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1 Spatio-temporal dynamics of attacks around 2 deaths of wolves: A statistical assessment of 3 lethal control efficiency in France

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17

18 Abstract

19 Evaluating the efficiency of lethal control of large carnivores such as wolves to reduce attacks on
20 livestock is important given the controversy surrounding this measure. We used retrospective data
21 over 10 years and an intra-site comparison approach to evaluate the effects of lethal control on the
22 distribution of attack intensities in the French Alps. We analyzed 278 legal killings of wolves between
23 2011 and 2020 and the 6110 attacks that occurred during a period of ± 90 days and within 10 km
24 around these lethal removals. This large number of attacks allowed us to perform an original
25 framework that combined both continuous spatial and temporal scales through 3D kernel
26 estimation. We also controlled the analysis for livestock presence, and explored different analysis
27 subsets of removals in relation to their locations, dates and proximity to other removals. This
28 statistical method provided an efficient visualization of attack intensity spatio-temporal distribution
29 before and after removals. A decrease of the intensity of attacks was the most common result after
30 the lethal removals of wolves. However, this outcome was not systematic for all subsets and
31 depended on the scale of the analysis. In addition, attacks tended to persist after removals while
32 showing frequent interruptions in time after but also before removals. We also observed localized
33 positive trends of attack intensities at varying distances from removals after they occurred. To
34 summarize, our results showed that considering the scale of the analysis is crucial and that effects
35 should be analyzed separately for each local context. As a next step, we recommend to move
36 forward from patterns to mechanisms by linking the effects of lethal control on wolves to their
37 effects on attacks through analysis of fine-scaled data on wolves and livestock.

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

40 1. Introduction

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

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

54 Also, retrospective studies have been conducted to answer the question of lethal control efficiency.
55 The data they used were not collected within a scientific frame but generally through management
56 (*e.g.* damages from compensation schemes). Most of retrospective studies on social canids (gray
57 wolves *Canis lupus*, dingoes *Dingo dingo*, coyotes *Canis latrans*) were correlative and tested for a
58 relationship between the number of livestock damages and the number of killed predators (Šuba et
59 al., 2023; Fernández-Gil et al., 2016; DeCesare et al., 2018; Conner et al., 1998; Allen, 2015; Kotal et
60 al., 2023). However, this approach is not suited to infer causality and is subject to high risks of
61 confounding factors and to analytical variability (Gould et al. 2023). For example, three correlative
62 studies which used the same dataset concluded differently on the effect of lethal removals of wolves
63 on livestock damages (Kompaniyets and Evans, 2017; Poudyal et al., 2016; Wielgus and Peebles,
64 2014).

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

75 Five of the seven comparative studies on social canids showed that lethal control significantly
76 decreased damage recurrence, whereas Santiago-Avila et al. (2018) and Kotal et al. (2023) found no
77 significant effect of lethal control on damages. Yet, results suggested variability in the efficiency of
78 lethal control. For example, Harper et al. (2008) detected that only the death of an adult wolf male
79 was significantly efficient, whereas Bradley et al. (2015) did not detect sex or age conditions on
80 efficiency. Variability could also result from the study designs themselves, as these studies used
81 different spatial and temporal scales to evaluate lethal control efficiency. Thus, small scale (*e.g.* 4 km
82 in Harper et al. (2008)), medium scale (*e.g.* pack territory in Bradley et al. (2015)) or large scale (*e.g.*
83 711 km² in Kotal et al. (2023)) could be used for space, sometimes within the same study (*e.g.*
84 Santiago-Avila et al., 2018). Time scale could also be disparate, going from several days or months

85 (e.g. Blejwas et al. (2002)) to two years (e.g. Kutal et al., 2023) or more (e.g. Bjorge and Gunson
86 (1985)). Most importantly, none of the mentioned retrospective studies have both used continuous
87 spatial and temporal scales, making it difficult to identify potential gradients of lethal control effects,
88 as those suggested in Santiago-Avila et al. (2018). Finally, most of these studies have not controlled
89 for livestock presence or abundance, yet the primary factor structuring damage risk and one of the
90 highest risks of confounding factor.

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

98 **2. Methods**

99 **2.1 Management context and study area**

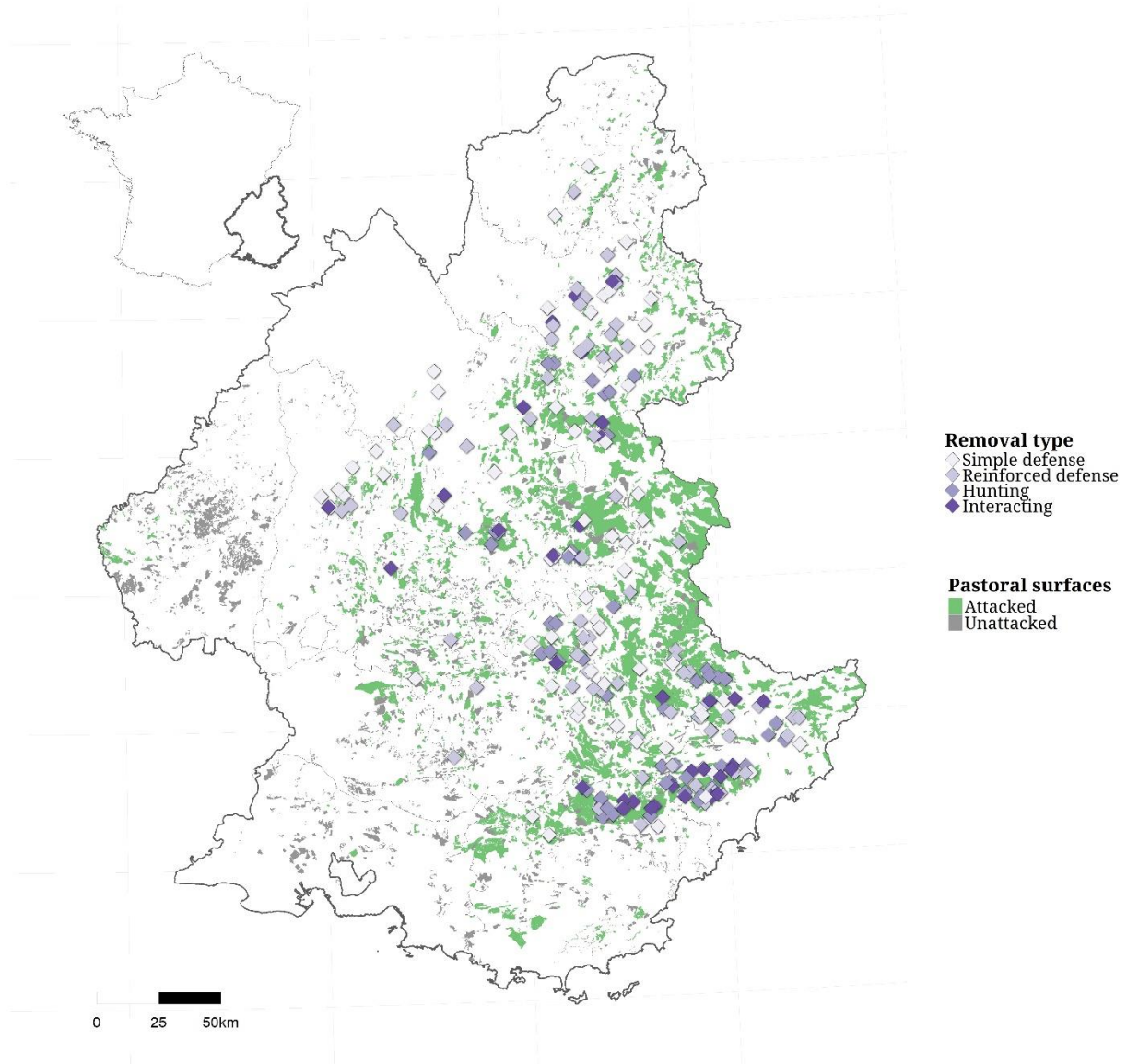
100 After historical campaigns of destruction, gray wolves disappeared from France at the beginning of
101 the twentieth century, despite being present on the whole metropolitan territory at the end of the
102 eighteenth century (de Beaufort, 1987). From the 1970s, the combination of protective legislation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

