Wolf depredation hotspots in France: Clustering analyses accounting for livestock availability

Oksana Grente*, Thibault Saubusse*, Olivier Gimenez, Eric Marboutin, Christophe Duchamp

*Both authors contributed equally to this work.

Author details

Oksana Grente (corresponding author)
Office Français de la Biodiversité, Unité Prédateurs Animaux Déprédateurs et Exotiques, Micropolis - La Bérardie 05000 Gap, France.
CEFE, Univ Montpellier, CNRS, EPHE, IRD, Université Paul Valéry Montpellier 3, Montpellier, France
oksana.grente@gmail.com

Thibaut Saubusse
Office Français de la Biodiversité, Unité Prédateurs Animaux Déprédateurs, et Exotiques Micropolis - La Bérardie 05000 Gap, France.

Olivier Gimenez
CEFE, Univ Montpellier, CNRS, EPHE, IRD, Université Paul Valéry Montpellier 3, Montpellier, France

Eric Marboutin
Office Français de la Biodiversité, Unité Ongulés sauvages, ZI Mayencin, F-38610 Gières, France

Christophe Duchamp
Office Français de la Biodiversité, Unité Prédateurs Animaux Déprédateurs et Exotiques, Micropolis - La Bérardie 05000 Gap, France.

Abstract

1. Depredation hotspots are the main source of conflict between humans and large carnivores. When locating depredation hotspots, previous studies have not adjusted for livestock availability, making it impossible for managers to discriminate hotspots resulting from underlying livestock clustering from those due to other factors such as environmental factors.
2. We studied hotspots of wolf depredation on sheep in France from the beginning of wolf recolonisation in 1994, up to 2018. For each year, we used spatial statistical analyses to determine the general depredation spatial pattern, then to locate depredation hotspots. We quantified the discrepancies between the analyses accounting or not for livestock availability.
3. We showed that ignoring livestock availability led to flawed inference about the depredation pattern, and resulted in a substantial number of unidentified hotspots, generally encompassing pastoral surfaces with small sheep availability.
4. Our results indicated that some large hotspots persisted in space and time whereas the distribution of depredations elsewhere in the study area tended to randomness and produced sporadic hotspots.
5. *Synthesis and applications*. Our methodology provides reliable information for managers to grasp the depredation pattern, to allocate resources and to evaluate management efficiency. In areas where depredations significantly persist, investigation on vulnerability is recommended.

Keywords

clustering analyses, conservation resource allocation, grey wolf, hotspots of depredation, human-carnivore conflict, livestock loss, spatial statistics

Introduction

The predations on domestic preys by large carnivores, called “depredation”, are the main driver of conflicts between humans and large carnivores. The financial and social costs associated to depredations reduce acceptance of these species and lead to retaliatory killings (Abade, Macdonald, & Dickman, 2014). Understanding the spatial and temporal patterns of depredations is a major challenge in large carnivore conservation to mitigate current conflicts and prevent future ones (Miller, 2015). To do so, two complementary approaches can be applied, namely spatial autocorrelation and risk modelling. Spatial autocorrelation quantifies the level of clustering or regularity (*i.e.* repulsion) of a depredation pattern (Baddeley et al., 2015; Hoffmann et al., 2019) and allows the identification of hotspots or coldspots, where events are unusually aggregating or scarce. Risk modelling aims to predict locations of future depredations, by quantifying the relationship between ecological or non-ecological features and depredation numbers or occurrences (Miller, 2015).

Spatial autocorrelation is often presented as a preliminary step to risk modelling and as of limited interest if applied alone (Gastineau, Robert, Sarrazin, Mihoub, & Quenette, 2019; Hoffmann et al., 2019). This may explain why risk modelling is more popular (*e.g.* Bradley & Pletscher, 2005; Fowler, Belant, & Beyer, 2019) than spatial autocorrelation analyses in the literature. However, risk models only reflect the depredation-factor relationships at a given point in time and space. These relationships may evolve because predator-prey systems are dynamic and carnivores can adapt their predation behaviour according to environmental or livestock management changes (Miller, 2015). This is especially true for (re)colonising large carnivore populations of plastic species such as the grey wolf (*Canis lupus*) which can embrace a large range of habitats. Risk models developed for this species were either restricted to a unique region and type of habitat (*e.g.* Clark et al., 2020) or showed a low predictive power when applied to habitats that differ from those originally used in the analysis (Hanley, Cooley, Maletzke, & Wielgus, 2018). Therefore, the outcomes of risk models are hardly transposable to other areas or on long-term periods, which makes their adoption by managers difficult (Miller, 2015). In contrast, information about current or past hotspot locations provided by spatial autocorrelation can directly help managers when allocating conservation resources such as subsidies of preventive measures. Prioritising on depredation hotspots is indeed recommended as recurrences of high levels of attacks in the same areas are likely to trigger negative attitudes and to undermine conservation efforts (Stahl, Vandel, Herrenschmidt, & Migot, 2001).

So far, several techniques of spatial autocorrelation for hotspot identification have been developed. The simplest one consists in defining an arbitrary threshold for a selected indicator such as the number of depredations which, if reached, turns the spatial unit into a hotspot. Units can be administrative areas (*e.g.* Dhungana et al., 2019) or simple shapes like circles (Stahl et al., 2001). To avoid arbitrary thresholds, some studies have applied spatial statistical analyses (*e.g.* Gastineau et al., 2019; Hoffmann et al., 2019; Packer et al., 2019). The spatial statistical analyses consider depredation events as a spatial point pattern, *i.e.* a dataset of observed spatial locations of a biological process (Baddeley et al., 2015). The areas exhibiting significantly more depredation events than expected under Complete Spatial Randomness (CSR) are statistically identified as hotspots. To gain understanding of the biological process, the spatial statistical analyses can also be conducted to determine the summarised spatial structure of the pattern, *i.e.*

the range of distances over which the pattern generally exhibits clustering, randomness or regularity (*e.g.* Kushnir et al., 2014 with lion attacks on humans).

However, these quantitative studies have not controlled for spatio-temporal livestock availability because the statistical method they used did not allow it or because the relevant data were not available. Yet the spatial pattern of depredation is inherent to the distributions of both large carnivores and livestock. Not only are conflicts exclusive to areas where both distributions overlap, but they are also dependent on livestock availability, which is related to the livestock count and to the time livestock spends in a specific area. If livestock distribution is ignored, it is difficult to disentangle the hotspots which exhibit high levels of livestock availability, from those where livestock densities are low and conflicts are due to environmental, predator-linked, social or other factors that management could attempt to identify, and which constitute priority areas for actions.

