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1 **Title**

2 Wolf depredation hotspots in France: Clustering analyses adjusting for livestock availability

3

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14

15 **Abstract**

16 Areas exhibiting high levels of predations on livestock generate conflicts between humans  
17 and large carnivores. Managers generally seek to identify these hotspots, in order to diagnose  
18 the causes that lead to hotspot formations and to provide financial or technical support to the  
19 involved livestock owners. When locating depredation hotspots, previous studies have not  
20 adjusted for livestock availability, making it difficult for managers to discriminate hotspots  
21 resulting from underlying livestock clusters from those due to other factors such as  
22 environmental factors. We studied hotspots of wolf depredation on sheep in France from the  
23 beginning of the natural wolf recolonisation in 1994 up to 2018. For each year, we applied the  
24 Ripley's  $K$ -function and Ripley's  $K_{inhom}$  to determine the general depredation spatial pattern  
25 and the Kulldorff statistic to locate depredation hotspots. We showed that omitting livestock  
26 availability in these analyses led to flawed inference about the depredation pattern, and  
27 resulted in a substantial number of unidentified hotspots, including pastoral surfaces with low

28 sheep availability. Our methodology provides reliable information for managers to understand  
29 the depredation pattern over space and time and to allocate resources.

### 30 **Keywords**

31 Human-carnivore conflict, depredation hotspot, conservation resource allocation, gray wolf,  
32 clustering analysis

### 33 **1. Introduction**

34 Predation on domestic prey by large carnivores, hereafter depredation, is the main driver of  
35 conflicts between humans and large carnivores (Lute et al., 2018). The financial and social  
36 costs associated to depredations reduce acceptance of these species and lead to retaliatory  
37 killings (Abade et al., 2014). Understanding the spatial and temporal patterns of depredation  
38 is a major challenge in large carnivore conservation to mitigate current conflicts and prevent  
39 future ones (Miller, 2015). To do so, two complementary approaches can be applied, namely  
40 the spatial correlation analysis and risk modelling. The spatial correlation analysis quantifies  
41 the level of clustering or regularity (i.e. repulsion) of a depredation pattern (Baddeley et al.,  
42 2015; Hoffmann et al., 2019) and enables the identification of hotspots or coldspots where  
43 events are unusually aggregating or scarce, respectively. Risk modelling aims at estimating  
44 the spatial risk of depredation, by quantifying the relationship between ecological or non-  
45 ecological features and depredation numbers or occurrences (Miller, 2015).

46 The spatial correlation analysis is often presented as a preliminary step to risk modelling and  
47 as of limited interest if applied alone (Gastineau et al., 2019; Hoffmann et al., 2019). This  
48 may explain why risk modelling is more popular (e.g. Bradley & Pletscher, 2005; Fowler,  
49 Belant, & Beyer, 2019) than spatial correlation analyses in the scientific literature. However,  
50 risk models only reflect the depredation-factor relationships at a given point in time and

51 space. These relationships may evolve because predator-prey systems are dynamic and  
52 carnivores can adapt their predation behaviour according to environmental or livestock  
53 management changes (Miller, 2015). This is especially true for (re)colonising large carnivore  
54 populations of plastic species such as the grey wolf (*Canis lupus*) which can embrace a large  
55 range of habitats (Llaneza et al., 2012; Mech and Boitani, 2003). Risk models developed for  
56 this species were either restricted to a unique region and type of habitat (e.g. Clark et al.,  
57 2020) or showed a low predictive power when applied to habitats that differ from those  
58 originally used in the analysis (Hanley et al., 2018). Therefore, the outcomes of risk models  
59 are hardly transposable to other areas or on long-term periods, which makes their adoption by  
60 managers difficult (Miller, 2015). In contrast, information about current or past hotspot  
61 locations provided by spatial correlation analyses can directly help managers when allocating  
62 conservation resources such as subsidies of preventive measures or when investigating the  
63 causes of depredation in situ. Prioritising conservation efforts on depredation hotspots is  
64 indeed recommended as recurrences of high levels of attacks in the same areas are likely to  
65 trigger negative attitudes (Stahl et al., 2001).

66 So far, several analyses of spatial correlation have been developed to identify depredation  
67 hotspots. The simplest one consists in defining an arbitrary threshold for a selected indicator  
68 like the number of depredations which, if reached, turns the spatial unit into a hotspot. Units  
69 can be administrative areas (e.g. Dhungana et al., 2019) or simple shapes like circles (Stahl et  
70 al., 2001). To avoid arbitrary thresholds, some studies have applied spatial statistical analyses  
71 (e.g. Gastineau et al., 2019; Hoffmann et al., 2019; Packer et al., 2019) where depredation  
72 events are considered as a spatial point pattern, i.e. a dataset of observed spatial locations of a  
73 biological process (Baddeley et al., 2015). The areas exhibiting significantly more  
74 depredation events than expected under Complete Spatial Randomness (CSR) are statistically  
75 identified as hotspots. To gain understanding of the biological process, the spatial statistical

76 analyses can also be conducted to determine the summarised spatial structure of the pattern,  
77 i.e. the range of distances over which the pattern generally exhibits clustering, randomness or  
78 regularity (Baddeley et al., 2015), as in Kushnir et al. (2014).

79

80 While studies on depredation risk modelling generally controlled for spatio-temporal  
81 livestock availability (e.g. Balbuena-Serrano et al., 2021; Fowler et al., 2019), quantitative  
82 studies of spatial correlation did not. The reason was that the statistical method they used did  
83 not allow it or because the relevant data were not available. Yet the spatial pattern of  
84 depredation is inherent to livestock risk exposure. Not only are conflicts exclusive to areas  
85 where carnivore and livestock distributions overlap, but they are also dependent on livestock  
86 availability, which is itself a by-product of livestock counts and time spent in a specific area.  
87 If livestock availability is ignored, it is difficult to disentangle the hotspots based on high  
88 levels of livestock availability from the hotspots where livestock densities are low but  
89 predation rates disproportionately high. In the latter cases, conflicts may be favoured by factors  
90 linked to, e.g., the environment, the predator or the husbandry practices which can be  
91 identified and managed to some extent.

92 The grey wolf has been naturally recolonising France since the early 1990s from the Italian  
93 Apennines. Since then, wolves have been expanding and densifying in the south-east part of  
94 France (Louvrier et al., 2018). The recolonisation has come along with a gradually increasing  
95 number of depredations, with more than 3,000 attacks on livestock in 2018, 90% of wolf  
96 attacks being on sheep (*Ovis aries*). French authorities have so far focused on hotspots to  
97 manage the conflict by subsidising preventive measures according to the level and recurrence  
98 of depredation events at the town level (Ministère de l'Agriculture et de l'Alimentation,  
99 2019), but without accounting for sheep availability at risk to identify hotspots.

100 Here, we aimed at conducting spatial statistical correlation analyses of wolf predations on  
101 sheep in south-east France, while accounting for sheep risk exposure. First, we determined the  
102 summarised spatial structure of the depredation pattern and second, we located the significant  
103 depredation hotspots. We compared how the adjustment for sheep availability in space and  
104 time affected the results. We conducted annual analyses, from 1994 to 2018, to study the  
105 temporal variations in depredation patterns and in hotspot locations throughout wolf  
106 recolonisation. We also explored the depredation patterns at a local scale, within the historic  
107 area of wolf recolonisation. The aims of the local scale analysis were to increase perceptibility  
108 of wolf territorial behaviour in the results, and to observe if years of wolf presence changed  
109 the depredation pattern over time compared to the regional scale where the colonisation  
110 process was still ongoing. Finally, we discuss the management implications of our results.