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

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

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

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



141

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

147 2.2 Datasets

148 2.2.1 *Lethal removals*

149 We used the records of deaths of wolves from 2011-2020 compiled by the regional French
150 administrations. We used the 362 records of wolves killed by legal shootings and that were
151 geolocated within the study area. Dates of lethal removals were recorded, but not the hour. The
152 number of lethal removals increased over time and could be divided into three periods, 2011-2014,
153 2015-2018 and 2019-2020, that represented respectively 8%, 44% and 48% of the dataset, for
154 annual means of 7 (\pm 6), 40 (\pm 6) and 87 (\pm 3) lethal removals respectively.

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

161 2.2.2 *Attacks on sheep*

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

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

173 2.2.3 *Spatio-temporal sheep distribution*

174 We used the data from the pastoral census of the two south-east regions Provence-Alpes-Côte-
175 d'Azur and Auvergne-Rhône-Alpes conducted by the National Research Institute for Agriculture,
176 Food and the Environment (Dobremez et al., 2016). The census indexed and delimited for the period
177 2012-2014 the pastoral units at medium or high altitude used by flocks, as well as the pastoral zones
178 at lower altitudes. Giving the relative stability of the use of the pastoral units and zones over time
179 (Grente et al., 2022), we assumed the information of the pastoral census was valid for our entire
180 study period. Pastoral units and zones delimited the spatio-temporal area where attacks could have
181 occurred. Therefore, our analysis was restricted to the pastoral area delimited by this census, in
182 order to control for livestock presence.

183

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

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

194

195 *2.2.4 Attributing attacks to pastoral units*

196 The attack dataset showed 59% of consistency with the dataset of pastoral surfaces, meaning that
197 59% attacks were within pastures that were in use according to the pastoral census. The other
198 attacks could be outside pastoral surfaces, or could have occurred in months for which pastoral
199 surfaces were not supposed to be in use according to the pastoral census. These mismatches could
200 result from changes in the spatial or temporal use of pastoral surfaces, from errors during the attack
201 record (*e.g.* geolocation approximation), or because attacks occurred in non-indexed pastoral
202 surfaces.

203 When attacks were within pastures and when difference between the month of their dates and the
204 sets of grazed months of their pastures did not exceed three months (9% of total attack dataset), we
205 only updated the pastoral census by adding the months of the attacks to the corresponding
206 pastures. Otherwise, we relocated attacks to their closest pastures within a 500 meters radius by
207 favoring pastures with the smallest difference between their sets of grazed months and the months
208 of the attacks. When these differences exceeded 3 months, or if no pastoral surface could be found
209 within a 500 meters radius around the attacks, we excluded these attacks (13% of total attack
210 dataset). Relocations were done at the closest point of the pastoral surfaces to the original attack
211 locations (19% of total attack dataset). When necessary, we added the months of the relocated
212 attacks to the sets of grazed months of their new pastoral surfaces. The final dataset of attacks had
213 19 302 events.

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

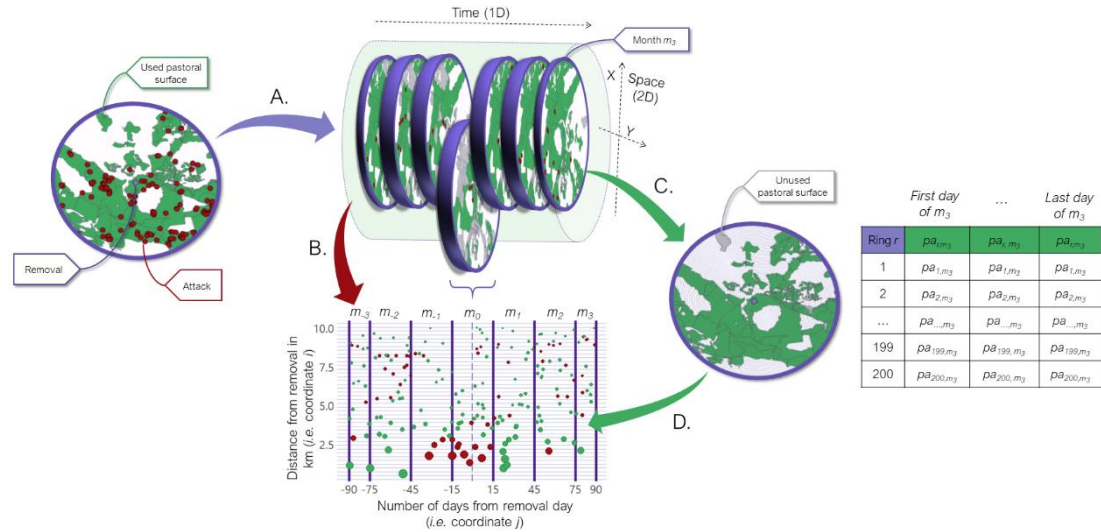
216 **2.3 Analysis**

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

221 *2.3.1 Construction of 3D buffers*

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

228



229
 230 *Figure 2. Data transformations for one lethal removal (purple point) occurring on 15th of August 2017 as an example. A.*
 231 *Attribution of the 3D spatio-temporal buffer around the removal. Each slice represents the occurrence of observed attacks*
 232 *(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*
 233 *partial (m_{-3} and m_3 , here only 15 days each). Monthly slices were chosen for visual convenience, but slices were daily in the*
 234 *analysis. Attacks (red points) in the buffer have 3 coordinates: 1 temporal (height of the cylinder), and 2 spatial (x,y). B.*
 235 *Reduction of 2D spatial coordinates of observed attacks of the 3D buffer to 1D, through the Euclidian distance to the*
 236 *removal (coordinate i , i.e. rows). Time coordinate becomes coordinate j (columns). C. Dividing one 10-km radius slice around*
 237 *the removal into 200 rings (here only 50 are represented for visual convenience) to calculate the total pastoral area pa that*
 238 *was used during the corresponding month of the slice. The column of pa is then duplicated into the number of days of the*
 239 *corresponding month (i.e. information about pastoral use was monthly). The operation is repeated for each slice of the 3D*
 240 *buffer. D. Simulation of coordinates i and j of attacks (green points) based on the matrix of pa from step C. The number of*
 241 *simulated attacks is the same as the number of observed attacks. The size of points represents the spatial correction $1/pa_r$,*
 242 *based on similar calculations as step C but achieved on the pastoral surfaces regardless of their use (i.e. as in the most left*
 243 *circle). Note that the observed and simulated datasets are placed on the same figure for visual convenience here, but were*
 244 *treated separately during the kernel estimations.*

