

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

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24 **Abstract**

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

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

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40

41 **Introduction**

42 Over the last decades, large carnivore populations have been recovering in Europe following
43 the implementation of conservation policies (Chapron *et al.*, 2014). Among the four species in
44 continental Europe is the brown bear *Ursus arctos*, which is widely distributed all over the
45 continent and split in numerous populations of varying sizes and ranges (Swenson, Taberlet
46 and Bellemain, 2011), including the large Swedish population (Kindberg *et al.*, 2011) or the
47 much smaller one living in the Italian Apennines (Gervasi *et al.*, 2012). One of the smallest
48 and most endangered of these populations resides in the Pyrenees mountains between
49 Southwestern France and Northeastern Spain and is considered to be critically endangered by
50 the IUCN (Huber, 2007). Its survival required the translocation of Slovenian individuals in
51 1996-97 and 2006 after only five individuals were detected in 1995, and it remains to this day
52 small and threatened by demographic stochasticity and inbreeding (Chapron *et al.*, 2009,
53 Swenson *et al.*, 2011).

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

61 The distribution of a wild population is a key element on which the IUCN relies to determine
62 its conservation status (IUCN, 2012). However, this state variable is difficult to assess in the
63 case of elusive species with large home ranges (Gittleman and Harvey, 1982), brown bear

64 making no exception, and requires their monitoring to rely on tracks and indirect observations
65 coupled with DNA analyses to identify the individuals (e.g., Bellemain *et al.*, 2005,
66 McDonald, 2004, Taberlet *et al.*, 1997). In the case of the French brown bear, its actual
67 distribution remains poorly studied. Martin *et al.* (2012) conducted a habitat suitability
68 analysis on the Cantabrian brown bear population in Spain and transferred their results using
69 presence data in the Pyrenees. Here, we intend to build on these results to address two main
70 issues in standard species distribution models.

71 First, when dealing with free-ranging populations, species detectability is most likely less than
72 1, which can lead to false negatives where animals are present but not seen during the survey
73 (Kéry, 2011). Falsely assuming perfect detection can lead to an underestimation of the actual
74 species distribution (Lahoz-Monfort, Guillera-Arroita and Wintle, 2014), which in turn can
75 have negative effects on the resolution of a conflict by generating distrust among stakeholders
76 (Redpath *et al.*, 2013). Site-occupancy models were specifically developed to explicitly
77 disentangle a non-detection from an actual absence through the modeling of the imperfect,
78 possibly heterogeneous, observation process (MacKenzie *et al.*, 2002). Second, another limit
79 of standard species distribution models is the assumption that the species always occupy the
80 most favorable area, and that dispersal allows reaching these ideal territories - both statements
81 originating from the ecological niche concept (Leibold, 1995). However, natural barriers or
82 dispersal limitations (such as being an extremely small population) may prevent a species
83 from reaching a favorable area (Araújo and Guisan, 2006). To address this issue, static
84 occupancy models were extended to account for colonization and extinction processes – so-
85 called dynamic or multi-season occupancy models (MacKenzie *et al.*, 2003). Although static
86 occupancy models have often been used on large carnivores (e.g., Bayne, Boutin and Moses,
87 2008, Carroll and Miquelle, 2006, Carroll *et al.*, 2003, Hines *et al.*, 2010), there are only few
88 applications of dynamic occupancy models (Miller *et al.*, 2013, Molinari-Jobin *et al.*, 2012).

