjacency matrix between the different subsections to specify the correlation matrix (Rousset and Ferdy, 2014). A likelihood ratio test (LRT) was performed to assess the significance of this temporal trend. These analyses were performed in R (RCoreTeam, 2013) with the 'unmarked' (Fiske and Chandler, 2011) and spaMM (Rousset and Ferdy, 2014) packages.

Results

1. Multi-stage model selection

The null model was selected during the first step, which means that we found no *year* or *survey* effects on any of the parameters ψ, γ, ε or p (Table 2). The ΔAICc of the next two best models (with a *year* effect on extinction ε and a *survey* effect on detection p respectively) was >2, therefore we used the null model as the basic structure for the next step. In the sequential model selection procedure with environmental and anthropogenic covariates, we found an effect of forest cover and roughness on detection probability, and effects of roughness on colonization γ, human diffusion on extinction ε and human density on initial occupancy ψ (Table 3).

2. The effect of covariates on parameters

Using the model best supported by the data, we investigated the relationships between the selected covariates and initial occupancy, colonization, extinction and detection probabilities, to assess the shape and intensity of the effects (Figure 2). Roughness was more influential on detection probability than forest cover (Figure 2A), with detection probability increasing with both covariates increasing. Initial occupancy ψ was strongly negatively correlated with human density (Figure 2B), with the least populated areas being much more likely to be occupied by bears, just like extinction ε was negatively correlated with human diffusion (Figure 2D). However, the link between roughness and colonization γ was weak, with only a slight increase of γ for the highest roughness values (Figure 2C).

3. Distribution maps

The initial occupancy map (Figure 3B) clearly showed two population cores (Western and Central), with the Central Core extending in Southeast Ariège and Southwest Aude and Pyrénées-Orientales (Figure 1). The extinction probability in the East of the Central core was high (Figure 3D), which is consistent with the disappearance of the bears from that area (Camarra *et al.*, 2012), while the colonization probability in the same mountain subsections were close to zero (Figure 3C). Detection was higher in the Central core than it was in the Western core (Figure 3A), which might be explained by the fact that the Central population core is much more populated than the Western one. The colonization map indicated that the Western population core was more likely to expand to the East, while the Central one was more likely to expand to the West (Figure 3C).

These last observations were confirmed by the yearly occupancy maps (Figure 4), which showed a strong decrease of the occupancy probability in the Eastern parts of the Central population core (Southeast Ariège, Southwest Aude and Pyrénées-Orientales). Occupancy in the West of the Western population core (Southwest of the Pyrénées-Atlantiques) also decreased while it remained constant in the East of that core (Southeast of the Hautes-Pyrénées). Overall, a shrinking of the bear population distribution between 2008 and 2014 was detected (slope = -0.011, standard error = 0.001, $\chi^2 = 78.13$, degree of freedom = 1, p-value<<0.01), with no new areas being colonized while others clearly went extinct.

Discussion

1. Environmental and anthropogenic effects on model parameters

Human density had a strong, negative effect on occupancy probability ψ, with the least densely populated areas being the most likely to be used by bears. This result confirms previous analyses suggesting that bears tend to live far from the areas with the most intense human activity (Long *et al.*, 2010, Martin *et al.*, 2010). Several factors such as the habituation of the bears (Wheat and Wilmers, 2016) or the need for female bears to shield themselves from sexual conflict (Steyaert *et al.*, 2016) may mitigate this effect – but the small current size of the Pyrenean brown bear population limits the immediate relevance of these factors as bears tend to disperse further at low densities, lowering the encounter rate of other individuals and for females the risk of sexually selected infanticide (Stoen *et al.*, 2006).