245 The spatio-temporal buffer was composed solely of the pastoral surfaces where attacks could occur.
 246 Therefore, the buffer was sparse, and remained empty where there was no pastoral surface around
 247 the removal event, or when the pastoral surface was not grazed according to the pastoral census.
 248

249 We set the radius of the cylinder at 10 km, in order to encompass more than one wolf territory
 250 radius, estimated at 7–8 km in France through telemetry and genetic tracking (Duchamp et al.,
 251 2012). Therefore, ripple effects, if any, could be observed up to 10 km from the lethal removal. The
 252 pastoral surfaces overlapping the spatial buffer were truncated to the spatial buffer.
 253

254 We set the height of the cylinder to 180 days, meaning that all attacks occurring 90 days before and
 255 90 days after the lethal removal were part of the temporal buffer. Thus, we analyzed the effect of
 256 lethal removal on a full season if the removal event occurred in the middle of the season, or on two
 257 successive seasons if not. The day of the removal was not part of the buffer, because we could not
 258 know if an attack recorded at the day of the removal occurred after of before the removal, having no
 259 information about the hour of both attacks and removals.
 260

261 Attacks were not homogeneously distributed across space and time (Grente et al., 2022). Increasing
 262 the radius or the height of buffers compressed the attack distribution towards the centers of buffers
 263 (i.e. at small spatial and temporal distances), and prevented an optimal reading of the results.
 264

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

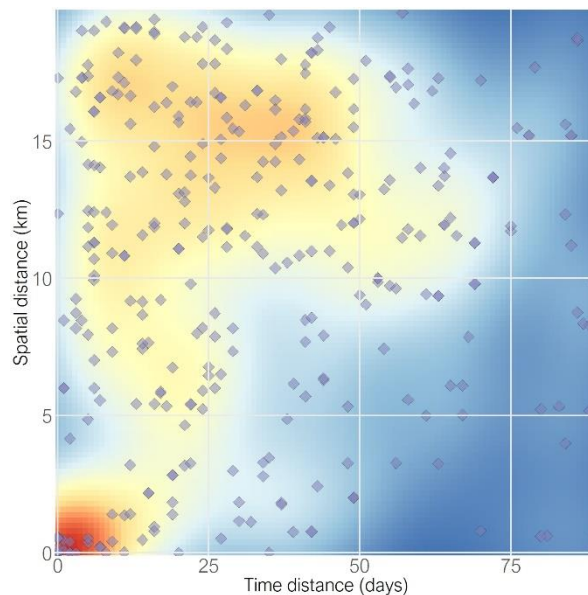
267 study area or occurring after the 1st October 2020, eventually leaving 278 analyzed lethal removals
268 (Figure 1).

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

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

285 We ended up with 232 spatio-temporal buffers, including 36 buffers of groups of interacting
286 removals, corresponding to a total of 6110 attacks. On average, a buffer included 26.3 attacks (\pm
287 20.7, range 0–100).

288



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

291 2.3.2 Reducing the number of spatial dimensions

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

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

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

309 To incorporate pastoral surfaces to the spatial correction, we sliced up the circle of each buffer into
310 200 rings r of progressive radius, from 0.025 to 9.975 km. Width of rings were therefore 50 m. We
311 calculated pa_r , the area of pastoral surfaces of each ring r . We then attributed to each attack from
312 the buffer the inverse of the pastoral area of its ring, $1/pa_r$ (Figure 2.B-D), corresponding to its
313 weight in the later analysis (part 2.3.4). Because attacks could only be located in pastoral surfaces
314 (part 2.2.4), pa_r of rings containing attacks could not be null.

315 2.3.3 *Simulating attacks according to livestock presence*

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

320 For each buffer, we used the same 200 rings r as in part 2.3.2. For each month m represented in the
321 temporal buffer, we calculated the set of $pa_{r,m}$ by considering only pastoral surfaces that were
322 grazed this month according to the pastoral census (Figure 2.C). Thus, we constructed a pa matrix $[r,$
323 $m]$ for each buffer, where columns were sorted following the order of months in the temporal
324 buffer. Each column m was then duplicated according to the number of days of this month included
325 in the temporal buffer. Thus, the matrix dimensions were 200 rows and 180 columns. Eventually, the
326 matrix coordinates (r, m) became similar to the coordinates (i, j) of the observed attacks, with a
327 slightly coarser spatial resolution of 50 meters (*i.e.* ring width) and the same temporal resolution of 1
328 day.

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

336 2.3.4 *Kernel estimates*

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

339 temporal j coordinates, with the spatial correction $1/pa$, as weight. We used two separate
340 bandwidth parameters for spatial distance and temporal lag, of 500 meters and 2 days. The choice of
341 the bandwidth parameters was *ad-hoc*, and met the needs of adopting a resolution close to the
342 matrices used to simulate attacks (*i.e.* cells of 50 meters and 1 day) while smoothing attack
343 intensities enough in order to obtain interpretable results. We also considered the spatio-temporal
344 distributions of attacks before removals ($j \in [1, 90]$) and after removals ($j \in [91, 180]$) as two separate
345 distributions by appropriately right- and left-truncating kernels in the time dimension for attacks
346 occurring before and after the date of removals, respectively. We corrected kernel estimates for
347 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
348 and Q_3 were the first and third quantiles of the estimated distribution of λ_{obs} (Walfish, 2006).

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

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

$$357 \quad \lambda_{corr}(i, j) = \lambda_{mean_sim}(i, j) - \lambda_{obs}(i, j) \quad (1)$$

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

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

$$363 \quad Y_{\lambda, s} = \frac{\sum_{i=1, j=91}^{i=I, j=91+J} \lambda'(i, j) - \sum_{i=1, j=90-J}^{i=I, j=90} \lambda'(i, j)}{(I \times J)/2} \times 100 \quad (2)$$

364 where I and J were the number of rows (spatial distance to removals) and columns (number of days
365 before or after removals) of scale s , $\lambda'(i, j)$ was the observed or corrected intensity at the coordinates
366 (i, j) rescaled over $[0, 1]$ for observed intensity or over $[-1, 1]$ for corrected intensity by using the
367 minimum and maximum values of $\lambda_{obs}(i, j)$ or $\lambda_{corr}(i, j)$ over the temporal range $90-J, 91+J$. The
368 rescaling allowed trend comparison between subsets of buffers. The division by $(I \times J)/2$ allowed
369 trend comparison between scales s of different sizes. We investigated trends of three spatio-
370 temporal scales s : the small scale ($s = 1$) of spatial range 0-2 km and of temporal range ± 15 days ($I =$
371 $40, J = 14$), the intermediate scale ($s = 2$) of spatial range 0-6 km and of temporal range ± 45 days ($I =$
372 $120, J = 44$) and the large scale ($s = 3$) of spatial range 0-10 km and of temporal range ± 90 days ($I =$
373 $200, J = 89$).