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

Here, we aimed to conduct spatial statistical analyses on wolf depredations on sheep in southeast France. First, we aimed to determine the summarised spatial structure of the depredation pattern and second to locate the significant depredation hotspots if any, both with methods controlling for sheep availability in space and time. We conducted year-to-year analyses, from 1994 to 2018, in order to study the temporal variations in the depredation patterns and in the hotspot locations throughout wolf recolonisation. We also explored the depredation patterns at a local scale, in the historic area of wolf recolonisation in France. The objectives of the local scale analysis were first to increase perceptibility of wolf territorial behaviour in the results if any, and second to observe if years of wolf presence changed the depredation pattern over time compared to the regional scale where colonisation fronts still persisted. Finally, we discussed the management implications of our results with regard to the decision-making process.

Materials and methods

Study area and study period

The study area covers the two southeast regions of France, Provence-Alpes-Côte-d’Azur and Auvergne-Rhône-Alpes, and includes all the French Alps and the east part of Massif Central mountains (102,483 km², **Fig. 1**). Habitats range from bush and coniferous forest under Mediterranean climate in the south, to mixed forest in the north and the east which are mountainous at high altitudes.

We defined the regional scale as the entire study area and the local scale as the Mercantour National Park and its surroundings (hereafter ‘MNP’), located in the very south-east of the study area (2146 km², **Fig. 1**). The MNP was characterised by a succession of alpine vegetation levels along a wide altitudinal range, from 600 to 3,200 m.

We settled the analyses for each wolf biological year *y*, starting from the 1st of April of year *y-1* to the 31th March of year *y*. The whole study period covers biological years (hereafter, ‘years’) from 1995 to 2018.

Depredation records

The large majority of depredations occurs between June and October, when most of sheep flocks are grazing in pastures. Up to 2019, the French Ministry of Ecology compensated for any killed farmed animal for which wolf responsibility could not be discarded, regardless of protective measures. Each claim was controlled and checked in the field by an accredited governmental agent who used a standardized protocol (Duchamp et al., 2012). Therefore, most depredations were reported if noticed, and the risk of false claims was low. We used the verified depredations on any type of livestock for which wolf responsibility could not be discarded to determine wolf distribution, and restricted the clustering analyses to depredations on sheep only as they constituted 90% of depredations. An event of depredation could correspond to one or several killed sheep. Because grazing activity may extend outside the official pastoral limits, or because of geolocation approximations, some depredation events were not located inside the geolocated pastoral surfaces (22% of the annual dataset on average). We assigned these depredations to the nearest pastoral surface and excluded depredations farther away than 500 meters (10% of the annual dataset on average).

Wolf distribution

The Wolf-Lynx French Network managed by the French Biodiversity Agency is in charge of the wolf monitoring in France. Its trained field experts opportunistically collect presence signs all year along, such as biological samples (mainly faeces), tracks or direct observations, which are geolocated and validated according to a standardized protocol and combined to genetic analysis when possible (Duchamp et al., 2012; Louvrier et al., 2018). To determine the annual wolf distribution, we combined the annual presence signs and the previously selected depredations within the study area. Wolf presence during year *y* was reported on a 10x10 km cell grid, and was defined as the collection of at least one presence sign or one depredation in the cell from *y*-1 to *y*-3 and from *y*-2 to *y* (see Marboutin et al., 2011).

Spatio-temporal sheep availability

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

We used two georeferenced censuses of pastoral surfaces in the study area carried out in 1996-1997 and in 2012-2014 by the National Research Institute of Science and Technology for the Environment and Agriculture (IRSTEA). For each pastoral surface, the two pastoral censuses included data about livestock species, livestock counts and grazing day numbers. The first census was incomplete in the low-altitudinal northern section. We therefore completed the missing parts with data from the second census. In the completed first census and the second census respectively, we selected the 6,241 and 5,099 pastoral surfaces with sheep. Mean pastoral surface area was 1.78 km² (sd=2.9) in the first census and 1.88 km² (sd=3.0) in the second census. In the first and second census respectively, mean pastoral surface sheep count was 474 (sd=543, range=1-9,200) and 516 (sd=547, range=1-6,000) and mean pastoral surface sheep grazing day number was 191 (sd=103, range=4-365) and 202 (sd=96, range=1-360). The spatio-temporal sheep availability was highly inhomogeneous across the study area at the regional or local scales (**Fig. 2**; **Fig. S1**).

For each biological 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, the pastoral surfaces came from the first census completed with the second one, and for years between 2006 to 2018, they exclusively came from the second census.

Analysis 1: Spatial structure of wolf depredations

For each year y, we analysed at the regional and local scales the spatial structure of the wolf depredation pattern considering sheep availability by using K_{inhom} (Baddeley et al., 2015).

First, we simulated the expected depredation pattern under CSR considering sheep availability. The simulated pattern was composed of n points called 'controls', in opposition to the n annual observed depredations called 'cases'. The distribution of controls was simulated over the pastoral surfaces at depredation risk according to an inhomogeneous Poisson Point Process (PPP). In this model, the number of controls falling into a pastoral surface u was expected to be equal to $\lambda(u)$, called 'intensity', that we defined as:

$$\lambda(u) = exp(a + b \ \times \log(pop_u) + c \ \times \log(time_u))$$

where pop_u and $time_u$ were the numbers of sheep and of grazing days of the pastoral surface u, and a, b and c were parameters to be estimated. Covariates were log-transformed because of their skewed distributions. Therefore, the controls were more likely to fall into the pastoral surfaces with the highest combinations of sheep count and grazing days number. For each year, we simulated 499 control patterns through this model.

Second, we computed K_{inhom} for the pattern of n cases. This function drew a circle of radius r around each depredation i covering more or less neighbouring depredations j. Then, the function summed the values $\frac{1}{\lambda(u_i)\lambda(u_j)}$ for all pairs of depredations i-j within this circle, $\lambda(u_i)$ and $\lambda(u_j)$ being the intensity values of the pastoral surface(s) containing i and j respectively. Therefore, for each tested r, K_{inhom} returned a surface. If the pattern was randomly distributed considering sheep availability, the surface should equal πr^2. Consequently, at a specific r, if the K_{inhom} value of the observed depredation pattern was higher or lower than πr^2, we could conclude that the depredations were respectively forming hotspots or coldspots of radius r.

However, the smaller the dataset, the larger the differences from the expected number of points within a circle, especially for high values of r. Therefore, a K_{inhom} value which differed from πr^2 was not necessarily the result of a non-randomly point pattern, but could be due to stochastic effects. To take this into account, we also computed K_{inhom} for the 499 control patterns and selected the 50th-lowest and 50th-highest values to build a control envelope. For a specific r, if the observed K_{inhom} was higher (or lower) than the upper (or lower) envelope limit, the depredations were significantly clustered (or regular, *i.e.* tended to avoid each other) at this distance considering sheep availability. The larger the differences, the more aggregated or regular the pattern.