Contrary to what we were expecting, human diffusion was negatively correlated with the probability of extinction. A possible explanation is the influence of demographic stochasticity in small populations (Gabriel and Bürger, 1992) which gives more weight to extinction events. In our study, human diffusion was lower in the Southeast of Ariège and Southwest of Aude and Pyrénées-Orientales (Figure A1) than it was in the other areas with high occupancy probability (Figure 3B), and was the place of several local extinction events in years 2010 and 2011 (Camarra *et al.*, 2012). The effect of stochasticity might also explain the weak, positive relationship between roughness and colonization, which seems to be driven by the effect of a very small number of subsections with very high values of the covariate (Figure 2C).

Finally, the positive correlation between the detection probability and both roughness and forest cover seems counter-intuitive, as we might think that bears are harder to spot in more densely forested areas with steeper slopes. However, this pattern may be explained by the characteristics of the monitoring, which was implemented a) through itineraries that used paths accessible to humans and b) through finding tracks that indirectly indicated bear presence instead of direct sightings and c) hair and camera traps being mostly installed in forested areas for practical reasons. Even though analyzing habitat preferences of animals at very fine scales is a difficult task (Johnson *et al.*, 2002), the paths used for systematic monitoring itineraries in rough and forested terrains are more likely to be used by bears as corridors (Graves *et al.*, 2007) due to a lack of other available options. Overall, species detection was imperfect and estimated below 0.6, therefore confirming the need to correct for it to avoid underestimating occupancy.

2. Brown bear distribution in the French Pyrenees

The occupancy maps for bears in the Pyrenees clearly showed the existence of two independent population cores, one located in the West and another in the Center of the Pyrenees (Figure 3B, Figure 4). The two cores remained unconnected during the timespan of the study. The dynamics of occupancy over the study period (Figure 4) showed that the population significantly shrunk overall. In particular, the extinction of the Eastern part of the Central core is consistent with the lack of bear tracks found in Southeast Ariège and Southwest Aude and Pyrénées-Orientales (Figure 1) since 2011 (Camarra *et al.*, 2012). These results demonstrate the usefulness of dynamic occupancy models to highlight trends in species distribution that cannot be identified by static models (MacKenzie *et al.*, 2003).

The negative correlation between human activity and bear presence was commonly found in previous studies (Apps *et al.*, 2004, Martin *et al.*, 2010, Martin *et al.*, 2012, Naves *et al.*, 2003, Nellemann *et al.*, 2007), and was also observed in the Pyrenees. The effects of roughness and forest cover, which were the second most commonly present in literature, were not retained (Apps *et al.*, 2004, Martin *et al.*, 2012, Naves *et al.*, 2003, Nellemann *et al.*, 2007), but roughness seemed to weakly affect colonization. These results confirm that anthropogenic effects supersede natural elements when it comes to habitat selection by brown bears (Nellemann *et al.*, 2007).

The fact that we found many mountain subsections with a high occupancy probability in the Western core despite the fact that only 2 to 3 bears were estimated to live there between 2008 and 2014 (Piédallu *et al.*, 2016b) suggests a violation of the closure assumption between our secondary occasions (July-November), because there were not enough bears in the population core to occupy all subsections at the same time. This means that we estimated the use of space by brown bears instead of the actual occupancy. For species that can attack livestock, presence does not have to be permanent to be a source of conflict, and therefore space use remains a relevant indicator in the case of large carnivores often characterized by their vast home ranges (Gittleman and Harvey, 1982) and their use of large areas without actually occupying much land at any given time.

3. Implications for human-wildlife conflict mitigation

We anticipate that our results will be useful as part of the “scientific evidence gathering” that is required for conflict mitigation (Redpath *et al.*, 2013). Attacks on livestock are one of the main causes of the negative attitudes towards carnivore presence in general (Kaczensky, Blazic and Gossow, 2004, Sponarski *et al.*, 2013) and towards brown bears in the Pyrenees in particular (Piédallu *et al.*, 2016a). There is an interest in mapping the areas which are more likely to host bears in the present and the future, and as such the "attack hotspots" (Miller, 2015). It could also be combined with a mapping of attitudes towards brown bears (Piédallu *et al.*, 2016a) to identify areas that combine positive attitudes towards bear presence and low attack risk, and as such could be primary targets of future management decisions. This might be the first step towards the development of socio-ecological models designed to mitigate human-wildlife conflicts (Aswani, 2011, Dupont *et al.*, 2011, Estoque and Murayama, 2014).