## 111 **2. Materials and methods**

### 112 *2.1 Study area and study period*

113 The study area covered the two south-east regions of France, Provence-Alpes-Côte-d'Azur  
114 and Auvergne-Rhône-Alpes, and included all the French Alps and the east part of Massif  
115 Central mountains (102 483 km<sup>2</sup>, **Fig. A.1**). Apart from the highest altitudes which are  
116 without forests, habitats range from bush to coniferous forest under Mediterranean climate in  
117 the south, to mixed forest in the north and the east.

118 We analysed the summarised spatial structure of the depredation pattern at two scales of the  
119 study area. First, the analyses were applied over the whole study area, i.e. the regional scale.  
120 Second, the analyses were applied over a sub-area of the study area, located in the very south-  
121 east of the study area (2 146 km<sup>2</sup>, **Fig. A.1**), i.e. the local scale. The local scale overlapped the  
122 Mercantour National Park and its surroundings (hereafter 'MNP'), which is a mountainous

123 area characterised by a succession of alpine vegetation levels along a wide altitudinal range,  
124 from 600 to 3 200 m, and by an important pastoral activity for meat production. The MNP is  
125 the oldest place where wolves and pastoralism are co-occurring in the country since wolf  
126 recolonisation in the 1990's from Italy.

127 In accordance with wolf biology, we defined the annual periods over which the analyses were  
128 applied as biological years  $y$ , starting from the 1<sup>st</sup> of April of year  $y-1$  (i.e. wolf pup birth) to  
129 the 31<sup>st</sup> March of year  $y$ . The whole study period covered biological years (hereafter, 'years')  
130 from 1995 to 2018.

## 131 *2.2 Depredation records*

132 Approximately three quarters of the depredations occurred between June and October, when  
133 most of sheep flocks were grazing in pastures. Up to 2019, the French Ministry of Ecology  
134 compensated for any killed farmed animal for which wolf responsibility could not be  
135 discarded, regardless of preventive measures. Each claim was controlled and checked in the  
136 field by an accredited governmental agent who used a standardized protocol (Duchamp et al.,  
137 2012). Therefore, most if not all depredations were reported if noticed, and the risk of false  
138 claims was low. We restricted the clustering analyses to depredations on sheep only as they  
139 constituted 90% of depredations on livestock. An event of depredation corresponded to at  
140 least one killed or wounded sheep by wolves. Because grazing activity may extend outside the  
141 official pastoral limits, or because of geolocation approximations, some depredation events  
142 were not located inside the geolocated pastoral surfaces (22% of the annual dataset on  
143 average). We excluded the depredations farther away from 500 meters of any pastoral surface  
144 (10% of the annual dataset on average) and assigned the remainder to their nearest pastoral  
145 surface.

### 146 **2.3 *Wolf distribution***

147 The Wolf-Lynx French Network managed by the French Biodiversity Agency is in charge of  
148 the national wolf monitoring in France. Its field experts are trained to opportunistically collect  
149 presence signs all year along, such as biological samples (mainly faeces, combined with  
150 genetic analysis), tracks or direct observations, which are geolocated and validated according  
151 to a standardized protocol (Duchamp et al., 2012; Louvrier et al., 2018). The annual wolf  
152 distribution was determined by combining the annual presence signs and all wolf depredations  
153 (i.e. on any type of livestock, including all those located outside the pastures) within the study  
154 area. Wolf presence during year  $y$  was reported on a 10x10 km cell grid, and defined as the  
155 collection of at least one presence sign or one depredation in the cell from  $y-1$  to  $y-3$  and from  
156  $y-2$  to  $y$  (see Marboutin et al., 2011). The use of depredation data to estimate the wolf  
157 distribution was necessary to identify the pastures that were at the edges of the wolf  
158 recolonisation area. Indeed, depredations (along with visual observations) are generally the  
159 first detections of wolves that settle in newly recolonized areas in France (Duchamp et al.,  
160 2012).

### 161 **2.4 *Spatio-temporal sheep availability***

162 Around 1 500 000 sheep are bred for meat or milk production each year in the study area  
163 (IDELE, 2018). During the summer period, a large part of these flocks becomes transhumant  
164 and moves to high-altitude pastures in the Alps. Otherwise, sheep are grazing in low- or mid-  
165 altitude pastures around farms. Sheep are in sheds during the whole winter except in the south  
166 where climate is mild (Gervasi et al., submitted).

167 Two georeferenced censuses of the pastoral surfaces in the study area were carried out in  
168 1996-1997 and in 2012-2014 by the National Research Institute of Science and Technology  
169 for the Environment and Agriculture (IRSTEA). For each pastoral surface, information about



170 the grazing livestock count per species and the annual number of grazing days was included.  
171 One or several herds, of one or multiple livestock species, could feed on a pastoral surface.  
172 We restricted the dataset to pastoral surfaces with grazing sheep, regardless of whether other  
173 species of livestock were present (**Fig. B.1**). For both censuses, the spatio-temporal sheep  
174 availability was inhomogeneous across the study area (**Fig. B.1**), particularly for grazing time  
175 between the north and the south of the regional scale due to climate differences and resulting  
176 grass phenology. The pastoral surfaces of the first census and of the second census were  
177 respectively 2.7 km<sup>2</sup> and 1.9 km<sup>2</sup> on average, and they hosted 606 sheep (sd=649) and 516  
178 sheep (sd=547), during 146 days (sd=96) and 202 days (sd=96) per year on average.  
179 For each year  $y$ , we identified the set of pastoral surfaces at depredation risk for both scales by  
180 selecting the pastoral surfaces which overlapped, even partially, with the wolf distribution.  
181 For years between 1995 to 2005, we used the 6 488 pastoral surfaces with sheep from the  
182 oldest census, and for years between 2006 to 2018, we used the 12 438 pastoral surfaces with  
183 sheep from the latest census. The oldest census did not include pastures in the west of the  
184 study area (i.e. outside the Alpine area), which explains the lower number of pastures  
185 compared to the latest census. However, the wolf distribution from 1995 to 2005 was mainly  
186 restricted to the east of the study area, within the Alpine area (**Fig. B.2**), where pastoral  
187 information in the oldest census was available. For example, using the latest census instead of  
188 the oldest census only provided a difference of 6.7% on average in the numbers of pastoral  
189 surfaces at depredation risk at the regional scale from 1995 to 2005. Thus, we considered this  
190 gap was of little impact.

191 IRSTEA did not carry out the census process every year for two reasons. First, the census  
192 process was the result of a long period of work, exceeding a year of work. The field work,  
193 which consisted in meetings with local contact persons, corresponded to 750 full working  
194 days on its own for the second census (F. Bray, pers. com.). Second, the use of pastoral

195 surfaces by farmers was relatively stable over time, because the environmental characteristics  
196 (area, topography, type of vegetation, weather...) of a pasture restricted the herd size the  
197 pasture could host and the time of grazing. Moreover, the large but limited number of pastures  
198 caused hard competition between livestock owners for access to pastoral resources. Livestock  
199 owners tended to secure their access by renting or buying these surfaces for a long period of  
200 time (C. Duchamp, *pers. com.*). For all these reasons, we assumed the information on spatio-  
201 temporal sheep distribution of a census was valid for several years before and after the census.

## 202 **2.5 Analysis 1: Summarised spatial structure of wolf depredations**

203 For each year  $y$ , we analysed at the regional and local scales the summarised spatial structure  
204 of the wolf depredation pattern considering sheep availability by using Ripley's  $K_{inhom}$   
205 (Baddeley et al., 2015). We used the package *spatstat* (Baddeley and Turner, 2005) in R 4.0.2  
206 (R Core Team, 2019) to perform the analysis.