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

378

379

380 2.3.4 Investigated categories of removals

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

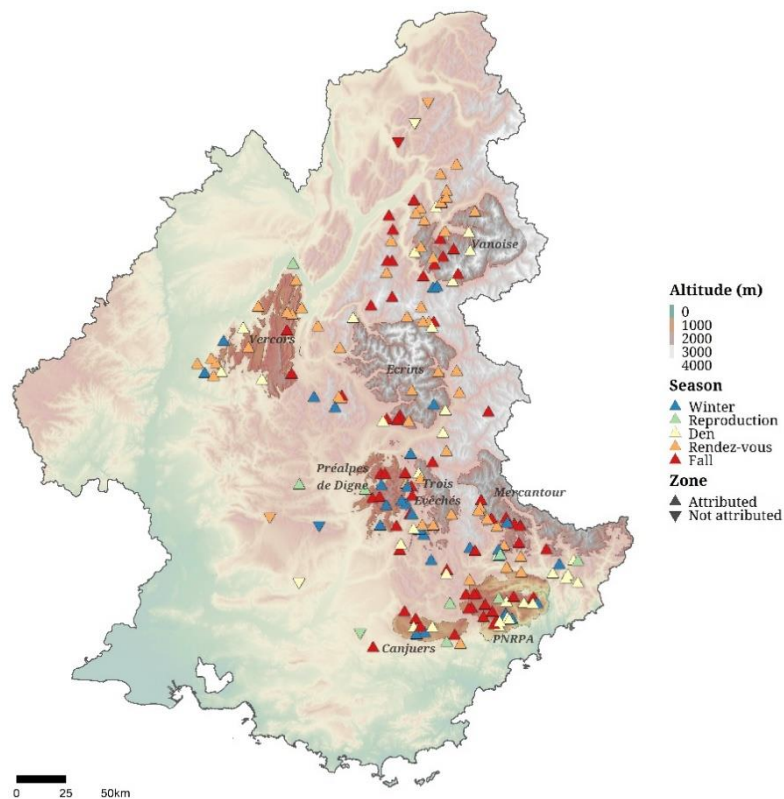


Figure 4. Topography of the study area, with the 8 highlighted zones from the Zone subcategory that were selected for the analysis. Upward and downward triangles represent lethal removals that could be attributed or not to one of the 27 zones, respectively. Colors show the subset from the Season subcategory.

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

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

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

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

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

406 **2.4 Implementation**

407 The analysis was conducted in R 4.2.3 (R Core Team, 2023). We used the R packages *tidyverse 2.0.0*
408 (Wickham et al., 2019), *readxl 1.4.2* (Wickham and Bryan, 2023), and *sf 1.0-12* (Pebesma and Bivand,
409 2023) to handle the datasets. We used the R package *spatstat 3.0-6* (Baddeley et al., 2015) to
410 simulate point patterns in part 2.3.3. We adapted the function *kde2d.weighted* from *ggtern 3.4.2*
411 (Hamilton and Ferry, 2018) to separate the kernel estimates before and after the removal date in
412 part 2.3.4. We used the package *osmdata 0.2.3* (Padgham et al., 2017) to extract limits of PNRPA and
413 of Canjuers military zone. We used the packages *RColorBrewer 1.1-3* (Neuwirth, 2022), *tidyterra*
414 *0.4.0* (Hernangómez, 2023), *geodata 0.5-8* (Hijmans et al., 2023), *scales 1.2.1* (Wickham and Seidel,
415 2022), *ggfx 1.0.1* (Pedersen, 2022a), *ggnewscale 0.4.9* (Campitelli, 2023), *metR 0.14.1* (Campitelli,
416 2021), *patchwork 1.1.2* (Pedersen, 2022b) and *ggtext 0.1.2* (Wilke and Wiernik, 2022) for data
417 visualisation. The datasets, codes and results are available online (Grente et al., 2024).

418 **3. Results**

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

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

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

436 **3.1 At small scale**

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

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

443 **3.2 At intermediate scale**

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

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

456 **3.3 At large scale**

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

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

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

471 **3.4 Differences between observed and controlled intensities in heatmaps**

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

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

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

483 **3.5 Attack intensities by spatial distances**

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

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

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

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

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

Category	Subcategory	Subset	Total	Figure	Scale 1		Scale 2		Scale 3	
					$Y_{\lambda_{obs},1}$	$Y_{\lambda_{corr},1}$	$Y_{\lambda_{obs},2}$	$Y_{\lambda_{corr},2}$	$Y_{\lambda_{obs},3}$	$Y_{\lambda_{corr},3}$
			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
Non-interacting		Season	Fall	63	S1.F	-17	-17	-48	-49	-33
	Rendez-vous		59	6.G	-10	-16	12	9	7	-8
	Denning		35	6.F	-62	-96	-26	-42	2	-12
	Reproduction	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	

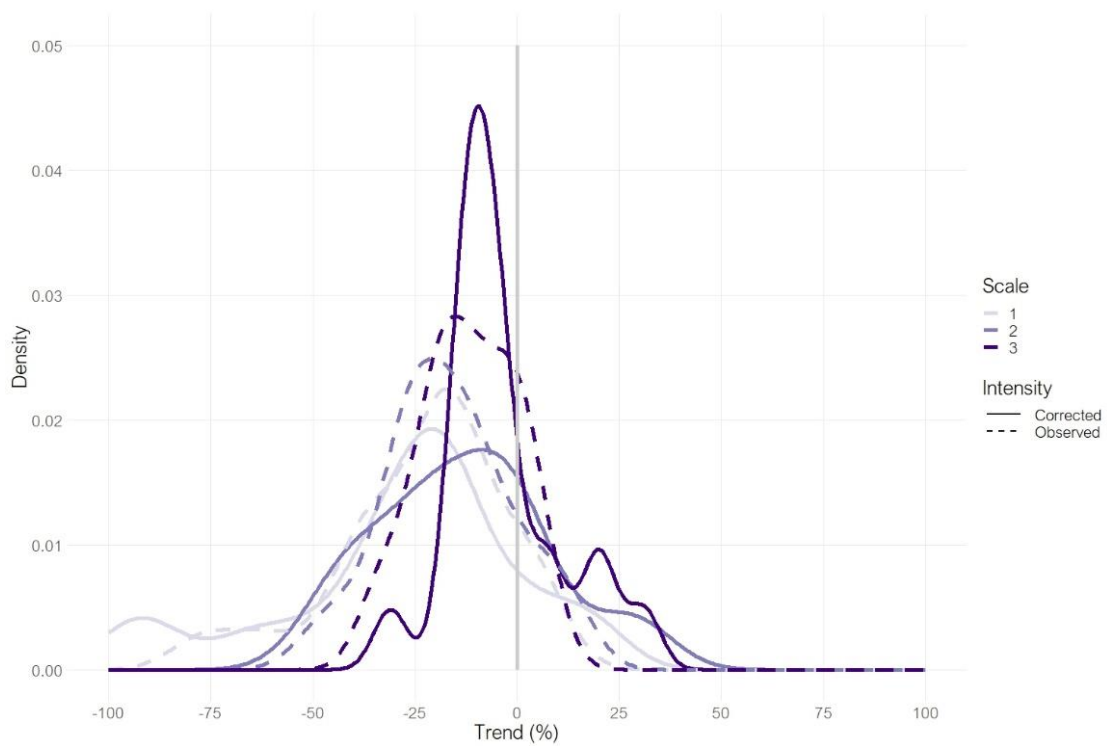
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Figure 5. Density distributions of the trends of observed (dotted lines) and corrected (solid lines) attack intensities after lethal removals at the spatio-temporal scales 1 (0-2 km, ± 15 days), 2 (0-6 km, ± 45 days) and 3 (0-10 km, ± 90 days) presented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

