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► To cite this version:

Oksana Grente, Thibault Saubusse, Olivier Gimenez, Eric Marboutin, Christophe Duchamp. Wolf depredation hotspots in France: Clustering analyses adjusting for livestock availability. *Biological Conservation*, 2022, 267, 10.1016/j.biocon.2022.109495 . hal-03647786

HAL Id: hal-03647786

<https://hal.science/hal-03647786>

Submitted on 25 Apr 2022

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1 **Title**

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

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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 disproportionally 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 km², **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 km², **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 1st of April of year $y-1$ (i.e. wolf pup birth) to
129 the 31st 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

the grazing livestock count per species and the annual number of grazing days was included. One or several herds, of one or multiple livestock species, could feed on a pastoral surface. We restricted the dataset to pastoral surfaces with grazing sheep, regardless of whether other species of livestock were present (**Fig. B.1**). For both censuses, the spatio-temporal sheep availability was inhomogeneous across the study area (**Fig. B.1**), particularly for grazing time between the north and the south of the regional scale due to climate differences and resulting grass phenology. The pastoral surfaces of the first census and of the second census were respectively 2.7 km² and 1.9 km² on average, and they hosted 606 sheep (sd=649) and 516 sheep (sd=547), during 146 days (sd=96) and 202 days (sd=96) per year on average. For each year y , we identified the set of pastoral surfaces at depredation risk for both scales by selecting the pastoral surfaces which overlapped, even partially, with the wolf distribution. For years between 1995 to 2005, we used the 6 488 pastoral surfaces with sheep from the oldest census, and for years between 2006 to 2018, we used the 12 438 pastoral surfaces with sheep from the latest census. The oldest census did not include pastures in the west of the study area (i.e. outside the Alpine area), which explains the lower number of pastures compared to the latest census. However, the wolf distribution from 1995 to 2005 was mainly restricted to the east of the study area, within the Alpine area (**Fig. B.2**), where pastoral information in the oldest census was available. For example, using the latest census instead of the oldest census only provided a difference of 6.7% on average in the numbers of pastoral surfaces at depredation risk at the regional scale from 1995 to 2005. Thus, we considered this gap was of little impact. IRSTEA did not carry out the census process every year for two reasons. First, the census process was the result of a long period of work, exceeding a year of work. The field work, which consisted in meetings with local contact persons, corresponded to 750 full working 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 λ was in ind/cell (i.e. ind/0.04km²), 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, πr^2 . Consequently, at a specific
226 r , if the K_{inhom} value of the observed depredation pattern was higher or lower than πr^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 πr^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 50th-lowest and 50th-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^2 . 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

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

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

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

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

Third, we simulated 499 sets of randomly distributed n controls over the depredated pastoral surfaces, proportionally to their sheep availabilities. The second step was repeated for each control set, to eventually compute the control distribution of the highest likelihood ratio $LR(Z)$. If the observed highest $LR(Z)$ were among the top 5% of this control distribution, 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 km² 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

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

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

The hotspot map provided the locations of areas where investigations in situ can be led to understand the unexpected high level of depredations. The most straightforward factor to investigate is husbandry. Generally, detailed husbandry practices or implementation of preventive measures are not available for spatial statistical analyses, as in our case study. Because a regional inventory of preventive measures is often difficult if not impossible to put in place, especially in the long term, it can be necessary to go in the field to check if preventive measures are implemented, but also suited to the local context. The involved farmers can receive technical support provided by the public authorities in the implementation 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

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

5. Conclusions

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

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

Acknowledgements

This work was partly funded by a grant from ‘Mission pour l’interdisciplinarité’ of CNRS, through its ‘Osez l’interdisciplinarité’ call. We are indebted to the governmental agents in charge of recording depredations and pastoral information and to the field experts from the Wolf-Lynx French Network who collected wolf presence signs. We are grateful to IRSTEA and the regional administration of Auvergne-Rhône-Alpes for the access to the pastoral and depredation databases. We thank A. Baddeley and E. Gabriel for valuable methodological advice, G. Loucougaray, F. Bray and M. Meuret from INRAE and L. Garde from CERPAM for advice on the pastoralism overview and diagnostic. We thank N. Drouet-Hoguet and S. Bauduin for comments on the first draft of the manuscript.