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Tables & Figures

Table 1: Definition of the environmental variables used for the occupancy analysis, and the parameters for which an effect was tested. ψ: initial occupancy probability, γ: colonization probability, ε: extinction probability, p: detection probability. +/-: predicted sign of the effect of the covariate on the parameter based on previous studies (see text for references). An absence of a +/- sign means that the effect was not tested.

Variable name	Description	ψ	γ	ε	p
Altitude	Mean altitude	+			
Roughness	Mean of the difference between the altitude of a cell and those of all surrounding cells	+	+		-
Forest cover	Percentage of forest cover	+	+		-
Shrub cover	Percentage of shrub cover	+			
Forest connectivity	Average percentage of forest cover in all bordering subsections		+		
Road length	Total length of roads	-		+	
Human density	Average human density	-	-	+	
Human diffusion	Average human density in all bordering subsections			+	

Table 2: Model selection with time-varying covariates. Models were ranked with AICc. ψ: initial occupancy probability, γ: colonization probability, ε: extinction probability, p: detection probability. *year*: year effect on the parameter, which relates to changes between primary occasions, i.e. from one year to another in our case. *survey*: survey effect on the parameter, which relates to the secondary occasions repeated within a year. ΔAICc: difference between the AICc of the current model and the AICc of the model with lowest AICc.

#	Model	AICc	ΔAICc
1	ψ(.) γ(.) ε(.) p(.)	577.1	0
2	ψ(.) γ(.) ε(*year*) p(.)	581.0	3.9
3	ψ(.) γ(.) ε(.) p(*survey*)	581.8	4.7
4	ψ(.) γ(.) ε(*year*) p(*survey*)	584.5	7.4
5	ψ(.) γ(*year*) ε(.) p(.)	584.5	7.4
6	ψ(.) γ(*year*) ε(.) p(*survey*)	588.0	10.9
7	ψ(.) γ(*year*) ε(*year*) p(.)	588.8	11.7
8	ψ(.) γ(*year*) ε(*year*) p(*survey*)	592.3	15.2

Table 3: Model selection with environmental and anthropogenic covariates. The starting model was the null model {ψ(.), γ(.), ε(.), p(.)} as shown in Table 2. The focal parameters are shown in the order in which they were considered during the model selection process. The covariates that were considered for each parameter are defined in Table 1. # models: number of models considered, equal to 2^n with n the number of covariates tested on that parameter. Best models: Among the # models we considered for selection, we only displayed the model with lowest AICc for a given focal parameter.

Focal parameter	# models	Best models	AICc
Detection probability p	4	ψ(.), γ(.), ε(.), p(roughness+forest cover)	[illegible]
Colonization probability γ	16	ψ(.), γ(roughness), ε(.), p(roughness+forest cover)	[illegible]
Extinction probability ε	8	ψ(.), γ(roughness), ε(*HDF*), p(roughness+forest cover)	[illegible]
Initial occupancy probability ψ	64	ψ(human density), γ(roughness), ε(human diffusion), p(roughness+forest cover)	[illegible]