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

93 **Material & Methods**

94 1. Study area and bear population

95 This study was performed on the French side of the Pyrenees at the border between
96 Northeastern Spain and Southwestern France (Figure 1). The bears that live here mostly
97 descend from individuals that were translocated from Slovenia to the Pyrenees in 1996-1997
98 (2 females and 1 male) and 2006 (4 females and 1 male), even though one bear's mother
99 belonged to the remnant of the original Pyrenean bear population which was thought to
100 include 5 individuals in 1995. Field observations suggest that two population cores exist on
101 the French side of the Pyrenees: the Western one is made of two male bears, and the Central
102 one accounts for the rest of the population. The Western core is located on two French
103 counties: the Southeast of the Pyrénées-Atlantiques, and the Southwest of the Hautes-
104 Pyrénées. The Central core, meanwhile, is currently located on the Southeast of the Haute-
105 Garonne county and the Southwest of the Ariège county, but until 2011 also extended on the
106 Southeast of Ariège and the Southwest of the Aude and Pyrénées-Orientales counties (Figure
107 1).

108 2. Bear data collection and monitoring

109 The data used for this analysis was gathered between 2008 and 2014 by members of the
110 national Brown Bear Network (135 professional members from government agencies and 228
111 unaffiliated amateur members) under the supervision of the French Game and Wildlife
112 Agency (ONCFS). A systematic monitoring protocol was followed using fixed itineraries

113 along which the agents looked for bear tracks such as hair, scats, claw marks or paw prints.
114 The Pyrenees were broken down in mountain massif subsections using ridge lines and the
115 bottom of valleys. Each one of the 84 investigated subsections of the mountain massif
116 included one itinerary, which could either be active or inactive each year. An itinerary was
117 assigned the inactive status after three years without any track discovered in the
118 corresponding subsection. Active itineraries were visited at least once every month from July
119 to November. Tracks and observations were validated by ONCFS experts, therefore
120 minimizing the risk of false positives due to species misidentification (Molinari-Jobin *et al.*,
121 2012).

122 3. Model building and selection

123 To estimate the probability of bear presence in all the mountain massif subsections, we built a
124 dynamic occupancy model (MacKenzie *et al.*, 2003) that was parameterized with the
125 probabilities of colonization γ (the probability for a subsection to become occupied while it
126 was unoccupied the year before), extinction ϵ (the probability for a subsection to become
127 unoccupied while it was occupied the year before) and initial occupancy ψ (the probability for
128 a subsection to be occupied the first year of the study), along with the species detection
129 probability p (the probability for a subsection to be seen as occupied when bears are present).
130 The subsections itineraries were visited every month between July and November. We used
131 years as primary occasions, between which colonization and extinction probabilities could be
132 estimated, and the months of July to November as secondary occasions during which we
133 considered the subsections' occupancy status to remain unchanged (the so-called closure
134 assumption). By focusing on the July-November period, we excluded the reproduction season
135 (April to June) during which male bears in particular are known to increase their movement
136 range while they look for females (Clevenger, Purroy and Pelton, 1990). Despite this

137 precaution, movements may still occur, and occupancy should be interpreted as use of the
138 subsections rather than the proportion of area occupied by the species (MacKenzie and
139 Nichols, 2004).

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

156 Due to the large number of covariate combinations, we used a multi-stage approach to model
157 selection (Dugger, Anthony and Andrews, 2011, Lee and Bond, 2015, MacKenzie *et al.*,
158 2012). We used Akaike's Information Criterion corrected for sample size (AICc, Burnham
159 and Anderson (2002)) to rank models at each stage. The covariates were standardized prior to
160 the analyses. Model selection proceeded as follows:

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

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

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

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

199 **Results**

200 1. Multi-stage model selection

201 The null model was selected during the first step, which means that we found no *year* or
202 *survey* effects on any of the parameters ψ , γ , ϵ or p (Table 2). The $\Delta AICc$ of the next two best
203 models (with a *year* effect on extinction ϵ and a *survey* effect on detection p respectively) was
204 >2 , therefore we used the null model as the basic structure for the next step. In the sequential
205 model selection procedure with environmental and anthropogenic covariates, we found an
206 effect of forest cover and roughness on detection probability, and effects of roughness on
207 colonization γ , human diffusion on extinction ϵ and human density on initial occupancy
208 ψ (Table 3).

