# Spatio-temporal dynamics of attacks around deaths of wolves: A statistical assessment of lethal control efficiency in France

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**Abstract**

Evaluating the efficiency of lethal control of large carnivores such as wolves to reduce attacks on livestock is important given the controversy surrounding this measure. We used retrospective data over 10 years and an intra-site comparison approach to evaluate the effects of lethal control on the distribution of attack intensities in the French Alps. We analyzed 278 legal killings of wolves between 2011 and 2020 and the 6110 attacks that occurred during a period of ± 90 days and within 10 km around these lethal removals. This large number of attacks allowed us to perform an original framework that combined both continuous spatial and temporal scales through 3D kernel estimation. We also controlled the analysis for livestock presence, and explored different analysis subsets of removals in relation to their locations, dates and proximity to other removals. This statistical method provided an efficient visualization of attack intensity spatio-temporal distribution before and after removals. A decrease of the intensity of attacks was the most common result after the lethal removals of wolves. However, this outcome was not systematic for all subsets and depended on the scale of the analysis. In addition, attacks tended to persist after removals while showing frequent interruptions in time after but also before removals. We also observed localized positive trends of attack intensities at varying distances from removals after they occurred. To summarize, our results showed that considering the scale of the analysis is crucial and that effects should be analyzed separately for each local context. As a next step, we recommend to move forward from patterns to mechanisms by linking the effects of lethal control on wolves to their effects on attacks through analysis of fine-scaled data on wolves and livestock.

***Keywords:*** *before-after* study design, *Canis lupus*, culling, depredation, French Alps, kernel density estimation, removal, sheep

## 1. Introduction

Lethal control of large carnivores aims to reduce damages on livestock by decreasing the encounter risk with livestock or by removing individuals inclined to predation on livestock (Lennox et al., 2018). The side effects of these management practices are often claimed to undermine the efficiency of lethal control or even to create more damages (Elbroch and Treves, 2023). In the specific case of social canids like wolves, studies have mostly pointed out additive human-caused breeder loss as a risk for increasing damages on livestock (Jęodrzejewska et al., 1996; Žunna et al., 2023). Social instability can indeed cause multiple reproduction (Ausband et al., 2017) or pack disruption (Cassidy et al., 2023), although their effects on damages have not been assessed.

Implementing controlled experiments to evaluate the efficiency of lethal control of large carnivores is extremely difficult, considering the involved large spatial and temporal scales. To date, no experimental study has been conducted for this matter (Treves et al., 2016, 2019). Only Allen (2014) conducted a controlled experiment to evaluate dingo's baiting efficiency but using the number of lactation failures as a proxy for calves lost to predation instead of direct cases of predation.

Also, retrospective studies have been conducted to answer the question of lethal control efficiency. The data they used were not collected within a scientific frame but generally through management (*e.g.* damages from compensation schemes). Most of retrospective studies on social canids (gray wolves *Canis lupus*, dingoes *Dingo dingo*, coyotes *Canis latrans*) were correlative and tested for a relationship between the number of livestock damages and the number of killed predators (Šuba et al., 2023; Fernández-Gil et al., 2016; DeCesare et al., 2018; Conner et al., 1998; Allen, 2015; Kutal et al., 2023). However, this approach is not suited to infer causality and is subject to high risks of confounding factors and to analytical variability (Gould et al. 2023). For example, three correlative studies which used the same dataset concluded differently on the effect of lethal removals of wolves on livestock damages (Kompaniyets and Evans, 2017; Poudyal et al., 2016; Wielgus and Peebles, 2014).

A smaller number of retrospective studies used a comparative approach. Harper et al. (2008), Bradley et al. (2015), Santiago-Avila et al. (2018) and Wagner and Conover (1999) compared situations where lethal control was used and situations where it was not, *i.e.* made inter-site comparison. Bjorge and Gunson (1985) and Blejwas et al. (2002) compared the situation before and after the implementation of lethal control within the same site. The intra-site comparison they used, also called *before-after control impact* study design, intends to reduce the risks for confounding factors of inter-site comparison because these risks are generally higher across space than across time. Kutal et al. (2023) was the only study to mix inter-site and intra-site comparisons, by combining comparisons before and after hunting season and between sites with and without hunted wolves.

Five of the seven comparative studies on social canids showed that lethal control significantly decreased damage recurrence, whereas Santiago-Avila et al. (2018) and Kutal et al. (2023) found no significant effect of lethal control on damages. Yet, results suggested variability in the efficiency of lethal control. For example, Harper et al. (2008) detected that only the death of an adult wolf male was significantly efficient, whereas Bradley et al. (2015) did not detect sex or age conditions on efficiency. Variability could also result from the study designs themselves, as these studies used different spatial and temporal scales to evaluate lethal control efficiency. Thus, small scale (*e.g.* 4 km in Harper et al. (2008)), medium scale (*e.g.* pack territory in Bradley et al. (2015)) or large scale (*e.g.* 711 km² in Kutal et al. (2023)) could be used for space, sometimes within the same study (*e.g.* Santiago-Avila et al., 2018). Time scale could also be disparate, going from several days or months

(*e.g.* Blejwas et al. (2002)) to two years (*e.g.* Kutal et al., 2023) or more (*e.g.* Bjorge and Gunson (1985)). Most importantly, none of the mentioned retrospective studies have both used continuous spatial and temporal scales, making it difficult to identify potential gradients of lethal control effects, as those suggested in Santiago-Avila et al. (2018). Finally, most of these studies have not controlled for livestock presence or abundance, yet the primary factor structuring damage risk and one of the highest risks of confounding factor.

The aim of our study was to evaluate the effects of the lethal control applied for gray wolves in France on the intensity of attacks on sheep. We used the data collected by the French administrations for the period 2011-2020. Given the retrospective nature of our study, we attempted to fill the gaps identified in the previously mentioned retrospective studies on the subject. For that purpose, we made intra-site comparisons, used continuous spatial and temporal study scales and controlled for livestock presence through an original framework of kernel estimation.

## 2. Methods

### 2.1 Management context and study area

After historical campaigns of destruction, gray wolves disappeared from France at the beginning of the twentieth century, despite being present on the whole metropolitan territory at the end of the eighteenth century (de Beaufort, 1987). From the 1970s, the combination of protective legislation across Europe and the increase of forested habitat allowed the recovery of the species in France through the dispersal of a few individuals from the Apennines population in Italy into the French Alps (Linnell and Cretois, 2018; Fabbri et al., 2007; Poulle et al., 1997). Nowadays, the French wolf population is still expanding but remains mainly restricted to the south-east corner of France, with only a few reproductive packs outside of this area (Louvrier et al., 2018).

South-east France is characterized by a variety of landscapes, including high altitude mountains, Piedmont plains, hills and garrigue lands, where mountain and Mediterranean climates converge. Livestock farming is generally extensive. Herds of cow are principally present in the north of the region, while those of sheep are present in the whole area (Dobremez et al., 2016). The pastoral practice of transhumance, consisting in moving all or part of herds from low to high altitude pastures during summer and vice versa during winter, is still important. Duration of grazing season increases following a north-south gradient, with some herds from low altitudes in the south grazing all year round (Grente et al., 2022). Livestock owners can share pastures, and even gather their herds to limit the cost of transport for transhumance and of herding. In the Alps, herds of cows are generally not mixed with flocks of sheep, but the latter can be occasionally mixed with goats. Mean size of transhumant flocks of sheep varies greatly between alpine departments and ranges between less than 250 sheep up to 2000 sheep (Agreste, 2021).

To prevent attacks, France subsidies non-lethal measures for protecting flocks of sheep or goat through livestock guarding dogs, fences and additional shepherds. Lethal removals by ground shooting are authorized in France through derogations to the strict protection provided by the Bern Convention and of the Habitats Directive to *Canis lupus*. Other forms of removals (*e.g.* trapping, aerial shooting) are prohibited. Conditions of application of ground shooting are defined by ministerial decrees (*e.g.* Ministère de la Transition Ecologique et Solidaire, 2018) and depend on the implementation of non-lethal protective measures and on the recurrence of attacks. If the conditions are met, the administration assigns the derogation to the livestock owner for a duration between two months and five years. The owner itself or a mandated hunter can shoot wolves during

an attack on its livestock (hereafter 'simple defense'). When attacks persist, governmental agents or special volunteers who are trained to shoot wolves may support owners in protecting their livestock (hereafter 'reinforced defense'). If the level of attacks escalates in an area, the administration can eventually decide to shoot a specific number of wolves under game hunting conditions (hereafter 'hunting').

Within the 2011-2020 studied period, lethal removals were for a large majority executed in south-east France. Only three lethal removals were outside this area and concerned lone wolves which dispersed far and whose territories were very isolated. Their deaths could only lead to an absence of attacks. This context was totally different from the one in the Alpine range where the wolf population was settled. Therefore, we restricted our study area to the two south-east regions, Provence-Alpes-Côte-d'Azur in its entirety and Auvergne-Rhône-Alpes restricted to its five most south-eastern departments, Ardèche, Drôme, Isère, Savoie and Haute-Savoie (Figure 1).

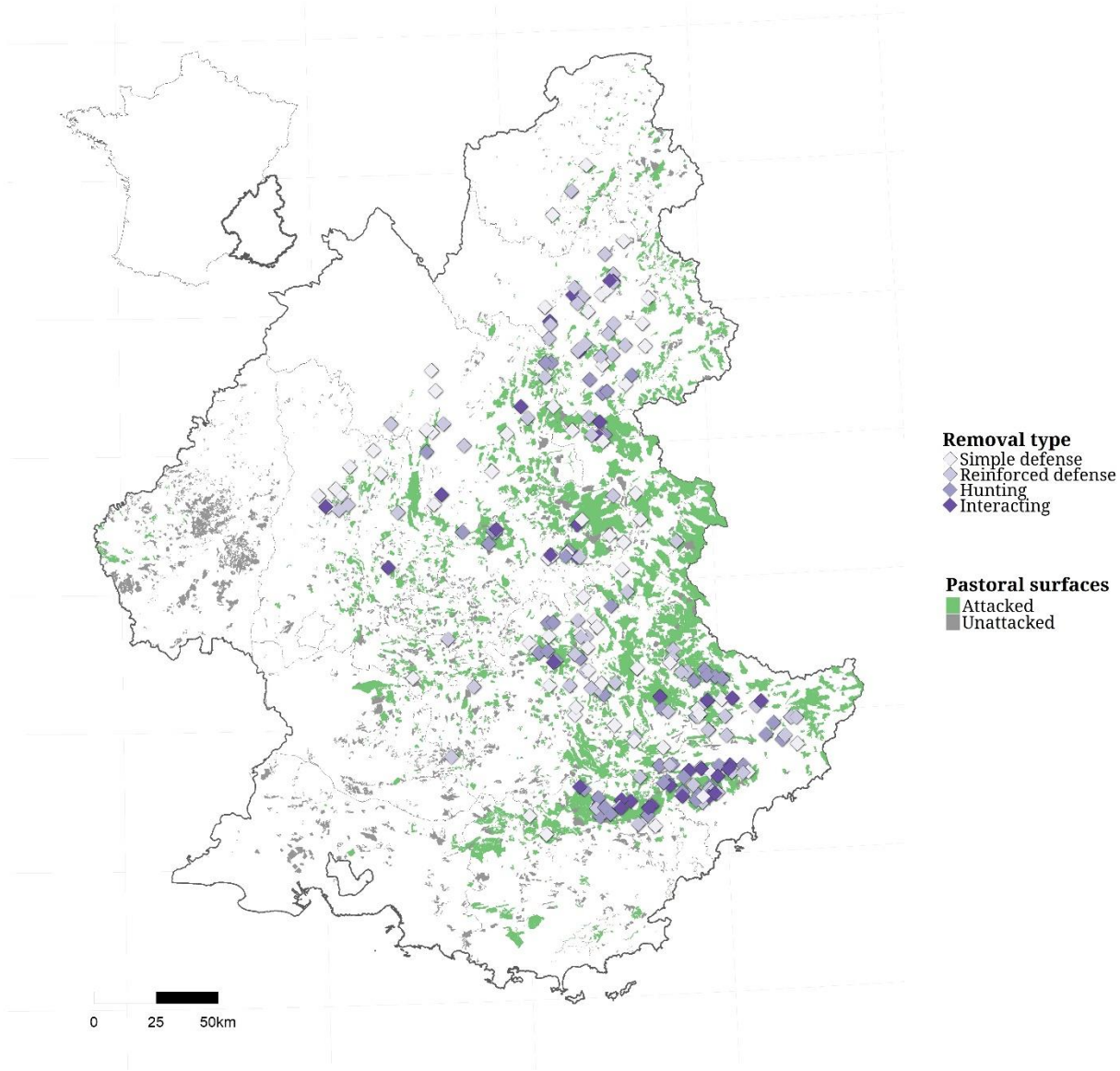



*Figure 1. Study area and location within France. Purple points represent locations of the 232 analyzed lethal removals of wolves, colored according to the three types of shooting implementation (simple defense, reinforced defense, hunting) and of the 32 groups of 'interacting' lethal removals of wolves that were combined for analysis (darkest color). Pastoral surfaces with or without attacks are shown in green and grey, respectively, after correction for inconsistencies between the pastoral and attack datasets (see part 2.2.4).*

## 2.2 Datasets

### *2.2.1 Lethal removals*

We used the records of deaths of wolves from 2011-2020 compiled by the regional French administrations. We used the 362 records of wolves killed by legal shootings and that were geolocated within the study area. Dates of lethal removals were recorded, but not the hour. The number of lethal removals increased over time and could be divided into three periods, 2011-2014, 2015-2018 and 2019-2020, that represented respectively 8%, 44% and 48% of the dataset, for annual means of 7 (± 6), 40 (± 6) and 87 (± 3) lethal removals respectively.

Almost half of the records were cases of reinforced defense (48%), while simple defense and hunting cases represented respectively 27% and 25% of the dataset. There were 58 records (16%) for which no wolf body was found after the shooting, but they were considered as killed because there was enough evidence for lethal injuries. For the remaining 304 records, information from the necropsy reports was available on the sex and the estimated age class (pup, subadult or adult) of the killed wolves and on the annual reproductive status for females.

### *2.2.2 Attacks on sheep*

We used the claims of attacks on livestock from 2010-2020 compiled by the French administration and for which wolf responsibility could not be discarded. Among the 25 948 available claims, we used the 23 645 claims that were geolocated within the study area. We then restricted the dataset to the 21 936 claims on sheep. Each claim corresponded to one or several dead or wounded sheep.

Apart very few specific cases, all claims were checked in the field by trained public agents. They followed a standardized procedure to estimate the date of the attack and if wolf responsibility could be discarded or not. Compensation was attributed regardless of non-lethal measures up to 2019. From 2020, compensations after two compensated attacks depended on the implementation of protective measures, with conditions of implementation varying locally according to the level of attacks of municipalities. Protective measures are widely implemented in south-east France (Meuret et al., 2020). We have therefore confidence in the level of reports of attacks noticed by breeders.

### *2.2.3 Spatio-temporal sheep distribution*

We used the data from the pastoral census of the two south-east regions Provence-Alpes-Côte-d'Azur and Auvergne-Rhône-Alpes conducted by the National Research Institute for Agriculture, Food and the Environment (Dobremez et al., 2016). The census indexed and delimited for the period 2012-2014 the pastoral units at medium or high altitude used by flocks, as well as the pastoral zones at lower altitudes. Giving the relative stability of the use of the pastoral units and zones over time (Grente et al., 2022), we assumed the information of the pastoral census was valid for our entire study period. Pastoral units and zones delimited the spatio-temporal area where attacks could have occurred. Therefore, our analysis was restricted to the pastoral area delimited by this census, in order to control for livestock presence.

Among the 3576 pastoral units and the 8862 pastoral zones of the census, we used the 3176 units and 8184 zones within the study area. We restricted the dataset to units and zones that were used for grazing sheep, regardless of the other livestock. The annual number of grazing sheep was on average 955 (standard deviation, hereafter '±', 764) for units (range 2—6000) and 412 (± 411) for zones (range 1—3600). The months for which the area was grazed were known for each pastoral unit. Only the seasons in use were available for pastoral zones. Therefore, we attributed to the pastoral zones the months corresponding to the seasons for which they were grazed (spring: March

to May, summer: June to August, fall: September to November, winter: December to February). The annual number of grazed months was on average 6.9 (range 1—12). The total size of our final dataset of pastoral units and zones, hereafter pastoral units, was 4987 (Figure 1).

#### *2.2.4 Attributing attacks to pastoral units*

The attack dataset showed 59% of consistency with the dataset of pastoral surfaces, meaning that 59% attacks were within pastures that were in use according to the pastoral census. The other attacks could be outside pastoral surfaces, or could have occurred in months for which pastoral surfaces were not supposed to be in use according to the pastoral census. These mismatches could result from changes in the spatial or temporal use of pastoral surfaces, from errors during the attack record (*e.g.* geolocation approximation), or because attacks occurred in non-indexed pastoral surfaces.

When attacks were within pastures and when difference between the month of their dates and the sets of grazed months of their pastures did not exceed three months (9% of total attack dataset), we only updated the pastoral census by adding the months of the attacks to the corresponding pastures. Otherwise, we relocated attacks to their closest pastures within a 500 meters radius by favoring pastures with the smallest difference between their sets of grazed months and the months of the attacks. When these differences exceeded 3 months, or if no pastoral surface could be found within a 500 meters radius around the attacks, we excluded these attacks (13% of total attack dataset). Relocations were done at the closest point of the pastoral surfaces to the original attack locations (19% of total attack dataset). When necessary, we added the months of the relocated attacks to the sets of grazed months of their new pastoral surfaces. The final dataset of attacks had 19 302 events.

Contrary to attacks, lethal removals did not require to be located within pastoral surfaces, as hunting did not necessarily occur within pastoral surfaces.

### 2.3 Analysis

Apart from being precisely geolocated, our data about attacks and lethal removals were very unbalanced in favor of attacks (19 302 attacks against 362 lethal removals). Consequently, we could adopt an original approach consisting in choosing removals as focal points through the use of 3D buffers, and in computing attack intensities over continuous spatial and temporal scales.

#### *2.3.1 Construction of 3D buffers*

We attributed to each lethal removal a spatio-temporal buffer, which can be visualized as a 3D cylinder centered on the lethal removal event. The circle base of the cylinder corresponded to the spatial dimensions (X, Y) and had the role to scan for attacks within the pastoral space around the lethal removal. The height of the cylinder corresponded to the temporal dimension, the left and right parts scanning for attacks that had occurred before or after the lethal removal, respectively (Figure 2.A).