For comparative purposes, we also annually applied at the regional scale only, the *K*-function which considered sheep availability as homogeneous. Contrary to K_{inhom}, the *K*-function used a homogeneous PPP where the number of controls falling into the spatial units of the analysis was expected to be equal over the whole analysis area (Baddeley et al., 2015). We tested two possibilities to define the spatial units. First, we used the pastoral surfaces at depredation risk as in the K_{inhom} analysis, in order to simulate a situation for which sheep distribution was known, but sheep availability was not. Second, we used the estimated wolf distribution cells, to simulate a situation for which pastoral data were totally unavailable.

Analysis 2: Wolf depredation hotspot location

For each year y, we located at the regional scale the significant wolf depredation hotspots by applying the first version of the Kulldorff statistic (Kulldorff, 1997) which adjusts for spatially inhomogeneous population at risk.

First, we defined the spatial unit, *i.e.* the smallest area that can be identified as a hotspot. To be consistent with the current management scale in France, we defined the pastoral surface as the spatial unit. We defined sheep availability within each pastoral surface u as $\omega(u) = pop_u \times time_u$. Then, the Kulldorff statistic defined the future zones that can be identified as hotspots, called zones *Z*. Each pastoral surface was defined as a zone *Z*. Other zones *Z* were defined by adding to these first zones the adjacent pastoral surfaces, and so on. We determined the limit size of a zone *Z* as following: a zone *Z* could not include more than 5% of the sum of $\omega(u)$ of all pastoral surfaces. Otherwise, the hotspots were too vast to be informative. In addition, we restricted the analysis to the depredated pastoral surfaces. The inclusion of pastoral surfaces without depredation into the analysis indeed increased sheep availabilities of certain zones, especially zones where depredated pastoral surfaces were surrounded by pastoral surfaces without depredation. This 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:

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

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 a null hypothesis (M_0) and an alternative hypothesis

(M_A), respectively $p_Z = q_Z$ and $p_Z > q_Z$. It calculated the likelihood ratio $LR(Z)$ as $\frac{L(Z)}{L_0}$. $L(Z)$ 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 $n \sim Poisson(p \times \sum \omega(u))$. The zones Z for which M_A was the most likely had the highest likelihood ratios.

Third, to test statistical significance, we simulated 499 sets of randomly distributed controls over the depredated pastoral surfaces, proportionally to sheep availability. 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 likelihood ratios were among the top 5% of this control distribution, then the corresponding zones were considered as significant hotspots.

We repeated this analysis with a simulated homogeneous sheep availability to point out the discrepancies when ignoring prey availability. In this analysis, each depredated pastoral surface had a sheep availability equal to the average observed sheep availability per depredated pastoral surface.

We performed the K_{inhom} and Kulldorff analyses with the packages *spatstat* (Baddeley & Turner, 2005) and *SpatialEpi* (Kim & Wakefield, 2018), respectively, in R (version 3.6.1, R Core Team, 2019).

Results

Trends in depredation risk and observed depredations

We collected 25,220 presence signs and 22,262 verified depredations on any type of livestock for which wolf responsibility could not be discarded, reported from 1995 to 2018 in the study area. The resulting estimated annual wolf distribution expanded year after year, and reached

40% of the study area in 2018 (**Fig. 3A; Fig. S2**). The annual proportion of pastoral surfaces at depredation risk within the total set of pastoral surfaces increased year after year at the regional scale, reaching 72% in 2018. This situation generated more and more depredations on sheep per year over time, starting from 49 depredation events in 1995 to 2,289 in 2018. However, the annual proportion of depredated pastoral surfaces among the pastoral surfaces at risk remained quite stable over time at the regional scale, with a mean of 16%. Most pastoral surfaces at depredation risk did not experience depredations, or only one or two per year at the regional scale (**Fig. S3**). One depredation event corresponded on average to 3.78 wounded or killed sheep (sd=0.29) without including indirect mortalities (*e.g.* collective falls).

The situation at the local scale differed from the regional scale. Because recolonisation started in the MNP, the majority of the local scale was recolonised by wolves by 2007. Almost all the pastoral surfaces were at depredation risk by 2003 and all of them by 2011 (**Fig. 3B**). Most depredated pastoral surfaces also experienced one or two depredations per year for the whole study period (**Fig. S3**). Because the number of pastoral surfaces at depredation risk quickly stabilised, the trend of the depredation numbers followed the trend of the proportion of depredated pastoral surfaces.

Analysis 1: Spatial structure of wolf depredations

The K_{inhom} function accounting for sheep-based intensity $\lambda(u)$ identified significant aggregation of the depredations for all years, with K_{inhom} values higher than the control envelope (**Fig. 4**; **Fig. S4**). The latter was thinner with time as the depredation pattern included more and more events. However, depending on years, the range of radiuses r for which aggregation was significant varied, as well as the aggregation intensity (*i.e.* differences between the observed and control envelope values). We identified four time periods.

During the first period (1995-1999), aggregation was significant for the whole range of radiuses r, up to 20-30 km around depredations. Aggregation tended to intensify with r, especially in 1996 and 1998. This was consistent with the depredation maps, where all depredations seemed conglomerated together without small-scaled structures (**Fig. 5; Fig. S2**).

During the second period (2000-2003), aggregation intensified only over the lowest r values, then its intensity decreased over the largest r values. Apart from 2000, the K_{inhom} values merged with the control envelope between 40 and 50 km. This indicated that depredation hotspots tended to emerge with wolf expansion, as observable in **Fig. 5**.

During the third period (2004-2012), a weak significant aggregation was only observed over the lowest r values, and turned into significant repulsion between 15 and 30 km. This was typical of a clustered pattern, with hotspots producing coldspot interzones (Hoffmann et al., 2019). These hotspots could correspond to the south-east and south areas where depredations were particularly densely distributed (**Fig. 5**).

Finally, the last period (2013-2018) showed significant aggregation over 25 to 50 km followed by randomness (except 2014 with continuous aggregation). In certain years, a weak repulsion was observed at the largest r values. Aggregation intensity was greater in 2013 compared to 2012, but it tended to decrease the following years, which brought the depredation pattern closer to randomness with time. This suggested that the former south and south-east hotspots, still noticeable (**Fig. 5**), were overlooked by the apparent randomness of depredations in the rest of the study area.

Using K_{inhom} or K provided comparable results only during the first period. But, from 1999-2000, the differences between the three analyses of K_{inhom} or K deepened (**Fig. 4**; **Fig. S4**). The K-function which considered sheep availability as homogeneous across pastoral surfaces only identified the typical hotspot structure (*i.e.* aggregation followed by repulsion) in 2009 and 2010 with a radius of 30 and 40 km respectively. The other years, aggregation was significant for all values of *r* and always more intense than the one obtained through K_{inhom}. When using the wolf distribution cells as the spatial units, the *K*-function analysed the pattern over larger values of *r* than the two previous analyses, because isolated distribution cells in the west of the study area could sporadically appear without overlapping with pastoral surfaces. Apart from 1995, this analysis only provided a significant aggregation which intensified with *r*.