209 2. The effect of covariates on parameters

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

219 3. Distribution maps

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

230 These last observations were confirmed by the yearly occupancy maps (Figure 4), which
231 showed a strong decrease of the occupancy probability in the Eastern parts of the Central
232 population core (Southeast Ariège, Southwest Aude and Pyrénées-Orientales). Occupancy in

233 the West of the Western population core (Southwest of the Pyrénées-Atlantiques) also
234 decreased while it remained constant in the East of that core (Southeast of the Hautes-
235 Pyrénées). Overall, a shrinking of the bear population distribution between 2008 and 2014
236 was detected (slope = -0.011, standard error = 0.001, $\chi^2 = 78.13$, degree of freedom = 1, p-
237 value $\ll 0.01$), with no new areas being colonized while others clearly went extinct.

238 **Discussion**

239 1. Environmental and anthropogenic effects on model parameters

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

249 Contrary to what we were expecting, human diffusion was negatively correlated with the
250 probability of extinction. A possible explanation is the influence of demographic stochasticity
251 in small populations (Gabriel and Bürger, 1992) which gives more weight to extinction
252 events. In our study, human diffusion was lower in the Southeast of Ariège and Southwest of
253 Aude and Pyrénées-Orientales (Figure A1) than it was in the other areas with high occupancy
254 probability (Figure 3B), and was the place of several local extinction events in years 2010 and
255 2011 (Camarra *et al.*, 2012). The effect of stochasticity might also explain the weak, positive

256 relationship between roughness and colonization, which seems to be driven by the effect of a
257 very small number of subsections with very high values of the covariate (Figure 2C).

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

270 2. Brown bear distribution in the French Pyrenees

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

280 The negative correlation between human activity and bear presence was commonly found in
281 previous studies (Apps *et al.*, 2004, Martin *et al.*, 2010, Martin *et al.*, 2012, Naves *et al.*,
282 2003, Nellemann *et al.*, 2007), and was also observed in the Pyrenees. The effects of
283 roughness and forest cover, which were the second most commonly present in literature, were
284 not retained (Apps *et al.*, 2004, Martin *et al.*, 2012, Naves *et al.*, 2003, Nellemann *et al.*,
285 2007), but roughness seemed to weakly affect colonization. These results confirm that
286 anthropogenic effects supersede natural elements when it comes to habitat selection by brown
287 bears (Nellemann *et al.*, 2007).

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

298 3. Implications for human-wildlife conflict mitigation

299 We anticipate that our results will be useful as part of the “scientific evidence gathering” that
300 is required for conflict mitigation (Redpath *et al.*, 2013). Attacks on livestock are one of the
301 main causes of the negative attitudes towards carnivore presence in general (Kaczensky,
302 Blazic and Gossow, 2004, Sponarski *et al.*, 2013) and towards brown bears in the Pyrenees in
303 particular (Piédallu *et al.*, 2016a). There is an interest in mapping the areas which are more

304 likely to host bears in the present and the future, and as such the “attack hotspots” (Miller,
305 2015). It could also be combined with a mapping of attitudes towards brown bears (Piédallu *et*
306 *al.*, 2016a) to identify areas that combine positive attitudes towards bear presence and low
307 attack risk, and as such could be primary targets of future management decisions. This might
308 be the first step towards the development of socio-ecological models designed to mitigate
309 human-wildlife conflicts (Aswani, 2011, Dupont *et al.*, 2011, Estoque and Murayama, 2014).

310

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314

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494 slope. *Marine Geodesy* 30, 3-35.
- 495

496

497 **Author contributions** Conceived and designed the experiments: BP, PYQ, OG. Performed
498 the experiments: BP, NB, AG, CM, PYQ. Analyzed the data: BP, OG. Contributed
499 reagents/materials/analysis tools: BP, PYQ, NB, AG, CM, OG. Wrote the paper: BP, PYQ,
500 OG.