207 First, we simulated the expected depredation pattern under CSR considering sheep  
208 availability. The simulated pattern was composed of  $n$  points called 'controls', in opposition  
209 to the  $n$  annual observed depredations called 'cases'. The distribution of controls was  
210 simulated on a grid of 200x200 m cells over the pastoral surfaces at depredation risk,  
211 according to an inhomogeneous Poisson Point Process (PPP). In this model, the number of  
212 controls falling into a cell  $g$  was expected to be equal to the intensity  $\lambda(g)$  defined as:

$$213 \quad \lambda(g) = \exp(a + b \times \log(pop_u) + c \times \log(time_u))$$

214 where  $pop_u$  and  $time_u$  were the numbers of sheep and of grazing days of the pastoral surface  
215  $u$  covered by  $g$ , and  $a$ ,  $b$  and  $c$  were model parameters to be estimated. Covariates were log-  
216 transformed because of their skewed distributions. Thus, the controls were more likely to fall

217 into the cells covering pastoral surfaces with high numbers of  $pop_u$  and  $time_u$ . For each year,  
218 we simulated 499 control patterns through this model.

219 Second, we computed  $K_{inhom}$  for the pattern of  $n$  cases. This function drew a circle of radius  $r$   
220 around each depredation  $i$  covering more or less neighbouring depredations  $\{j\}$ . Then, the  
221 function summed the values  $1/(\lambda(g_i)\lambda(g_j))$  for all pairs of depredations  $i$ - $j$  within this  
222 circle,  $\lambda(g_i)$  and  $\lambda(g_j)$  being the intensity values of the cell(s) containing  $i$  and  $j$  respectively.  
223 Because the unit of measurement of  $\lambda$  was in ind/cell (i.e. ind/0.04km<sup>2</sup>),  $K_{inhom}$  returned a  
224 surface for each tested  $r$ . If the pattern was randomly distributed considering sheep  
225 availability, the surface should equal the surface of the circle,  $\pi r^2$ . Consequently, at a specific  
226  $r$ , if the  $K_{inhom}$  value of the observed depredation pattern was higher or lower than  $\pi r^2$ , we  
227 could conclude that the depredations were respectively forming hotspots or coldspots of  
228 radius  $r$ . A large set of continuous radiuses  $r$  was tested.

229 However, the smaller the dataset, the larger the likelihood of differences from the expected  
230 number of points within a circle, even if the dataset has a random pattern. Therefore, a  $K_{inhom}$   
231 value which differed from  $\pi r^2$  was not necessarily the result of a non-randomly point pattern,  
232 but could be due to stochastic effects. To take this into account, we also computed  $K_{inhom}$  for  
233 the 499 control patterns and selected the 50<sup>th</sup>-lowest and 50<sup>th</sup>-highest values to build a ‘control  
234 envelope’. For a specific  $r$ , if the observed  $K_{inhom}$  was higher (or lower) than the upper (or  
235 lower) envelope limit, the depredations were significantly clustered (or regular, i.e. tended to  
236 avoid each other) at this distance considering sheep availability. The larger the differences  
237 with the envelope, the more aggregated or regular the pattern.

238 We also annually applied the Ripley’s  $K$ -function at the regional scale. The PPP of the  $K$ -  
239 function was homogeneous. Hence, the number of controls falling into the cells was expected  
240 to be equal over the whole analysis area (Baddeley et al., 2015). We tested two possibilities to

241 define the grid of 200x200 m cells. First, we simulated the same grid over the pastoral  
242 surfaces at depredation risk as in the  $K_{inhom}$  analysis, in order to simulate a situation for which  
243 sheep distribution was known, but sheep availability was not. Second, we simulated the grid  
244 over the wolf distribution, to simulate a situation for which pastoral data were totally  
245 unavailable.

## 246 **2.6 Analysis 2: Wolf depredation hotspot location**

247 For each year  $y$ , we located at the regional scale the significant wolf depredation hotspots by  
248 applying the first version of the Kulldorff statistic (Kulldorff, 1997) which adjusts for  
249 spatially inhomogeneous population at risk. We used the package *SpatialEpi* (Kim and  
250 Wakefield, 2018) in R 4.0.2 (R Core Team, 2019) to perform the analysis.

251 First, we defined all the possible zones  $Z$  which could be later identified as hotspot by the  
252 Kulldorff statistic. We defined the pastoral surface as the smallest possible zone  $Z$ . Then, a  
253 circle was put on the centroid of each pastoral surface, with a progressively increasing radius.  
254 Each time the growing circles encompassed the centroid of an adjacent pastoral surface, a new  
255 zone  $Z$  was defined. The sheep availability of a zone  $Z$  was calculated as the sum of the sheep  
256 availability  $\omega(u)$  of all the pastoral surfaces  $u$  whose centroids were in  $Z$ . We determined the  
257 limit size of a zone  $Z$  as following: a zone  $Z$  could not include more than 5% of the sum of  
258  $\omega(u)$  of all pastoral surfaces. Otherwise, the hotspots were too vast to be informative  
259 (Kulldorff, 1997). Because information on the pastoral area was omitted in this analysis, we  
260 included this information in the definition of the sheep availability of a pastoral surface  $\omega(u)$ ,  
261 as  $\omega(u) = pop_u \times time_u \times area_u$ , where  $area_u$  was the surface  $u$  in km<sup>2</sup>. Therefore, the  
262 larger a pastoral surface, the larger its risk of depredation. We indeed considered that two  
263 flocks of the same size and grazing time should have a different depredation risk depending  
264 on the size of their pastures. Farmers generally used the entire pasture for their flock, either by

265 dividing the flock into smaller flocks or by moving the flock within the pasture. Increasing the  
266 pasturing area should make the flock more exposed to depredation by increasing the risk of  
267 encounters with wolves. In addition, we restricted the analysis to the depredated pastoral  
268 surfaces. The inclusion of pastoral surfaces without depredation into the analysis would  
269 indeed have increased sheep availabilities of certain zones, especially zones where depredated  
270 pastoral surfaces were surrounded by pastoral surfaces without depredation. This would have  
271 reduced the capacity of the analysis to identify such zones as hotspots.

272 Second, the Kulldorff statistic modelled the total number of observed depredations  $n$  as:

$$273 \quad n \sim \text{Poisson}(p_Z \times \omega(u \in Z) + q_Z \times \omega(u \notin Z))$$

274 with the probabilities  $p_Z$  and  $q_Z$  that a depredation event occurred within or outside  $Z$ ,  
275 respectively, and  $\omega(u \in Z)$  and  $\omega(u \notin Z)$  the sum of  $\omega(u)$  inside and outside  $Z$ , respectively.  
276 For each  $Z$ , the Kulldorff statistic tested the null hypothesis  $p_Z = q_Z$  ( $M_0$ ) and the alternative  
277 hypothesis  $p_Z > q_Z$  ( $M_A$ ). It calculated the likelihood ratio  $LR(Z)$  as  $L(Z)/L_0$ .  $L(Z)$   
278 corresponded to the result of the likelihood function  $L$  of the model under  $M_A$  for the zone  $Z$ .  
279  $L_0$  corresponded to the result of the likelihood function  $L$  of the model under  $M_0$ , which was  
280 the same for all zones because under  $M_0$  the model can be reduced to  $n \sim \text{Poisson}(p \times$   
281  $\sum \omega(u))$ . The zones  $Z$  for which  $M_A$  was the most likely had the highest  $LR(Z)$ .