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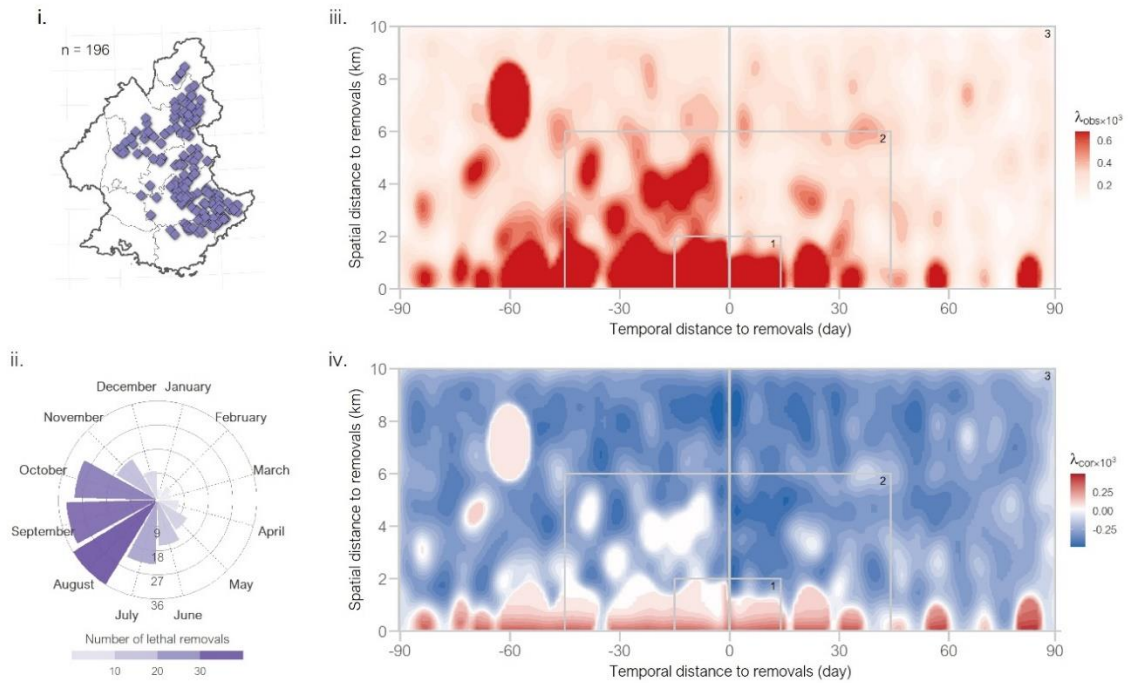
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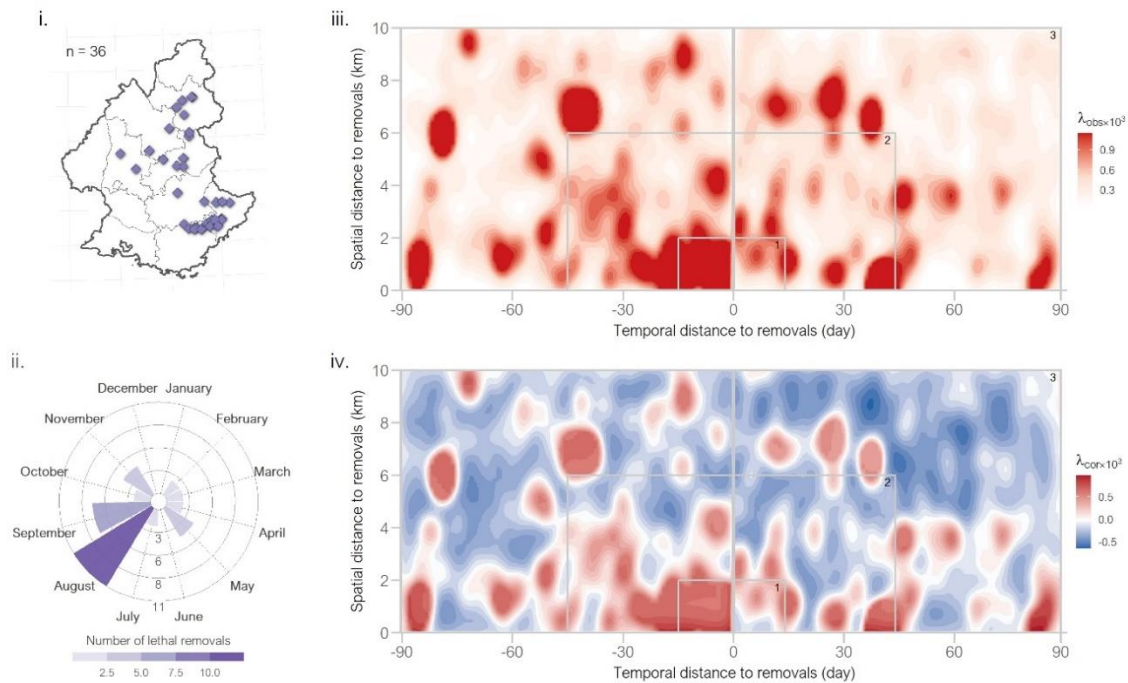
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A. Non-interacting lethal removals