501

502 **Biographical sketches** Blaise Piédallu is a population ecologist interested in human-wildlife
503 conflicts with a focus on large carnivores. Pierre-Yves Quenette is an ecologist who leads the
504 ONCFS brown bear program. Nicolas Bombillon is an ecologist interested in wildlife
505 conservation. Adrienne Gastineau is an ecologist interested in the behavior of large
506 carnivores. Christian Miquel is a population geneticist interested in promoting non-invasive
507 monitoring methods. Olivier Gimenez is a biostatistician interested in population dynamics of
508 large carnivores.

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512 **Tables & Figures**

513 **Table 1:** Definition of the environmental variables used for the occupancy analysis, and the
 514 parameters for which an effect was tested. ψ : initial occupancy probability, γ : colonization
 515 probability, ε : extinction probability, p : detection probability. +/-: predicted sign of the effect
 516 of the covariate on the parameter based on previous studies (see text for references). An
 517 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			+	

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

#	Model	AICc	Δ AICc
1	$\psi(\cdot) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$	577.1	0
2	$\psi(\cdot) \gamma(\cdot) \epsilon(\textit{year}) p(\cdot)$	581.0	3.9
3	$\psi(\cdot) \gamma(\cdot) \epsilon(\cdot) p(\textit{survey})$	581.8	4.7
4	$\psi(\cdot) \gamma(\cdot) \epsilon(\textit{year}) p(\textit{survey})$	584.5	7.4
5	$\psi(\cdot) \gamma(\textit{year}) \epsilon(\cdot) p(\cdot)$	584.5	7.4
6	$\psi(\cdot) \gamma(\textit{year}) \epsilon(\cdot) p(\textit{survey})$	588.0	10.9
7	$\psi(\cdot) \gamma(\textit{year}) \epsilon(\textit{year}) p(\cdot)$	588.8	11.7
8	$\psi(\cdot) \gamma(\textit{year}) \epsilon(\textit{year}) p(\textit{survey})$	592.3	15.2

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527

528 **Table 3:** Model selection with environmental and anthropogenic covariates. The starting
 529 model was the null model $\{\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)\}$ as shown in Table 2. The focal parameters are
 530 shown in the order in which they were considered during the model selection process. The
 531 covariates that were considered for each parameter are defined in Table 1. # models: number
 532 of models considered, equal to 2^n with n the number of covariates tested on that parameter.
 533 Best models: Among the # models we considered for selection, we only displayed the model
 534 with lowest AICc for a given focal parameter.