282 Third, we simulated 499 sets of randomly distributed  $n$  controls over the depredated pastoral  
283 surfaces, proportionally to their sheep availabilities. The second step was repeated for each  
284 control set, to eventually compute the control distribution of the highest likelihood ratio  
285  $LR(Z)$ . If the observed highest  $LR(Z)$  were among the top 5% of this control distribution,  
286 then the corresponding zones were significant hotspots.

287 We repeated this analysis with a simulated homogeneous sheep availability to show the  
288 discrepancies when ignoring prey availability: each depredated pastoral surface had then a  
289 sheep availability equal to the mean observed sheep availability of the depredated pastoral  
290 surfaces.

## 291 **3. Results**

### 292 *3.1 Trends in depredation risk and observed depredations*

293 We collected 25 220 wolf presence signs and 18 764 verified depredations on any type of  
294 livestock, reported from 1995 to 2018 in the study area. The resulting estimated annual wolf  
295 distribution expanded along the years, and reached 40% of the study area in 2018 (**Fig. A.2A;**  
296 **Fig B.2**). The annual proportion of pastoral surfaces at depredation risk within the total set of  
297 pastoral surfaces increased at the regional scale, reaching 70% in 2018. This overlap  
298 generated more and more depredations on sheep per year, starting from 49 depredation events  
299 in 1995 to 2 289 in 2018. However, the annual proportion of depredated pastoral surfaces  
300 among all surfaces at risk remained quite stable over time at the regional scale, with a mean of  
301 18%. Most of these pastoral surfaces experienced one or two depredations per year (**Fig. B.3**).  
302 One depredation event corresponded on average to 3.8 wounded or killed sheep (sd=0.3)  
303 when removing indirect mortalities (e.g. fall from cliff).  
304 The situation at the local scale differed from the regional scale (**Fig. A.2B**). The majority of  
305 the local scale was recolonised by wolves from 2003. Almost all the pastoral surfaces were at  
306 depredation risk from 2003. Most depredated pastoral surfaces also experienced one or two  
307 depredations per year (**Fig. B.3**). Because the number of pastoral surfaces at depredation risk  
308 quickly stabilised, the trend of the depredation numbers followed the trend of the proportion  
309 of depredated pastoral surfaces.

### 310 *3.2 Analysis 1: Summarised spatial structure of wolf depredations*

311 At the regional scale, the  $K_{inhom}$  function identified significant aggregation of the depredations  
312 for all years, with some  $K_{inhom}$  values higher than the control envelope (**Fig. 1; Fig. B.4**). The  
313 control envelope was thinner with time as the depredation pattern included more and more  
314 events. However, depending on years, the range of radiuses  $r$  for which aggregation was  
315 significant varied, as well as the aggregation intensity (i.e. difference between the observed  
316 and control envelope values at the same  $r$ ). We identified four time periods.

317 The first period ranged from 1995 to 1999. In 1995, aggregation was significant up to 20 km.  
318 The depredation pattern exhibited randomness beyond. From 1996, aggregation was  
319 significant for the whole range of computed radiuses  $r$ , up to 15-30 km around depredations.  
320 Aggregation tended to intensify with  $r$ , especially in 1996 and 1998. This suggested that the  
321 depredation pattern showed no particular spatial structure, except in 1995. During the second  
322 period from 2000 to 2003, aggregation intensity decreased at the largest computed  $r$  values.  
323 From 2001, the  $K_{inhom}$  values merged with the control envelope between 40 and 50 km,  
324 suggesting a locally emerging clustered pattern. During the third period from 2004 to 2012, a  
325 weak significant aggregation was only observed over the lowest  $r$  values, and turned into  
326 significant repulsion between 15 and 35 km. This was typical of a clustered pattern, with  
327 hotspots producing coldspot interzones (Hoffmann et al., 2019). Finally, the last period from  
328 2013 to 2018 showed significant aggregation over 25 to 40 km followed by randomness  
329 (except 2014 with continuous aggregation). In certain years, a weak repulsion was observed at  
330 the largest  $r$  values. Aggregation intensity was greater in 2013 compared to 2012, but it  
331 tended to decrease the following years, which brought the depredation pattern closer to  
332 randomness with time.

333 Using  $K_{inhom}$  or the  $K$ -function provided comparable results only during the first period. But,  
334 from 1999-2000, the differences between the analysis of  $K_{inhom}$  and the two analyses of the  $K$ -  
335 function increased (**Fig. 1; Fig. B.4**). The first analysis with the  $K$ -function which considered  
336 sheep availability as homogeneous across pastoral surfaces identified the typical hotspot  
337 structure (i.e. aggregation followed by repulsion) only in 2009 and 2010 with a radius of 30  
338 and 40 km respectively. The other years, aggregation was significant for all values of  $r$  and  
339 always more intense than the one obtained through  $K_{inhom}$ . When the analysis grid was only  
340 based on the wolf distribution, the  $K$ -function analysed the pattern over larger values of  $r$  than  
341 the previous analyses because isolated distribution cells in the west of the study area could  
342 sporadically appear without overlapping with pastoral surfaces. This analysis only identified  
343 significant aggregation which, in most years, intensified with  $r$ .

344 At the local scale, the  $K_{inhom}$  function provided two main findings. First, from 1995 to 2011,  
345 the analysis identified significant aggregation over 12 to 17 km, occasionally followed by  
346 randomness at large radiuses (**Fig. B.4**). Repulsion was never observed, except in 2004 where  
347 depredations seemed clustered into three single zones (**Fig. B.2**). Second, the aggregation  
348 intensity was generally decreasing with time from 2013, even though the control envelopes  
349 were of equivalent thickness. The pattern tended to randomness for all values of  $r$  from 2015,  
350 with almost complete randomness observed in 2016. Therefore, the depredations were  
351 increasingly widespread at the local scale and were no longer significantly clustering in the  
352 last years of the study period, long after the full recolonisation of the MNP by wolves.

### 353 **3.3 Analysis 2: Wolf depredation hotspot location**

354 The number of hotspots identified by the Kulldorff statistic adjusting for sheep availability  
355 tended to increase over time in the study area, from 2 hotspots in 1995 to 32 in 2018 (**Fig.**  
356 **2A**). The annual proportion of depredated pastoral surfaces into hotspots was higher for the



357 period 2012-2018 (mean=29.2%, sd=3.8%) than for the period 1995-2011 (mean=23.5%,  
358 sd=5.9%) (**Fig. 2B**). Hotspots were of various sizes but generally did not exceed 50 km<sup>2</sup> of  
359 pastoral area (**Fig. 2C**). The average number of pastoral surfaces within hotspots tended to  
360 increase with time, from 3.0 in 1995 (sd=0) to 7.8 in 2018 (sd=11.5). Hotspots could be  
361 located at different places within the study area (**Fig. 3A; Fig. B.5**). They could be sporadic,  
362 appearing for one year. But others could persist over time, such as in the MNP where hotspots  
363 were present during the whole study period, and in the south for the period 2013-2018.

364 In contrast to the analysis adjusting for sheep availability (hereafter ‘first Kulldorff analysis’),  
365 the results of hotspot identification changed in the analysis with simulated homogeneous  
366 sheep availability (hereafter ‘second Kulldorff analysis’). For almost all years, the numbers of  
367 hotspots were lower in the second Kulldorff analysis than in the first one (**Fig. 2A**). The  
368 annual proportion of depredated pastoral surfaces into hotspots was always lower than in the  
369 second Kulldorff analysis and exceeded 20% only in 2014 and 2017 (**Fig. 2B**). The pastoral  
370 surfaces identified as hotspots in the second Kulldorff analysis were generally identified as  
371 hotspots in the first Kulldorff analysis (e.g. **Fig. 3B; Fig. B.5**). The unidentified hotspots in  
372 the second Kulldorff analysis generally encompassed small pastoral surfaces where sheep  
373 availability was low as well as the number of depredations. Thus, annual means of sheep  
374 counts, of grazing time and of depredations of the pastoral surfaces within hotspots were  
375 significantly larger in the second Kulldorff analysis than in the first one (Wilcoxon tests:  
376  $P < 0.001$ ,  $\alpha = 0.05$ ).