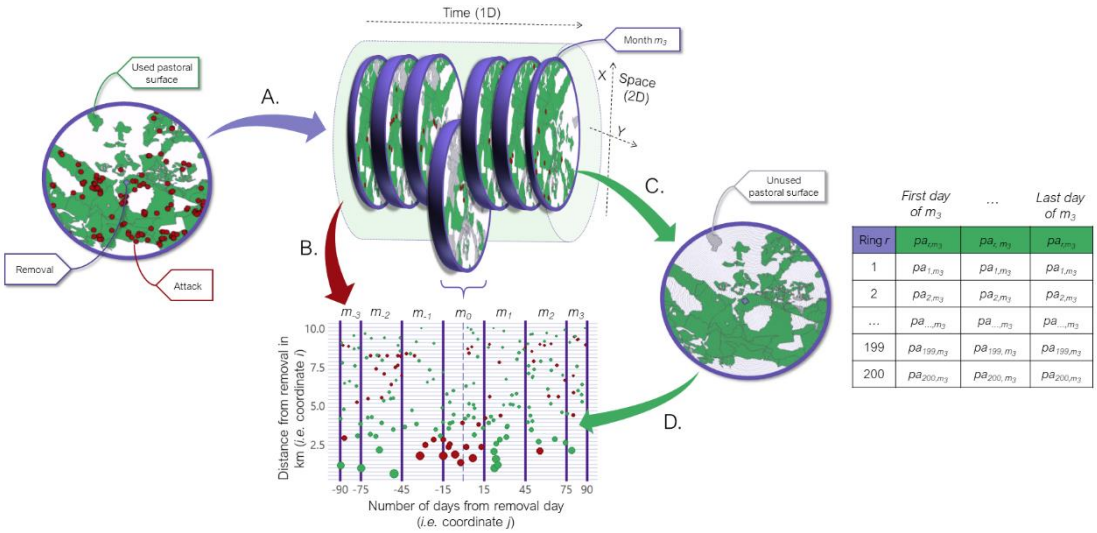



*Figure 2. Data transformations for one lethal removal (purple point) occurring on 15th of August 2017 as an example.* ***A.*** *Attribution of the 3D spatio-temporal buffer around the removal. Each slice represents the occurrence of observed attacks (red points) in a radius of 10 km around the removal in a given month m. Months could be complete (from $m_{-2}$ to $m_2$) or partial ($m_{-3}$ and $m_3$, here only 15 days each). Monthly slices were chosen for visual convenience, but slices were daily in the analysis. Attacks (red points) in the buffer have 3 coordinates: 1 temporal (height of the cylinder), and 2 spatial (x,y).* ***B.*** *Reduction of 2D spatial coordinates of observed attacks of the 3D buffer to 1D, through the Euclidian distance to the removal (coordinate i, i.e. rows). Time coordinate becomes coordinate j (columns).* ***C.*** *Dividing one 10-km radius slice around the removal into 200 rings (here only 50 are represented for visual convenience) to calculate the total pastoral area pa that was used during the corresponding month of the slice. The column of pa is then duplicated into the number of days of the corresponding month (i.e. information about pastoral use was monthly). The operation is repeated for each slice of the 3D buffer.* ***D.*** *Simulation of coordinates i and j of attacks (green points) based on the matrix of pa from step C. The number of simulated attacks is the same as the number of observed attacks. The size of points represents the spatial correction $1/pa_r$ based on similar calculations as step C but achieved on the pastoral surfaces regardless of their use (i.e. as in the most left circle). Note that the observed and simulated datasets are placed on the same figure for visual convenience here, but were treated separately during the kernel estimations.*

The spatio-temporal buffer was composed solely of the pastoral surfaces where attacks could occur. Therefore, the buffer was sparse, and remained empty where there was no pastoral surface around the removal event, or when the pastoral surface was not grazed according to the pastoral census.

We set the radius of the cylinder at 10 km, in order to encompass more than one wolf territory radius, estimated at 7–8 km in France through telemetry and genetic tracking (Duchamp et al., 2012). Therefore, ripple effects, if any, could be observed up to 10 km from the lethal removal. The pastoral surfaces overlapping the spatial buffer were truncated to the spatial buffer.

We set the height of the cylinder to 180 days, meaning that all attacks occurring 90 days before and 90 days after the lethal removal were part of the temporal buffer. Thus, we analyzed the effect of lethal removal on a full season if the removal event occurred in the middle of the season, or on two successive seasons if not. The day of the removal was not part of the buffer, because we could not know if an attack recorded at the day of the removal occurred after of before the removal, having no information about the hour of both attacks and removals.

Attacks were not homogeneously distributed across space and time (Grente et al., 2022). Increasing the radius or the height of buffers compressed the attack distribution towards the centers of buffers (*i.e.* at small spatial and temporal distances), and prevented an optimal reading of the results.

We ensured that the buffers did not overlap geographic areas or periods without data about attacks. We removed the 84 lethal removals occurring at less than 10 km from the terrestrial limits of the

study area or occurring after the 1st October 2020, eventually leaving 278 analyzed lethal removals (Figure 1).

Most buffers overlapped in space and in time, with a total of 86% of buffers overlapping with at least another one. However, only few removal events were simultaneously close in space and time (Figure 3), with 82 removals separated by less than 5 km and less than 25 days. In these cases, we considered that the risks of interaction between removals were high enough. We called these removals, 'interacting removals'. We pooled the interacting removals into 36 groups, with each corresponding to a set of interacting removals. For the special case where two removals were not interacting, but were both interacting with a third removal, we considered these three removals were part of the same group of interacting removals. On average, 2.28 wolves (± 0.45, range 2—3) were killed per group.

We attributed a single buffer to each group of interacting removals, of 10 km radius, of 180 days height and centered on the centroid of the interacting removals of the group. To compare the attack intensity before and after each group of interacting removals, we excluded the attacks recorded between the date of the first removal of the group and the date of the latest removal of the group. The exclusion period lasted 7.5 days on average (± 8.38, range 0—27). In cases where interacting removals occurred the same day, only the date of the removals was not part of the buffer, as previously.

We ended up with 232 spatio-temporal buffers, including 36 buffers of groups of interacting removals, corresponding to a total of 6110 attacks. On average, a buffer included 26.3 attacks (± 20.7, range 0—100).

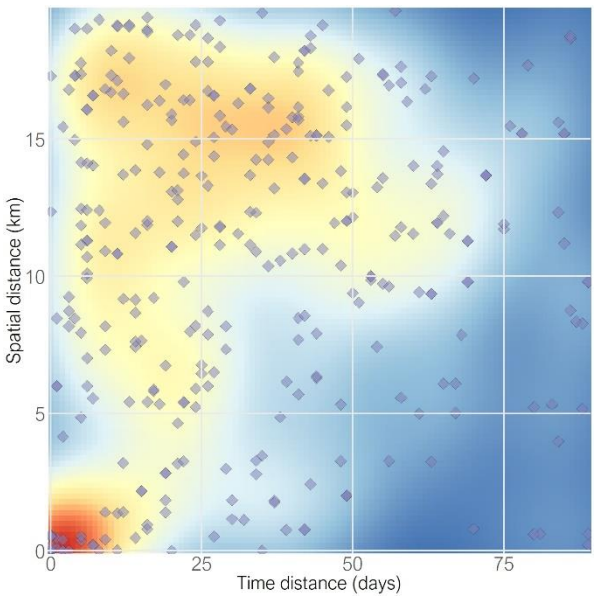



*Figure 3. Spatial and temporal distances between the 352 pairs of lethal removals whose spatio-temporal buffers overlapped.*

### *2.3.2 Reducing the number of spatial dimensions*

Methods for the analysis of interactions of several types of datasets with three dimensions are yet to be developed and may suffer from the curse of dimensionality (Wikle et al., 2019). Therefore, we followed standard geostatistical practices and reduced the two spatial dimensions of the buffers to one by computing the Euclidian distance of each attack to the center of the buffer. In other words,

we converted the spatial circle of buffers to a line. The temporal dimension corresponded to the difference in days between each attack and the date of the removal of the buffer. In the case of interacting removals, we used the first (or last) date of the group if the attack occurred before (or after) the exclusion period. Thus, each attack occurring in a buffer had then two coordinates *(i, j)* corresponding to the spatial *i* and temporal *j* distances from the center of the buffer (Figure 2.B).

Nevertheless, converting a 2D circle into a 1D line always induces a spatial bias that gives more representation of points farther away, simply because the circle perimeter increases linearly with circle radius. Therefore, we should have applied a spatial correction of 1/*i* to each attack of a buffer, with *i* the Euclidian distance of the attack to the buffer center. However, the buffers were delimited by pastoral surfaces that were not homogeneously distributed around the buffer center. In other words, the spatial bias did not increase linearly with the radius, but according to the perimeter fraction that intersects with pastoral surfaces. For example, the spatial bias could be low at the furthest distances of the buffers if pastoral surfaces were almost non-existent at these distances.

To incorporate pastoral surfaces to the spatial correction, we sliced up the circle of each buffer into 200 rings *r* of progressive radius, from 0.025 to 9.975 km. Width of rings were therefore 50 m. We calculated $pa_r$, the area of pastoral surfaces of each ring *r*. We then attributed to each attack from the buffer the inverse of the pastoral area of its ring, $1/pa_r$ (Figure 2.B-D), corresponding to its weight in the later analysis (part 2.3.4). Because attacks could only be located in pastoral surfaces (part 2.2.4), $pa_r$ of rings containing attacks could not be null.

### *2.3.3 Simulating attacks according to livestock presence*

We controlled for livestock presence in each buffer by randomly simulating attacks with a distribution defined according to the locations of pastoral surfaces of the buffer and their grazed months. The simulated dataset corresponded to the expected distribution of attacks if they were only dependent on the livestock presence.

For each buffer, we used the same 200 rings *r* as in part 2.3.2. For each month *m* represented in the temporal buffer, we calculated the set of $pa_{r,m}$ by considering only pastoral surfaces that were grazed this month according to the pastoral census (Figure 2.C). Thus, we constructed a *pa* matrix *[r, m]* for each buffer, where columns were sorted following the order of months in the temporal buffer. Each column *m* was then duplicated according to the number of days of this month included in the temporal buffer. Thus, the matrix dimensions were 200 rows and 180 columns. Eventually, the matrix coordinates *(r, m)* became similar to the coordinates (*i, j)* of the observed attacks, with a slightly coarser spatial resolution of 50 meters (*i.e.* ring width) and the same temporal resolution of 1 day.

We converted the matrix into a two-dimensional pixel image. We generated a random point pattern, with the pixel image acting as the probability density of the points. We generated the same number of points as the number of observed attacks in the buffer. We extracted the coordinates *(i, j)* of each point, hereafter called simulated attack, corresponding to its spatial and temporal distances to the buffer center. We also attributed the spatial correction $1/pa_r$ for each simulated attack, following the same calculations as in 2.3.2 (Figure 2.D). We repeated the simulation 1000 times for each buffer.

### *2.3.4 Kernel estimates*

For a subset of buffers (see subset definition in the next section 2.3.5), we applied an anisotropic Gaussian kernel estimation of the observed attacks, based on the distribution of their spatial *i* and

temporal *j* coordinates, with the spatial correction $1/pa_r$ as weight. We used two separate bandwidth parameters for spatial distance and temporal lag, of 500 meters and 2 days. The choice of the bandwidth parameters was *ad-hoc*, and met the needs of adopting a resolution close to the matrices used to simulate attacks (*i.e.* cells of 50 meters and 1 day) while smoothing attack intensities enough in order to obtain interpretable results. We also considered the spatio-temporal distributions of attacks before removals ($j \in [1, 90]$ and after removals ($j \in [91, 180]$) as two separate distributions by appropriately right- and left-truncating kernels in the time dimension for attacks occurring before and after the date of removals, respectively. We corrected kernel estimates for outliers by capping the estimated observed attack intensities $\lambda_{obs}(i, j)$ to $Q_3 + 1.5\times(Q_3-Q_1)$, where $Q_1$ and $Q_3$ were the first and third quantiles of the estimated distribution of $\lambda_{obs}$ (Walfish, 2006).

We repeated the Gaussian kernel estimation for the simulated buffers in the same conditions. To this end, we combined the simulated attacks of the same subset of buffers for each of the 1000 simulations. The kernel estimation was applied on each of the 1000 combined simulations. We then calculated the mean estimated simulated attack intensities $\lambda_{mean_sim}(i, j)$ of the 1000 kernel estimations. The mean kernel estimation obtained corresponded to the expected attack intensities given pastoral use.

To control the observed kernel estimation for livestock presence, we calculated the corrected intensities $\lambda_{corr}(i, j)$ as:

$$\lambda_{corr}(i,j) = \lambda_{mean_{sim}}(i,j) - \lambda_{obs}(i,j) \quad (1)$$

Thus, a value of $\lambda_{corr}(i, j)$ lower, equal or higher than zero indicated that the observed attack intensity at coordinates *(i, j)* was lower, equal or higher, respectively, than the attack intensity expected according to pastoral use.

We calculated the general trends of observed or corrected attack intensities at different spatio-temporal scales *s* as:

$$Y_{\lambda,s} = \frac{\sum_{i=1,j=91}^{i=I,j=91+J} \lambda'(i,j) - \sum_{i=1,j=90-J}^{i=I,j=90} \lambda'(i,j)}{(I \times J)/2} \times 100 \quad (2)$$

where I and J were the number of rows (spatial distance to removals) and columns (number of days before or after removals) of scale *s*, $\lambda'(i, j)$ was the observed or corrected intensity at the coordinates *(i, j)* rescaled over [0,1] for observed intensity or over [-1,1] for corrected intensity by using the minimum and maximum values of $\lambda_{obs}(i, j)$ or $\lambda_{corr}(i, j)$ over the temporal range 90-J, 91+J. The rescaling allowed trend comparison between subsets of buffers. The division by $(I \times J)/2$allowed trend comparison between scales *s* of different sizes. We investigated trends of three spatio-temporal scales *s*: the small scale (*s* = 1) of spatial range 0-2 km and of temporal range ± 15 days (I = 40, J = 14), the intermediate scale (*s* = 2) of spatial range 0-6 km and of temporal range ± 45 days (I = 120, J = 44) and the large scale (*s* = 3) of spatial range 0-10 km and of temporal range ± 90 days (I = 200, J = 89).

In addition, we investigated the potential spatial shift of attack intensities at large scale s = 3 by applying Equation 2 separately for each spatial coordinate *i* ($i \in [0,200]$). There was no need to adjust results by $(I \times J)/2$ as we only investigated shift at s = 3. Namely, we transformed Equation 2 into Equation 3: $Y_\lambda(i) = (\sum_{j=91}^{180} \lambda'(i,j) - \sum_{j=1}^{90} \lambda'(i,j)) \times 100$.

### 2.3.4 *Investigated categories of removals*

The subsets of buffers on which we applied the kernel calculations were divided into 2 general categories. The first category corresponded to the whole subset of interacting groups of removals (‘*Interacting’*, n = 36, corresponding to 82 lethal removals). The second category corresponded to the whole subset of removals that were not interacting (‘*Non-interacting*’, n = 196).

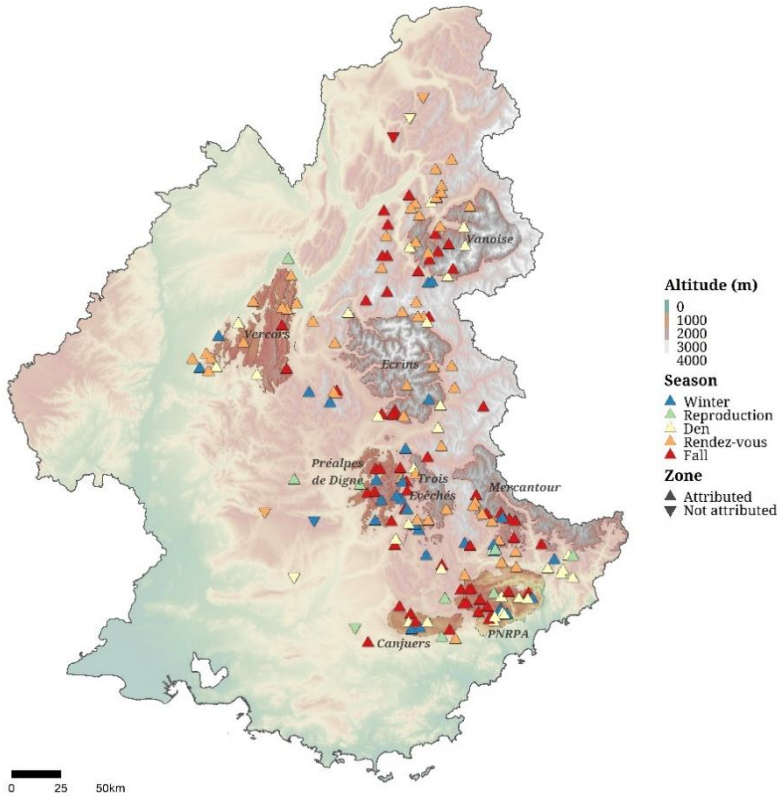



*Figure 4. Topography of the study area, with the 8 highlighted zones from the Zone subcategory that were selected for the analysis. Upward and downward triangles represent lethal removals that could be attributed or not to one of the 27 zones, respectively. Colors show the subset from the Season subcategory.*

We also divided the second category into 4 subcategories. The first subcategory corresponded to subsets defined according to removal locations. We delimited zones by using 25 Alpine mountain ranges defined by hydrography and orography (Knopf, 2019) and the limits from OpenStreetMap of the protected area *Parc Naturel Régional des Préalpes d’Azur* (PNRPA) and of the military zone *Canjuers*, both in the south of the study area. We attributed removals to their closest zone to a limit of 15 km. We selected the 8 subsets with at least 10 removals (Figure 4): *PNRPA* (n = 33), *Mercantour* (23), *Vercors* (18), *Les Trois-Evêchés* (18), *Vanoise* (15), *Préalpes de Digne* (12), *Ecrins* (12) and *Canjuers* (11).

The second subcategory corresponded to the 5 subsets defined according to the wolf seasons during which removals occurred (Figure 4): *Winter* (November — December, n = 30), *Reproduction* (February — March, 9), *Denning* (April — June, 35), *Rendez-vous* (July — August, 59) and *Fall* (September — October, 63).

The third subcategory corresponded to the 3 subsets defined according to removals administrative types (Figure 1): *Simple defense* (n = 69), R*einforced defense* (75) and *Hunting* (52).

The fourth subcategory corresponded to the 2 subsets defined according to the sex of the killed wolf when known: *Male* (n = 83) and *Female*, (n = 78). At the necropsy, 7 females of our final dataset of lethal removals were declared as being reproductive at least the year they were killed, which we considered too low to constitute a subset. Annual reproductive status of males was unknown.

In addition, we considered that the distribution of lethal removals among the three age classes when known was too unbalanced to investigate a potential effect of age class (177 adults, 24 subadults and 16 pups).

### 2.4 Implementation

The analysis was conducted in R 4.2.3 (R Core Team, 2023). We used the R packages *tidyverse 2.0.0* (Wickham et al., 2019), *readxl 1.4.2* (Wickham and Bryan, 2023), and *sf 1.0-12* (Pebesma and Bivand, 2023) to handle the datasets. We used the R package *spatstat 3.0-6* (Baddeley et al., 2015) to simulate point patterns in part 2.3.3. We adapted the function *kde2d.weighted* from *ggtern 3.4.2* (Hamilton and Ferry, 2018) to separate the kernel estimates before and after the removal date in part 2.3.4. We used the package *osmdata 0.2.3* (Padgham et al., 2017) to extract limits of PNRPA and of Canjuers military zone. We used the packages *RColorBrewer 1.1-3* (Neuwirth, 2022), *tidyterra 0.4.0* (Hernangómez, 2023), *geodata 0.5-8* (Hijmans et al., 2023), *scales 1.2.1* (Wickham and Seidel, 2022), *ggfx 1.0.1* (Pedersen, 2022a), *ggnewscale 0.4.9* (Campitelli, 2023), *metR 0.14.1* (Campitelli, 2021), *patchwork 1.1.2* (Pedersen, 2022b) and *ggtext 0.1.2* (Wilke and Wiernik, 2022) for data vizualisation. The datasets, codes and results are available online (Grente et al., 2024).

## 3. Results

Trends in the observed and corrected attack intensities for all analyzed subsets and for all spatio-temporal scales *s* are displayed in Table 1. Distributions of these trends are displayed in Figure 5. Heatmaps of observed and corrected kernel estimates of subsets are displayed in Figure 6 and Figure S1. Trends as a function of spatial coordinate *i* are displayed in Figure 7 for all subsets.

Subsets generally presented a general pattern of observed or corrected intensities that formed patches of high intensities at low distances from removals, below 2 km (*e.g. Non-interacting* [Figure 6.A], *Denning* [Figure 6.F], *Reinforced defense* [Figure 6.J]). Some subsets also showed patterns that progressively moved away from this general pattern, starting from subsets showing supplementary patches of high intensities at higher spatial distances such as *Fall* (Figure S1.F), to subsets splitting up their patches of low and high intensities at all analyzed scales such as *Ecrins* (Figure S1.B).