At the local scale, the K_{inhom} function accounting for sheep availability provided two main findings. First, from 1998 to 2011, the analysis identified significant aggregation over 12 to 17 km, followed by randomness in some but not all years (**Fig. 6**; **Fig. S4**). Repulsion was never observed, except in 2004. This year, depredations seemed conglomerated into three distinct groups (**Fig. 7**). Second, the aggregation intensity was generally decreasing with time from 2008, even though the control envelopes were of equivalent thickness. Eventually, the pattern tended to randomness for all values of *r* from 2015, with almost complete randomness observed in 2016.

Analysis 2: Wolf depredation hotspot location

The number of hotspots identified by the Kulldorff statistic accounting for sheep availability increased over time in the study area, from one hotspot in 1995 to 20 in 2018 (**Fig. 8A**). However, the annual proportion of depredated pastoral surfaces into hotspots in the whole set of depredated pastoral surfaces remained stable (**Fig. 8B**), with an annual mean of 13%. Except during the first years, the hotspots were of various sizes but generally did not exceed 5,000 pastoral ha (**Fig. 8C**). Annual means of sheep counts and grazing time were significantly lower for the pastoral surfaces within hotspots than for those outside hotspots (respectively, t-test: $P<0.001$, $\alpha=0.05$; Wilcoxon test: $P<0.05$, $\alpha=0.05$). Hotspots could be located at different places within the study area (**Fig. 9A; Fig. S5**). They were mostly sporadic, appearing for one year.

But some could persist over time, such as in the MNP where they were present during the whole study period, and in the south during the period 2010-2018. These long-lasting hotspots generally encompassed several adjacent pastoral surfaces.

In contrast, the results of hotspot identification drastically changed when ignoring sheep availability heterogeneity. For most years, the number of hotspots was lower (**Fig. 8A**) but their sizes were generally higher (**Fig. 8C**) than in the previous results accounting for sheep availability heterogeneity. In 2017 for example, the south-east identified hotspot was made of the smaller hotspots that were identified in the analysis accounting for sheep heterogeneity (**Fig. 9**). In addition, small hotspots, which encompassed only one or a few small depredated pastoral surfaces were not systematically identified in the analysis ignoring sheep heterogeneity (***e.g.* Fig. 9; Fig. S5**). Annual means of sheep counts and grazing time of pastoral surfaces within hotspots were significantly larger in the analysis ignoring sheep heterogeneity than in the analysis accounting for sheep heterogeneity (t-tests: $P<0.001$, $\alpha=0.05$).

Discussion

Wolves are opportunistic predators. The number of wolf attacks on a specific prey generally increases with prey availability, because of higher risks of encounters (Mech & Boitani, 2003). The same rule has been observed for depredations (*e.g.* Gula, 2008). Therefore, ignoring livestock availability in clustering analyses of depredations prevents the distinction between sheep and depredation clustering. We quantified the discrepancies between clustering analyses considering or not livestock availability and distribution. These discrepancies were minimal from 1995 to 1999, at the early stage of wolf colonisation, then became visible from 2000 once the wolf population increased and expanded. Firstly, ignoring sheep availability in the depredation pattern analysis mostly led to a pattern of complete aggregation at all distances for almost all years, rather representing the underlying heterogenous sheep availability than the depredation clustering itself. These results were consistent with the hotspot identification analysis ignoring sheep availability, which tended to identify hotspots with larger flock size and grazing time, but not those with low sheep availabilities and numbers of depredations. Secondly, ignoring sheep distribution in the *K*-function intensified the aggregation observed when ignoring only sheep availability, because of the inclusion of area where depredations were not possible. In contrast, accounting for sheep availability (and therefore for sheep distribution too) was necessary to identify the typical clustered pattern (*i.e.* aggregation followed by repulsion; Hoffmann et al., 2019) through K_{inhom} and to provide a finer-grained analysis of hotspots through the Kulldorff statistic. This is of great interest for management when allocating prevention tools or derogations of wolf removals for the most pressing situations.

Wolves are territorial animals. They live in packs or alone within a delimited territory that they actively defend against conspecifics. This behaviour creates buffer zones between territories that wolves tend to avoid because of intraspecific strife risks. A lower risk of predation has been observed in buffer zone compared to the predation risk within territories (Mech & Boitani, 2003). The typical clustered pattern observed in our K_{inhom} analysis could be the result of such spatial variation in predation risk, where the aggregation and repulsion would respectively correspond to core territories and buffer zones. However, at the regional scale, the hotspot radius was estimated between 15 and 50 km, which did not match with the 7-8 km wolf territory radius estimated in France through telemetry and genetic tracking (Duchamp et al., 2012). Even at the local scale, where we expected a better perceptibility of wolf territorial behaviour, the hotspot radiuses were still too high to match with field observations, the lowest estimation being 12 km. Nevertheless, pack cohesion is low during summer and pack members may not forage together (Metz, Vucetich, Smith, Stahler, & Peterson, 2011), which can potentially increase the pack foraging surface. Moreover, lone wolves in dispersion may roam around pack territories in these buffer zones, where they have less risk to encounter territorial wolves (Mech & Boitani, 2003). These ecology features could contribute to smooth the clustering pattern.

Wolves share parental care among pack members to increase pup survival, and have high dispersal abilities (Mech & Boitani, 2003). These features partially explain why wolves were able to recolonise almost half of mainland France in only two decades. Our 24-year depredation dataset allowed an original analysis of the trends in the depredation patterns through wolf recolonisation. During the first period of recolonisation (1995-1999), large spaces were vacant and pack territories were not adjacent to avoid competition (Louvrier et al., 2018). This could explain why only aggregation in the depredation pattern was observed during this period. Once wolf distribution homogenised across the study area from 2000, aggregation started to weaken at the largest analysed distances (2nd period, 2000-2003) and then turned into repulsion between 15 and 30 km (3rd period, 2004-2012). The densification of wolf territories therefore seemed to create the typical clustering pattern (hotspots separated by coldspots). However, from 2013 to 2018, the results at the regional scale showed that, apart from large hotspots which persisted in space and time, the distribution of depredations elsewhere in the study area tended to form sporadic small hotspots and overall tended to randomness. This result could be explained by the wolf expansion that produced very high rates of depredations spreading out all over the study area. The randomisation was also observed at the local scale once depredations reached around 500 from 2013. The randomisation could also be explained by the depredation risk homogenisation among pastoral surfaces, because of the increasing number of farmers who protected their flocks against wolf depredations (MTES & MAA, 2018). The sporadic hotspots could therefore result from occasional environmental or pastoral conditions favouring only briefly depredation (*e.g.* fog, protection fails). This was consistent with the right-skewed distribution of the number of attacks per pastoral surface: in a given year, most pastoral surfaces were not experiencing depredations, or only one or two. On the other hand, the long-lasting hotspots encompassed a large number of depredations. They could result from environmental, topographic or pastoral vulnerability to depredation, or from wolf accommodation to livestock depredations and transmission of this behaviour through generations (Meuret, Lescureux, & Garde, 2018). The observed trends in the depredation patterns could also result from a temporal change in sheep availability, for which we only had two censuses (1996 and 2012). However, the data consistency between the censuses suggested that this risk was reduced. In any case, we demonstrated the underlying livestock availability was of particular importance to any study on depredation hotspots.