#### 377 **4. Discussion**

378 To reduce the number of depredations in an area, managers seek to act on the factors driving  
379 depredation. Depredations primarily rely on the rate of encounters between predators and  
380 livestock (Mech and Boitani, 2003), and therefore on livestock availability (Balbuena-Serrano

381 et al., 2021; Bradley and Pletscher, 2005). The room for maneuver on livestock availability is  
382 however generally limited for managers. Other factors can favour depredations, such as  
383 environmental, husbandry or predator-linked factors, or a combination of these factors  
384 (Fowler et al., 2019). There is therefore a strong interest for managers to easily identify the  
385 areas where the high number of depredations is not only caused by the primary livestock  
386 availability factor, but also by other factors.

387

388 Depredation spatial risk modelling studies have generally integrated livestock availability.  
389 However, the produced risk maps do not allow managers to clearly disentangle between areas  
390 with significant depredation clustering given livestock availability (e.g. Balbuena-Serrano et  
391 al., 2021; Fowler et al., 2019). If adjusted for livestock availability, the depredation hotspot  
392 analysis can allow for such identification. In our case study, we showed that adjusting or not  
393 for livestock availability modified the results, whether it was for the summarised depredation  
394 pattern or the hotspot map. These two analyses are complementary to help managers to  
395 identify the causes favouring depredations.

396

397 The hotspot map provided the locations of areas where investigations in situ can be led to  
398 understand the unexpected high level of depredations. The most straightforward factor to  
399 investigate is husbandry. Generally, detailed husbandry practices or implementation of  
400 preventive measures are not available for spatial statistical analyses, as in our case study.  
401 Because a regional inventory of preventive measures is often difficult if not impossible to put  
402 in place, especially in the long term, it can be necessary to go in the field to check if  
403 preventive measures are implemented, but also suited to the local context. The involved  
404 farmers can receive technical support provided by the public authorities in the implementation  
405 of appropriate preventive tools (Littlewood et al., 2020). Other factors can encompass larger

406 spatial scales than the sole pasture (e.g. environmental factors as type of vegetation, or  
407 wolves). Investigation of such factors is difficult if the hotspot definition is based on each  
408 spatial unit without considering the other units, as it is currently done by the French  
409 administration. Our approach has the benefit of identifying groups of spatial units belonging  
410 to the same hotspot, and therefore to facilitate the investigation of large-scale factors.

411

412 The analysis of the summarised depredation pattern can also help to understand the spatial  
413 scale of the depredation pattern, and therefore the scale relevant to management. The hotspot  
414 radiuses were estimated between 12 and 50 km in our  $K_{inhom}$  analysis at the local and regional  
415 scales. This did not match with the 7-8 km wolf territory radius estimated in France through  
416 telemetry and genetic tracking (Duchamp et al., 2012). Therefore, these results suggest that  
417 most of the hotspots encompassed more than one pasture, but also more than one wolf  
418 territory. In other words, the depredation clustering was not linked to one ‘problematic’ wolf  
419 or pack, or one isolated unprotected flock. Instead, these results suggest that a local context  
420 could favour depredations, e.g. a lack of wild preys or environmental conditions making an  
421 efficient guarding difficult (as bushy environments). The  $K_{inhom}$  analysis also showed that  
422 depredation pattern tended to randomise through time. This randomisation pattern did not  
423 seem to be linked to the increase of the area recolonised by wolves, as the randomisation  
424 occurred at the local scale long after wolves recolonised the MNP. The depredation risk  
425 homogenisation among pastoral surfaces could result from the increasing number of farmers  
426 who protected their flocks against wolf depredations during wolf recolonisation (MTES and  
427 MAA, 2018), as suggested by Meuret et al. (2021).

428

429 Besides the identification of the causes favouring depredation, the results provided by the  
430 hotspots maps can help in resource allocation. For example, France currently allocates its

431 highest level of subsidies for preventive measures in depredation hotspots. Each year hotspots  
432 are defined as the municipality with a mean of at least 15 depredations over the last three  
433 years, and all its adjacent municipalities. This definition accounts neither for the surface of the  
434 municipality nor for the surface of pastures. This definition creates biases, large  
435 municipalities having higher chances to be identified as hotspots than others (DREAL  
436 Auvergne-Rhône-Alpes et al., 2020). Moreover, relying on three years to define hotspots  
437 prevents the detection of emerging hotspots in time. In our case study, the methodology we  
438 used corrected these biases. Correcting for livestock availability also allowed us to detect  
439 hotspots of pastoral surfaces with low sheep counts and grazing time. The current  
440 administrative definition of hotspots does not account for the size of flocks or the time spent  
441 on pastures. Therefore, hotspots with low livestock availability can remain undetected by the  
442 administration. Yet, the consequences of depredations for the involved livestock owners are  
443 high in these situations because a high proportion of the flock is lost to predation (Stahl et al.,  
444 2001).

445

446 Thus, the spatial correlation analyses are powerful tools for large carnivore conservation.  
447 They help to better define priority conservation areas. These areas can receive a specific  
448 attention from managers, whether it is for preventive measures subsidies or for investigating  
449 the effective implementation of these measures, as recommended by Bautista et al., 2019. The  
450 methodology we presented could then optimize the cost-effectiveness of public funds. The  
451 user interface we developed to present the hotspot maps (Fig B.5) should also facilitate the  
452 adoption of the tool by managers.

453

454 For both the  $K_{inhom}$  and the Kulldorff analyses, information about livestock availability was of  
455 paramount importance to detect the depredation pattern and hotspot locations. This

456 information is usually hard to obtain, even more at a regional scale. This explains why the  
457 studies on depredation hotspots generally do not adjust for livestock information (e.g.  
458 Hoffmann et al., 2019) or only for livestock distribution (e.g. Gastineau et al., 2019). Here,  
459 our information on livestock availability was limited in time to two censuses which in total  
460 covered a period of 5 years. Limiting our study period to this 5-year period would have been  
461 possible and still informative to show the discrepancies in the results of  $K_{inhom}$  and of the  
462 Kulldorff statistic when adjusting or not for livestock availability. However, the extension of  
463 the use of livestock information to years surrounding the census' periods brought valuable  
464 information about the dynamics of the depredation pattern. Indeed, grazing time and flock  
465 size are highly constrained by the climate that differs greatly between the north and the south  
466 of the studied area. If it is possible that flocks may have grazed more or less before or after  
467 each census, we do not expect these differences to overcome the benefits of using the pastoral  
468 censuses that allowed the integration of seasonal differences between pastures in the analysis.  
469

470

## 471 **5. Conclusions**

472 We encourage the use of clustering analyses adjusted for livestock availability in the context  
473 of large predator conservation and of the management of their predations on livestock.  
474 Contrary to the conventional wisdom which relegates clustering analyses to a preliminary step  
475 in risk modelling, the estimation of hotspot locations is a full-fledged decision-making tool.  
476 Hotspots are the first targets for allocation of conservation resources, or for investigation in  
477 situ of the causes favouring depredation. The livestock owners in hotspots can be supported,  
478 financially or technically, to quickly adapt their husbandry practices according to the pastures  
479 they use and the predator they face. Using spatial statistical analyses with  $K_{inhom}$  or with the

480 Kulldorff statistic combined with livestock availability data would substantially improve the  
481 reliability of the estimates of depredation pattern and hotspot locations, and therefore the use  
482 of these quantities for conservation.