Trends in totals of attack intensities leaned towards a decrease of intensities after removals, with their main modes located between -21% and -9% (Figure 5). However, this general decrease concealed disparities between subsets. Indeed, from subset trends in Table 1 or from heatmaps, we could observe three main possible types of attack intensity changes after lethal removals, *i.e.* decrease, no change and increase of attack intensities. Most importantly, the results did not only vary according to subsets, but also according to the analyzed scales *s*, to the correction of analysis for livestock presence and to the spatial distance to lethal removals.

### 3.1 At small scale

At small scale *s* = 1, 17 subsets over 20 showed an observed negative trend of attack intensity after removals (Table 1). Only the subsets of *Canjuers* and *Hunting* showed a positive observed trend after removals (Table 1). *PNRPA* was the only subset showing an almost zero observed trend.

The control for livestock increased the strength of two-thirds of negative trends and of all positive trends at scale 1 (Table 1). Thus, the corrected trend distribution flattened the observed trend distribution at scale 1, and reinforced its distribution tails (Figure 5).

### 3.2 At intermediate scale

Results at the intermediate scale *s* = 2 showed the same proportions of observed negative, positive or zero trends as those at scale 1. However, the classification of subsets within each type of result could change. For example, the subset of *Hunting*, formerly showing a weak but positive trend (4%) at scale 1, was the second subset showing the highest negative trend (-40%) at scale 2. Conversely, *Vercors*, formerly the fifth subset showing the highest negative trend (-35%) at scale 1, had the second highest positive trend (11%) at scale 2. *Ecrins* was now the zero-trend subset. Others were consistent across scales, such as *Préalpes de Digne* that remained in the first three subsets showing the highest negative trends at both scales.

Contrary to scale 1, the control for livestock presence at scale 2 reduced the strength of half of negative and of two-thirds of positive observed trends (Table 1). Thus, the main mode of the corrected trend distribution at scale 2 increased from -21% to -9%, and its right tail extended toward higher values than the observed trend distribution (Figure 5).

### 3.3 At large scale

At large scale s = 3, the subsets showing an observed negative trend were still dominant, with 15 subsets concerned over 20, whereas three subsets showed an observed positive trend. The observed zero trend subsets were again different from the other scales: *Vercors* and *Simple defense* (Table 1).

The differences between the observed and corrected intensities were important at scale 3. Thus, the control for livestock presence changed the trend sign in 5 subsets over the 20 analyzed, for only 2 at scale 1 and 1 at scale 2 (Table 1). The control for livestock at scale 3 reduced the strength of two-thirds of negative and of positive trends (Table 1).

Thus, the main mode of the trend distribution at scale 3 increased from -15% to -9.5% when corrected, but contrary to scale 2, the main mode narrowed instead of flattening (Figure 5). In addition, two minor modes emerged when using corrected intensities, at -31% and at 20%. In other words, control for livestock exacerbated the emergence of three types of results at scale 3: a moderate decrease, a small decrease and a moderate increase. The subset of *Reproduction* corresponded to the negative mode of -31%, and the subsets of *Vercors*, *Préalpes de Digne* and *Winter* particularly contributed to the positive mode of 20% (Table 1).

### 3.4 Differences between observed and controlled intensities in heatmaps

Some subsets showed large differences between the panel ii of observed intensities and the panel iv of corrected intensities (Figures 6 and S1), such as *Préalpes de Digne* (Figure 6.D), *Vercors* (Figure 6.E), *Reinforced defense* (Figure 6.J), *Winter* (Figure 6.H) or *Female* (Figure S1.I).

Yet, not all of these subsets were associated with high differences between observed and corrected trends at scale 3. For example, the subset of *Reinforced defense* had a trend difference of 5%, against 54% for the *Winter* subset. In the case of *Reinforced defense* subset, the effect of livestock control was the same before and after removals (*i.e.* time 0, Figure 6.J), whereas in the case of

*Winter* subset, the correction decreased the intensities before removals and increased those after removals (Figure 6.H). These differences lay on the monthly distribution of removals. Corrections varied more greatly along the temporal axis when removals occurred at the limit between an intense and calm grazing period, like removals of the *Winter* subset (Figure 6.H.ii).

### 3.5 Attack intensities by spatial distances

When looking at the observed attack intensity trends as a function of spatial distance to removals, three types of results were observed, with balanced proportions (Figure 7): A decrease or an increase over all distances (6/20 subsets, *e.g. Interacting* subset), phases of decrease interrupted by phases of weak increase (7/20 subsets, *e.g. Male* subset) and phases of decrease interrupted by phases of strong increase (7/20 subsets, *e.g. Ecrins* subset).

Repeating the same exercise for corrected attack intensity trends led to the same three types of results, but with a large majority of subsets presenting decrease phases interrupted by strong increase phases (14/20 subsets) and only two subsets, *Vercors* and *Winter*, presenting no trend sign shifts over all spatial distances.

Most of the time, trends shifted from negative to positive values, sometimes several times. *Vanoise* and *Male* were the only subsets to show an observed or corrected positive trend after removals at 0 km while presenting trend shifts. Distances at which first trend shifts appeared ranged from less than 1 km (*Ecrins*) up to 7 km (*Hunting*). On average, 1.7 trend shifts occurred over 10 km.

The two subsets of *Ecrins* and *Canjuers* showed a multimodal distribution of trend shifts, with shifts equally apart of approximately 1 km. In these cases, as in most subsets presenting trend shifts, there was no symmetry between negative and positive phases, *e.g.* there could be an intense decrease in attack intensity after removals at low distances, and only one or several weak increases in attack intensity after removals at higher distances, such as the subsets of *Vanoise* and *Reproduction*.

*Table 1. Trends (%) of observed attack intensities $Y_{\lambda_{obs},s}$ and of corrected attack intensities $Y_{\lambda_{corr},s}$ after lethal removals calculated over three different spatio-temporal scales s, 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days) following Equation 2, separately for each subset. All trends are comparable because intensities were rescaled and trends were relative to the number of involved rows and columns. Column "Total" indicates the number of lethal removals of each subset or of groups of lethal removals for the category "Interacting". Column "Figure" gives the corresponding figure number of heatmaps. Gradient of colors ranges from dark blue for the lowest value to dark red for the highest value, while the middle color in white corresponds to zero.*

| | | | | | Scale 1 | | Scale 2 | | Scale 3 | |
|---|---|---|---|---|---|---|---|---|---|---|
| Category | Subcategory | Subset | Total | Figure | $Y_{\lambda_{obs},1}$ | $Y_{\lambda_{corr},1}$ | $Y_{\lambda_{obs},2}$ | $Y_{\lambda_{corr},2}$ | $Y_{\lambda_{obs},3}$ | $Y_{\lambda_{corr},3}$ |
| *Non-interacting* | | | 196 | 6.A | -16 | -14 | -28 | -23 | -18 | -8 |
| | Geographic zone | *PNRPA* | 33 | 6.C | 1 | -1 | -9 | -15 | -10 | -15 |
| | | *Mercantour* | 23 | S1.D | -39 | -54 | -27 | -23 | -21 | -10 |
| | | *Trois Evêchés* | 18 | S1.C | -34 | -29 | -24 | -3 | -19 | 6 |
| | | *Vercors* | 18 | 6.E | -35 | -38 | 11 | 31 | 0 | 19 |
| | | *Vanoise* | 15 | S1.E | -18 | -30 | -27 | -38 | -5 | -11 |
| | | *Ecrins* | 12 | S1.B | -15 | -21 | 0 | 2 | 3 | 9 |
| | | *Préalpes de Digne* | 12 | 6.D | -77 | -67 | -30 | -2 | -23 | 21 |
| | | *Canjuers* | 11 | S1.A | 6 | 13 | 2 | 0 | -3 | -8 |
| | Season | *Fall* | 63 | S1.F | -17 | -17 | -48 | -49 | -33 | -11 |
| | | *Rendez-vous* | 59 | 6.G | -10 | -16 | 12 | 9 | 7 | -8 |
| | | *Denning* | 35 | 6.F | -62 | -96 | -26 | -42 | 2 | -12 |
| | | *Winter* | 30 | 6.H | -33 | -17 | -16 | 25 | -23 | 31 |
| | | *Reproduction* | 9 | S1.G | -23 | -40 | -8 | -15 | -17 | -31 |
| | Class | *Reinforced defense* | 75 | 6.J | -14 | -15 | -8 | -3 | -11 | -6 |
| | | *Simple defense* | 69 | 6.I | -20 | -27 | -19 | -26 | 0 | -3 |
| | | *Hunting* | 52 | 6.K | 4 | 20 | -40 | -39 | -33 | -16 |
| | Sex | *Male* | 83 | S1.H | -21 | -25 | -19 | -12 | -14 | -3 |
| | | *Female* | 78 | S1.I | -5 | 1 | -15 | -10 | -13 | -2 |
| *Interacting* | | | 36 | 6.B | -44 | -88 | -14 | -28 | -7 | -13 |

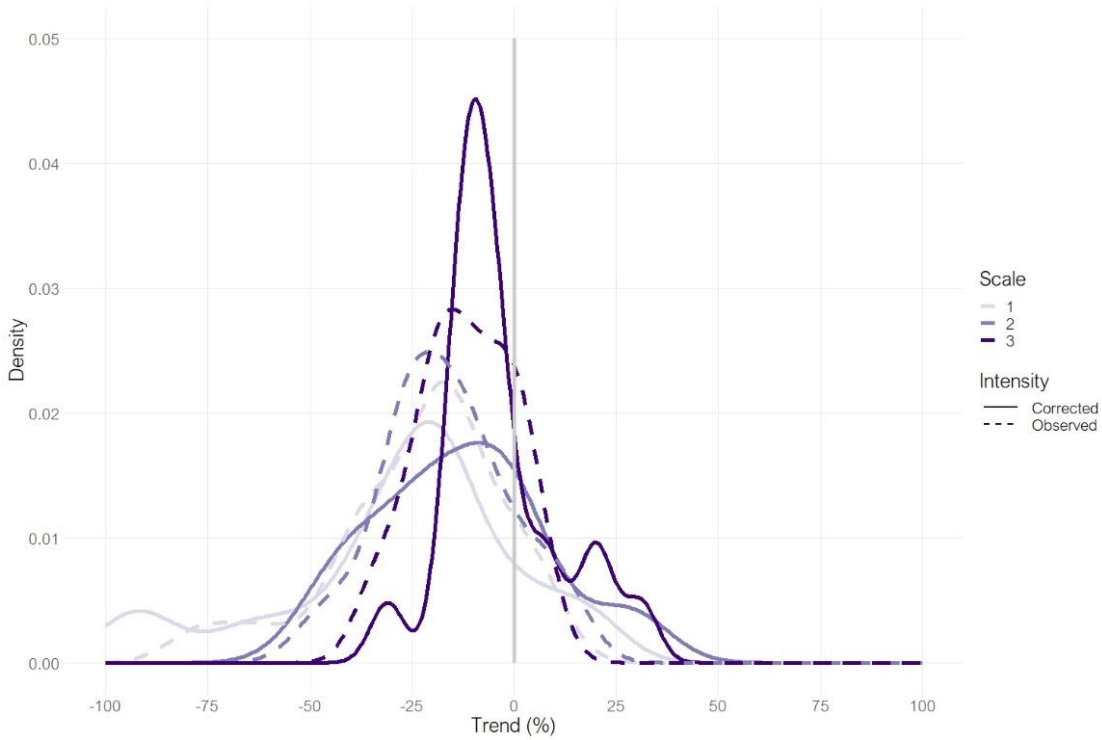



*Figure 5. Density distributions of the trends of observed (dotted lines) and corrected (solid lines) attack intensities after lethal removals at the spatio-temporal scales 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days) presented in Table 1 (n = 20 subsets per distribution).*

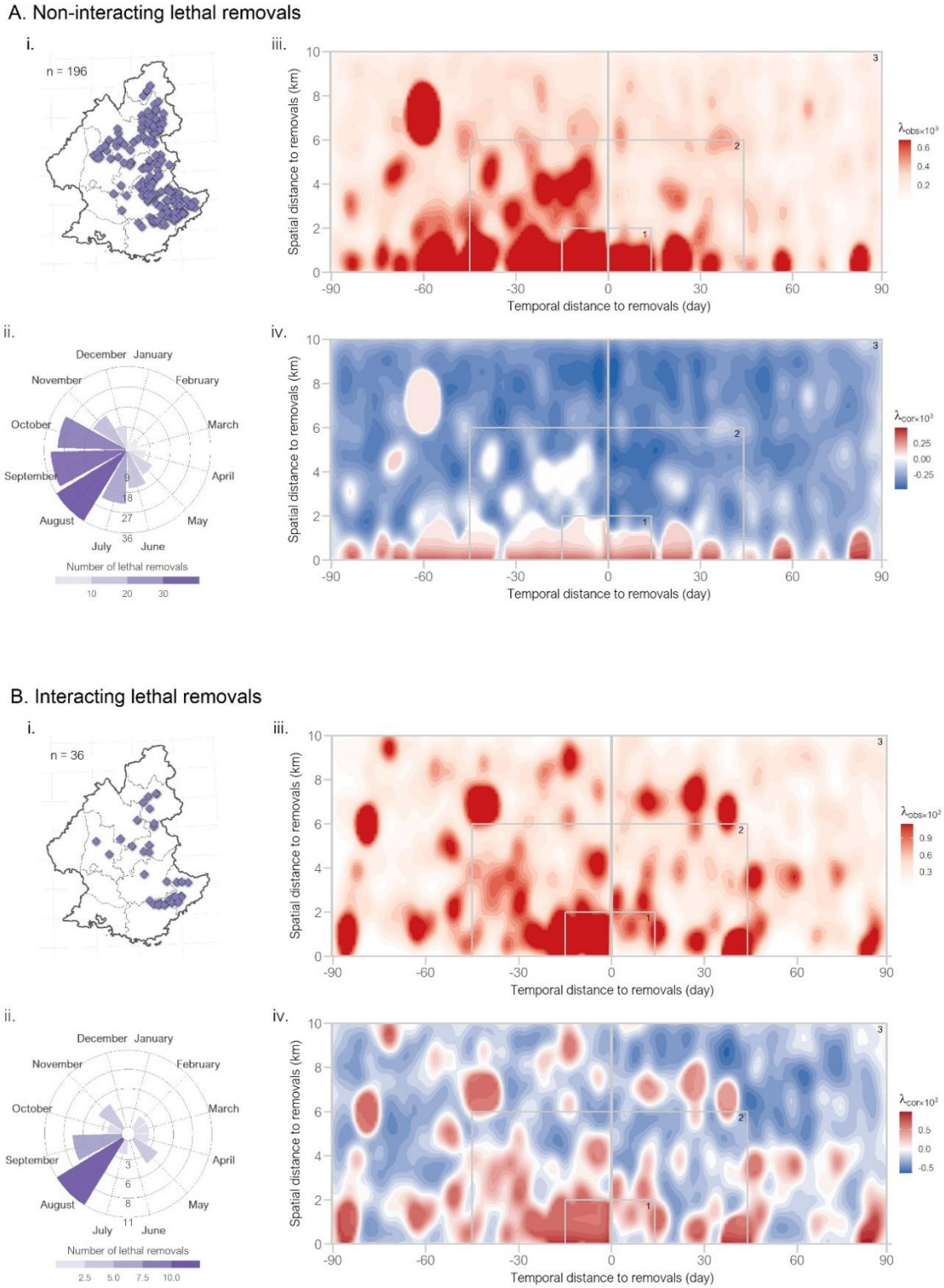



*Figure 6. Results of kernel estimation of attack intensities surrounding lethal removals, detailed for each analyzed subset of removals (all panels except B.) or groups of removals for the subset of interacting removals (B.). Each panel includes (i) the map of the removal locations or of the centroids of the groups, with the annotated number of involved removals or groups, (ii) the monthly distribution of the removal dates or of the middle dates of the groups, (iii) the observed attack intensities $\lambda_{obs}$ and (iv) the corrected attack intensities $\lambda_{corr}$. Intensities are given along the continuous temporal axis (x-axis) and spatial axis (y-axis). The coordinate (0,0) indicates the date and the location at which removals or groups of interacting removals occurred. Grey rectangles of subpanels iii and iv delimit the three analysis scales 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days). A value of $\lambda_{corr}$ lower, equal or higher than zero indicated that the observed attack intensity was lower, equal or higher, respectively, than the attack intensity expected according pastoral use. (Part 1/4)*