Management implications

Reliable estimates of hotspot locations can inform risk models (Hoffmann et al., 2019). However, they also constitute a full management tool, especially to allocate resources for protective measures. For example, year-to-year analysis of hotspot identification allows the localisation of long-lasting hotspots which crystallise conflicts (Stahl et al., 2001). The involved farmers could be helped in the understanding of the causes favouring depredations and in the implementation of appropriate preventive tools. This tool is already applied in France, but the descriptive statistics used by the French authorities could be improved by our methodology. The latter indeed guarantees that the identified hotspots are not the result of livestock availability but only of other factors favouring depredations, such as environmental, pastoral or predator-linked factors. Moreover, our methodology allows the localisation of hotspots with small flocks or with flocks grazing for a short period of time. If the K_{inhom} analysis is not necessary for locating hotspots, it allows a general understanding of the depredation pattern at the regional and local scales and its evolution through time, which can help managers to grasp the situation.

Authors' contributions

O Grente, TS, CD, EM and O Gimenez conceived the ideas and designed methodology; O Grente and TS analysed the data; O Grente and TS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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 to the field experts from the Wolf-Lynx French Network who collected wolf presence signs. We also thank IRSTEA and the regional administration of Auvergne-Rhône-Alpes which provided 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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Figures

Figure 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).

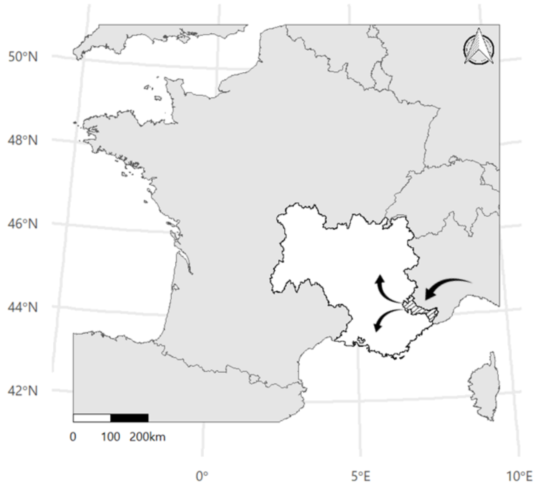


Figure 2: Pastoral information from the 2012-2014 census of the study area, including the MNP (hatched). See Fig. S1 for the 1996-1997 census completed with information from the second census.

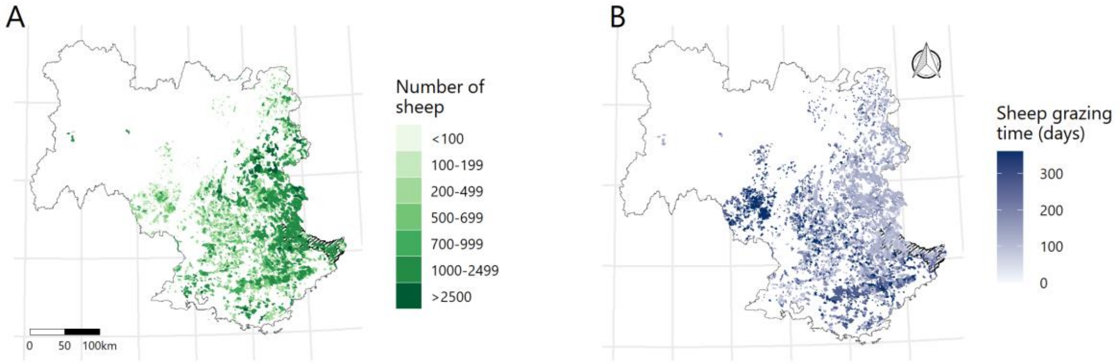


Figure 3: Proportion of 10x10km cells within wolf distribution (yellow), proportion of pastoral surfaces under wolf depredation risk in the whole set of pastoral surfaces (light green), proportion of pastoral surfaces with at least one reported wolf depredation on sheep in the set

of pastoral surfaces at depredation risk (dark green), and number of wolf depredations on sheep (solid red) per year in the area. At the A) regional scale, B) local scale.

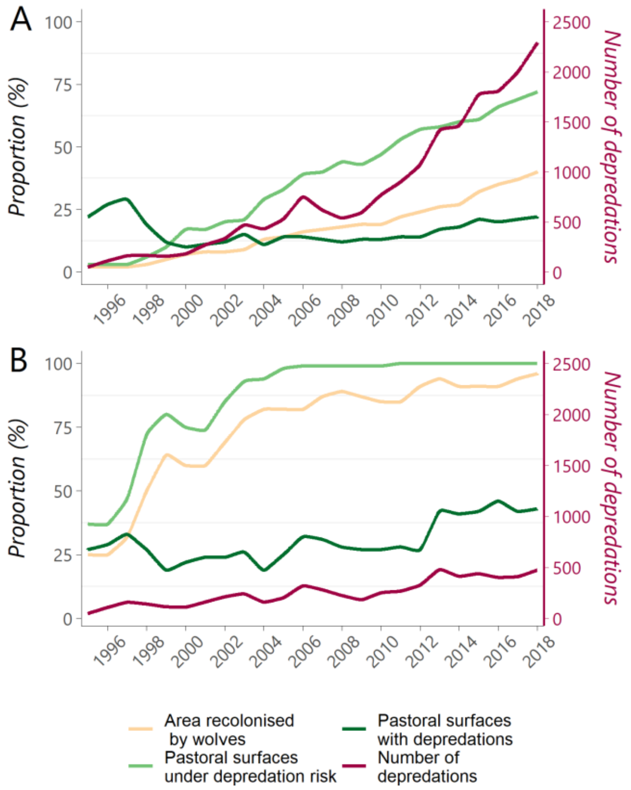


Figure 4: Results at the regional scale of the K_{inhom} function (solid yellow line) and of the K-function where the analysis area was defined as the pastoral surfaces at depredation risk (dotted dark blue line) or as the wolf distribution cells (dotted light blue line), against their corresponding control envelopes, for the years 1995, 2001, 2010 and 2018. The shown distances of r were delimited to those computed by the K_{inhom} function. See Fig. S4 for all years.