483

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494

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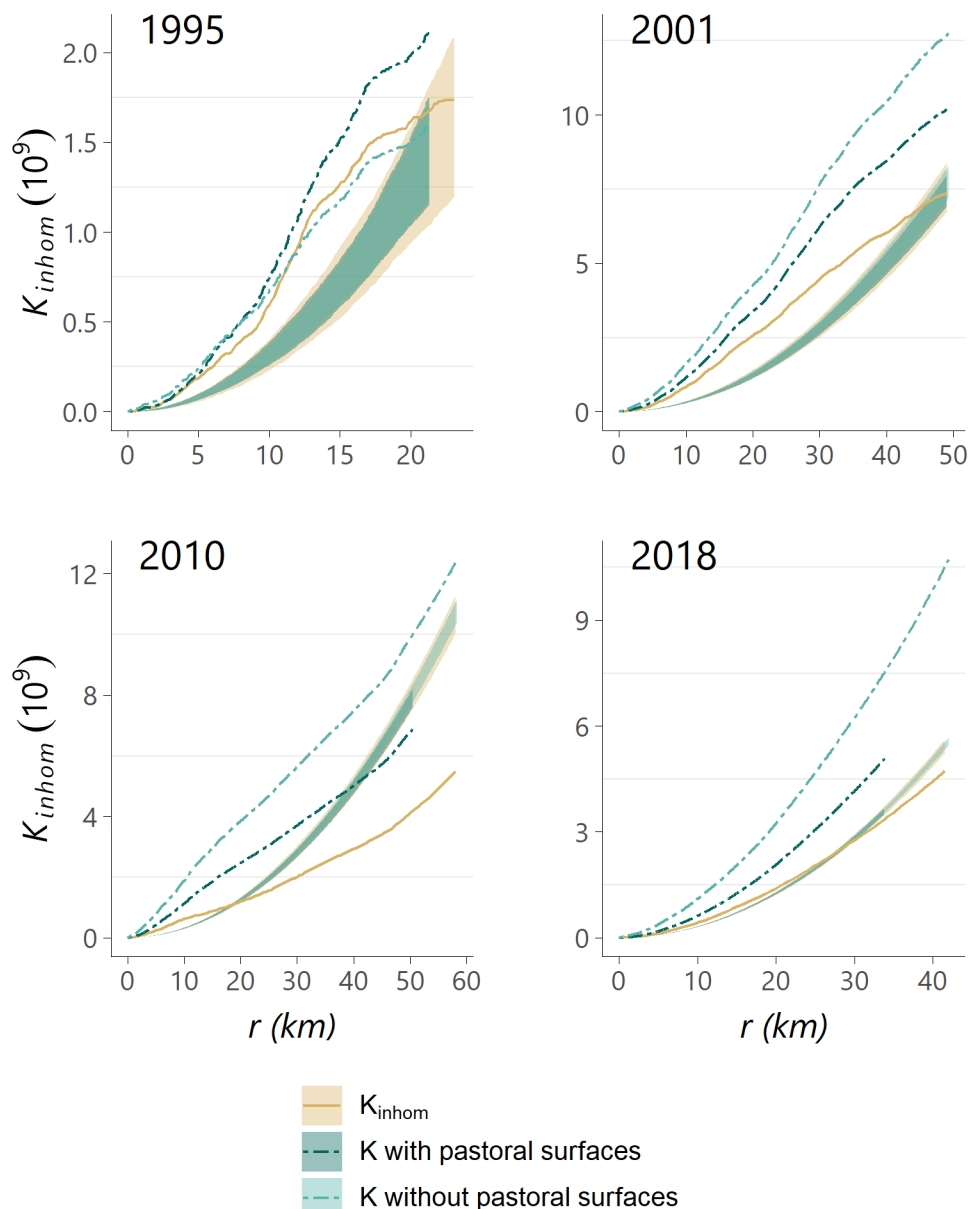
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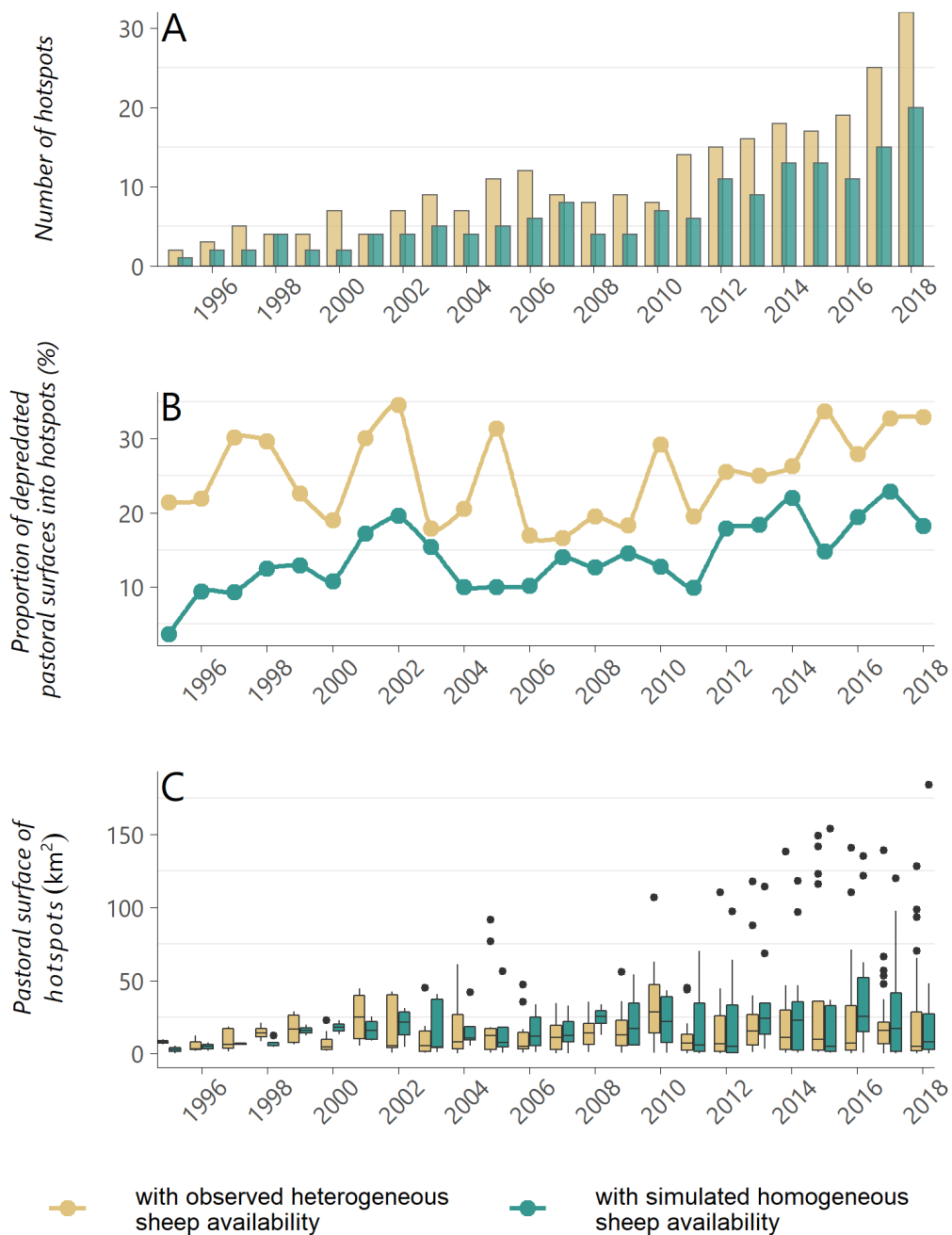
604 **Figures**

605 Color should be used for all figures in print.

606 Figure 1: Results at the regional scale of the  $K_{inhom}$  function (solid yellow line) and of the  $K$ -  
607 function where the analysis grid was simulated over the pastoral surfaces at depredation risk  
608 (dotted dark blue line) or over the wolf distribution (dotted light blue line), against their  
609 corresponding control envelopes, for years  $y$  1995, 2001, 2010 and 2018. The  $r$  distances were  
610 limited in the figure to those computed by the  $K_{inhom}$  function. See Fig. B.4 for all years and  
611 all computed  $r$ .