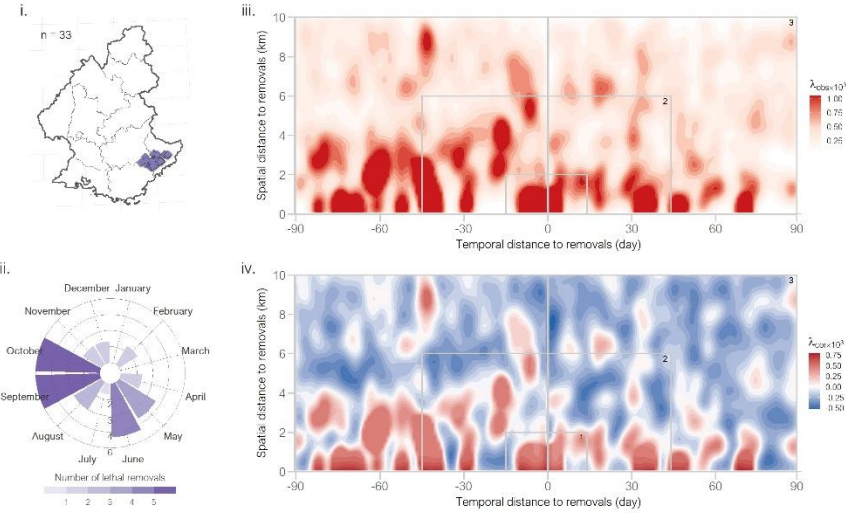
B. Interacting lethal removals



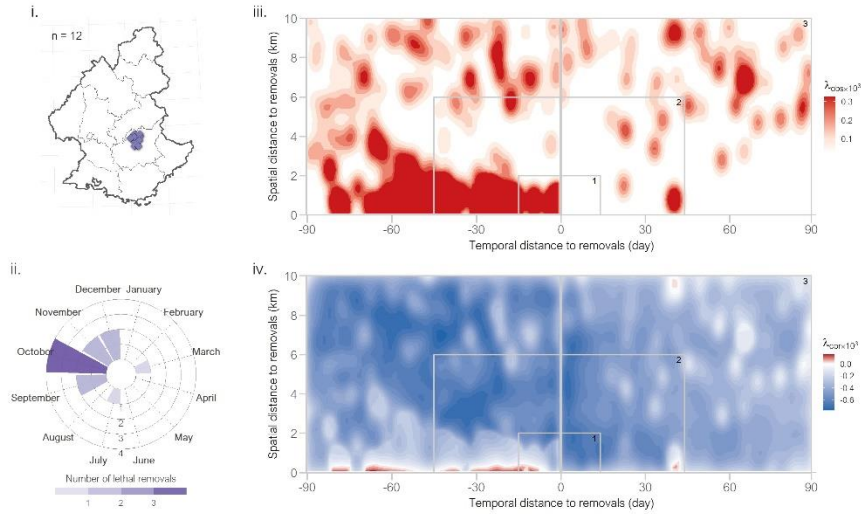
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541 *Figure 6. Results of kernel estimation of attack intensities surrounding lethal removals, detailed for each analyzed subset of*
 542 *removals (all panels except B.) or groups of removals for the subset of interacting removals (B.). Each panel includes (i) the*
 543 *map of the removal locations or of the centroids of the groups, with the annotated number of involved removals or groups,*
 544 *(ii) the monthly distribution of the removal dates or of the middle dates of the groups, (iii) the observed attack intensities*
 545 *λ_{obs} and (iv) the corrected attack intensities λ_{corr} . Intensities are given along the continuous temporal axis (x-axis) and spatial*
 546 *axis (y-axis). The coordinate (0,0) indicates the date and the location at which removals or groups of interacting removals*
 547 *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)*
 548 *and 3 (0-10 km, ± 90 days). A value of λ_{corr} lower, equal or higher than zero indicated that the observed attack intensity was*
 549 *lower, equal or higher, respectively, than the attack intensity expected according pastoral use. (Part 1/4)*

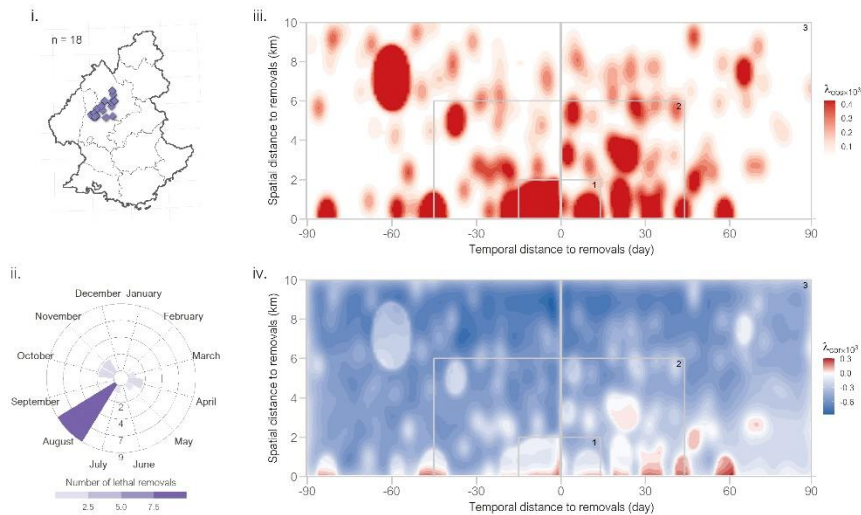
C. PNRPA



D. Préalpes de Digne



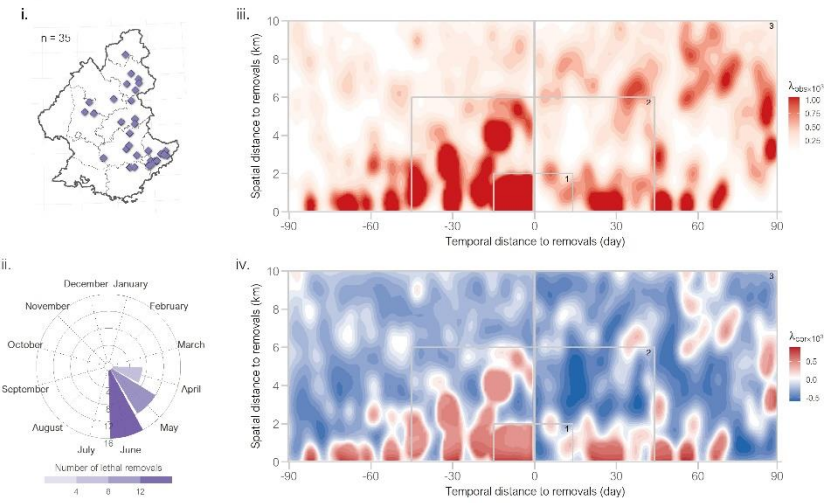
E. Vercors



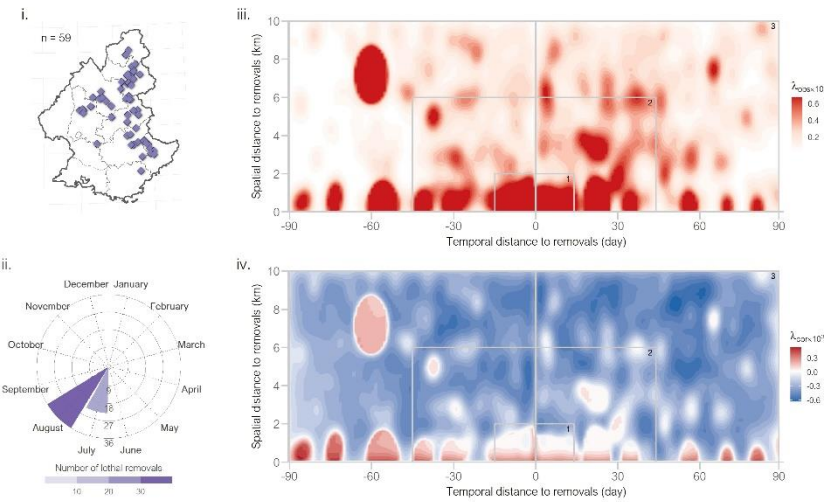
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551 Figure 6. (Part 2/4)