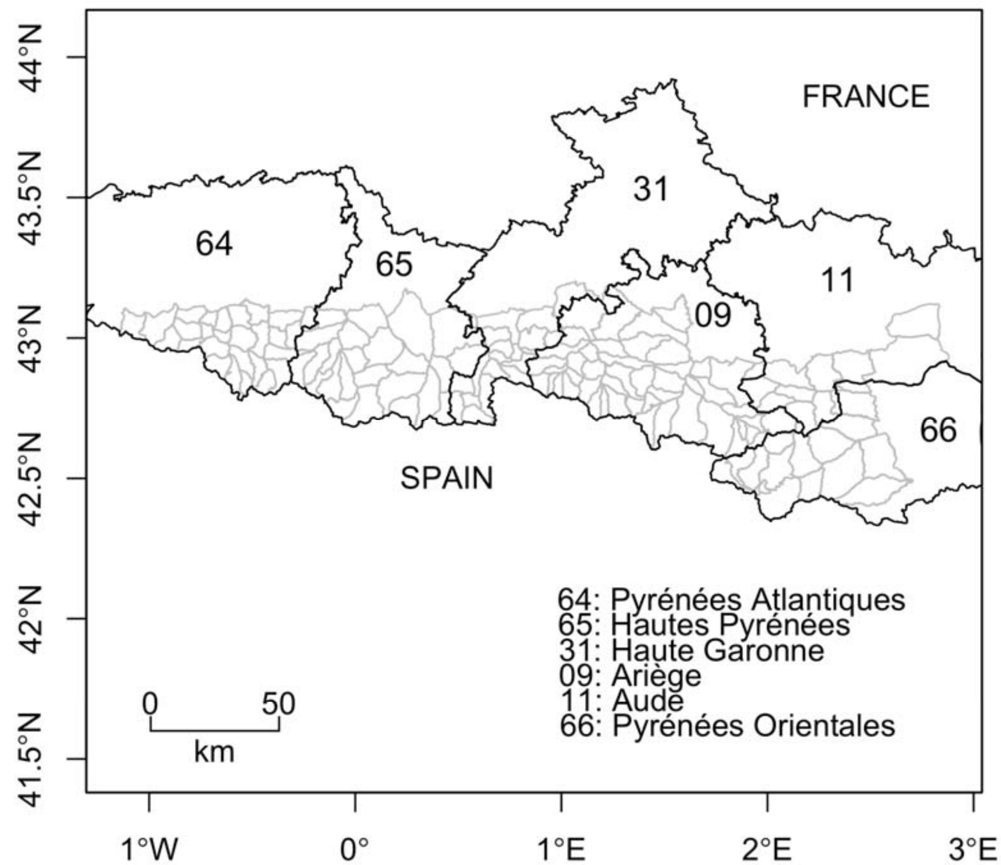

Figure 1: Map of the counties and mountain subsections in the French Pyrenees. Dark lines: county borders. Gray lines: limits between mountain subsections.