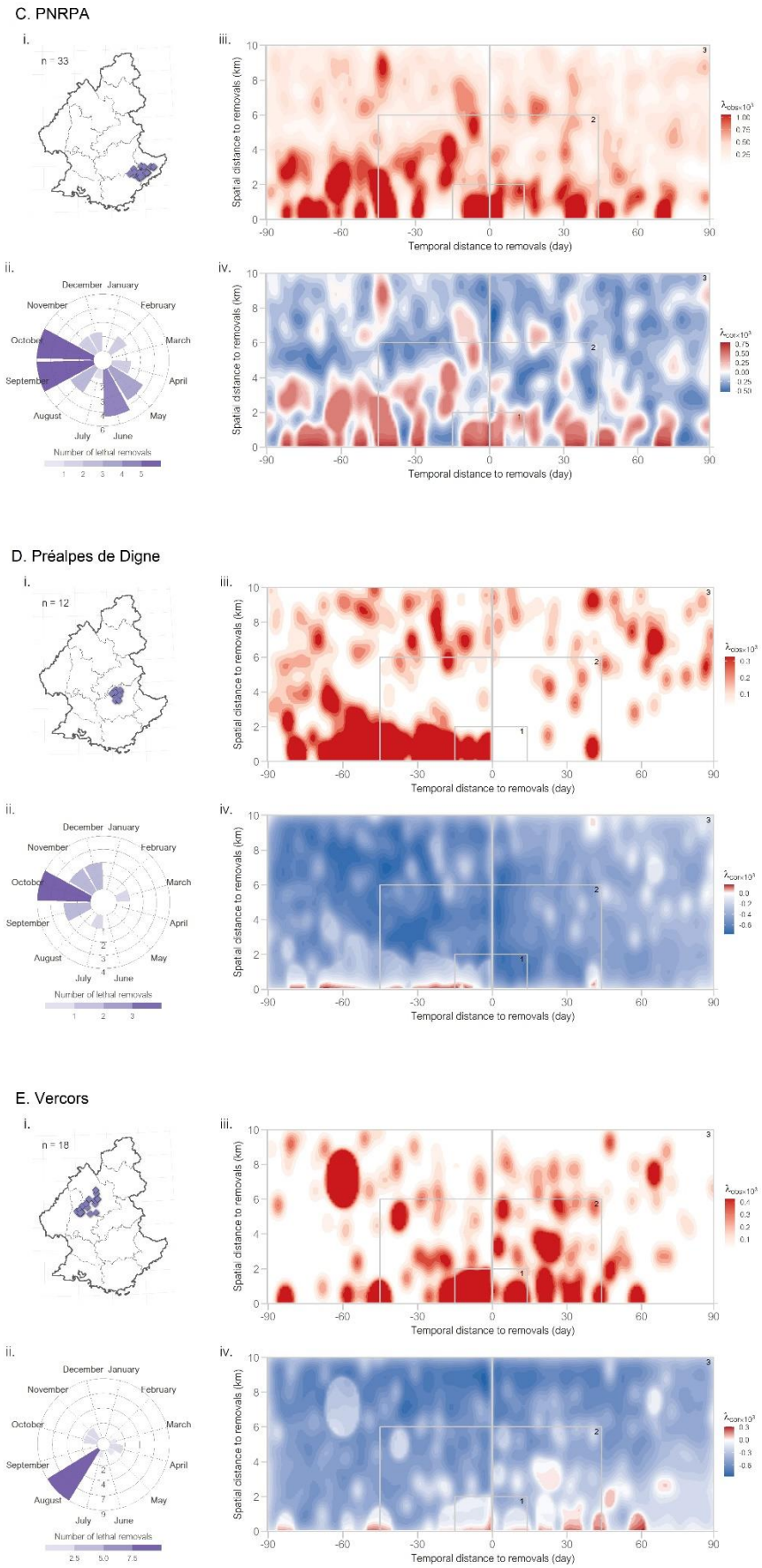



*Figure 6. (Part 2/4)*

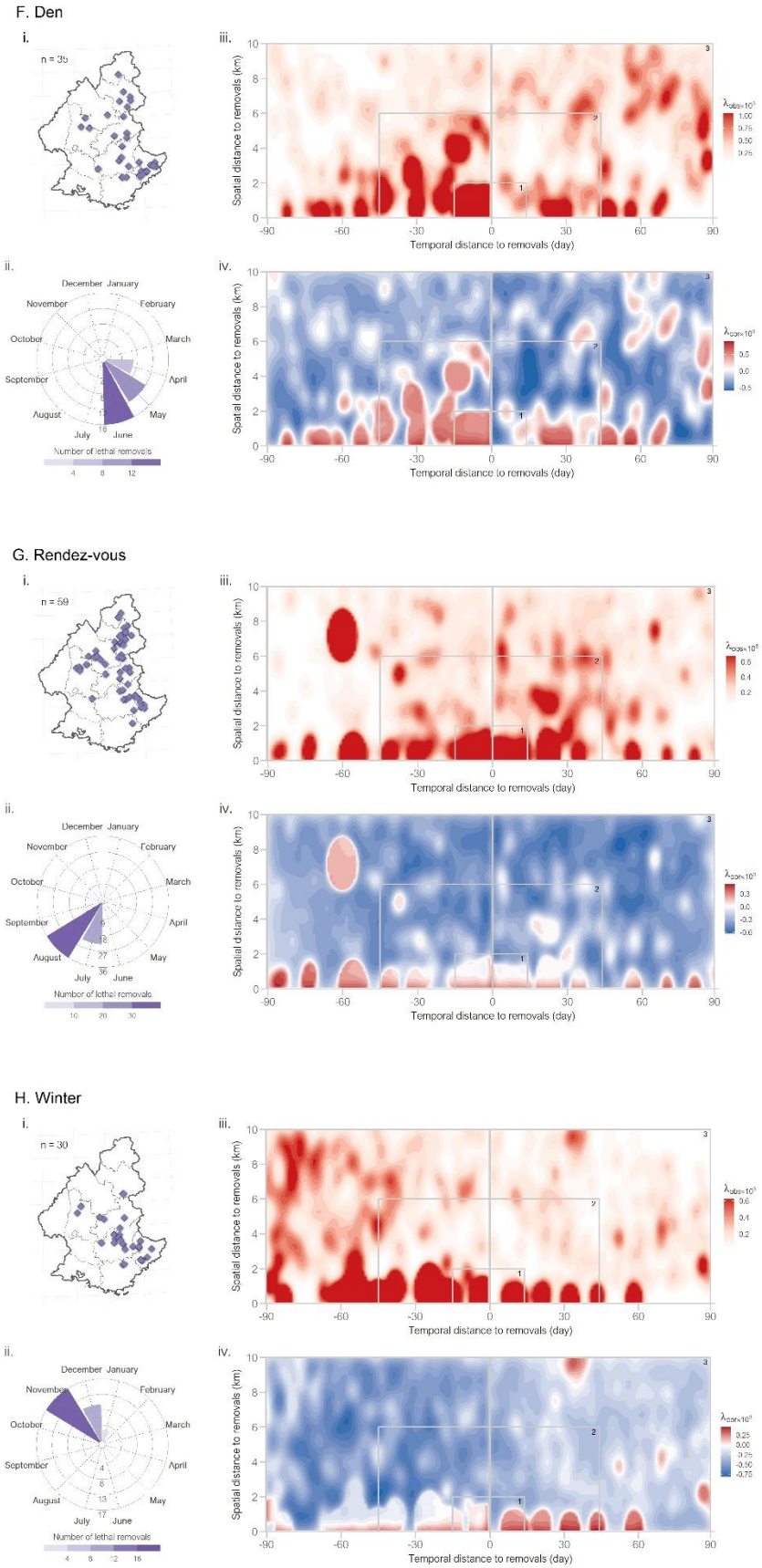



*Figure 6. (Part 3/4)*

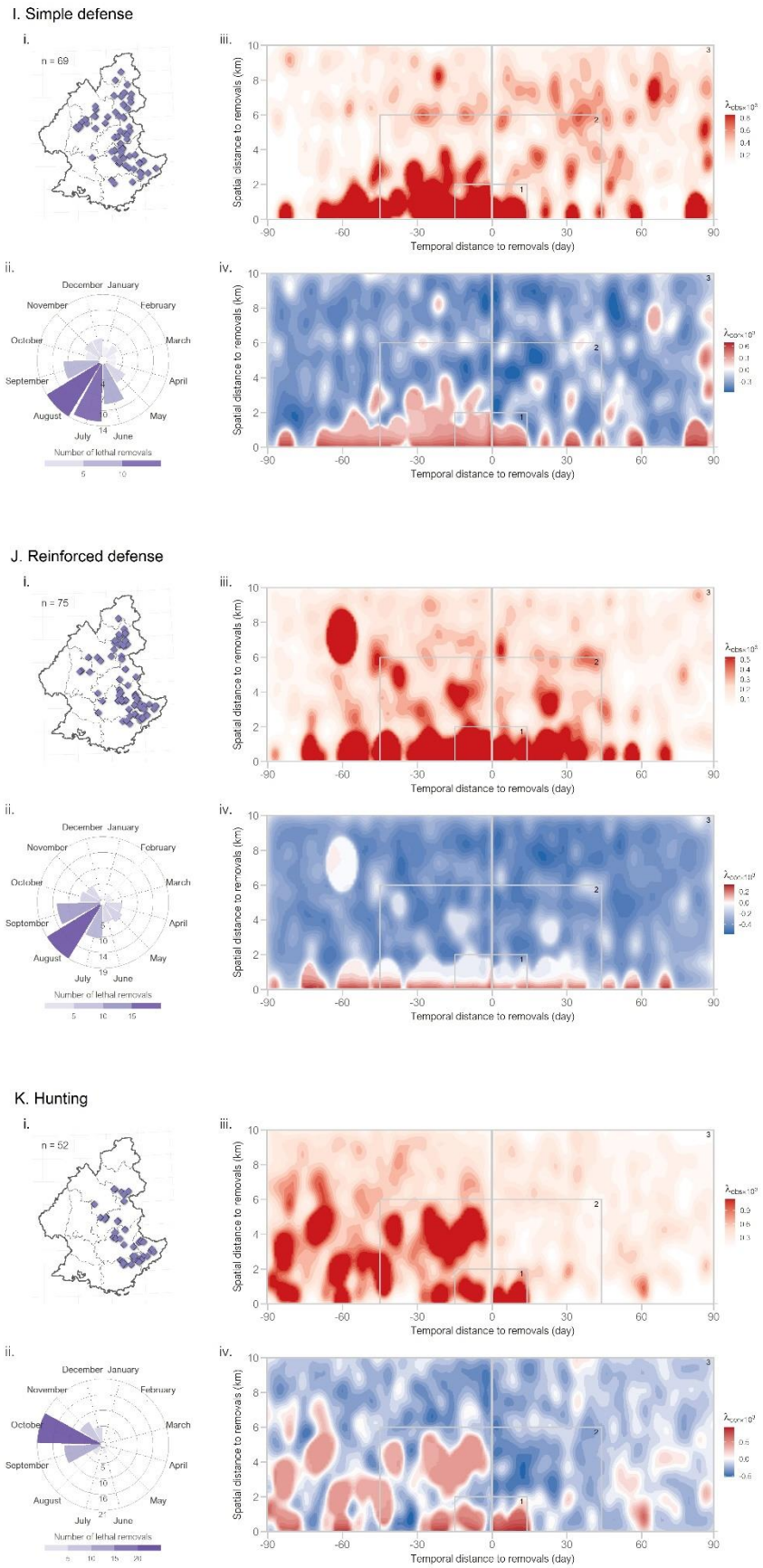



*Figure 6. (Part 4/4)*

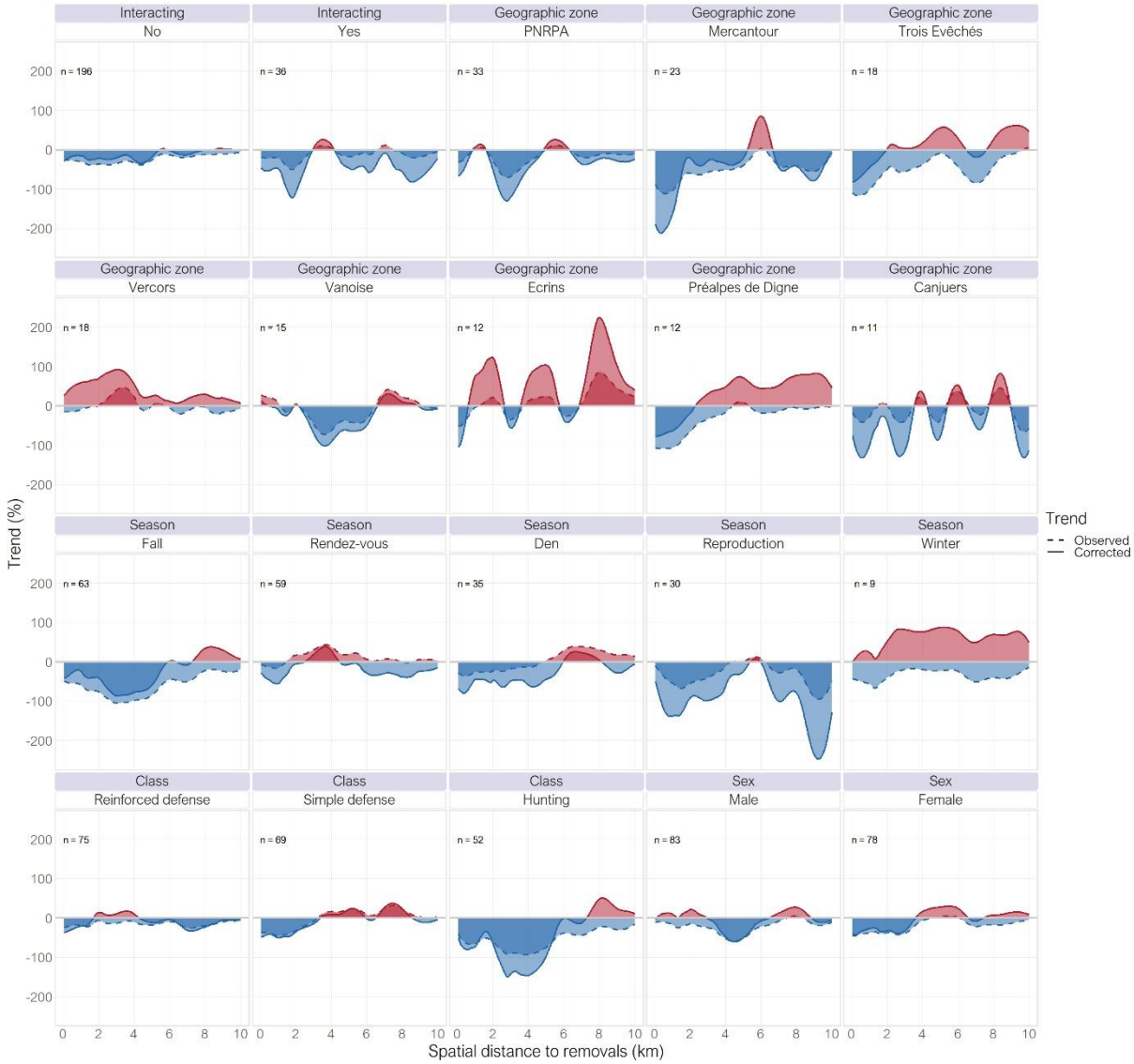



*Figure 7. Trends (%) of observed attack intensities $Y_{\lambda_{obs}}$ (dotted line) and of corrected attack intensities $Y_{\lambda_{corr}}$ (solid lines) after lethal removals calculated along the spatial scale of 10 km with a fixed temporal scale of ± 90 days following Equation 3, separately for each subset. Top facet strips indicate the category or subcategory of the subset, and the bottom facet strips indicate the subset name. All trends are comparable because intensities were rescaled.*

## 4. Discussion

We evaluated the effects of lethal control of wolves on attack intensity distribution through a kernel density estimation that had never been used before for this topic. Our method contrasted with the Cox proportional hazard models commonly used by previous studies to estimate the risk of recurrence of a single attack over a fixed area (Bradley et al., 2015; Harper et al., 2008; Santiago-Avila et al., 2018).

We conducted the analysis on 20 subsets of lethal removals of wolves in France, for a total of 278 analyzed lethal removals occurring between 2011 and 2020. Subsets were based on interactions between removals, administrative type, location or date of removals, or on sex of killed wolves. We corrected attack intensities by sheep presence according to a pastoral census from 2012-2014. We conducted the analysis over 10 km around removals and 90 days before and 90 days after removals. This method provided an efficient visualization of attack intensity distribution in the form of heatmaps over continuous spatial and temporal scales. We also computed attack intensity trends

after removals and added two smaller spatio-temporal analysis scales (0-6 km and ± 45 days; 0-2 km and ± 15 days) to the computations.

### 4.1 Common features among subsets and scale influence

Heatmaps revealed a high variability of patterns in spatio-temporal distributions of attacks across subsets (Figure 6, Figure S1), although two features tended to be common to all subsets. First, removals were generally preceded by high attack intensities at their locations, meaning they were applied in response to attacks, in accordance with French legislation. Second, attacks tended to aggregate below 2 km from removal locations, regardless of time and of other possible aggregation spots. Therefore, the attack process was generally a persistent phenomenon at these locations, although showing possible interruptions in time, even before removals (*e.g.* subset of *Rendez-vous*).

Trends of attack intensities once removals occurred (Table 1) and their distributions (Figure 5) broke down the variability observed in heatmaps into three possibilities: Decrease in attack intensity, zero or almost zero trend, and increase in attack intensity. Proportions of each type varied according to the analysis scale and the use of livestock control, but decrease in attack intensity remained over-represented in all cases (75-85% of subsets). Nevertheless, for about half of the subsets, the greater the analysis scale, the lesser the decrease. Thus, 96% of decrease in corrected attack intensities were observed for the *Denning* subset at the smallest scale (0-2 km, ± 15 days), against only 12% of decrease at the largest scale (0-10 km, ± 90 days). If considering the uncorrected results, this was even worse, as the 62% of decrease at scale 1 became a 2% increase at scale 3 for this subset. Conversely, the three subsets showing a zero trend or an increase of attack intensities after removals at scale 1 showed negative trends at larger scales (*PNRPA*, *Canjuers*, *Hunting* subsets). The other half of subsets presented a non-linear effect of scales, with intermediate scale 2 (0-6 km, ± 45 days) showing the highest or lowest trends (*e.g. Rendez-vous*, *Non-interacting* subsets). Overall, the effects of lethal control according to spatio-temporal analysis scale were difficult to predict.

### 4.2 Ripple effects of lethal removals

When focusing on the variation of attack intensities after lethal removals along the spatial scale of 10 km with a fixed temporal scale of ± 90 days (Figure 7), we frequently observed localized positive trends, although this distance greatly varied across subsets.

Shifts in the location of attack could result from pack dissolution (Cassidy et al., 2023), especially if killed wolves were breeders. Yet, only 7 killed females among the 105 necropsied females were evaluated as breeders in our dataset. Nevertheless, this number could have been underestimated, and reproductive status of males were unknown. In addition, the analyzed spatial and temporal scale (10 km, 90 days) may also not be enough considering the large dispersal abilities of wolves (Mech, 2020), although this spatial scale was sufficient for Santiago-Avila et al. (2018) to detect potential attack shifts. In our case, the persistence of high intensities of attacks below 2 km from removals, frequently quickly after removals and on the long term, weakened the pack dissolution hypothesis, as settlement of new wolves was unlikely to be as fast, even in the dense population of the Western Alps.

Remaining wolves from targeted packs could also have shifted part of their attacks toward other flocks, possibly because of removals without necessarily implying pack dissolution. This shift could also simply result from changes in the spatio-temporal distribution of sheep flocks. Control for livestock presence was designed to correct for this bias. However, correction was applied on a monthly basis. Shepherds may change the grazing zone or pastoral surface of their flocks from one week to another. These changes would not be corrected by our monthly correction for livestock

presence, especially since our correction was based on a ten-yearly pastoral census and may not be up-to-date. The multimodal distributions of *Ecrins* and *Canjuers* subsets (Figure 7) could reflect such bias, potentially exacerbated by the lower number of their removals (n = 12 and n = 11) regarding other subsets.

### 4.3 Causality inference

Potential ripple effects of removals raise the more general question of the contribution of removals in the trends we observed. As the variability of subsets showed, the attack process could seem inconstant, with intensity irregularly turning on and off at the same spatial distances even before removals. If contribution of removals in changing the dynamics and intensities of attacks at low spatial and temporal scales could be easily considered, our confidence in such causal relationship was decreasing as analysis scale increased. For example, in the subset of *Non-interacting* removals (Figure 6.A), is the disappearance, after removals, of the patch of high attack intensity between 6 and 8 km from removals present at -60 days before removals the result of removals? Apart from livestock presence, many confounding factors can also affect attack intensity distribution, starting with wolves themselves, *e.g.* their varying density. If dividing removals into seasonal subsets may smoothen differences between removals due to the wolf annual biological cycle, they could not entirely erase random biological events that rhythmed wolf lives, as dispersal, settlement, or natural deaths. Restricting the analysis at scale 1 could greatly reduce such bias. As an example, our correction for livestock presence greatly impacted results at scale 3 but not at scale 1. However, because wolves move over large territories, we acknowledge that focusing on changes happening only in close proximity to removals could not be enough to evaluate removal effects (Treves et al., 2016).

### 4.4 Exploring variability in the spatio-temporal distribution of attacks

Keeping these limits in mind, we are confident that our results showed that there could not be a single type of changes in attack intensities after lethal control, but several, and that they form a gradient noticeable in the heatmaps. First, after lethal control, attack intensity could decrease on the long term (observed results of the subsets of *Préalpes de Digne*, or of *Trois-Evêchés*) or on the short term only (*Denning*). Second, attack intensity could decrease but not immediately after lethal control (*Hunting*, *Female*, *Fall*, *Reproduction*, *Mercantour*). Third, the duration of high intensity patches (*Simple defense*) or their spatial expansion (*Non-interacting*, *PNRPA*, *Male*, *Fall*) or both at the same time (*Interacting*, *Ecrins*), could decrease after lethal control. Fourth, no major changes in attack intensity could be observed after lethal control even on the long term (*Reinforced defense*, *Vanoise*, *Canjuers*). Fifth, the spatial expansion of high intensity patches could increase (*Rendez-vous*). Sixth, the attack intensity could be sliced into several patches of high intensity increasing with time (*Vercors*, *Winter*).

The origins of these variations between subsets were hard to explain. They could originate from pastoral practices, including non-lethal measures, combined to other environmental differences such as altitude that can modify wild ungulate distributions or wolf distribution (Miller et al., 2016). The choices we made to define subsets were an attempt to group removals applied in similar conditions or giving similar results (sex of killed wolf), expecting common patterns of attack intensity distribution would emerge. Ideally, we could have grouped removals according to location and season (and even years) at the same time, but we were limited by the number of removals per subset. On the contrary, pooling a large number of removals, as in the *Non-interacting* subset, may be counterproductive because a large subset would include situations that are too various to lead to

similar effects of lethal control, therefore preventing patterns in attack intensity distribution from emerging.