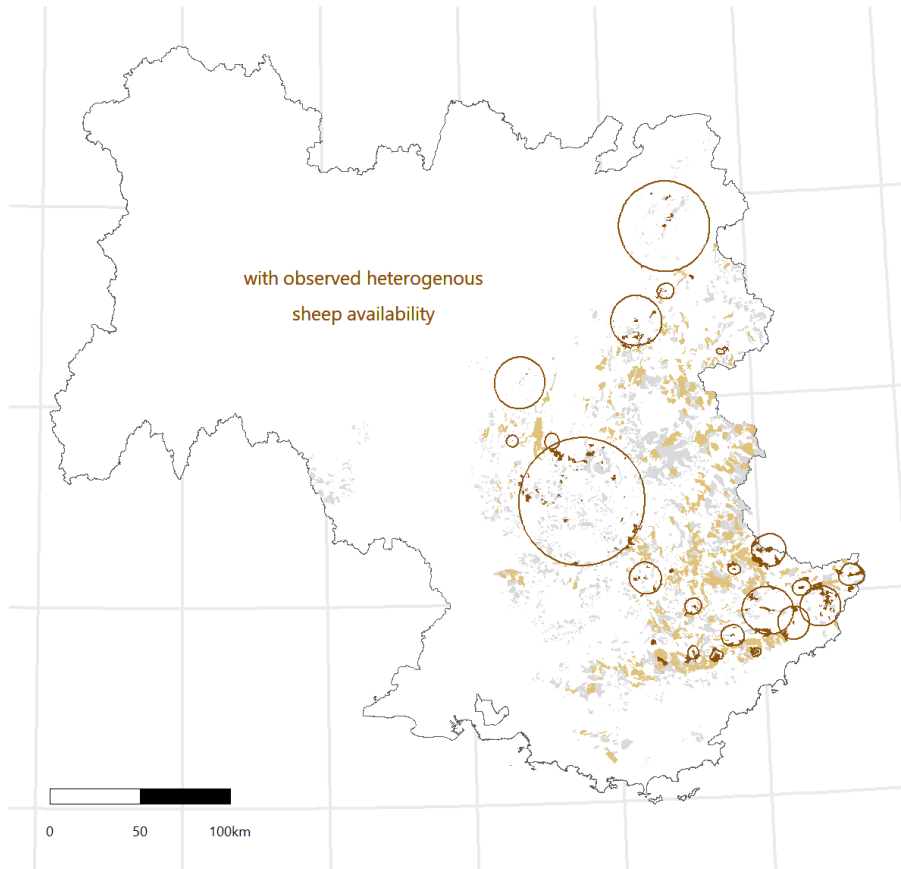
612 Figure 2: Descriptive results of the Kulldorff statistic used with the observed heterogeneous  
 613 (yellow) or simulated homogeneous (blue) sheep availability, for each year, within the study  
 614 area. (A) Number of significant hotspots; (B) Proportion of degraded pastoral surfaces into  
 615 significant hotspots in the whole set of degraded pastoral surfaces; (C) Distribution of the  
 616 sum of the areas of the pastoral surfaces included into each hotspot (with outliers as black  
 617 dots).



618

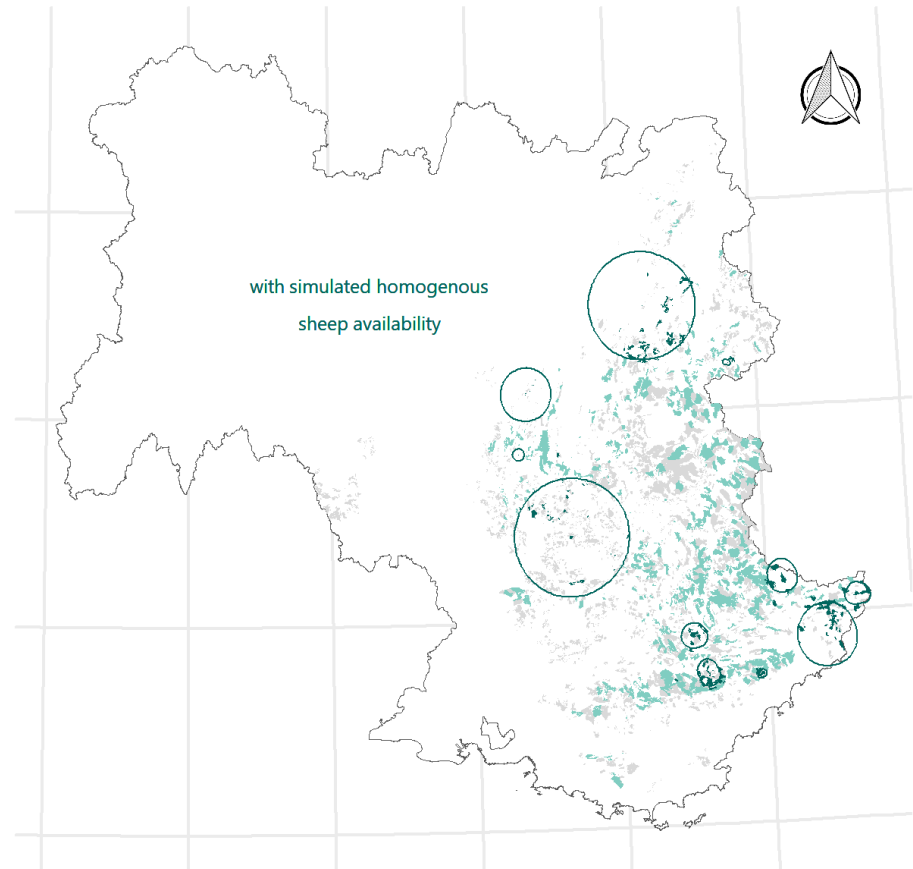
619 Figure 3: Locations of depredated pastoral surfaces identified as hotspots (dark colour) or not  
620 (light colour) in the study area in 2017 according to the Kulldorff statistic results adjusted for  
621 the observed heterogeneous (A) or simulated homogeneous (B) sheep availability. Pastoral  
622 surfaces within the same circles belonged to the same hotspot. Pastoral surfaces which were  
623 not depredated (grey) were shown for information but were not used in the statistical analysis.  
624 See Fig. B.5 for all years.