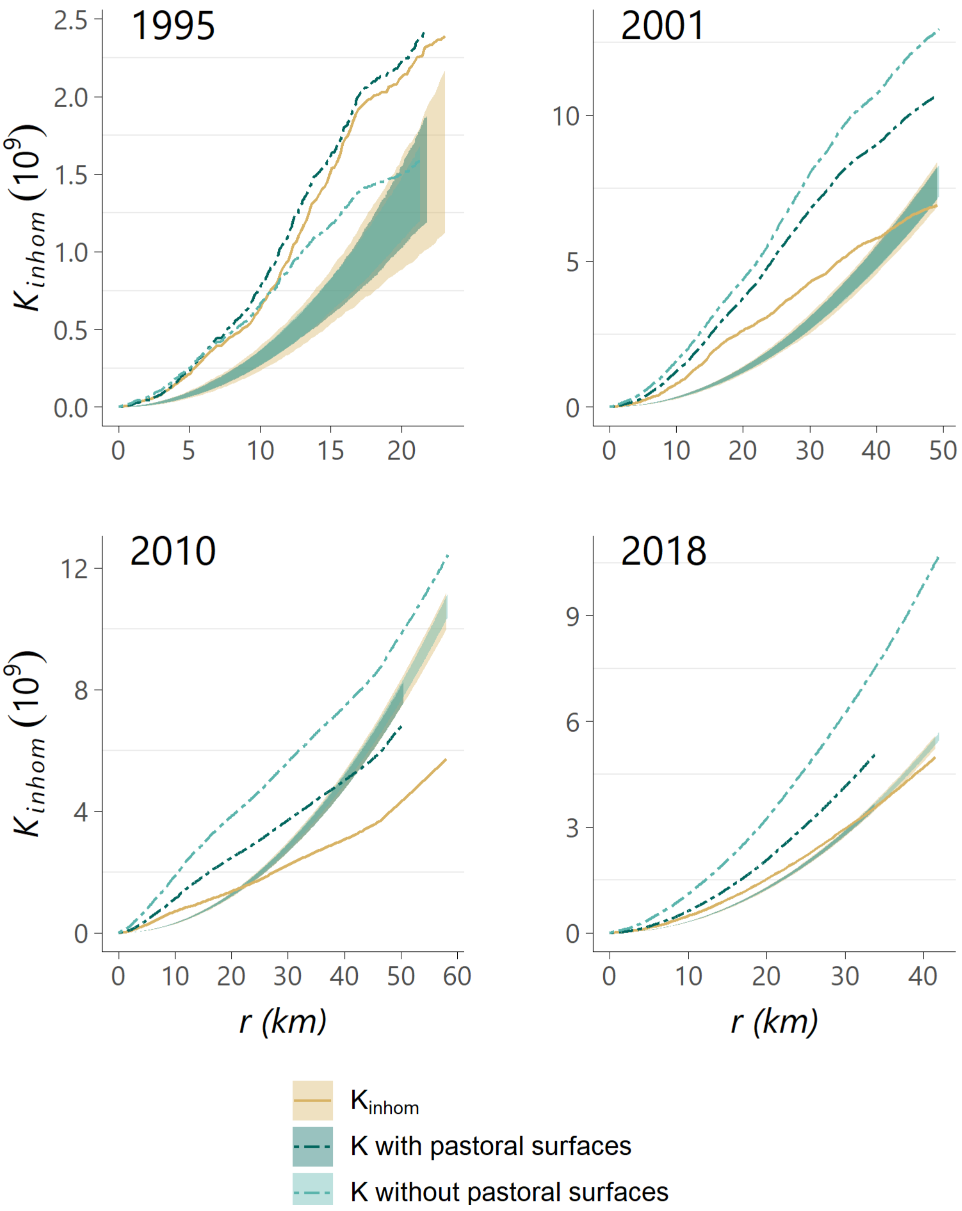


Figure 5: Annual distributions of pastoral surfaces at depredation risk and of verified wolf depredations on sheep at the regional scale for the years 1995, 2001, 2010 and 2018. See Fig. S2 for all years.

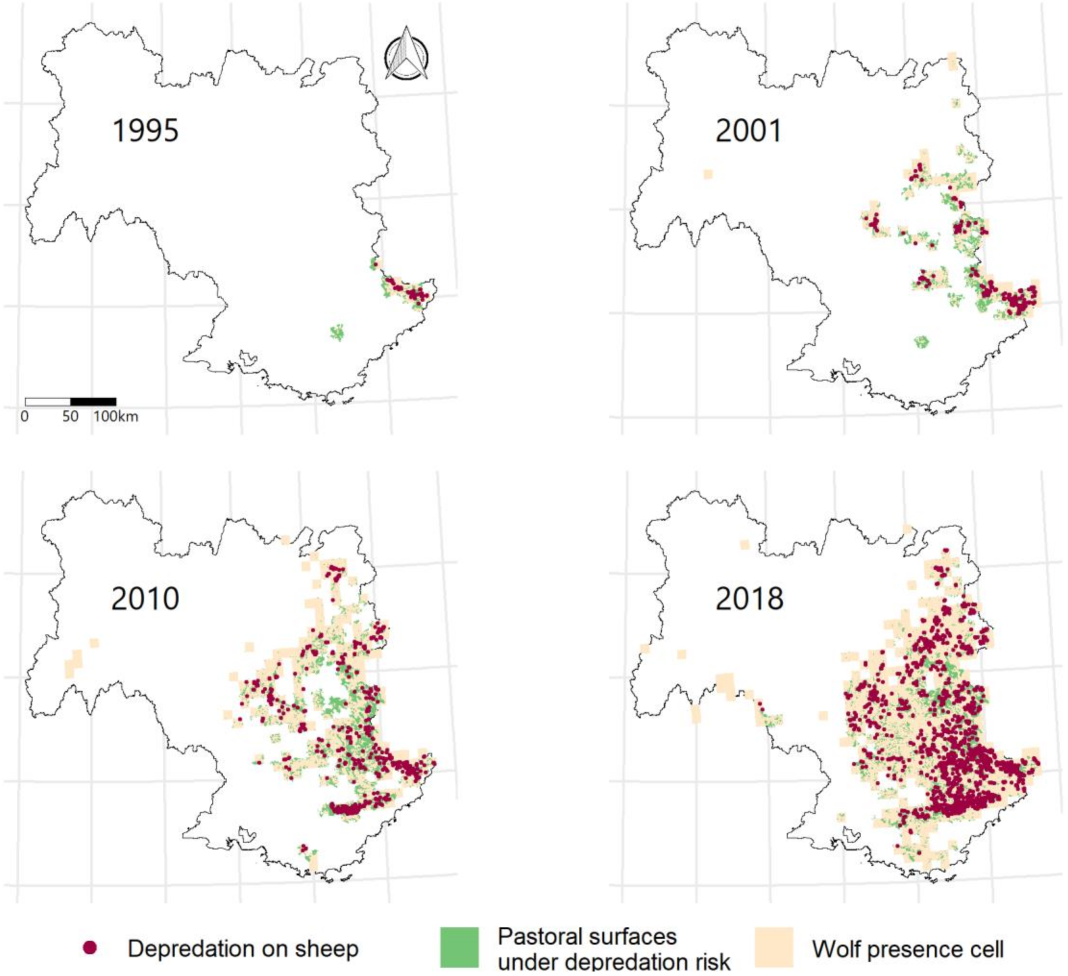


Figure 6: Results at the local scale of the K_{inhom} function for the years 1999, 2004, 2010 and 2018. See Fig. S4 for all years.