Some hypotheses concerning the variability of results could be made. They rest upon consideration of local and temporal context. For example, at scales 1 and 2, the removals from the *Simple defense* subset appeared more efficient than those of the *Reinforced defense* subset to reduce attack intensities (Table 1, Figures 6.I, 6.J). This result could originate from the fact that reinforced defense removals were allowed when the protected flocks, or other flocks from the same municipality, have recurrent attacks despite simple defense removals (Ministère de la Transition Ecologique et Solidaire, 2018). In other words, reinforced defense removals were supposed to be applied in situations that were not mitigated through simple defense removals, maybe because of a higher wolf density. However, the removals of the *Hunting* subset, supposed to be applied in situations that were not mitigated through both defense removals, were associated with a decrease of attack intensities that did not appear immediately after removals but that was long-lasting. This result could originate from the fact that hunting removals occurred essentially in October, contrary to the defense removals mainly occurring in August. It could have been easier, in the winter context, to maintain attack intensity at the level they were expected (*e.g.* flocks in fold during the night). In addition, the analyzed reinforced defense removals were mostly applied in the last years of the study period (58% in 2019-2020), whereas the hunting removals were mostly applied in 2015-2016 (51%). Estimated wolf population size increased greatly between these two years, being 341 [95% IC 266-463] in 2015 and 624 [95% IC 414-834] in 2020 (Réseau Loup-Lynx, 2021).

Thus, reducing attack intensity in summer whereas wolf population was densifying appeared a difficult task for reinforced defense removals. Reducing locally and temporarily wolf density could have improved lethal control efficiency, as found by Bradley et al. (2015). In our results, killing more than one wolf in less than 5 km and less than 25 days, as interacting removals did, indeed appeared more efficient to reduce attack intensities than killing only one wolf, even if patches of high intensity still persisted after interacting removals (Figure 6.A-6.B, Table 1).

### 4.5 Consistency with previous studies

Our most common result of a moderate and temporary decrease of attack intensity following lethal control, tempered by a large variability depending on contexts and on analysis scales, was consistent with most of the previous comparative studies (*e.g.* Bradley et al., 2015; Harper et al., 2008; Santiago-Avila et al., 2018) and the apparent discrepancy on the subject (Lennox et al., 2018; Treves et al., 2016).

Some disparity with previous studies also appeared. Contrary to Bjorge and Gunson (1985) or Bradley et al. (2015) who reported total or high efficiency of lethal control on reducing attacks in time, the time duration effectiveness in our results was generally much lower. However, very different management contexts applied in North America where these studies were conducted compared to the French context. Our most intense removals (on average 2.3 wolves for interacting removals) corresponded to the least intense in these studies (*e.g.* 2.2 wolves for partial removal in Bradley et al. (2015)). In addition, the Western Alps are close to saturation in wolf packs (Marucco et al., 2023). Therefore, we cannot expect the same recurrence of attacks nor the same effectiveness in lethal control in both situations.

Compared to the previous studies, the strength of our analysis was to demonstrate the variability of lethal control effects on both continuous spatial and temporal scales by computing attack intensities through kernel density estimates. Last but not least, the control for livestock presence, even if

perfectible with more updated data, reduced the risk of confounding factors and improved inference of this non-experimental study. For some subsets as *Winter*, control for livestock presence drastically changed the results.

### 4.6 Management implications

For conditions similar to the application of lethal control in France, managers should keep in mind that applying lethal removals may reduce attack intensities at small scale (i.e. below 2 km and 15 days), but with several drawbacks. First, attacks are likely to persist after removals, including at high intensity. Second, absence of changes or even increase of attack intensities after removals are still possible. Third, trends in attack intensity are more variable at larger scales. In other words, lethal control can contribute to management of wolf attacks but cannot be expected to cancel by itself predation on livestock on large timescales or on large areas with removal intensities as those analyzed, even if its implementation goes along with non-lethal measures as in the Western Alps.

In addition, the high variability and context-specificity of our results support a management which is itself contextualized, but the lack of understanding of this variability prevents us to give more specific management implications per context. Our results cannot be considered as predictions of lethal control effects on attack distribution, even per subset, as too many factors influence the attack process beyond the characteristic of the subset and may evolve.

Moreover, managers cannot easily handle the unit of measure of intensity we used, *i.e.* the number of attacks over a small spatio-temporal area (50 meters – 1 day) corrected for spatial bias and for livestock presence. If managers can do so with intensity trends from Table 1, we strongly caution, however, to read Table 1 without the corresponding heatmaps. Indeed, the heatmaps provided the detailed range of changes of the attack intensity distribution after removals, and therefore the potential responses of wolves to removals in its full complexity. On the contrary, Table 1 could only indicate three tendencies (decrease, null, increase) that tended to oversimplify lethal control effects by concealing other components of the evaluation (e.g. frequency of intense attack events, duration, potential attack shifts…).

### 4.7 Perspectives

Evaluation of the effects of lethal control on attacks made by large carnivores on livestock remains a technical challenge. Our results showed that consideration of analysis scale is crucial and that effects should be analyzed separately for each local context.

To fully understand the effects of lethal control, we need more precise and long-term data related to carnivores for example about their age, their pack affiliations or their reproductive status, through genetics or telemetry. We also need up-to-date information about livestock presence and more precise data about pastoral practices (*e.g.* livestock non-lethal protection). Collection of these datasets and their analysis are particularly feasible at small scale, for example at the scale of one wolf territory and their neighbors. In addition, small scale analysis is consistent with the need to contextualize evaluation of lethal removal effects. Effects of lethal control on wolves and their attacks may then be evaluated through promising methods such as animal social network analysis, which was applied to study the resilience of other social animals to human-induced removals (*e.g.* Downing et al., 2023; Goldenberg et al., 2016).

The side effect of focusing on a specific context is to restrict the number of cases and to fail to extract a general pattern if any. A solution would be to upgrade the analysis of observed data by simulations. For example, Wiśniewska et al. (2022) used individual-based modelling to simulate

poaching effects on elephant social structures. This type of modelling is useful to reproduce biological processes even for socially complex species as wolves. Haight et al. (2002) already used this method to simulate management of attacks of wolves by lethal control, but it lacked several biological processes that have been implemented in new population models since that could be used for this purpose (*e.g.* Bauduin et al., 2020).

Thus, combination of analysis based on observed data as social network analysis and simulations through individual based-models may be the next step to evaluate lethal control effects on social carnivores while understanding the biological responses of the targeted species to lethal control.

## Appendices

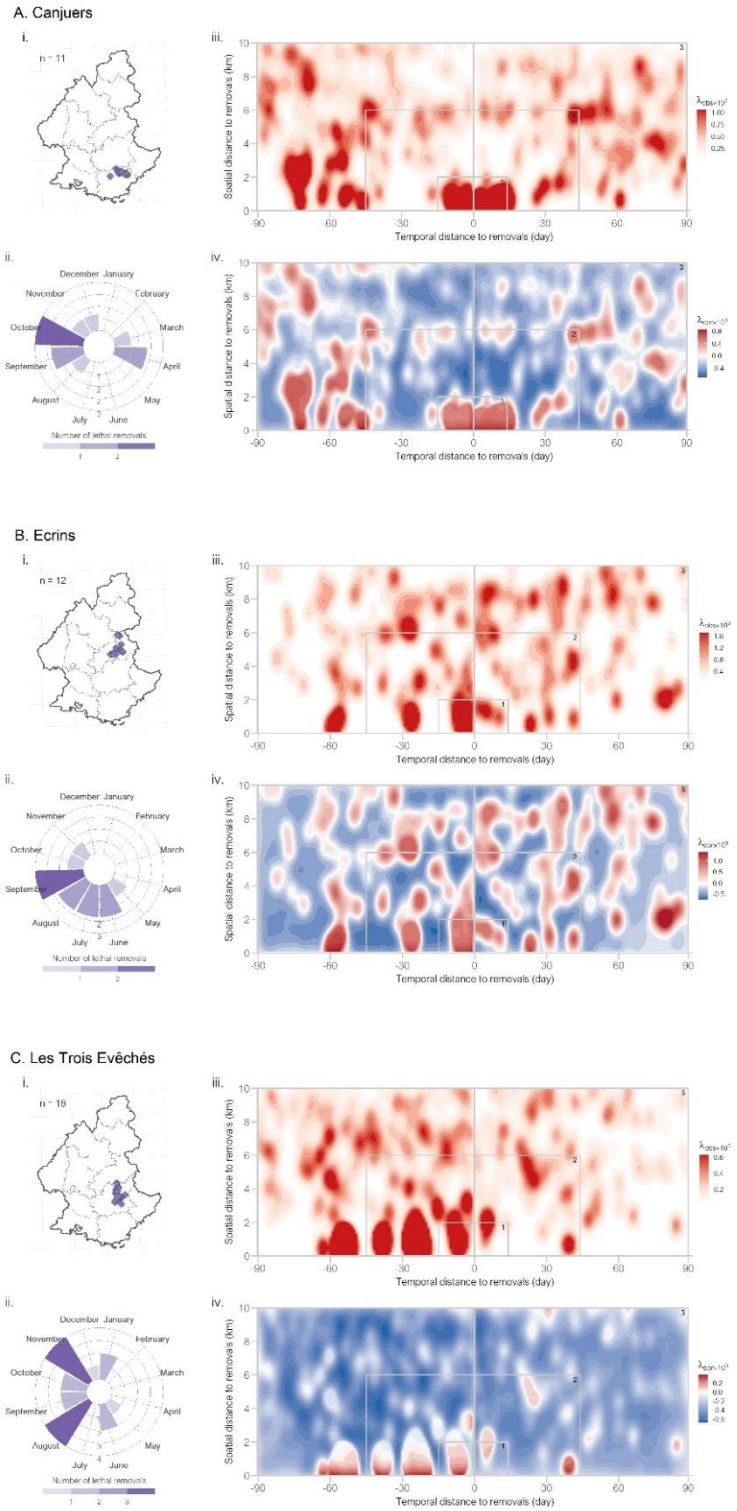
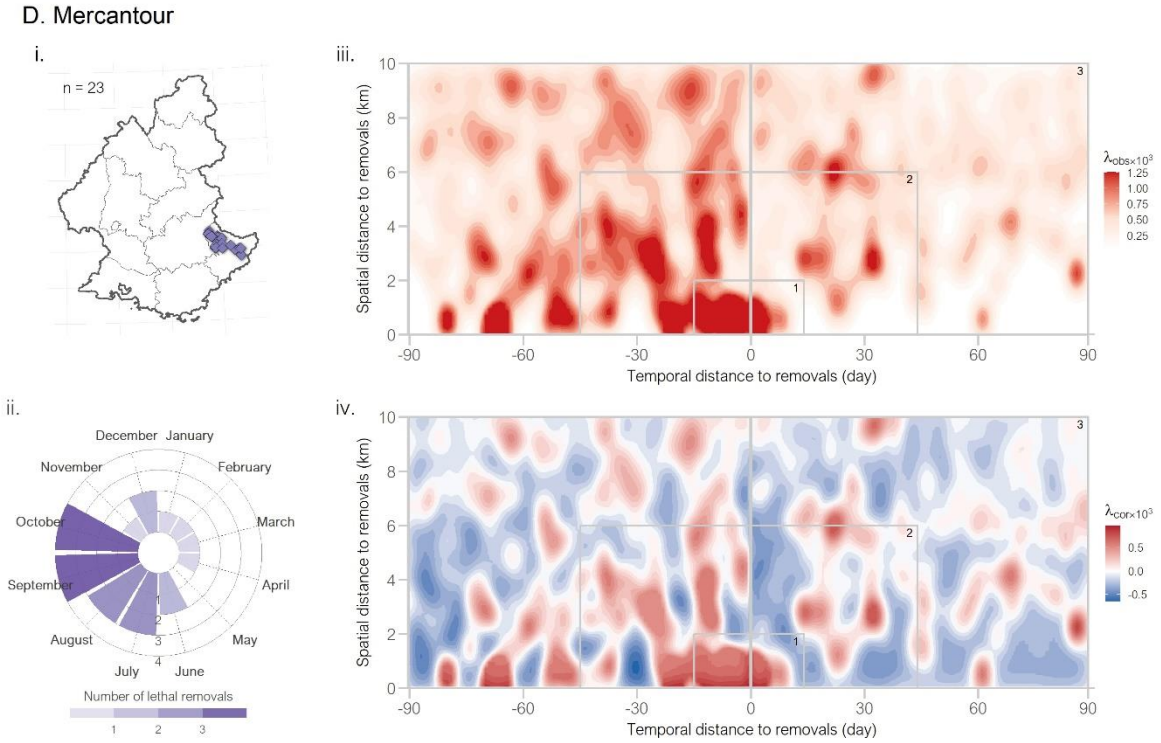



*Figure S1. Results of kernel estimation of attack intensities surrounding lethal removals, detailed for each analyzed subset of removals. Each panel includes (i) the map of the removal locations with the annotated number of involved removals, (ii) the monthly distribution of the removal dates, (iii) the observed attack intensities $\lambda_{obs}$ and (iv) the corrected attack intensities $\lambda_{corr}$. Intensities are given along the continuous temporal axis (x-axis) and spatial axis (y-axis). The coordinate (0,0) indicates the date and the location at which removals occurred. Grey rectangles of subpanels iii and iv delimit the three analysis scales 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days). A value of $\lambda_{corr}$ lower, equal or higher than zero indicated that the observed attack intensity was lower, equal or higher, respectively, than the attack intensity expected according pastoral use. (Part 1/4)*



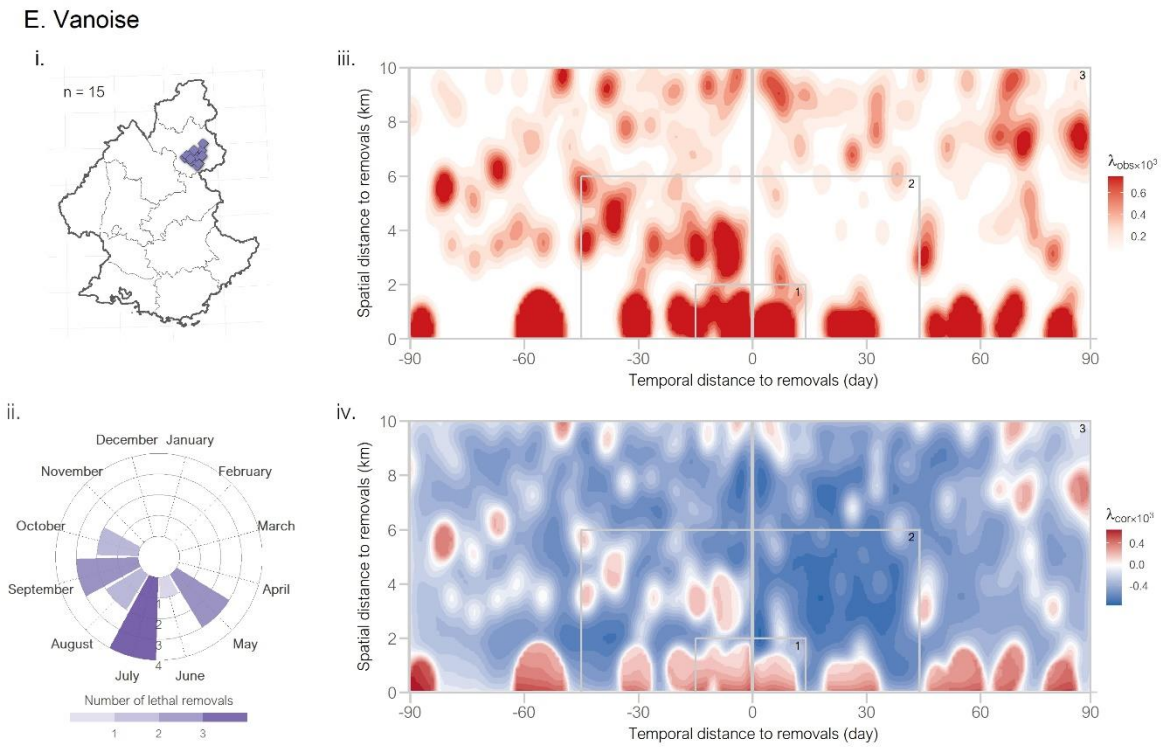




*Figure S1. (Part 2/4)*

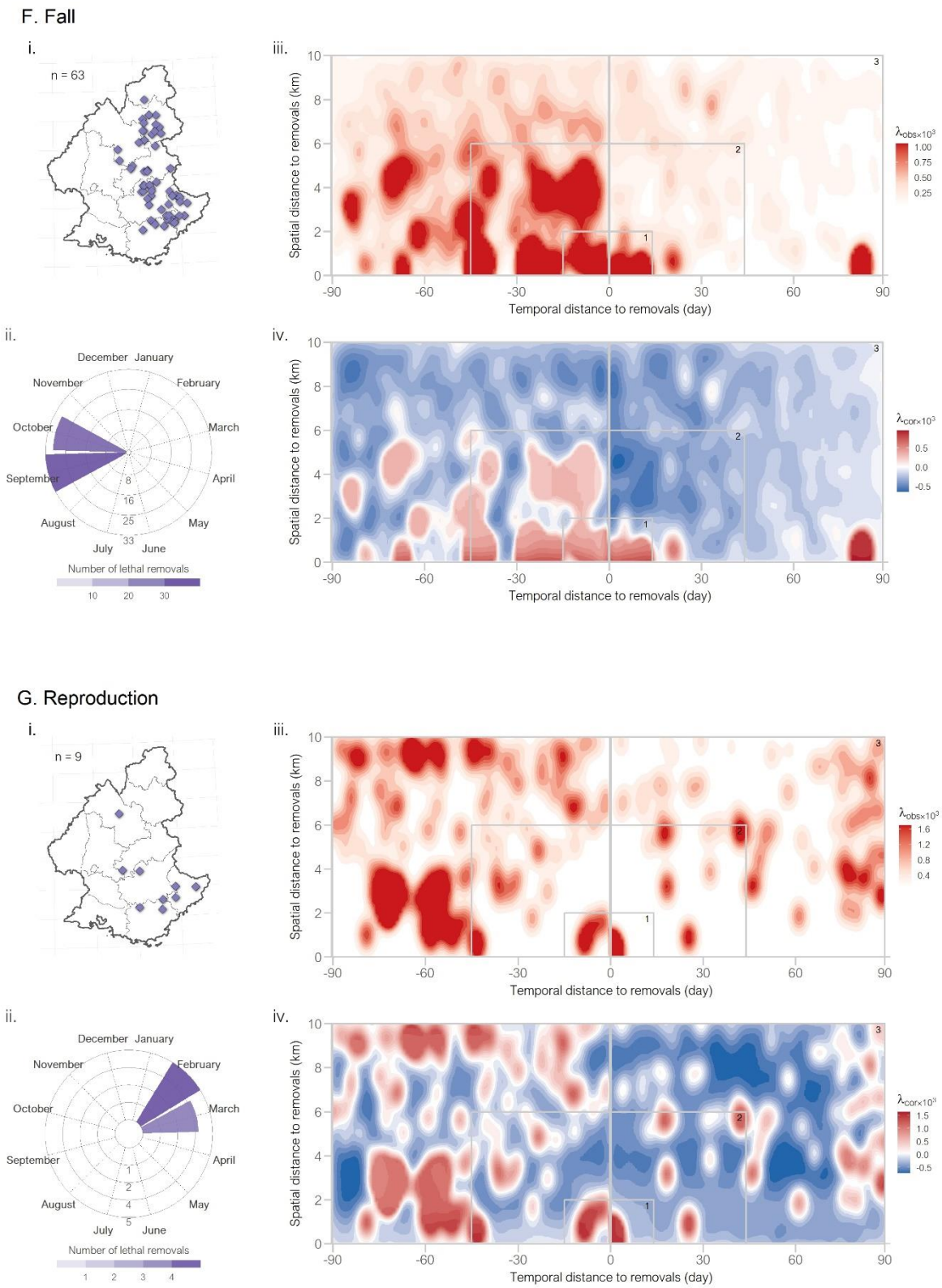
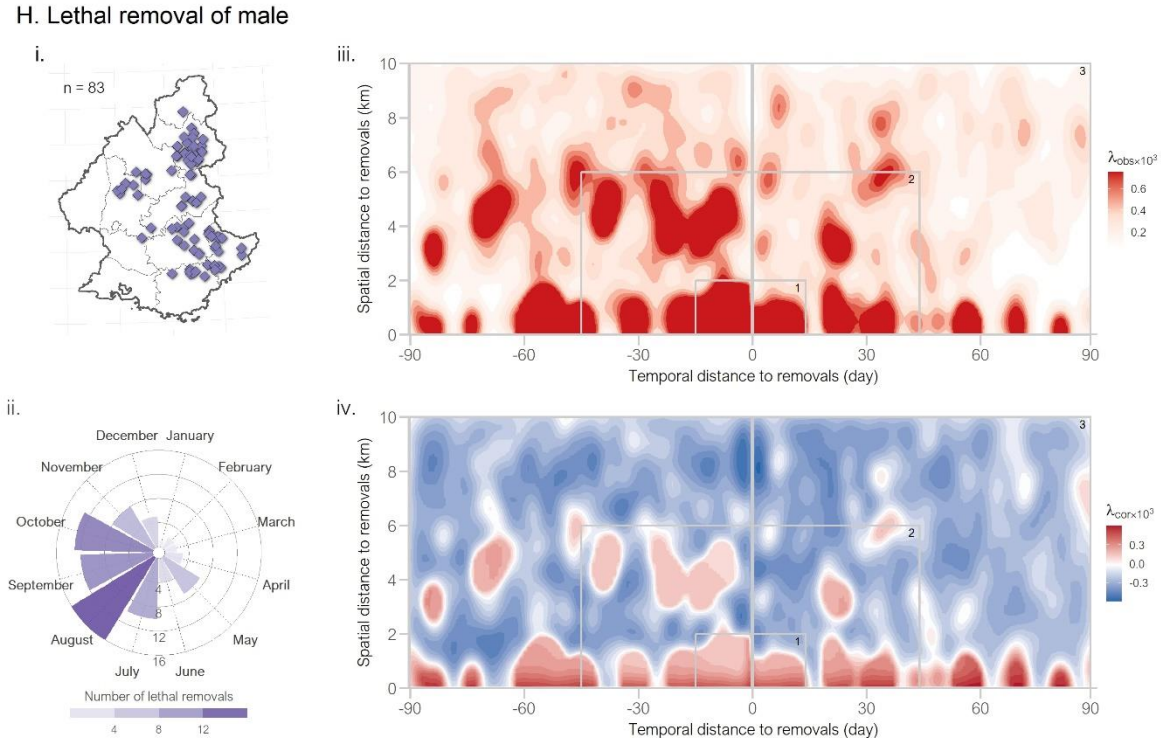