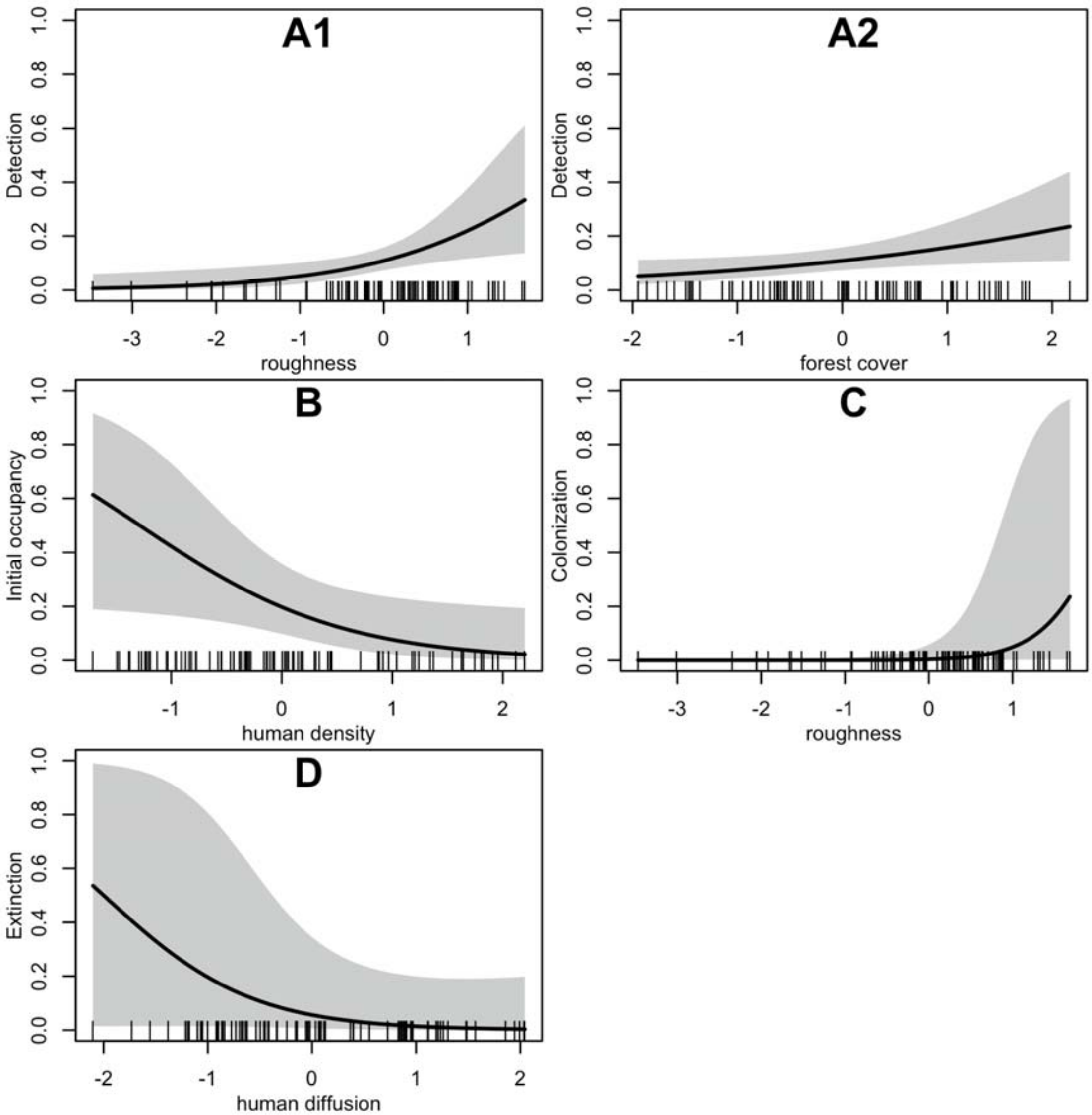

Figure 2: Relationships between the model parameters and the standardized covariates selected in the best model {ψ(human density), γ(roughness), ε(human diffusion), p(roughness+forest cover)}. The dashes on the x-axis indicate the observed covariate values. A: Detection p, with A1: detection as a function of roughness (forest cover set at its mean) and A2: detection as a function of forest cover (roughness set at its mean). B: Initial occupancy ψ as a function of human density. C: Colonization γ as a function of roughness. D: Extinction ε as a function of human diffusion.