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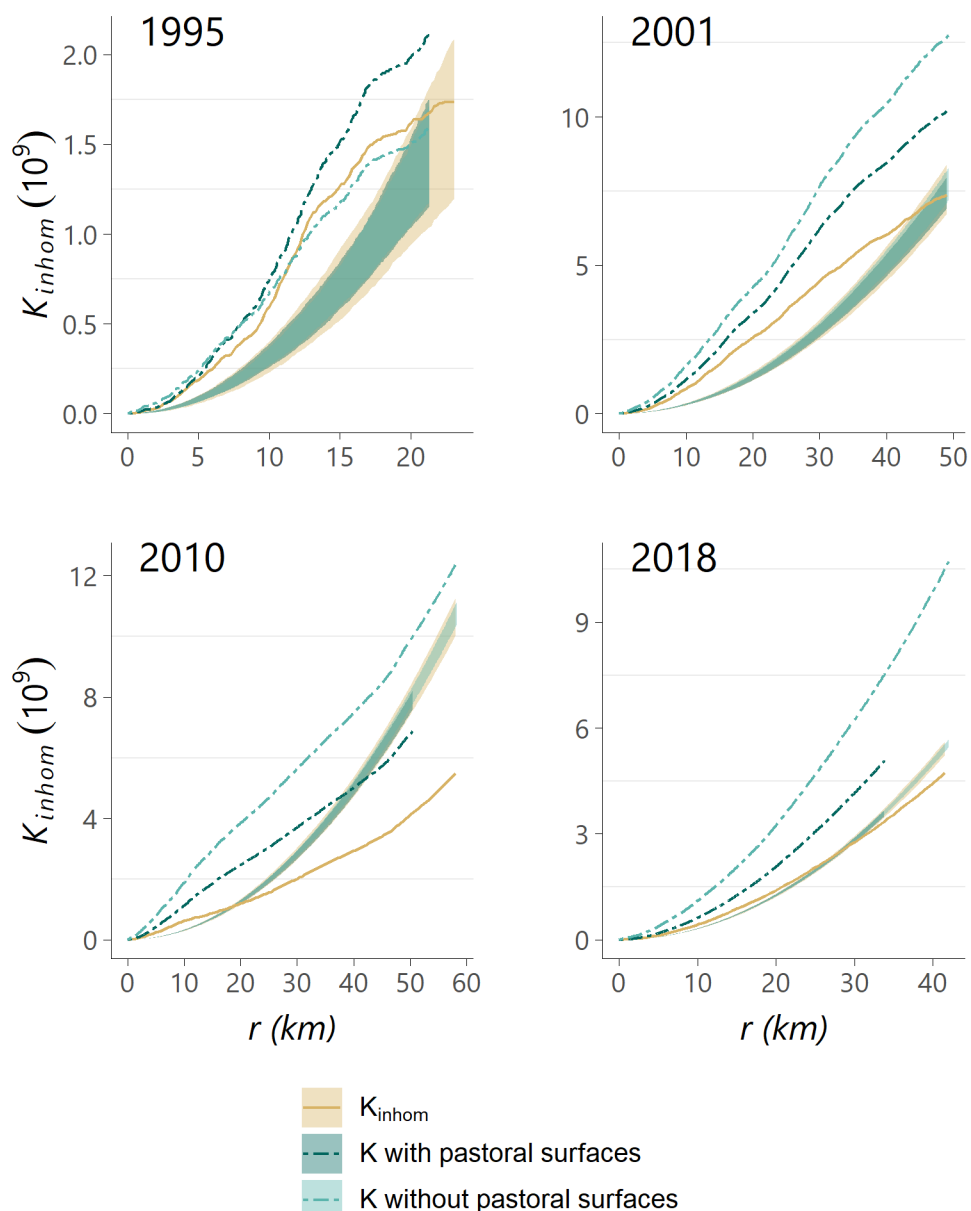