*Figure S1. (Part 3/4)*



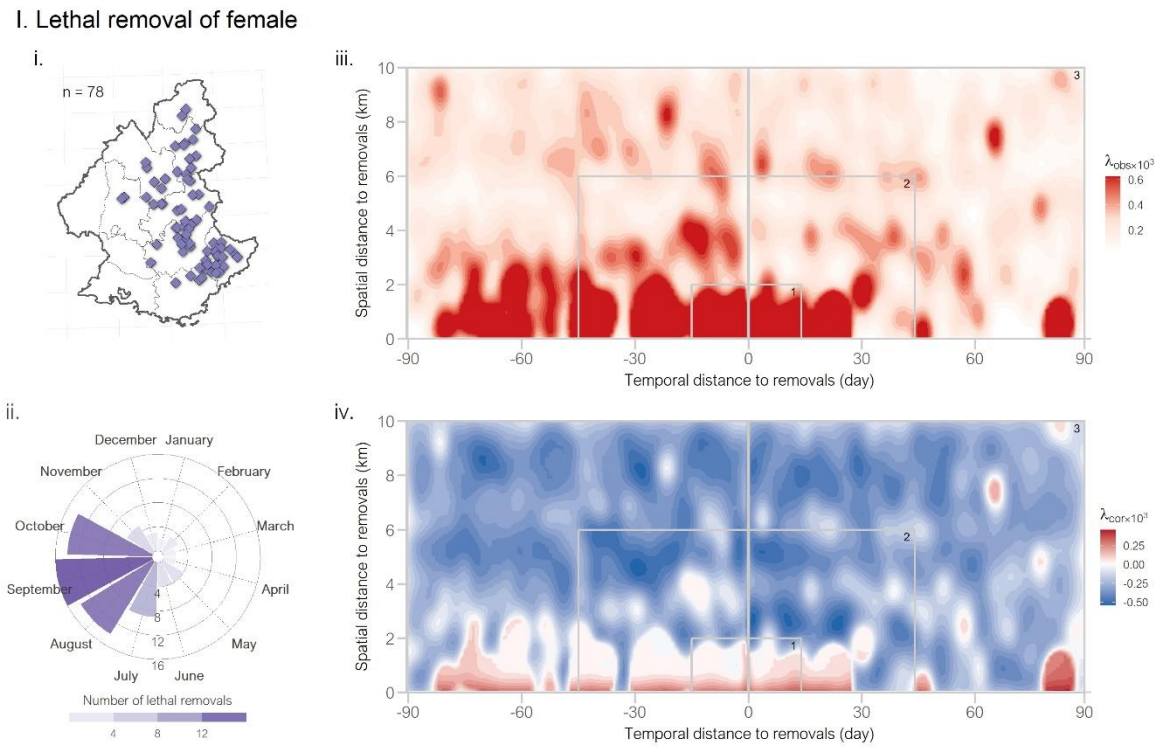




*Figure S1. (Part 4/4)*

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**Data, scripts and code**

Data, scripts and code are available online: https://doi.org/10.5281/zenodo.12772868 and https://gitlab.com/oksanagrente/Kernel_wolf_culling_attacks_p

**Conflict of interest disclosure**

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

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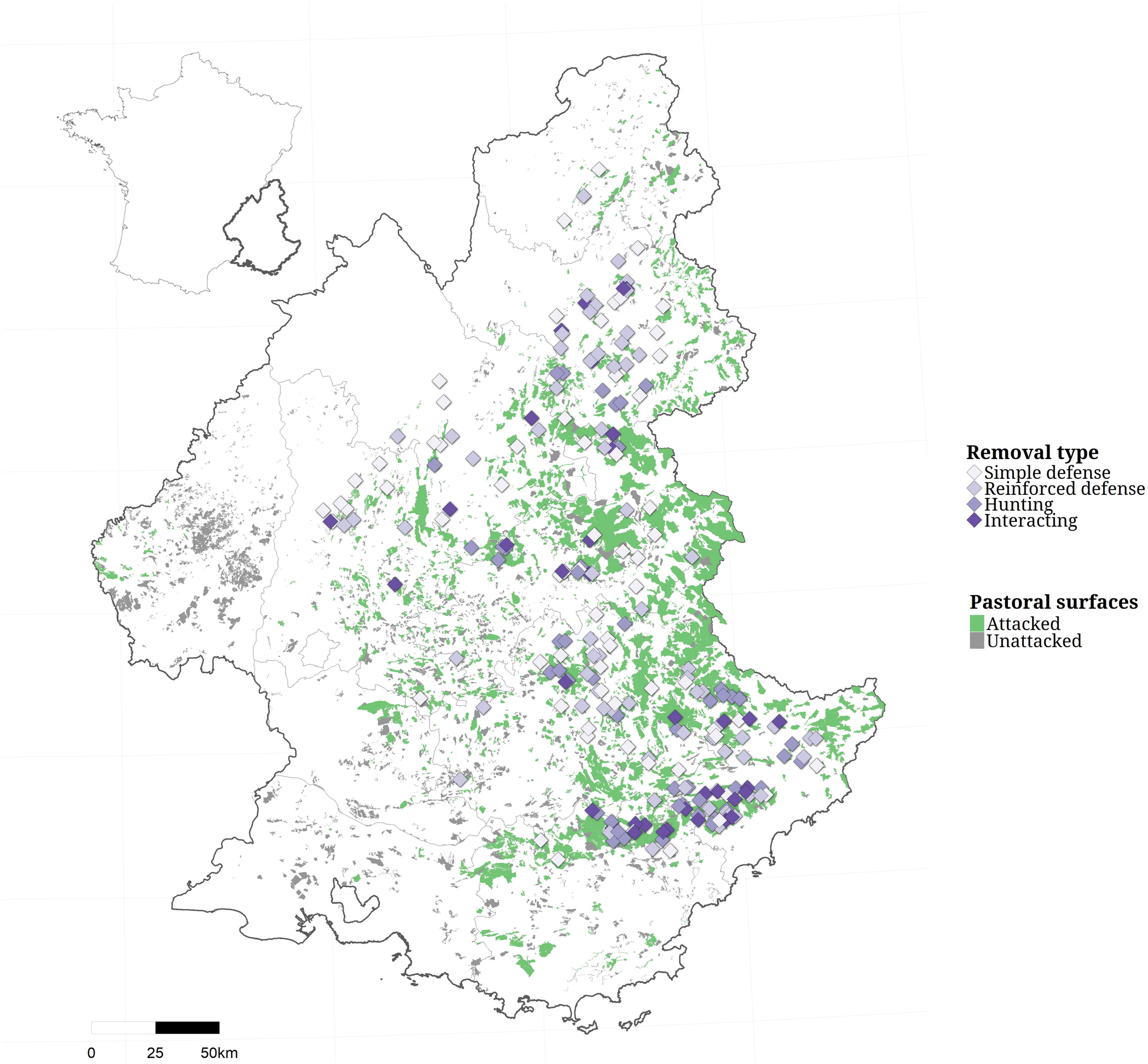
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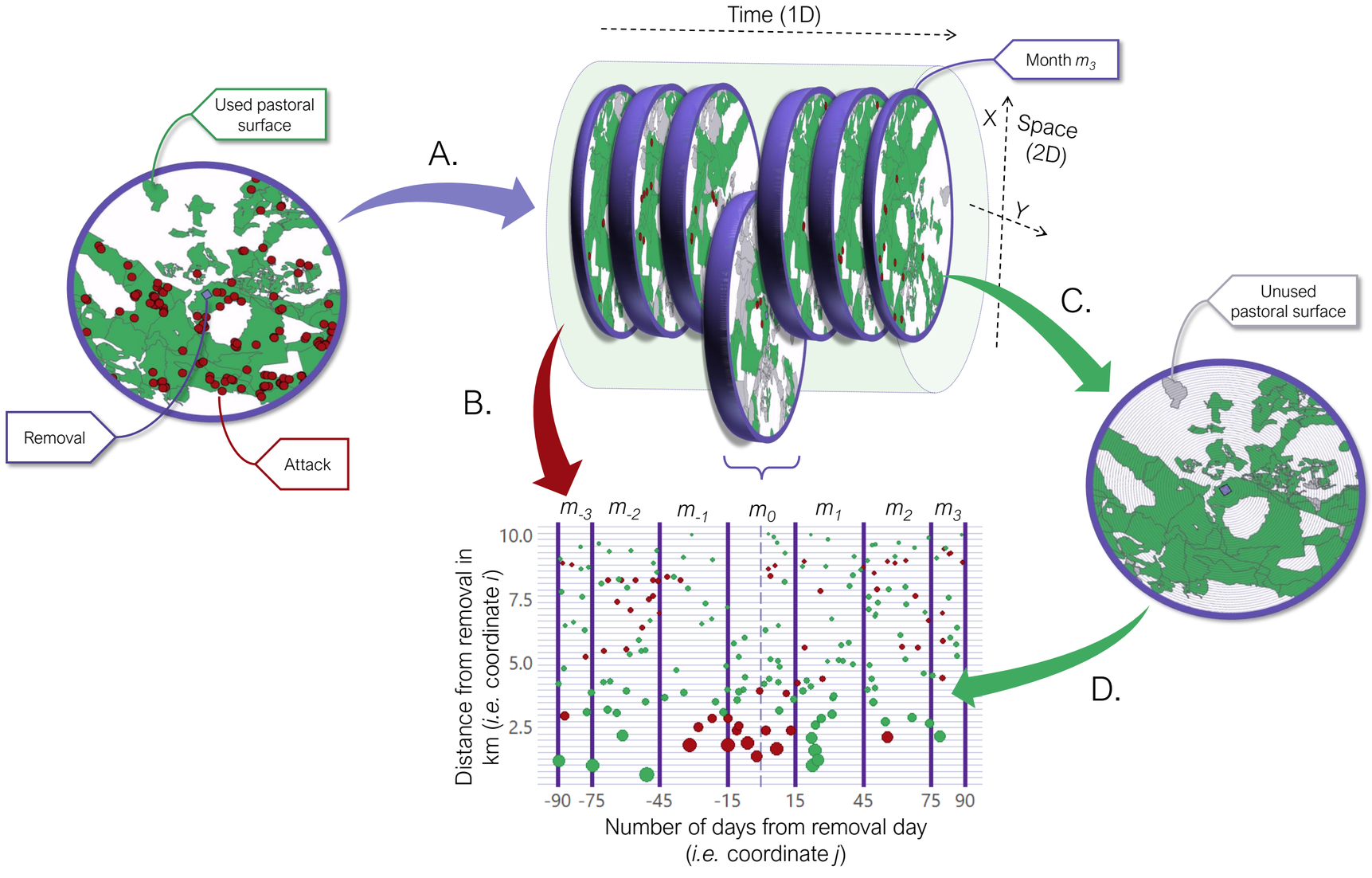