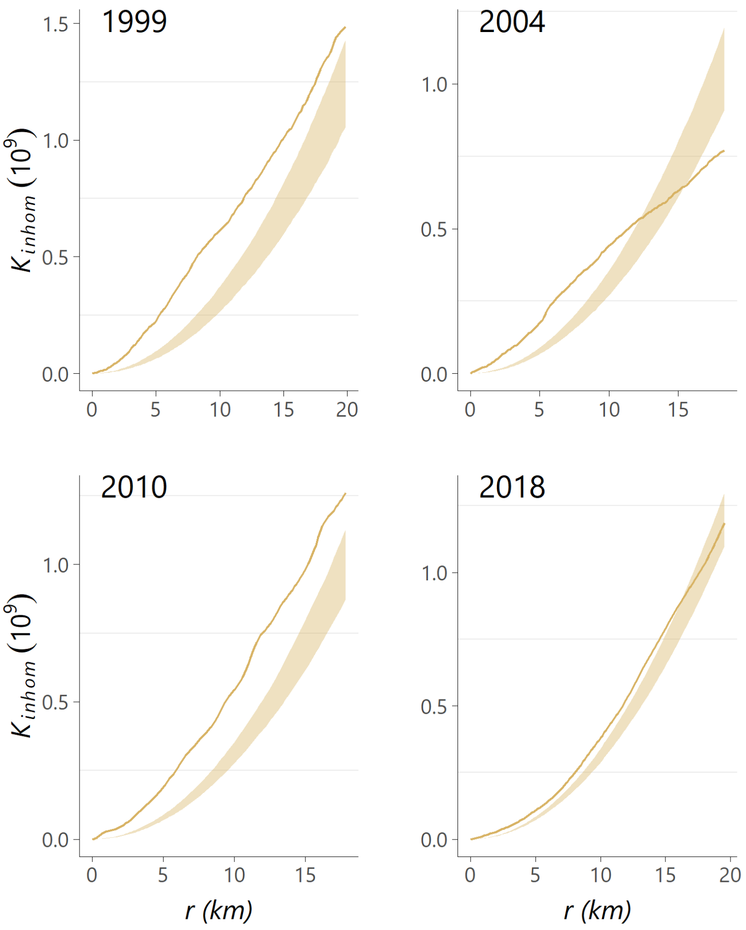


Figure 7: Annual distributions of pastoral surfaces at depredation risk and of verified wolf depredations on sheep at the local scale for the years 1999, 2004, 2010 and 2018. See Fig. S2 for all years.

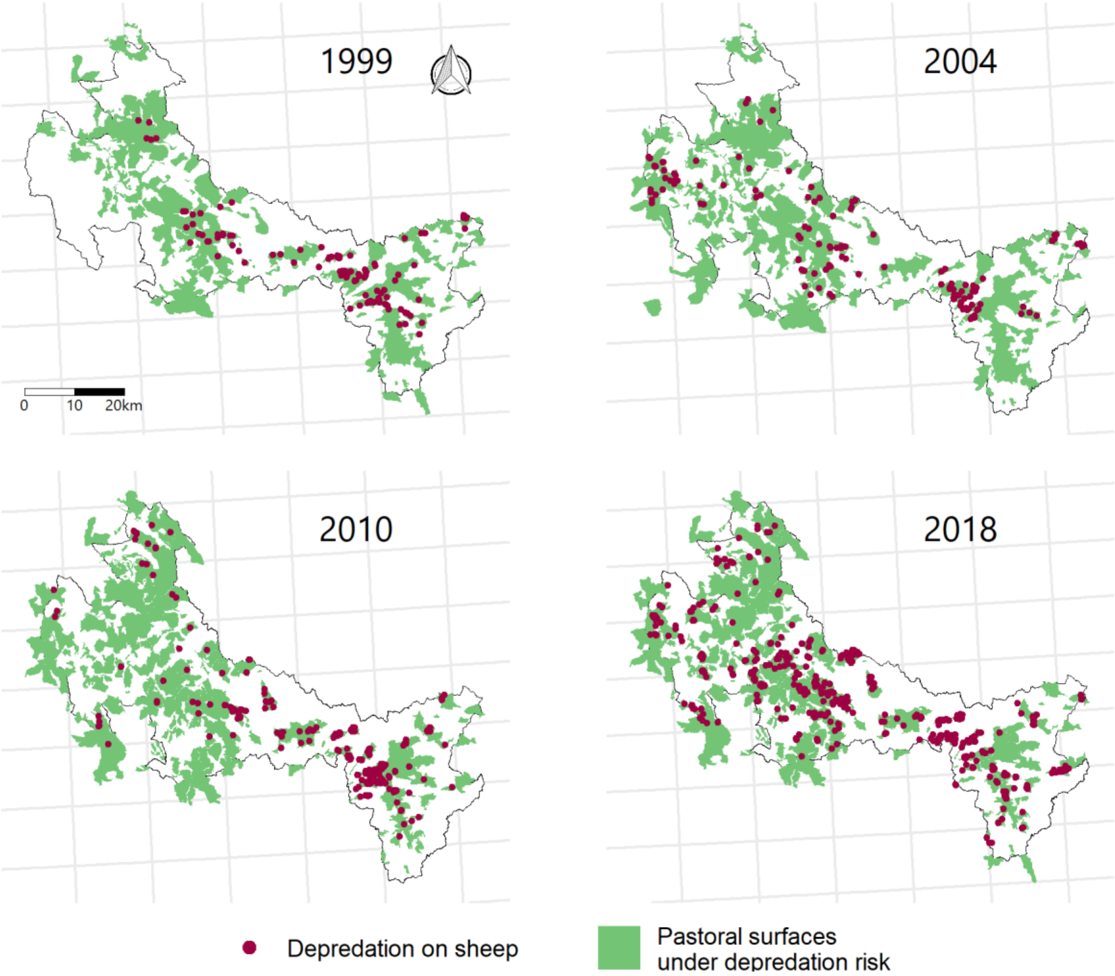


Figure 8: Descriptive results of the Kulldorff statistic used with the observed heterogeneous (yellow) or simulated homogeneous (blue) sheep availability, for each year within the study area. (A) Number of significant hotspots, (B) Proportion of depredated pastoral surfaces into significant hotspots in the whole set of depredated pastoral surfaces, (C) Distribution of the sum of the areas of the pastoral surfaces included into each hotspot (with outliers as black dots).