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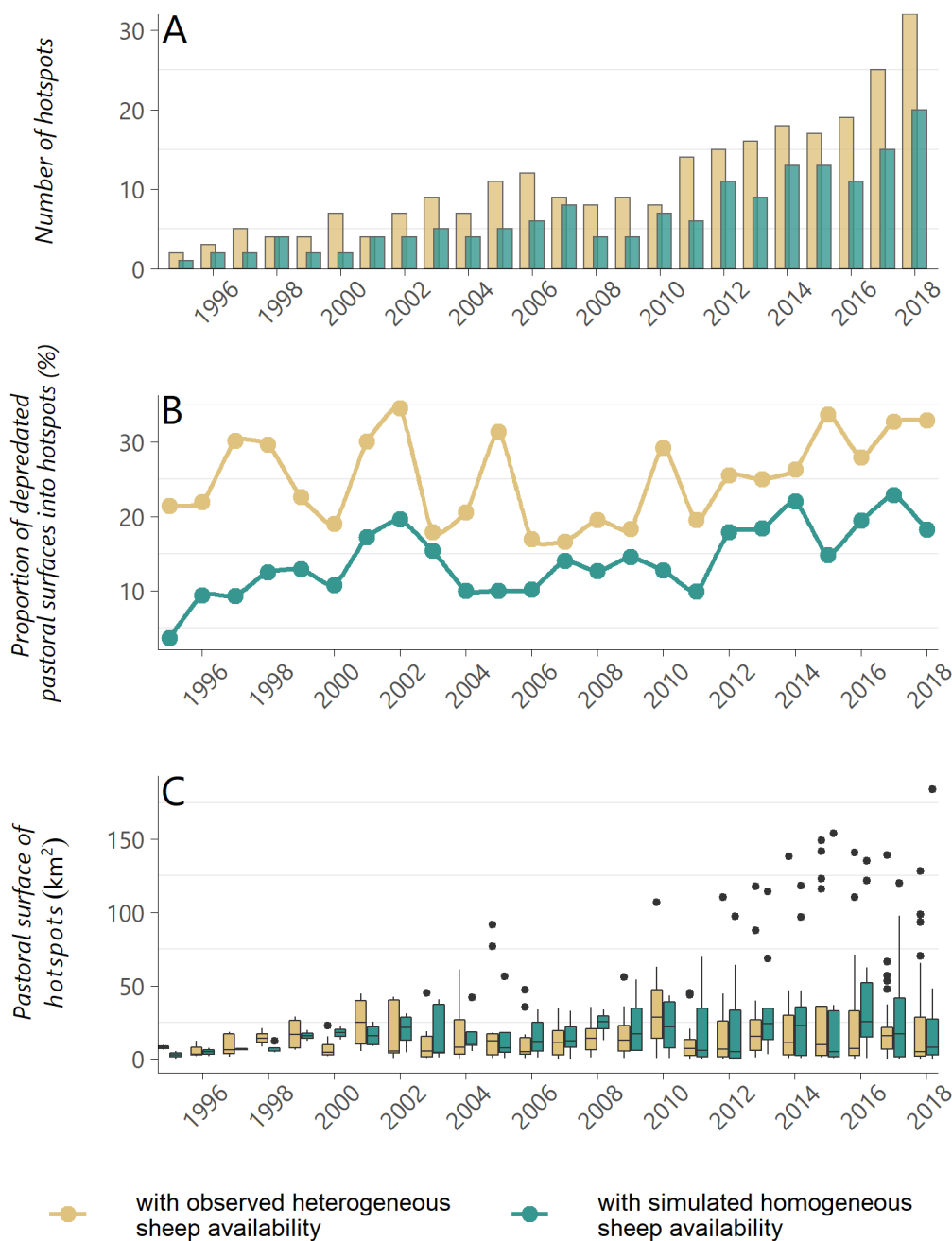
604 Figures