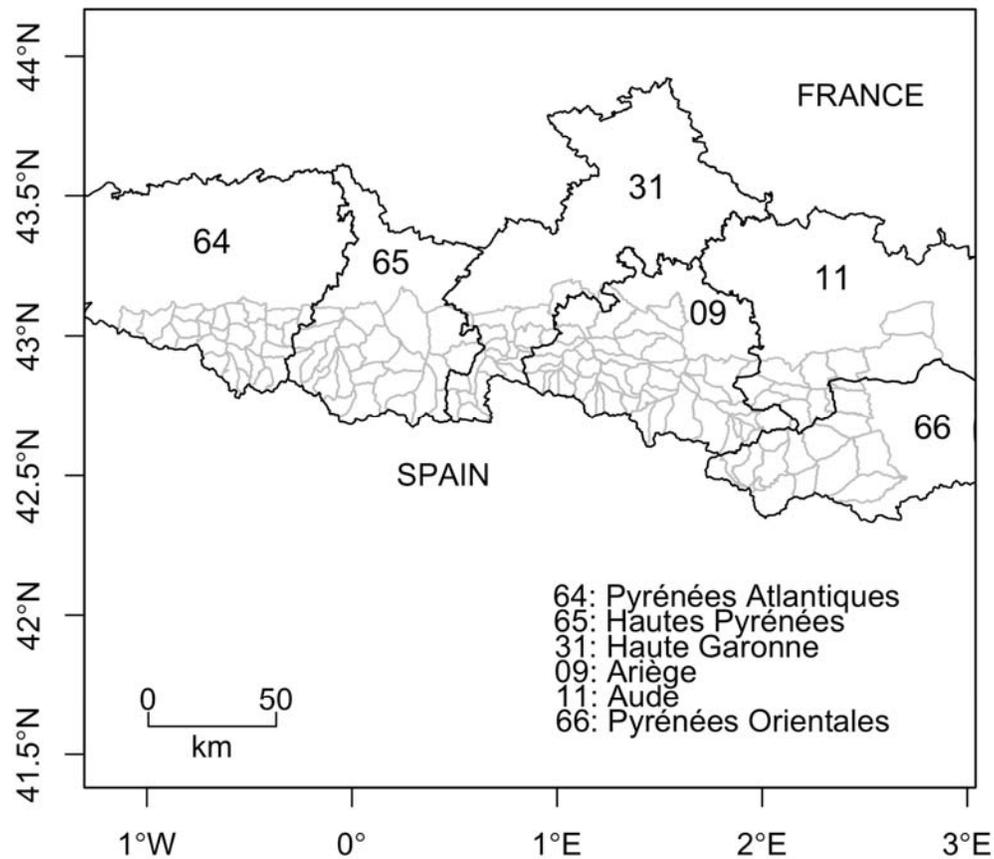
Focal parameter	# models	Best models	AICc
Detection probability p	4	$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{roughness+forest cover})$	□ □̃ □
Colonization probability γ	16	$\psi(\cdot), \gamma(\text{roughness}), \varepsilon(\cdot), p(\text{roughness+forest cover})$	□ □ □̃ □
Extinction probability ε	8	$\psi(\cdot), \gamma(\text{roughness}), \varepsilon(\text{HDF}), p(\text{roughness+forest cover})$	□ □̃ i □
Initial occupancy probability ψ	64	$\psi(\text{human density}), \gamma(\text{roughness}), \varepsilon(\text{human diffusion}), p(\text{roughness+forest cover})$	□ □ □̃