A



■ Not depredated ■ No hotspot ■ Hotspot

B

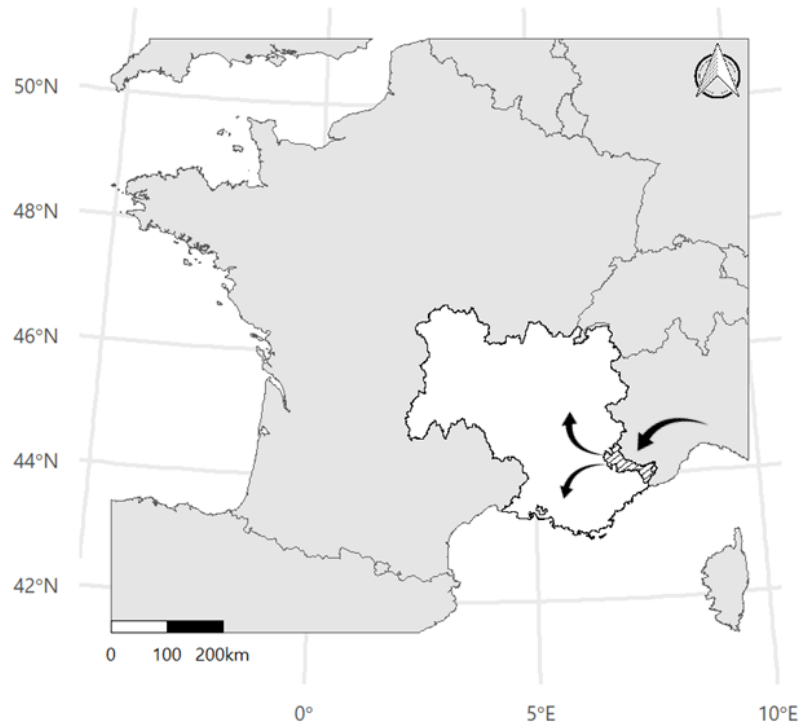


■ Not depredated ■ No hotspot ■ Hotspot

626 **Supplementary material**

627 **Appendix A - Figures**

628 **Fig. A.1** – Location of the study area (white) within France, and of the MNP (hatched) within the  
629 study area, from which wolves from Italy recolonised France (black arrows).



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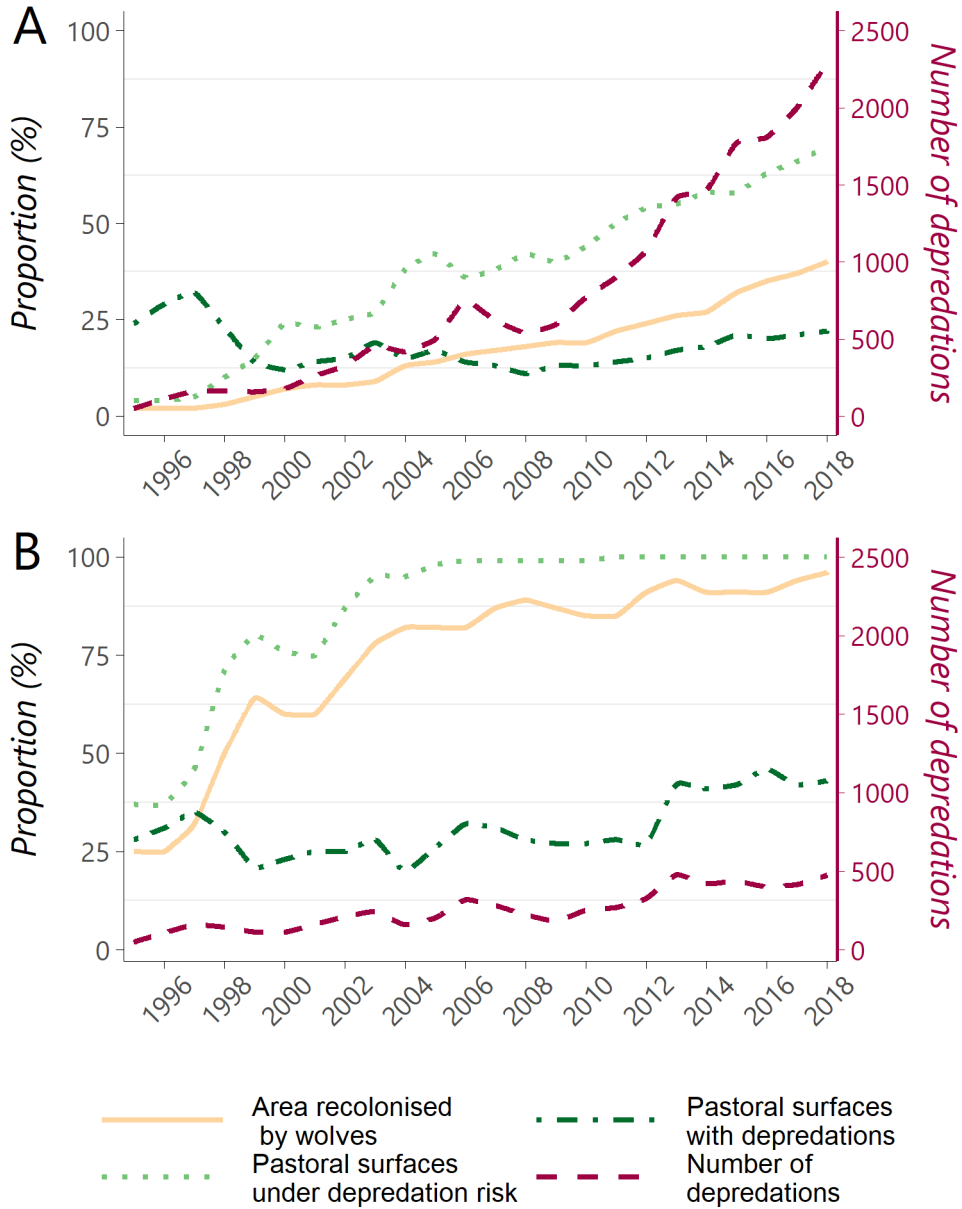
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644 **Fig. A.2** – Proportion of 10x10km cells of the study area within wolf distribution (solid yellow),  
 645 proportion of pastoral surfaces within wolf distribution in the whole set of pastoral surfaces (dotted  
 646 light green), proportion of pastoral surfaces with at least one reported wolf depredation on sheep in  
 647 the set of pastoral surfaces within wolf distribution (dot-dashed dark green), and number of wolf  
 648 depredations on sheep (dashed red) per year in the area. At the A) regional scale, B) local scale.



649

650

651 **Supplementary material**

652 **Appendix B – Interactive figures**

653 **Fig. B.1** – Pastoral information of the study area, from the census of 1996-1997 and from the census  
 654 of 2012-2014. <https://oksanagreente.shinyapps.io/Hotspots-SuppFig1/>

655 **Fig. B.2** – Annual distributions of wolf presence, pastoral surfaces at depredation risk and verified  
 656 wolf depredations on sheep in the study area between biological years 1995 and 2018.

657 <https://oksanagreente.shinyapps.io/Hotspots-SuppFig2/>

658 **Fig. B.3** – Annual distributions of the number of wolf depredations on sheep per pastoral surface, at  
659 the regional and local scales between biological years 1995 and 2018.

660 <https://oksanagrente.shinyapps.io/Hotspots-SuppFig3/>

661 **Fig. B.4** – Annual results between biological years 1995 and 2018 of the  $K_{inhom}$  analysis and of the two  
662 *K-function* analyses (one with the analysis grid simulated over the pastoral surfaces at depredation  
663 risk, the other only over the wolf distribution) at the regional and local scales.

664 <https://oksanagrente.shinyapps.io/Hotspots-SuppFig4/>

665 **Fig. B.5** – Annual locations between biological years 1995 and 2018 of depredated pastoral surfaces  
666 identified or not as hotspots, according to the Kulldorff statistic used with the observed  
667 heterogeneous sheep availability or the simulated homogeneous sheep availability at the regional  
668 scale. <https://oksanagrente.shinyapps.io/Hotspots-SuppFig5/>

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#### 670 **Author contributions**

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672 **Oksana Grente:** Methodology, Software, Validation, Formal analysis, Investigation, Data curation,  
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675 draft preparation, Writing - Review & Editing, Visualization. **Olivier Gimenez:** Validation, Resources,  
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