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 .

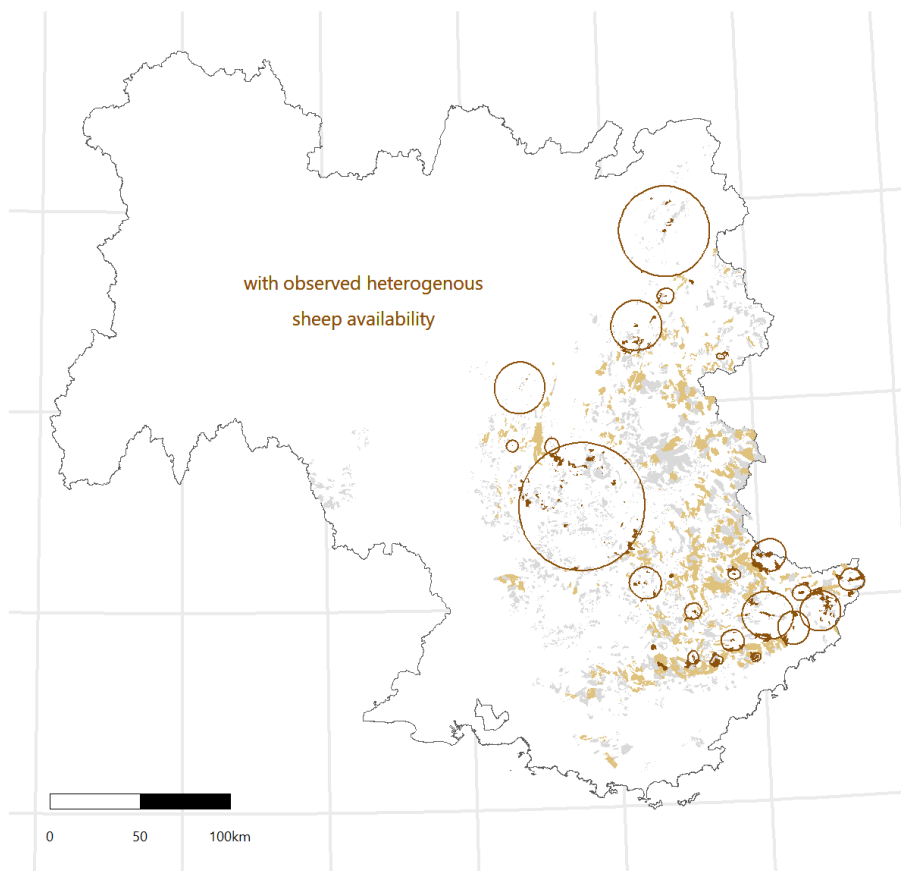


612 Figure 2: Descriptive results of the Kulldorff statistic used with the observed heterogeneous
 613 (yellow) or simulated homogeneous (blue) sheep availability, for each year, within the study
 614 area. (A) Number of significant hotspots; (B) Proportion of depredated pastoral surfaces into
 615 significant hotspots in the whole set of depredated 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).



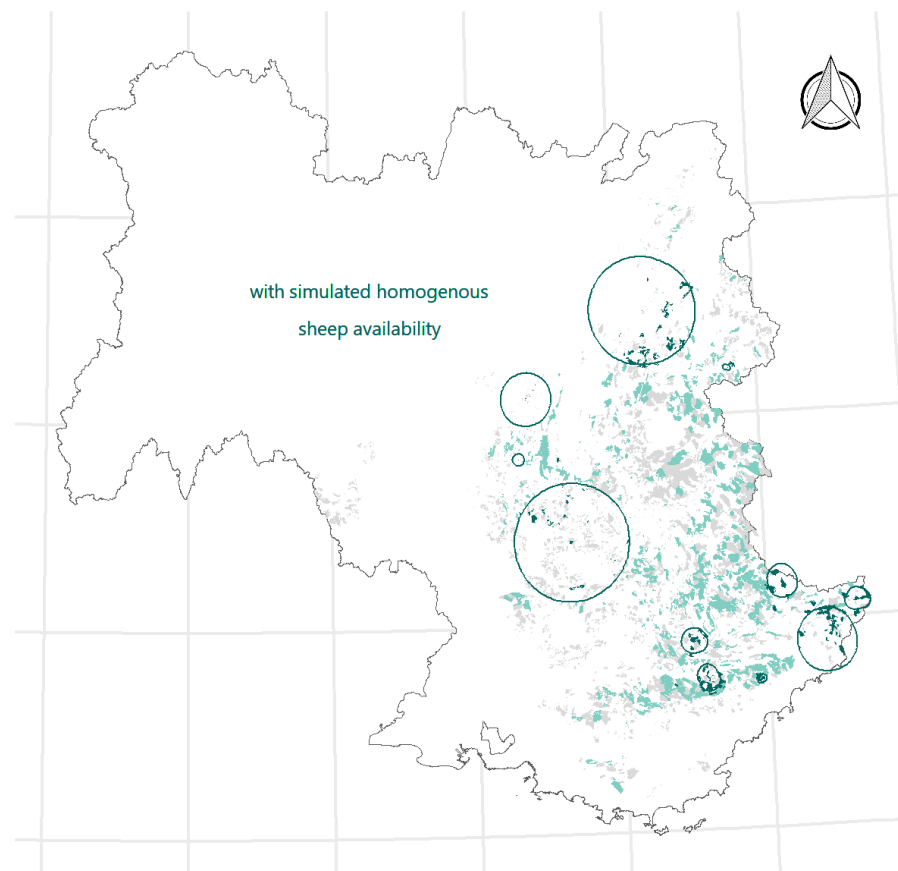
619 Figure 3: Locations of depredated pastoral surfaces identified as hotspots (dark colour) or not
620 (light colour) in the study area in 2017 according to the Kulldorff statistic results adjusted for
621 the observed heterogeneous (A) or simulated homogeneous (B) sheep availability. Pastoral
622 surfaces 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