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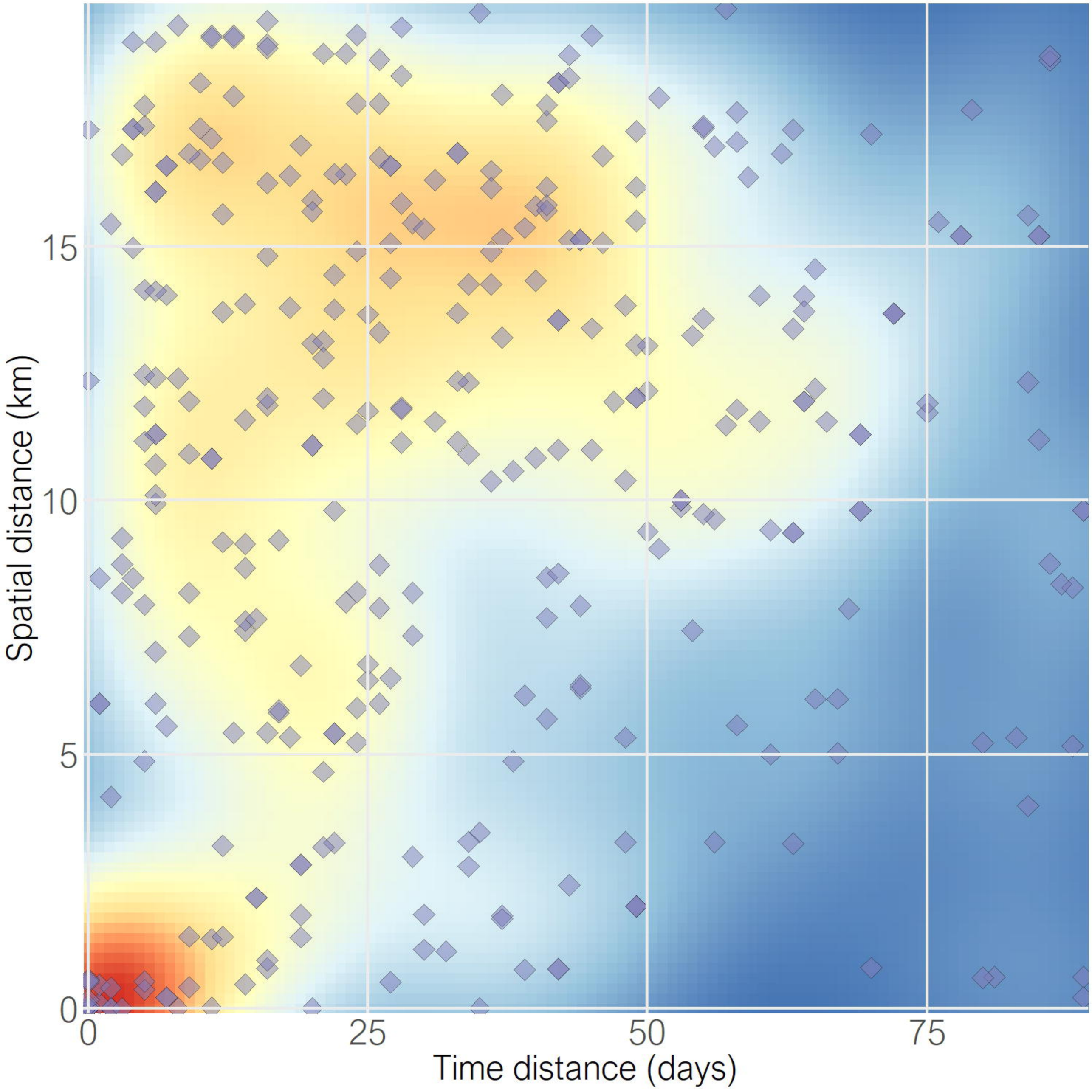
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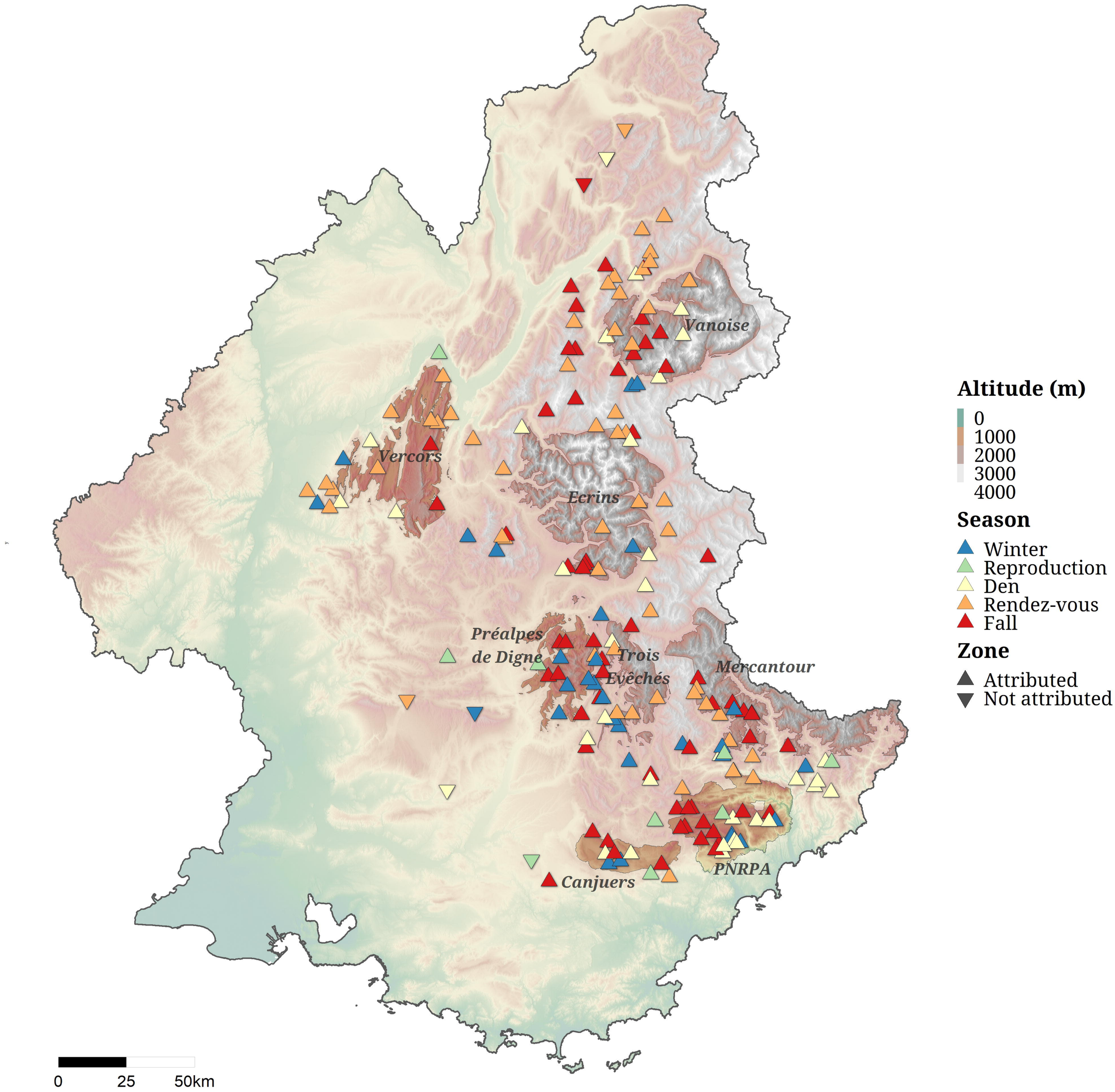
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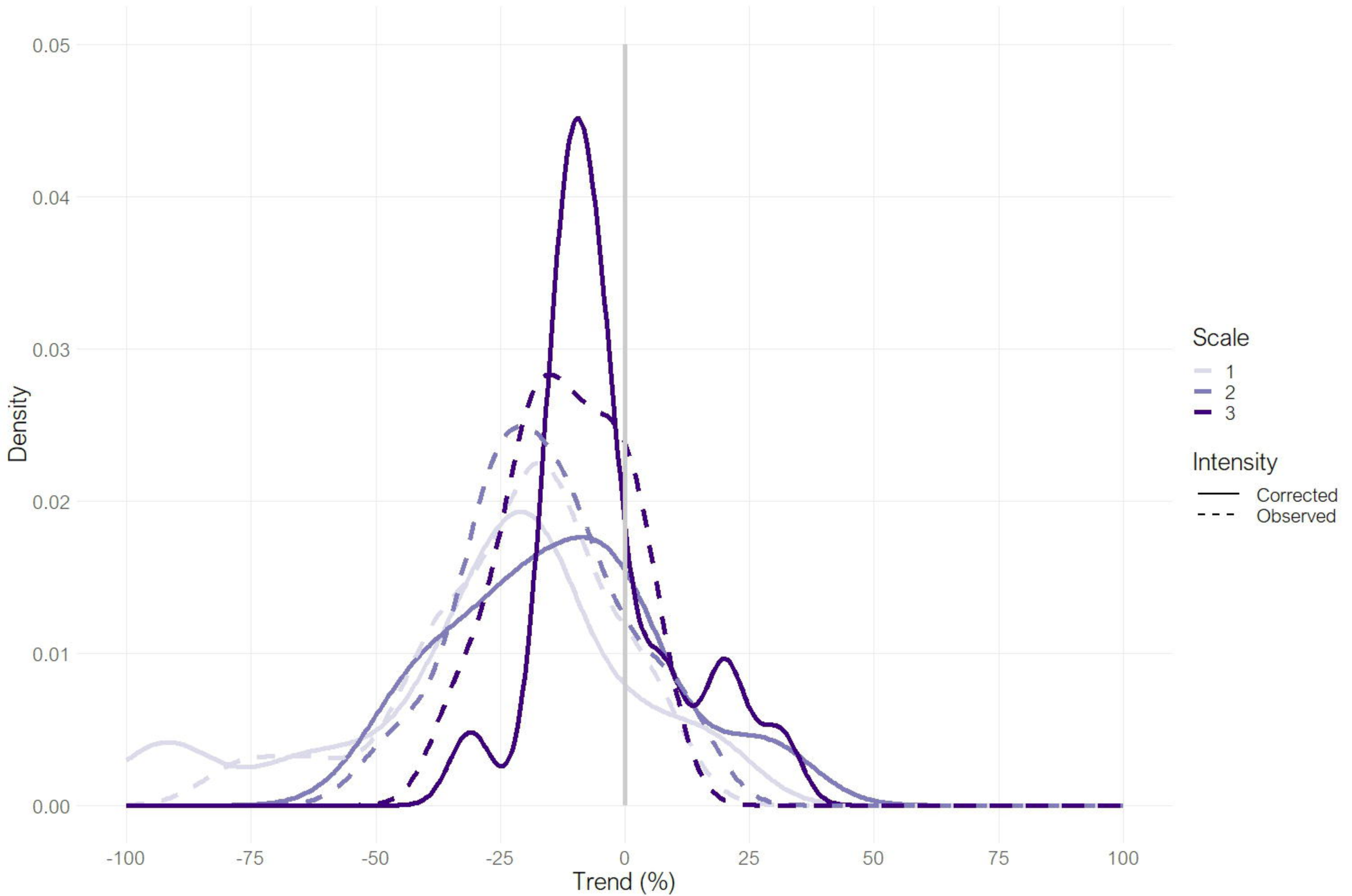
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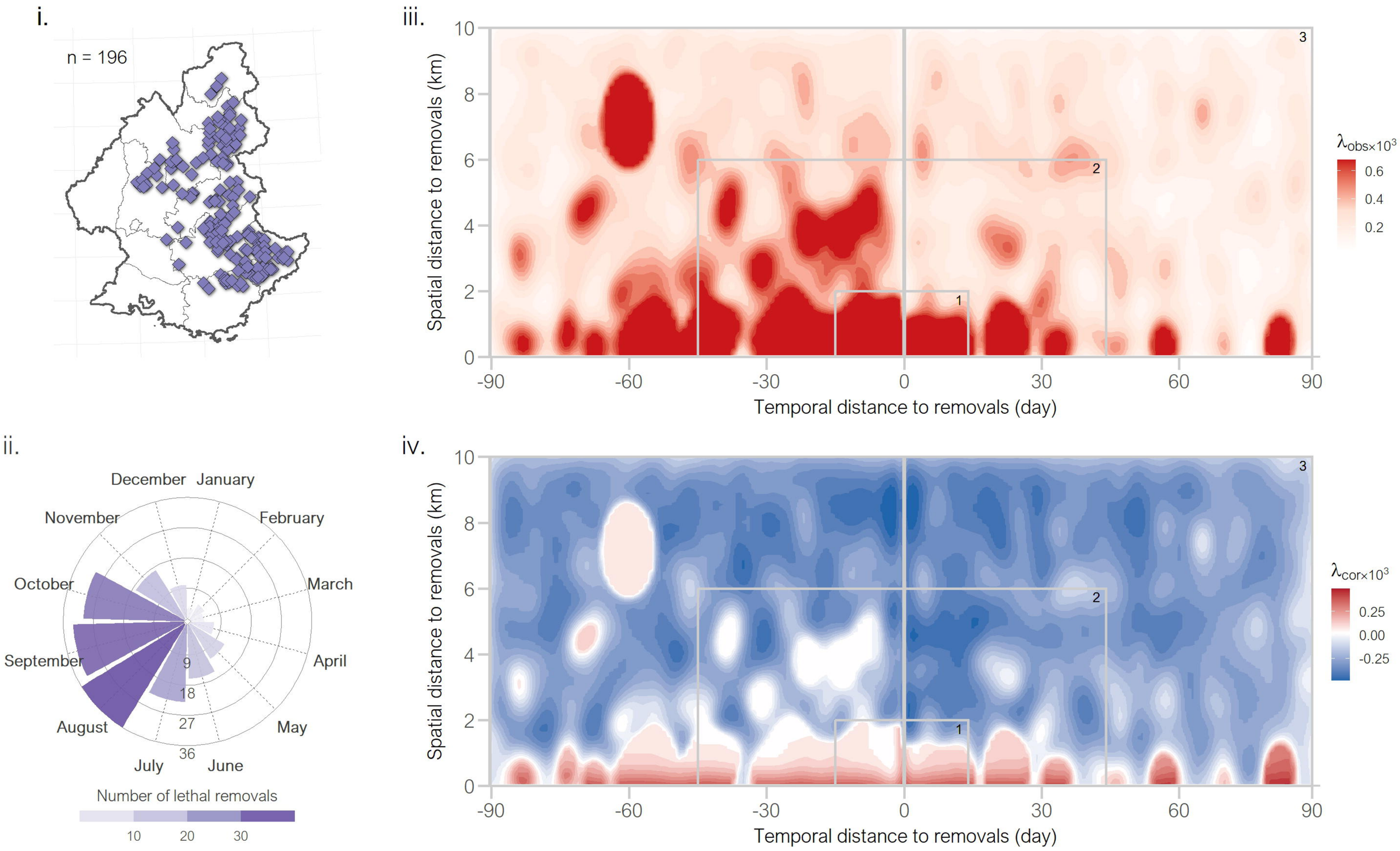
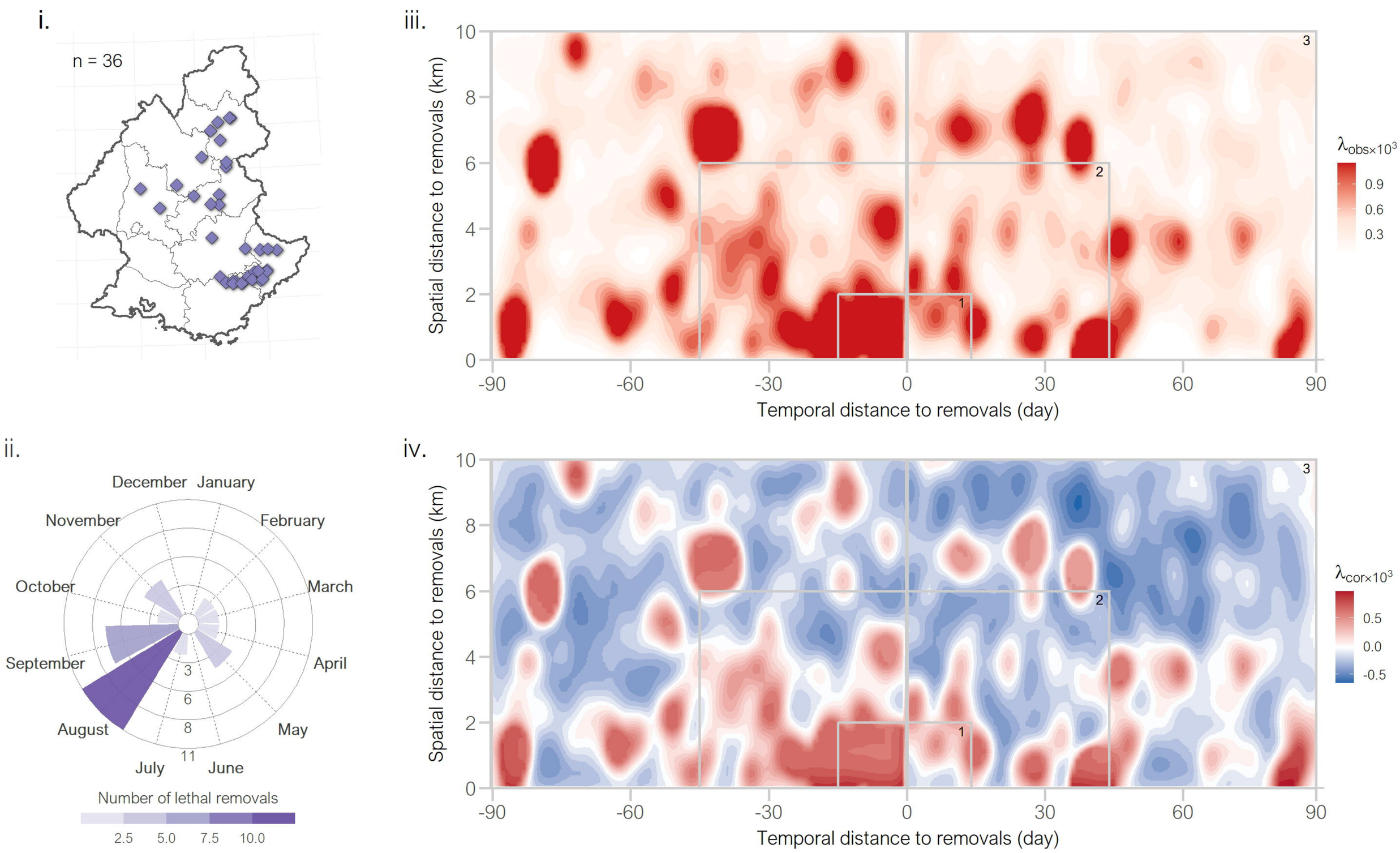
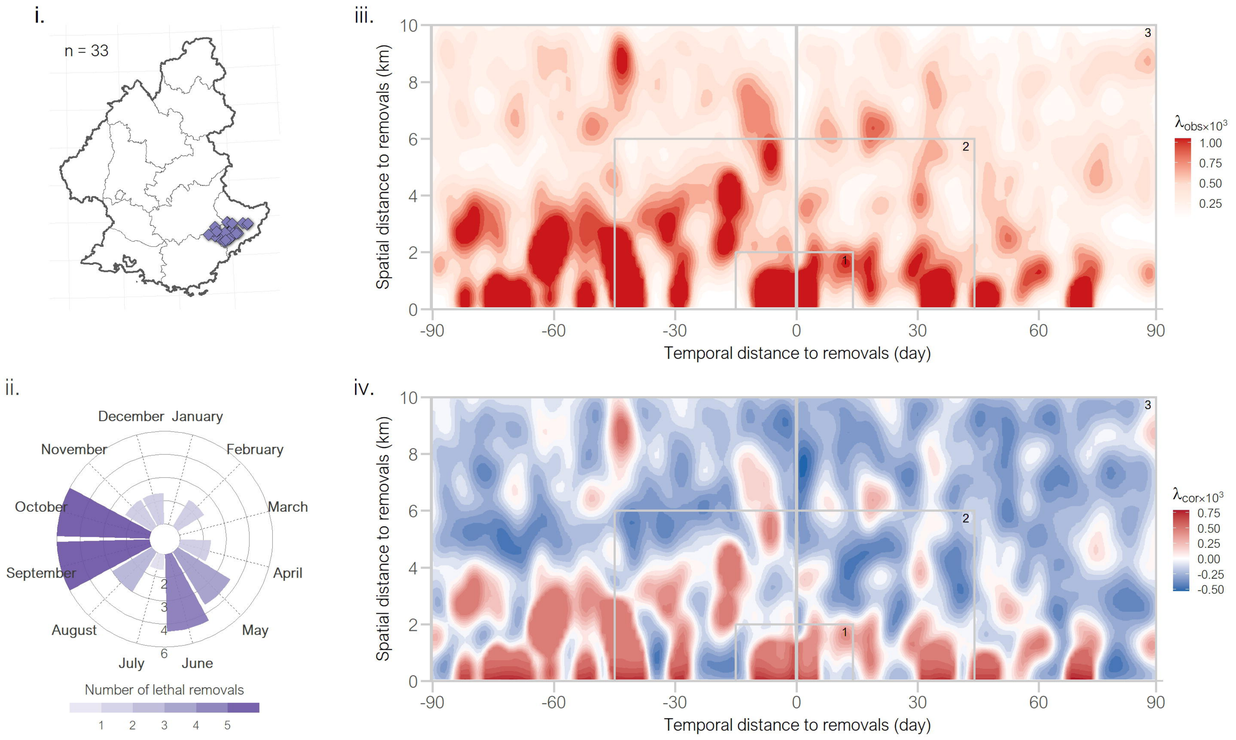
## A. Non-interacting lethal removals