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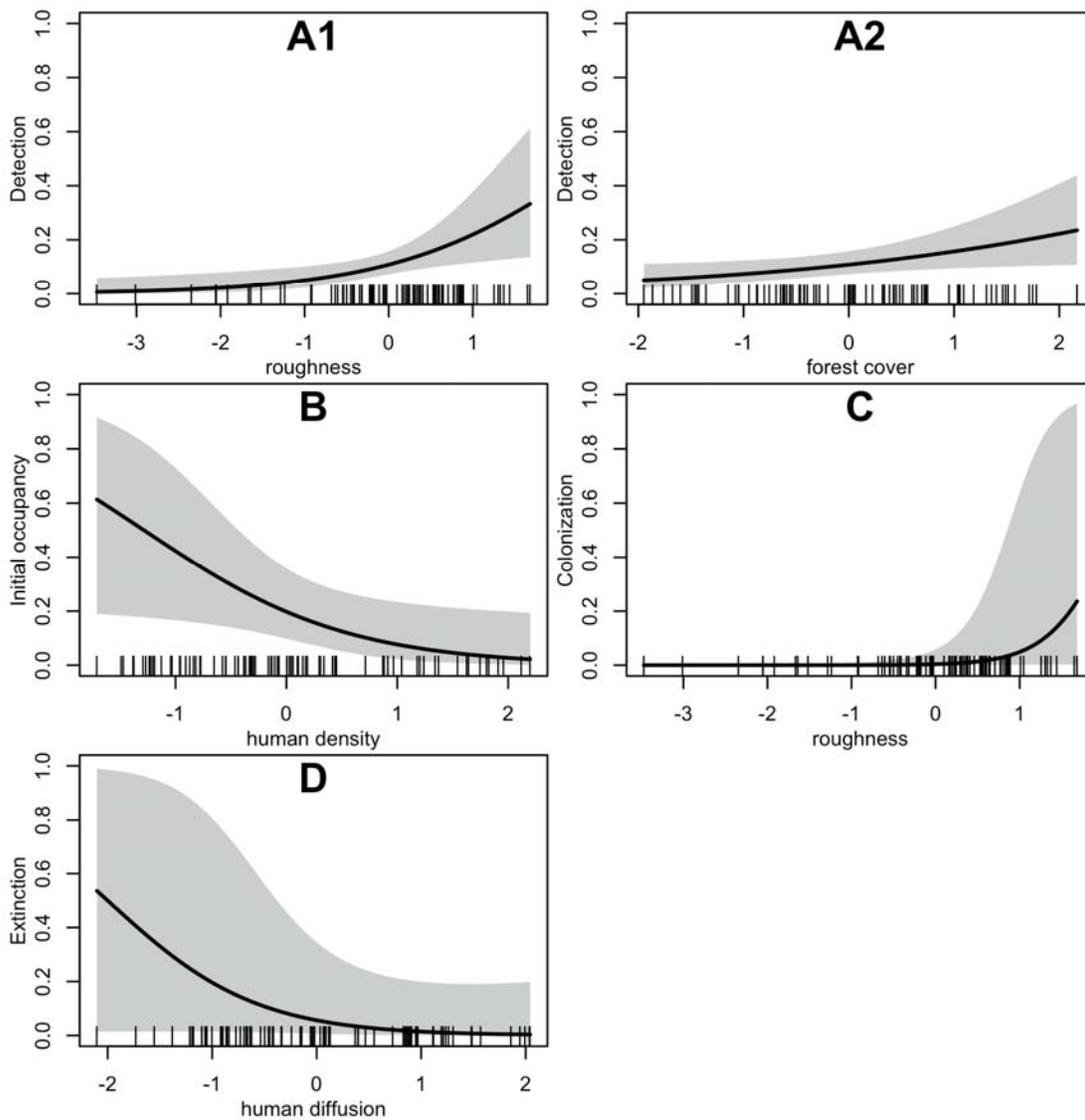
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540 **Figure 1:** Map of the counties and mountain subsections in the French Pyrenees. Dark lines:

541 county borders. Gray lines: limits between mountain subsections.