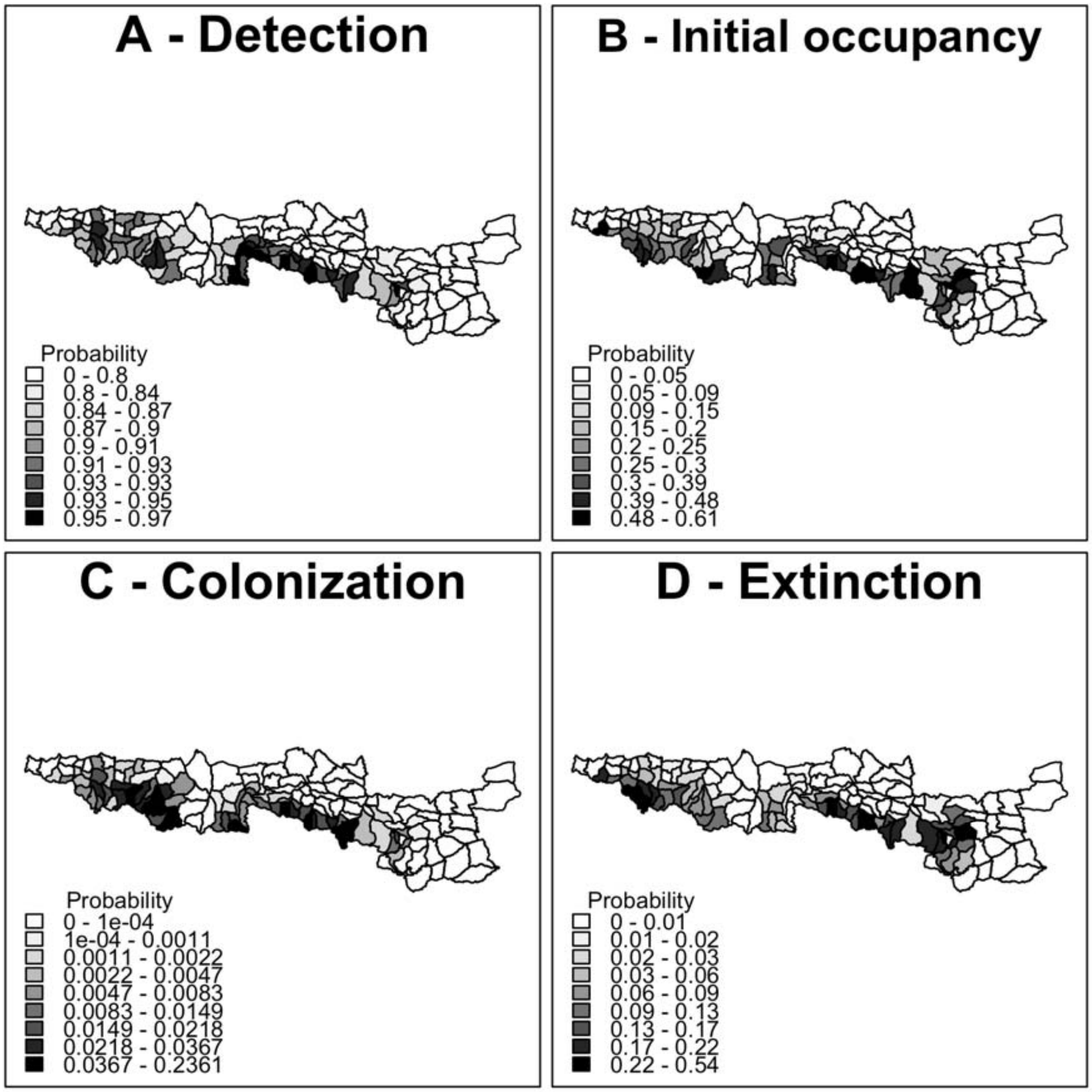

Figure 3: Maps of the model parameters in the various mountain subsections of the French Pyrenees, estimated using the results obtained from the best model {ψ(human density), γ(roughness), ε(human diffusion), p(roughness+forest cover)}. A: Detection probability, B: Initial occupancy probability, C: Colonization probability, D: Extinction probability. Covariates were set at their mean.