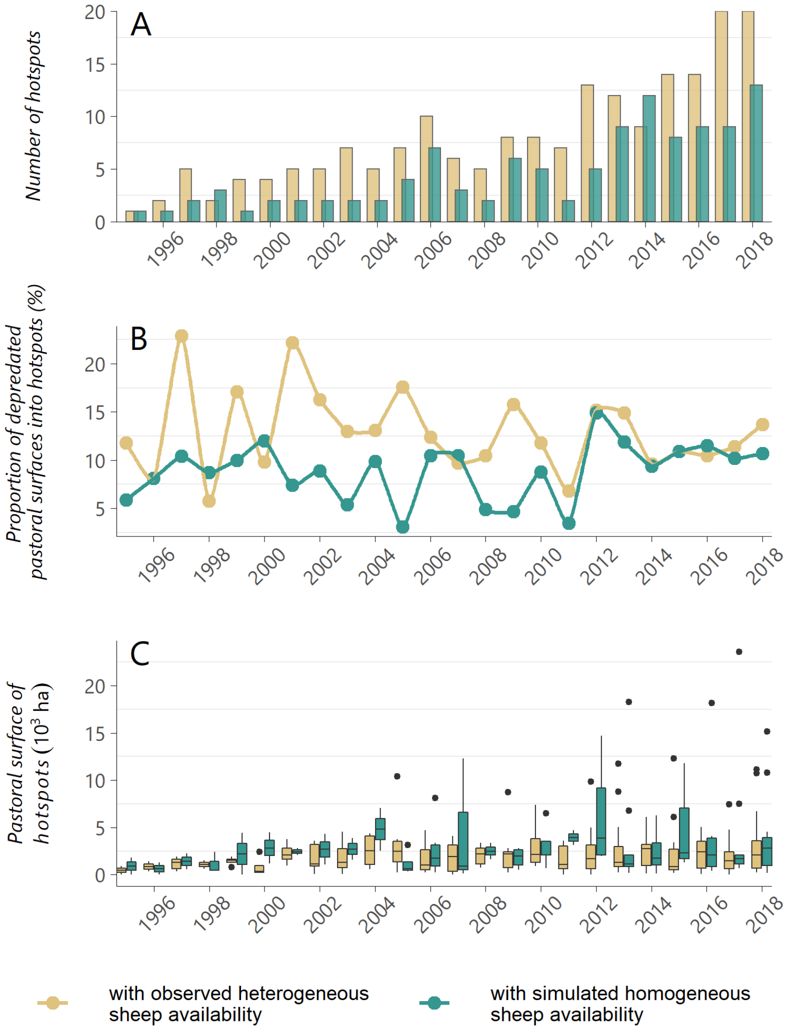
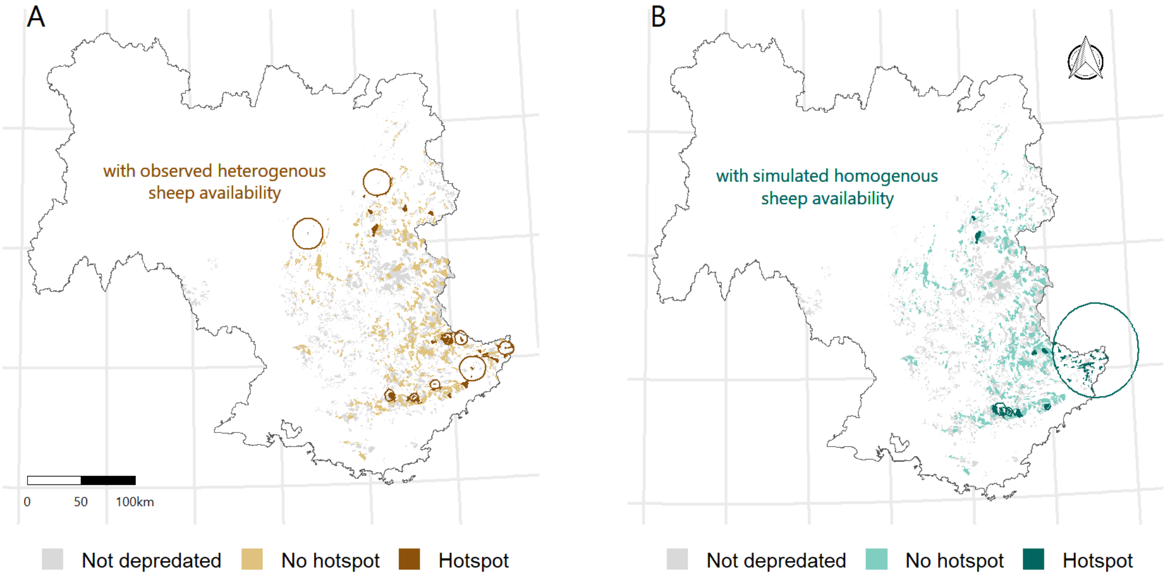


Figure 9: Locations of depredated pastoral surfaces identified as hotspots (dark colour) or not (light colour) in the study area in 2017 according to the Kulldorff statistic results using the observed heterogeneous (A) or simulated homogeneous (B) sheep availability. Pastoral surfaces within the same circles belonged to the same hotspot. Pastoral surfaces which were not depredated (grey) were shown for information but were not used in the statistical analysis. See Fig. S5 for all years.



Supporting Information

Fig. S1 – Pastoral information of the study area, from the census of 1996-1997 (completed with information from the 2012-2014 census) or from the census of 2012-2014. https://oksanagrente.shinyapps.io/Hotspots-SuppFig1/

Fig. S2 – Annual distributions of wolf presence, pastoral surfaces and verified wolf depredations on sheep in the study area between 1995 and 2018. https://oksanagrente.shinyapps.io/Hotspots-SuppFig2/

Fig. S3 – Annual distributions of the number of wolf depredations on sheep per pastoral surface at depredation risk, at the regional and local scales between 1995 and 2018. https://oksanagrente.shinyapps.io/Hotspots-SuppFig3/

Fig. S4 – Annual results between 1995 and 2018 from the K_{inhom} function from the K-function with the analysis units defined as the pastoral surfaces at depredation risk or as the wolf distribution cells. https://oksanagrente.shinyapps.io/Hotspots-SuppFig4/

Fig. S5 − Annual locations between 1995 and 2018 of depredated pastoral surfaces identified or not as hotspots, according to the Kulldorff statistic used with the observed heterogeneous or simulated homogeneous sheep availability at the regional scale. https://oksanagrente.shinyapps.io/Hotspots-SuppFig5/