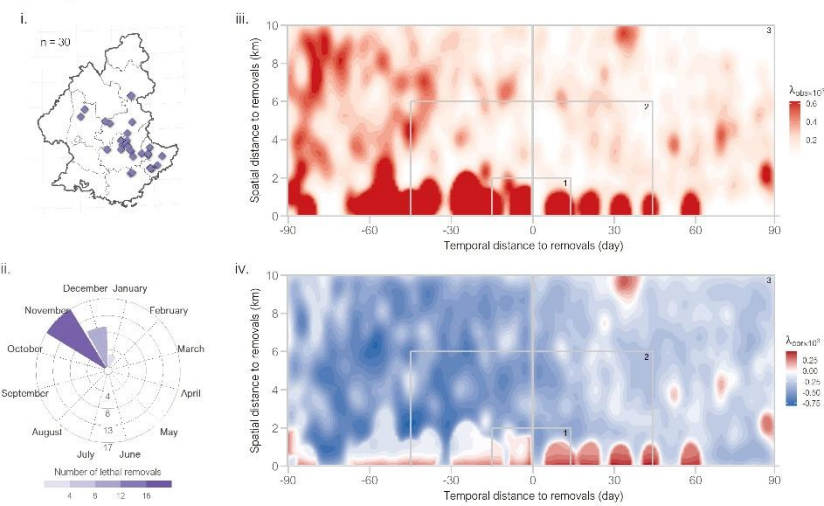
F. Den



G. Rendez-vous



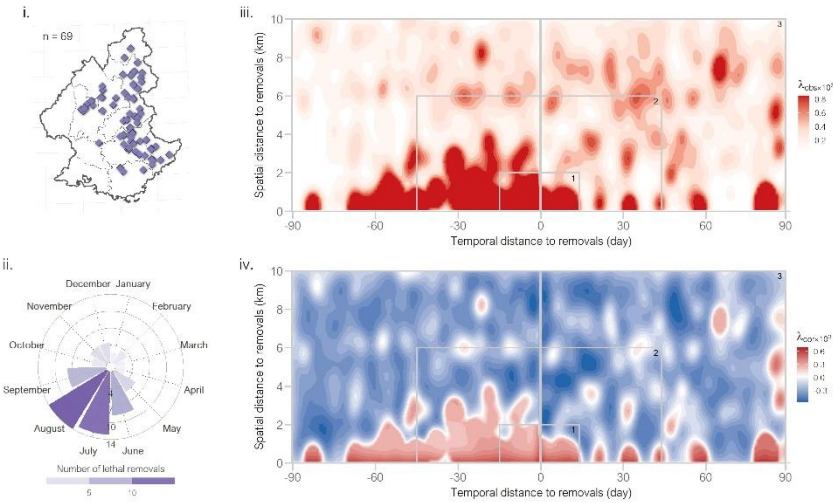
H. Winter



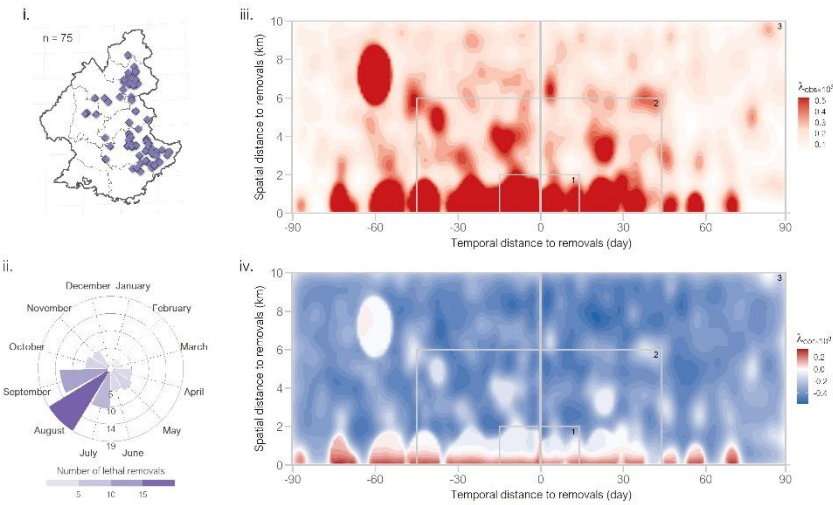
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553 *Figure 6. (Part 3/4)*

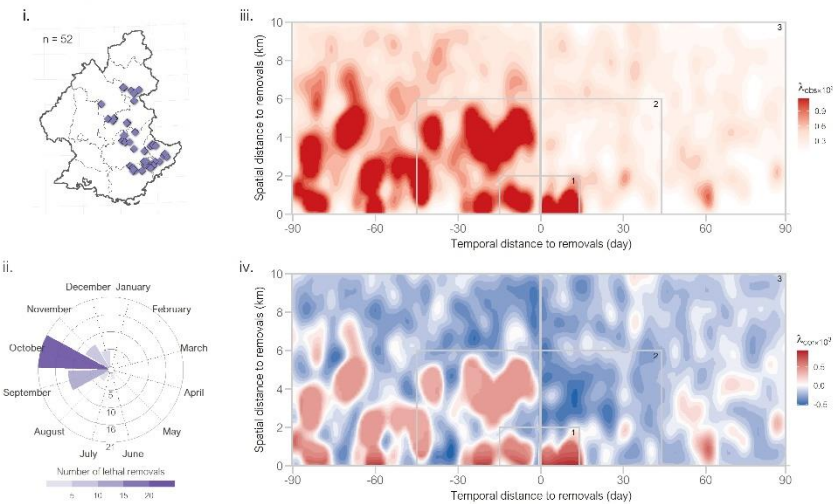
I. Simple defense



J. Reinforced defense

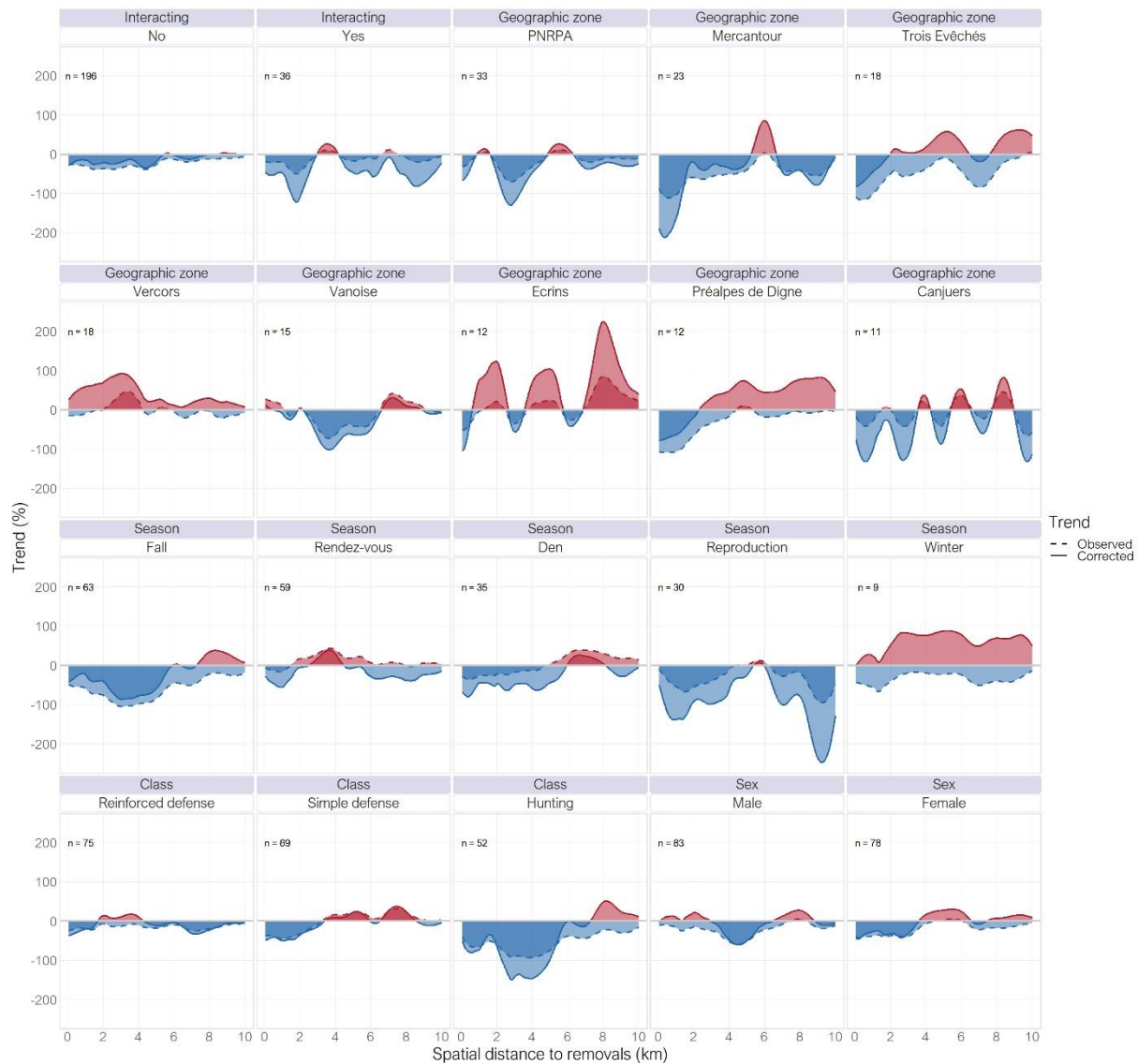


K. Hunting



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555 *Figure 6. (Part 4/4)*



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557 *Figure 7. Trends (%) of observed attack intensities $Y_{\lambda_{obs}}$ (dotted line) and of corrected attack intensities $Y_{\lambda_{corr}}$ (solid lines)*
 558 *after lethal removals calculated along the spatial scale of 10 km with a fixed temporal scale of ± 90 days following Equation*
 559 *3, separately for each subset. Top facet strips indicate the category or subcategory of the subset, and the bottom facet*
 560 *strips indicate the subset name. All trends are comparable because intensities were rescaled.*