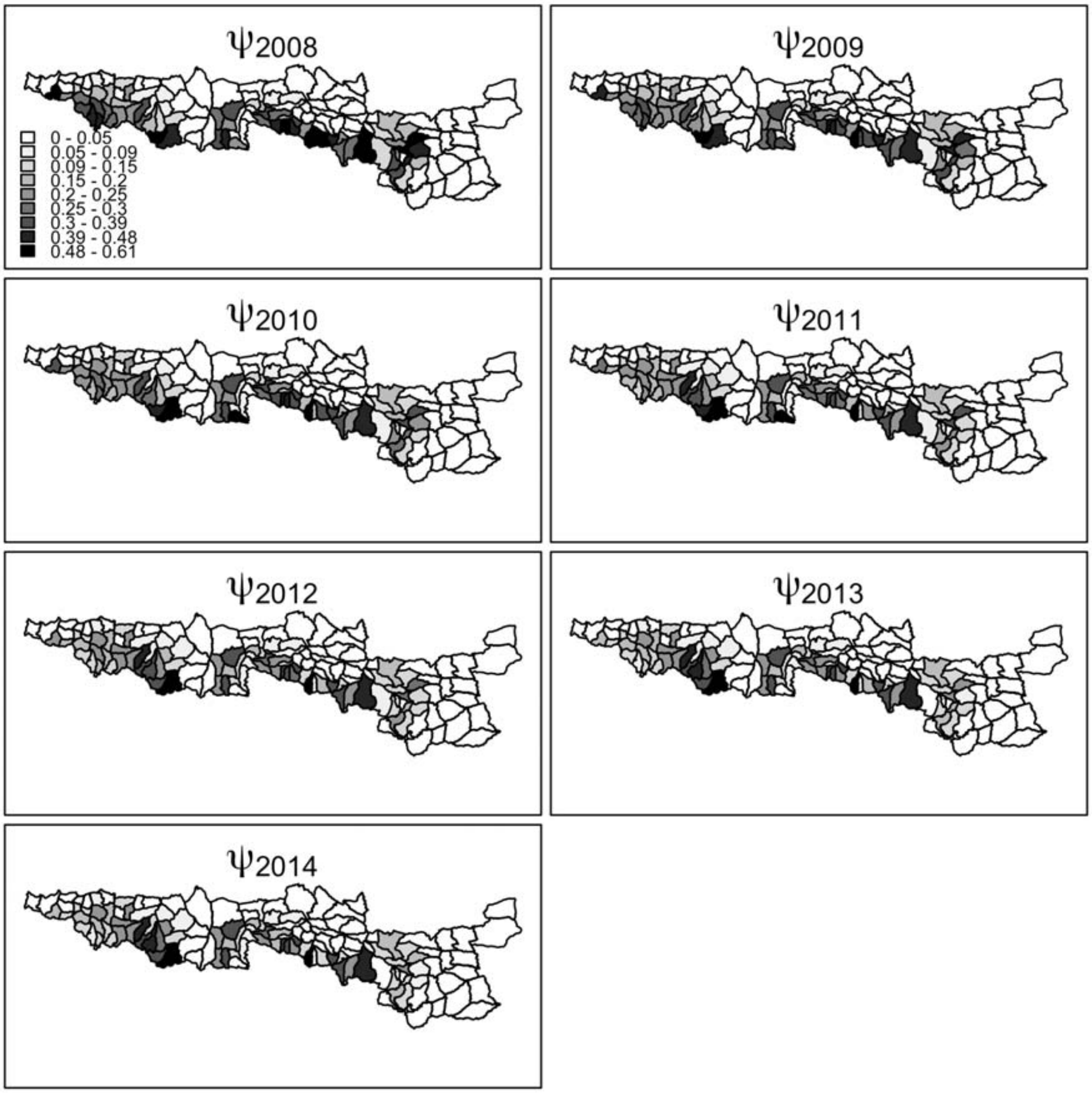

Figure 4: Maps of the yearly occupancy probability ψ_t from t = 2008 to t = 2014 in the various mountain subsections of the French Pyrenees, estimated using the results obtained from the best model {ψ(human density), γ(roughness), ε(human diffusion), p(roughness+forest cover)} by using the formula $\psi_{t+1} = (1-\psi_t)\,\gamma + \psi_t\,(1-\varepsilon)$ (MacKenzie *et al.*, 2002). Covariates were set at their mean.