Supplementary material

Appendix A - Figures

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

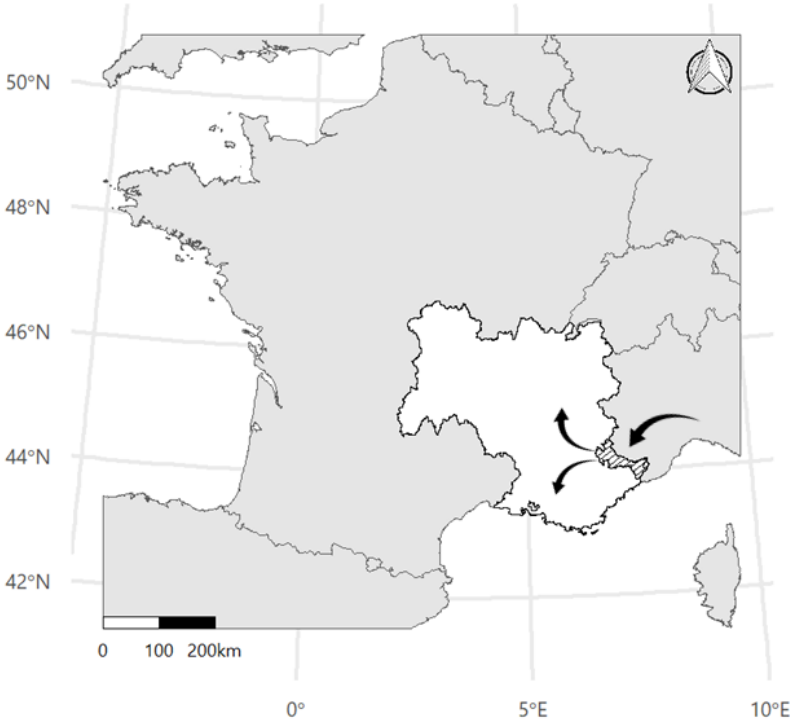
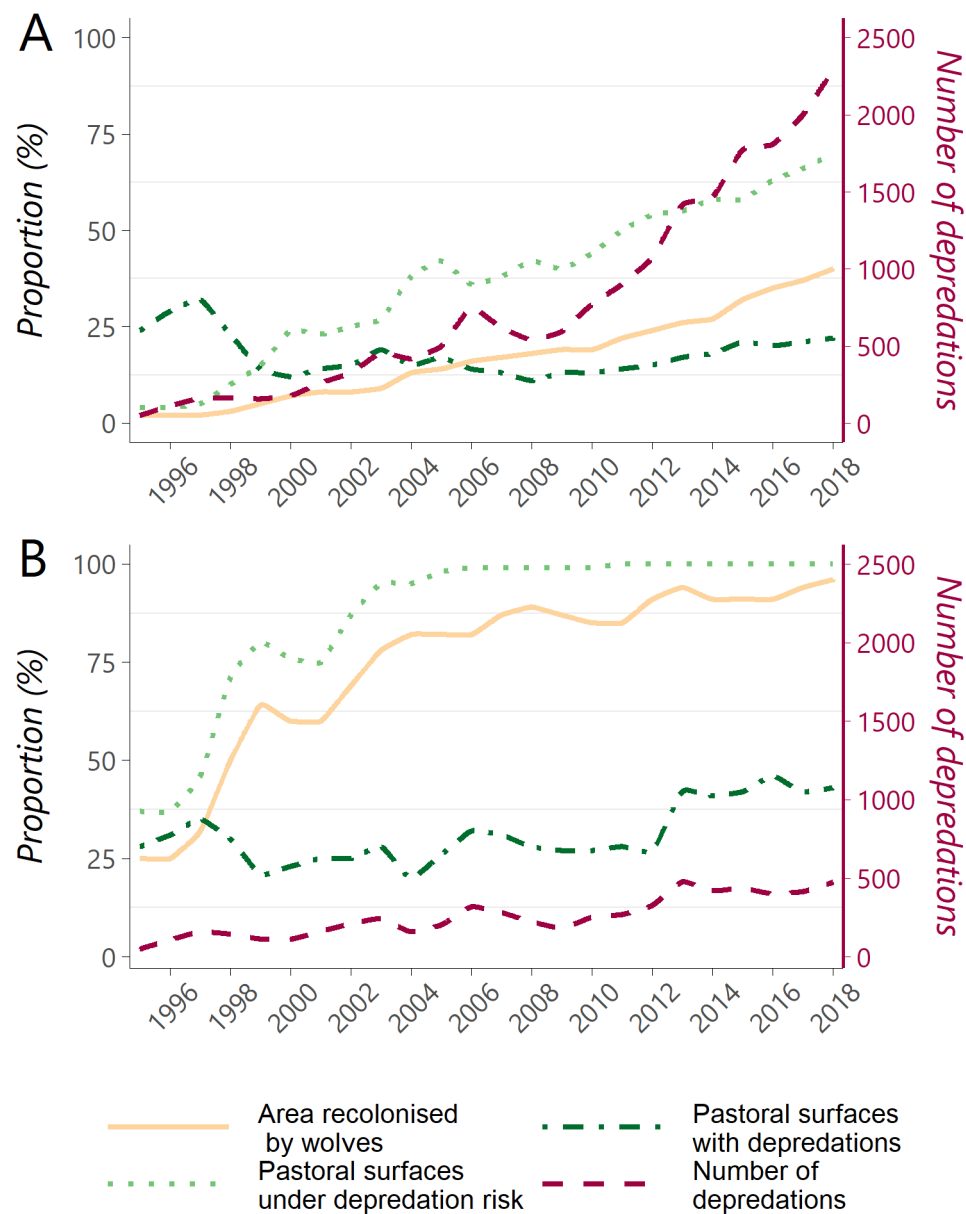


Fig. A.2 – Proportion of 10x10km cells of the study area within wolf distribution (solid yellow), proportion of pastoral surfaces within wolf distribution in the whole set of pastoral surfaces (dotted light green), proportion of pastoral surfaces with at least one reported wolf depredation on sheep in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



Supplementary material

Appendix B – Interactive figures

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

Fig. B.2 – Annual distributions of wolf presence, pastoral surfaces at depredation risk and verified wolf depredations on sheep in the study area between biological years 1995 and 2018. <https://oksanagrente.shinyapps.io/Hotspots-SuppFig2/>

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

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

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

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

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

Author contributions

Oksana Grente: Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing- Original draft preparation, Writing - Review & Editing, Visualization. **Thibaut Saubusse:** Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing- Original draft preparation, Writing - Review & Editing, Visualization. **Olivier Gimenez:** Validation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. **Eric Marboutin:** Resources, Writing - Review & Editing, Project administration, Funding acquisition. **Christophe Duchamp:** Conceptualization, Methodology, Validation, Resources, Data Curation, Writing - Review & Editing, Supervision, Project administration.