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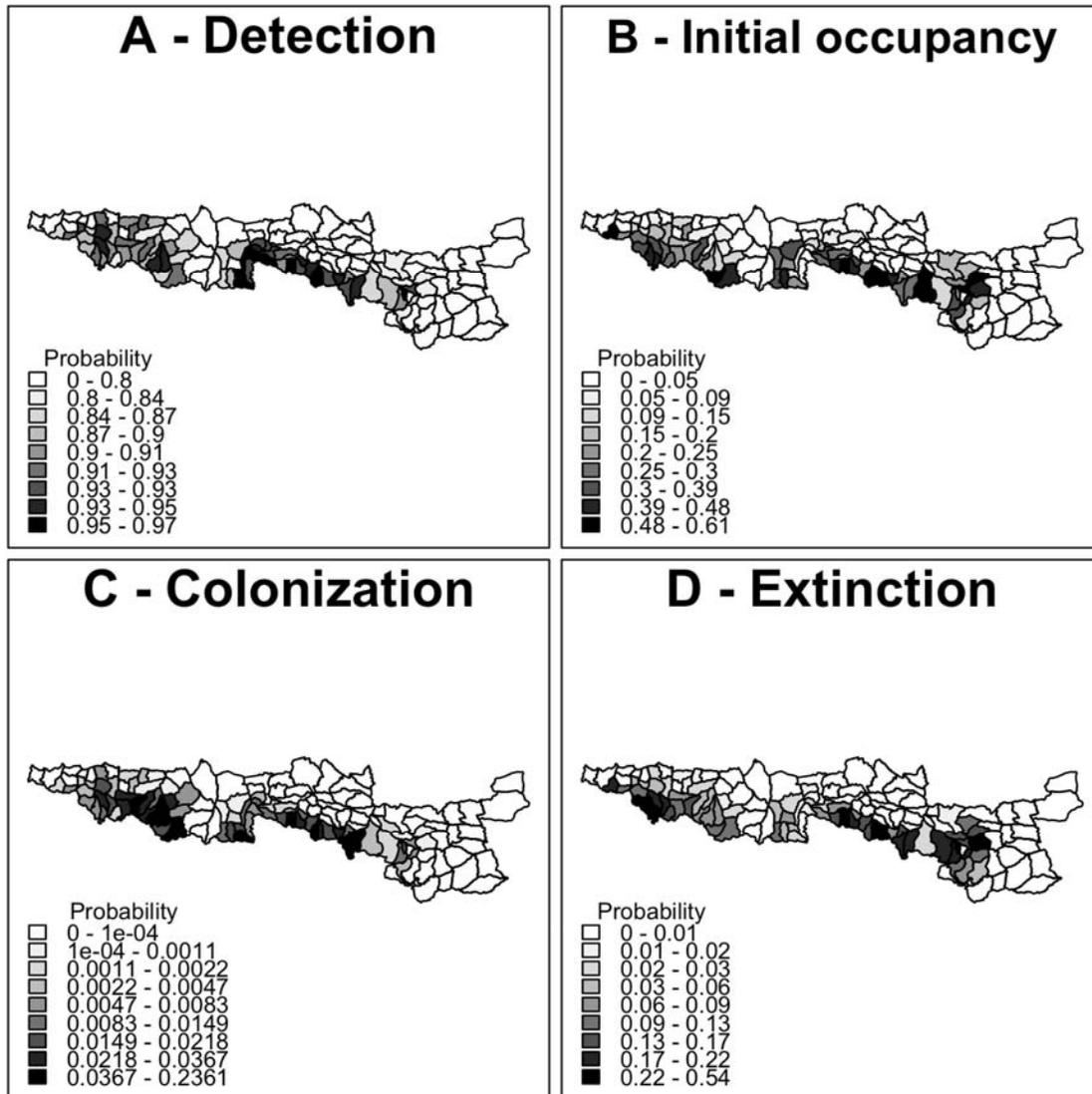
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545 **Figure 2:** Relationships between the model parameters and the standardized covariates
546 selected in the best model $\{\psi(\text{human density}), \gamma(\text{roughness}), \varepsilon(\text{human diffusion}),$
547 $p(\text{roughness}+\text{forest cover})\}$. The dashes on the x-axis indicate the observed covariate values.
548 A: Detection p , with A1: detection as a function of roughness (forest cover set at its mean)
549 and A2: detection as a function of forest cover (roughness set at its mean). B: Initial
550 occupancy ψ as a function of human density. C: Colonization γ as a function of roughness. D:
551 Extinction ε as a function of human diffusion.