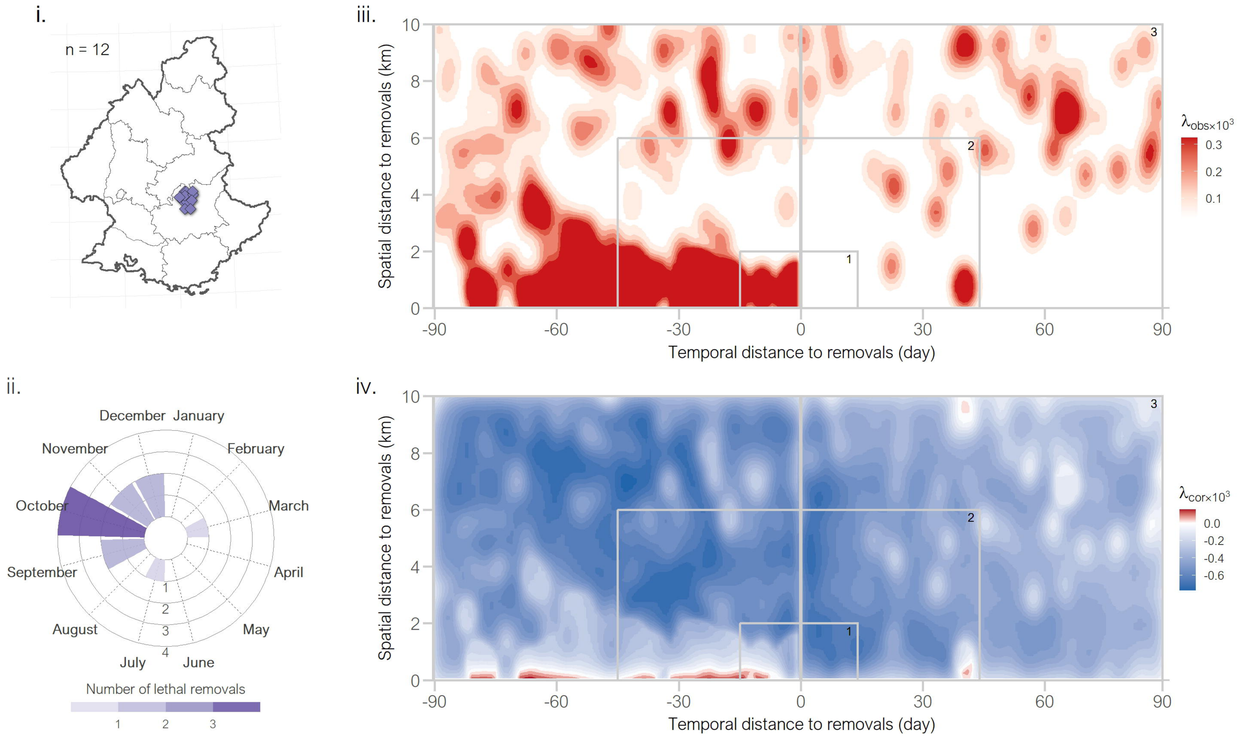

## B. Interacting lethal removals



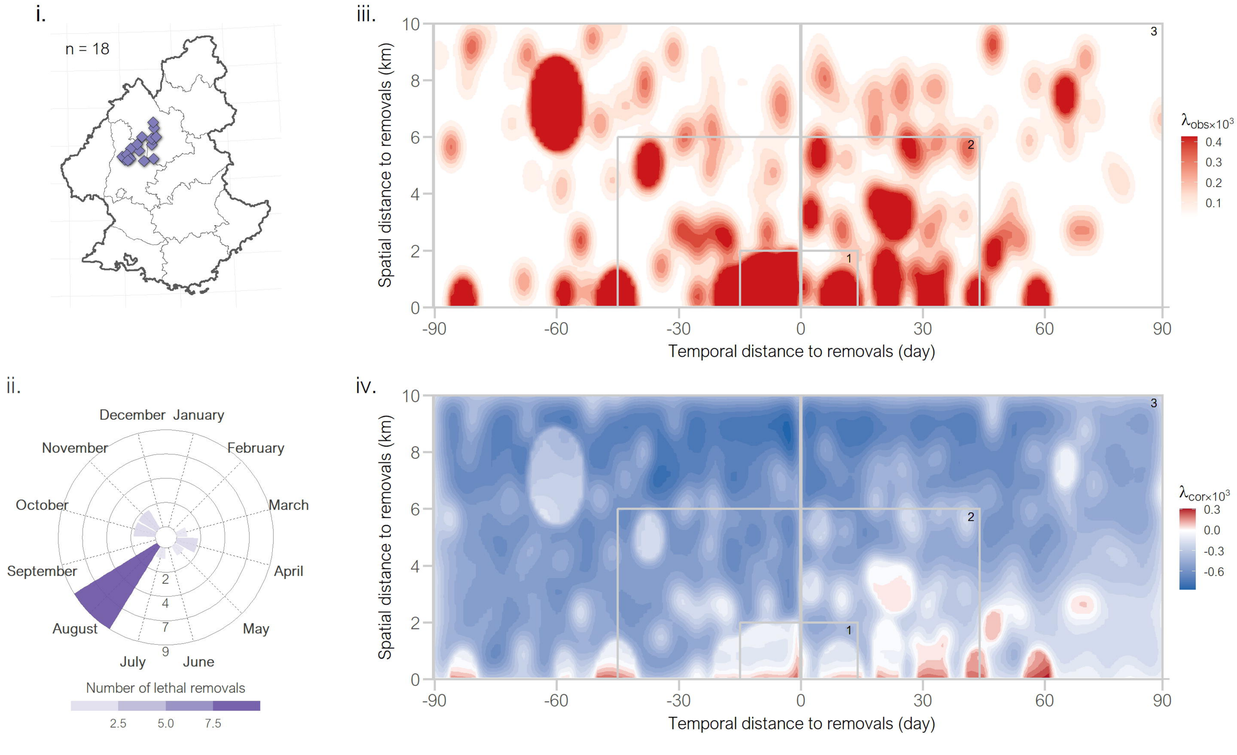
## C. PNRPA



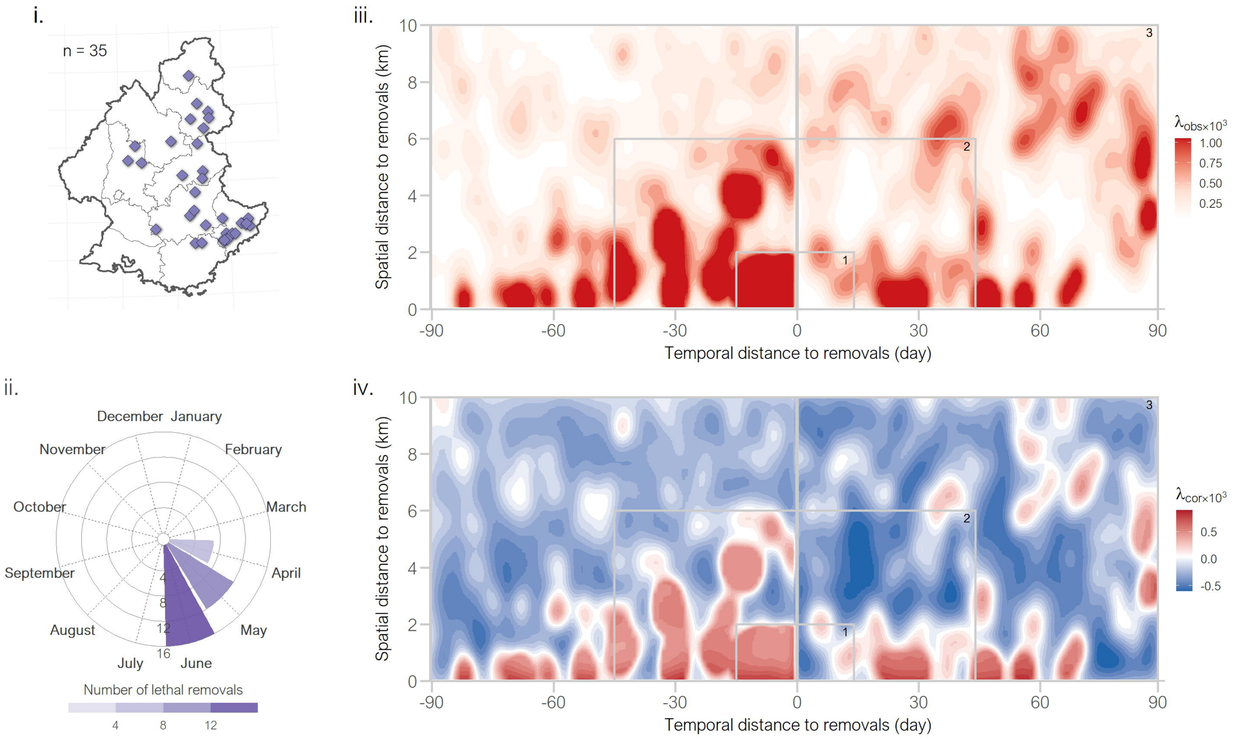

## D. Préalpes de Digne



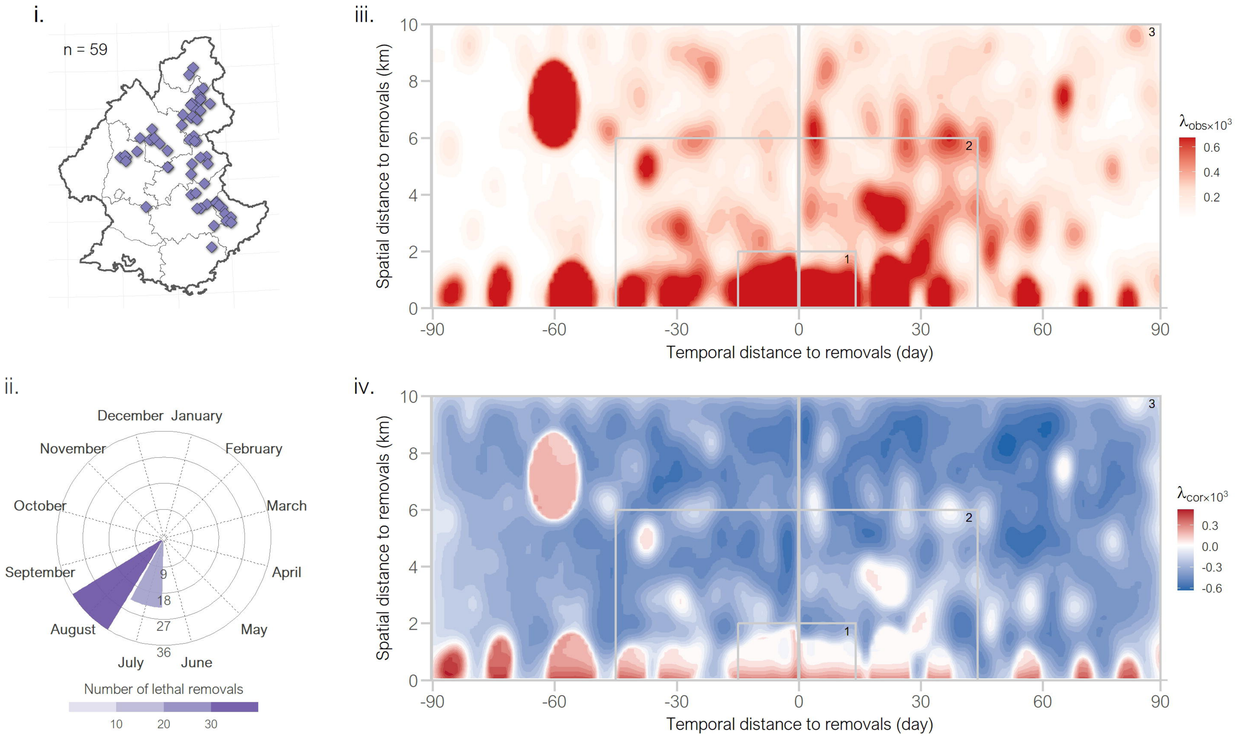

## E. Vercors



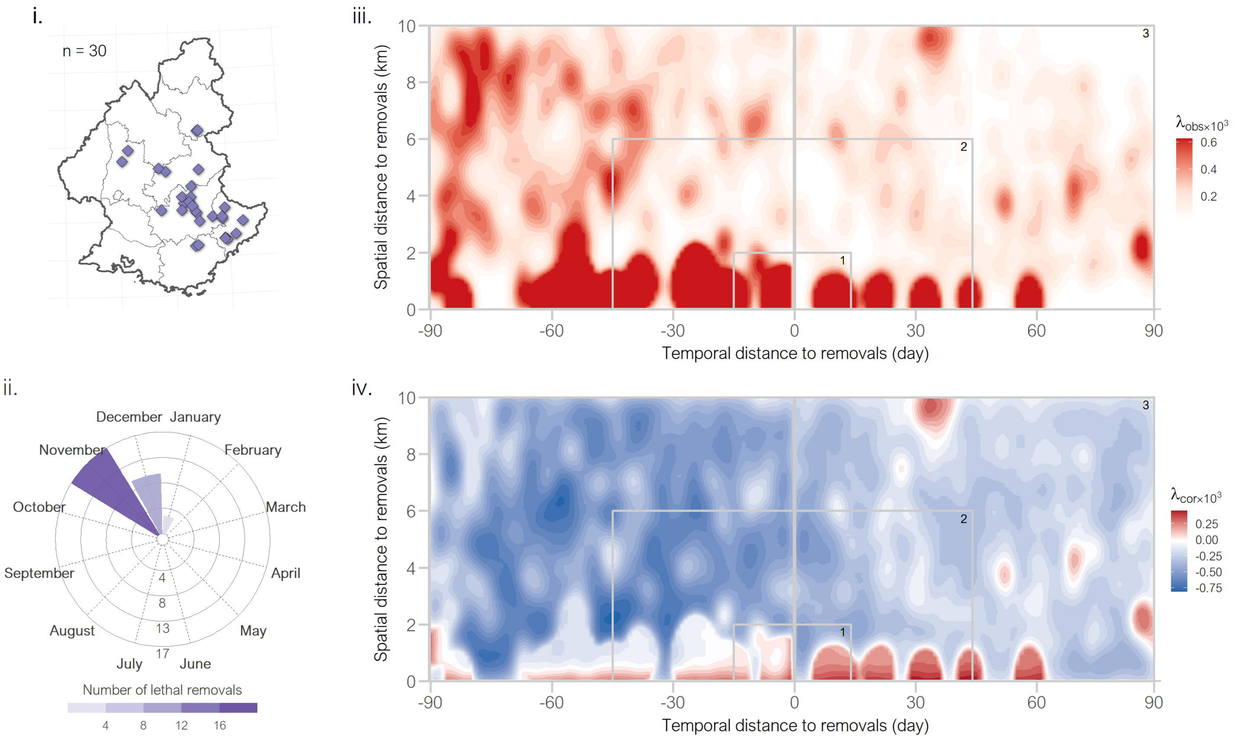
## F. Den



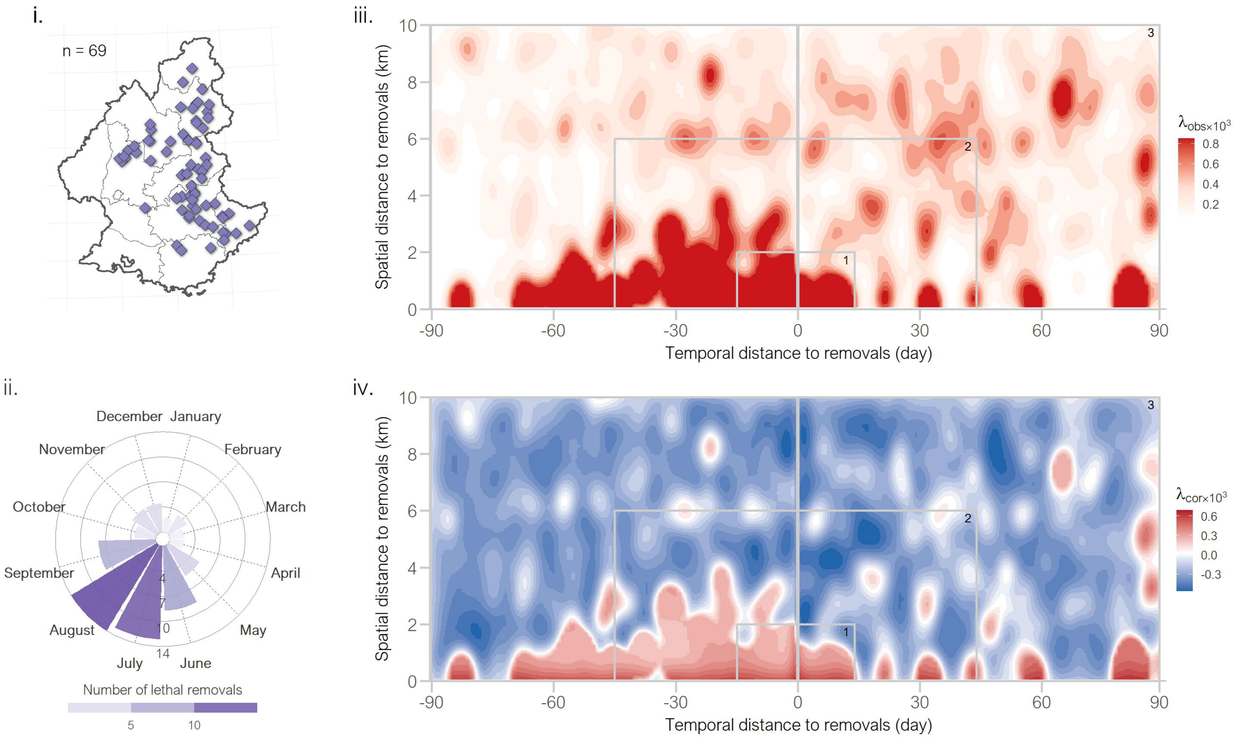

## G. Rendez-vous



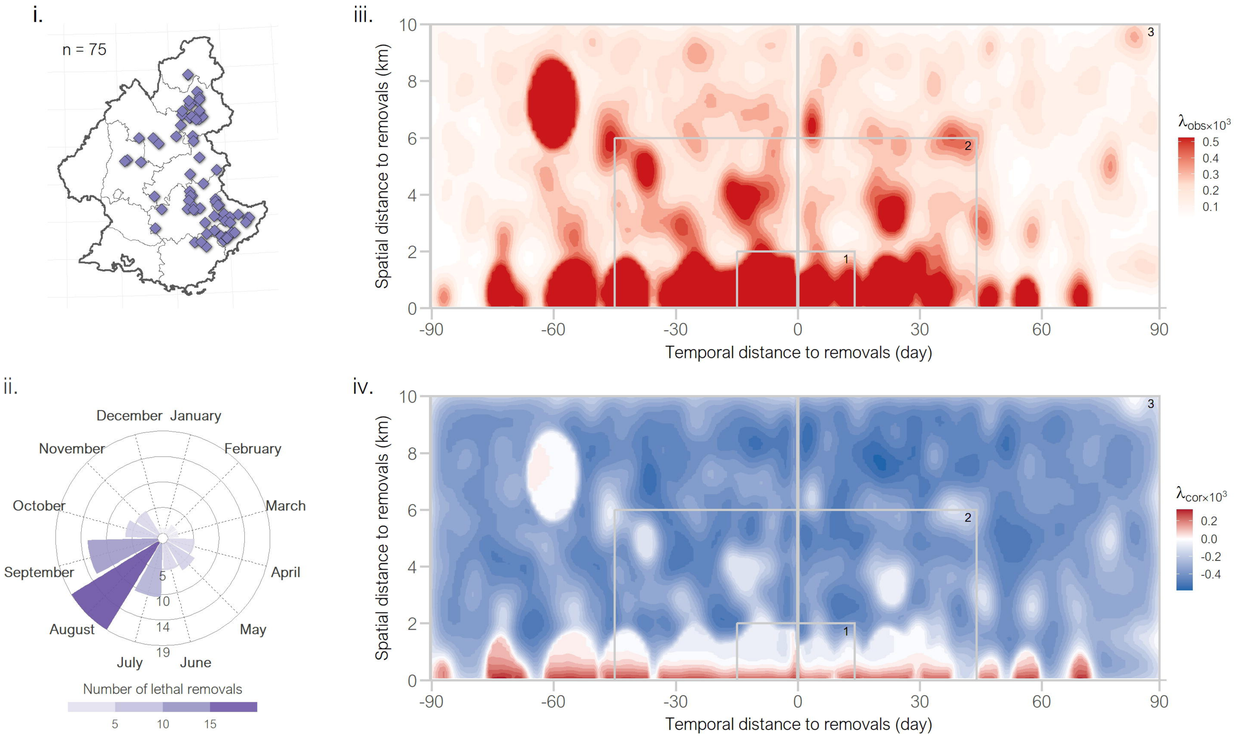

## H. Winter



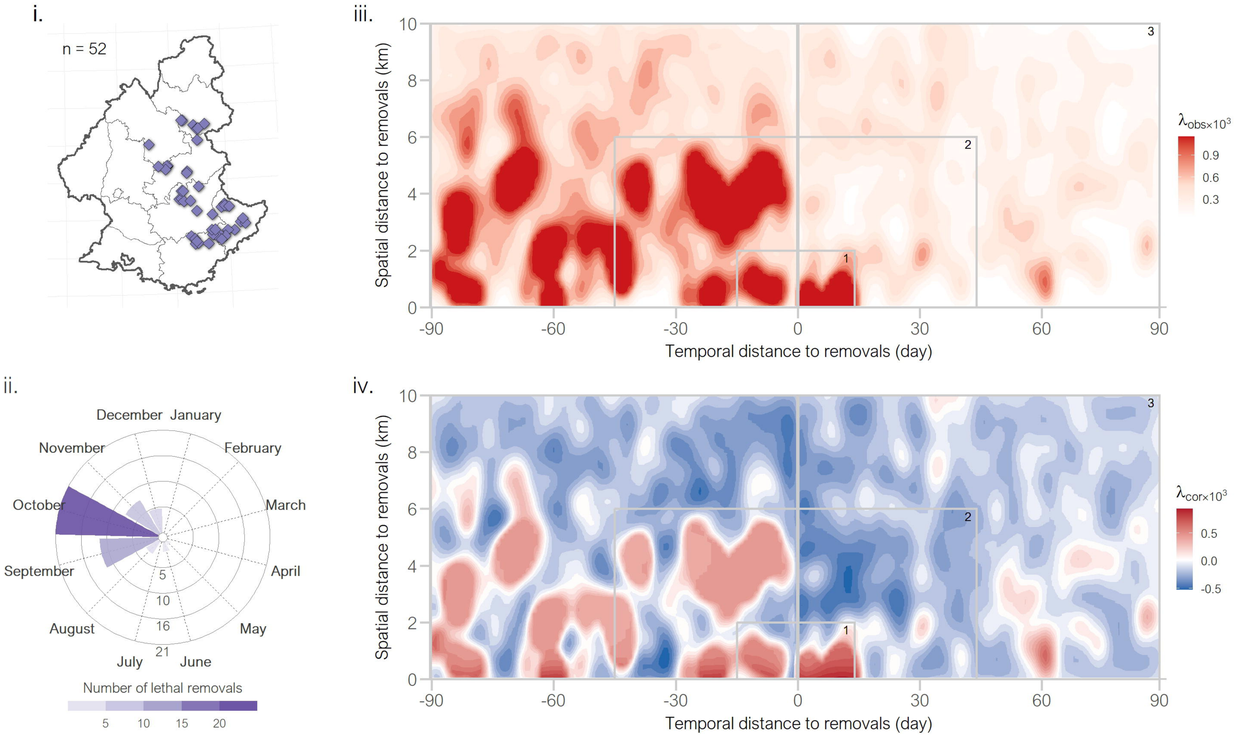
## I. Simple defense




## J. Reinforced defense




## K. Hunting



Interacting
No
n = 196
Interacting
Yes
n = 36
Geographic zone
PNRPA
n = 33
Geographic zone
Mercantour
n = 23
Geographic zone
Trois Evêchés
n = 18
Geographic zone
Vercors
n = 18
Geographic zone
Vanoise
n = 15
Geographic zone
Ecrins
n = 12
Geographic zone
Préalpes de Digne
n = 12
Geographic zone
Canjuers
n = 11
Season
Fall
n = 63
Season
Rendez-vous
n = 59
Season
Den
n = 35
Season
Reproduction
n = 30
Season
Winter
n = 9
Class
Reinforced defense
n = 75
Class
Simple defense
n = 69
Class
Hunting
n = 52
Sex
Male
n = 83
Sex
Female
n = 78
Trend (%)
200
100
0
-100
-200
0
2
4
6
8
10
Spatial distance to removals (km)
Trend
Observed
Corrected