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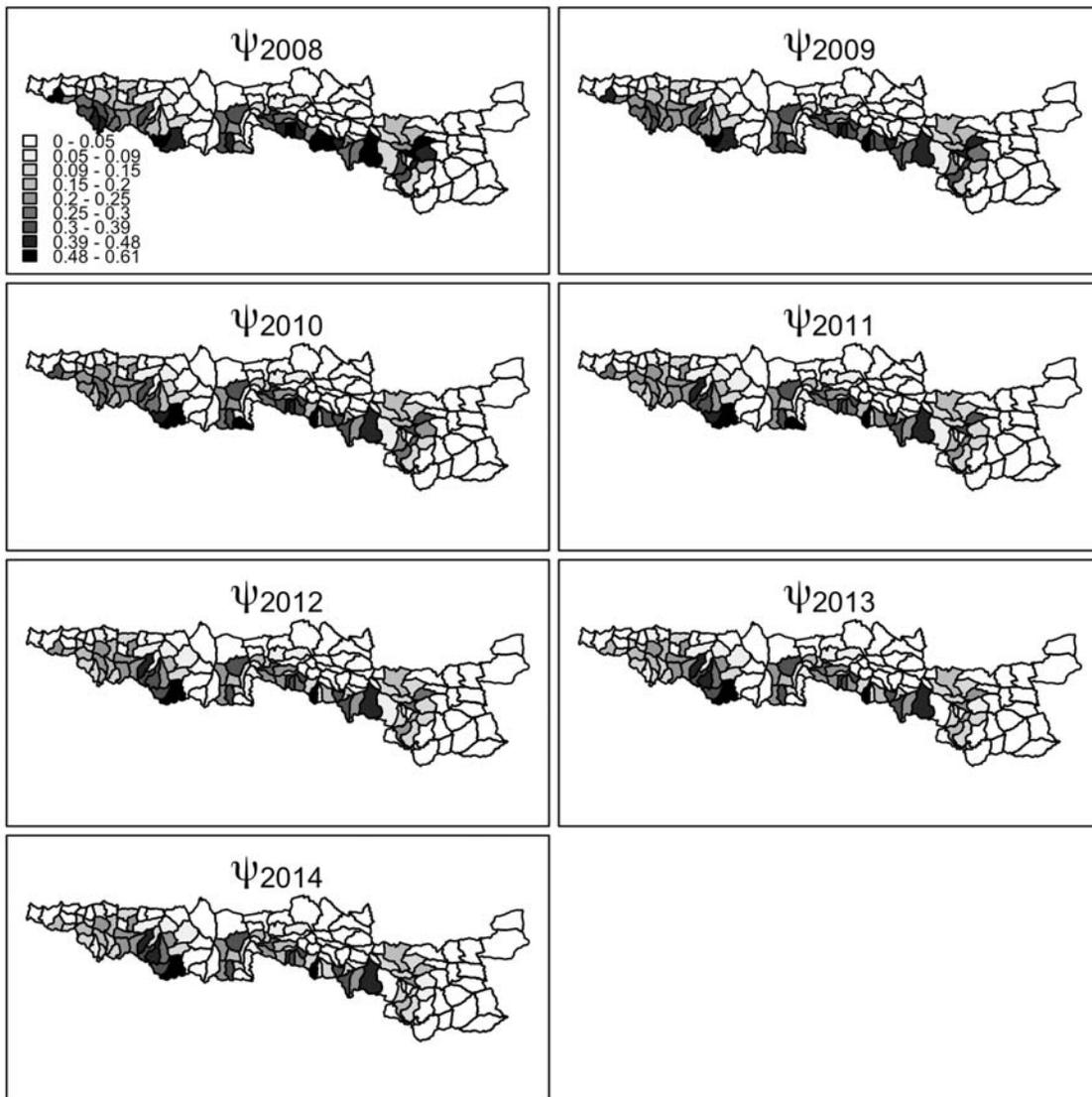


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554 **Figure 3:** Maps of the model parameters in the various mountain subsections of the French
555 Pyrenees, estimated using the results obtained from the best model $\{\psi(\text{human}$
556 density), $\gamma(\text{roughness})$, $\epsilon(\text{human diffusion})$, $p(\text{roughness}+\text{forest cover})\}$. A: Detection
557 probability, B: Initial occupancy probability, C: Colonization probability, D: Extinction
558 probability. Covariates were set at their mean.

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562 **Figure 4:** Maps of the yearly occupancy probability ψ_t from $t = 2008$ to $t = 2014$ in the
563 various mountain subsections of the French Pyrenees, estimated using the results obtained
564 from the best model $\{\psi(\text{human density}), \gamma(\text{roughness}), \epsilon(\text{human diffusion}),$
565 $\rho(\text{roughness+forest cover})\}$ by using the formula $\psi_{t+1} = (1-\psi_t) \gamma + \psi_t (1-\epsilon)$ (MacKenzie *et al.*,
566 2002). Covariates were set at their mean.