561 **4. Discussion**

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

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

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

576 **4.1 Common features among subsets and scale influence**

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

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

598 **4.2 Ripple effects of lethal removals**

599 When focusing on the variation of attack intensities after lethal removals along the spatial scale of
600 10 km with a fixed temporal scale of \pm 90 days (Figure 7), we frequently observed localized positive
601 trends, although this distance greatly varied across subsets.

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

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

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

622 **4.3 Causality inference**

623 Potential ripple effects of removals raise the more general question of the contribution of removals
624 in the trends we observed. As the variability of subsets showed, the attack process could seem
625 inconstant, with intensity irregularly turning on and off at the same spatial distances even before
626 removals. If contribution of removals in changing the dynamics and intensities of attacks at low
627 spatial and temporal scales could be easily considered, our confidence in such causal relationship
628 was decreasing as analysis scale increased. For example, in the subset of *Non-interacting* removals
629 (Figure 6.A), is the disappearance, after removals, of the patch of high attack intensity between 6
630 and 8 km from removals present at -60 days before removals the result of removals? Apart from
631 livestock presence, many confounding factors can also affect attack intensity distribution, starting
632 with wolves themselves, *e.g.* their varying density. If dividing removals into seasonal subsets may
633 smoothen differences between removals due to the wolf annual biological cycle, they could not
634 entirely erase random biological events that rhythm wolf lives, as dispersal, settlement, or natural
635 deaths. Restricting the analysis at scale 1 could greatly reduce such bias. As an example, our
636 correction for livestock presence greatly impacted results at scale 3 but not at scale 1. However,
637 because wolves move over large territories, we acknowledge that focusing on changes happening
638 only in close proximity to removals could not be enough to evaluate removal effects (Treves et al.,
639 2016).

640 **4.4 Exploring variability in the spatio-temporal distribution of attacks**

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

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

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

664 Some hypotheses concerning the variability of results could be made. They rest upon consideration
665 of local and temporal context. For example, at scales 1 and 2, the removals from the *Simple defense*
666 subset appeared more efficient than those of the *Reinforced defense* subset to reduce attack
667 intensities (Table 1, Figures 6.I, 6.J). This result could originate from the fact that reinforced defense
668 removals were allowed when the protected flocks, or other flocks from the same municipality, have
669 recurrent attacks despite simple defense removals (Ministère de la Transition Ecologique et
670 Solidaire, 2018). In other words, reinforced defense removals were supposed to be applied in
671 situations that were not mitigated through simple defense removals, maybe because of a higher
672 wolf density. However, the removals of the *Hunting* subset, supposed to be applied in situations that
673 were not mitigated through both defense removals, were associated with a decrease of attack
674 intensities that did not appear immediately after removals but that was long-lasting. This result
675 could originate from the fact that hunting removals occurred essentially in October, contrary to the
676 defense removals mainly occurring in August. It could have been easier, in the winter context, to
677 maintain attack intensity at the level they were expected (*e.g.* flocks in fold during the night). In
678 addition, the analyzed reinforced defense removals were mostly applied in the last years of the
679 study period (58% in 2019-2020), whereas the hunting removals were mostly applied in 2015-2016
680 (51%). Estimated wolf population size increased greatly between these two years, being 341 [95% IC
681 266-463] in 2015 and 624 [95% IC 414-834] in 2020 (Réseau Loup-Lynx, 2021).

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

688 **4.5 Consistency with previous studies**

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

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

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

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

709 **4.6 Management implications**

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

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

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

732 **4.7 Perspectives**

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

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

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

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

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

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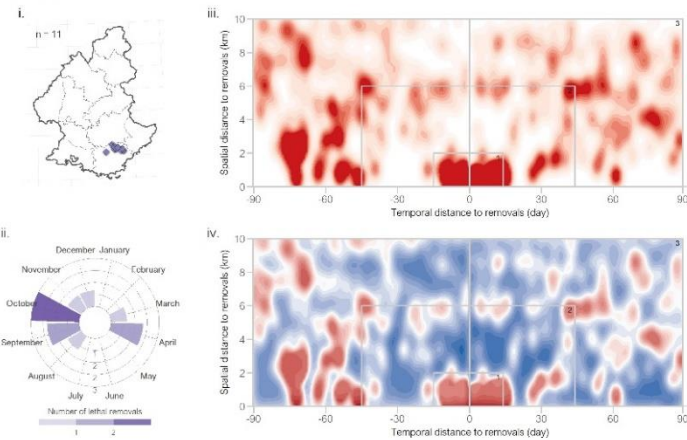
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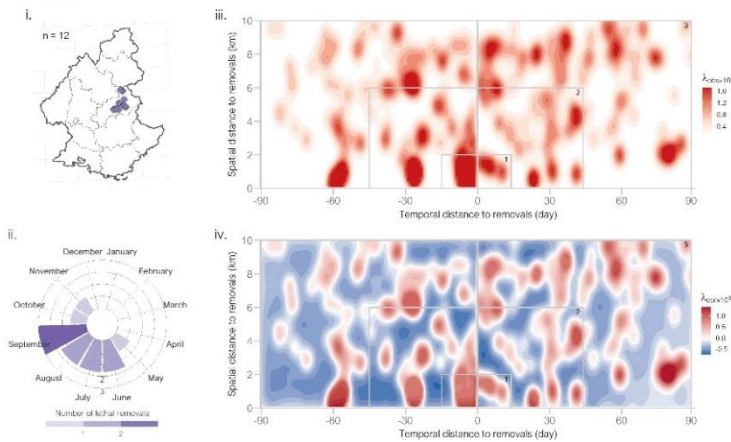
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782 Appendices

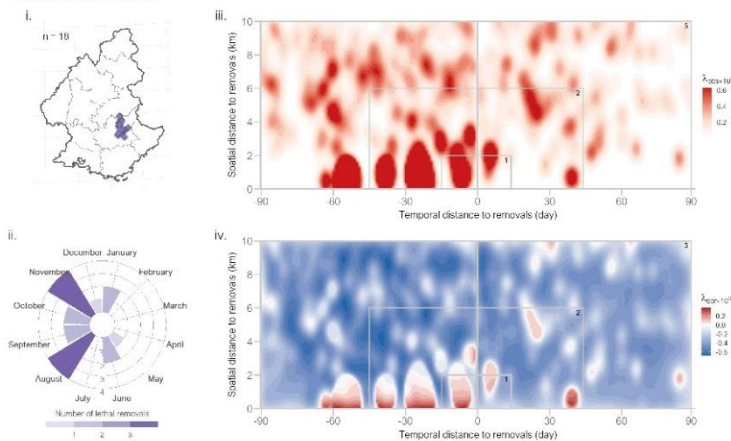
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B. Ecrins



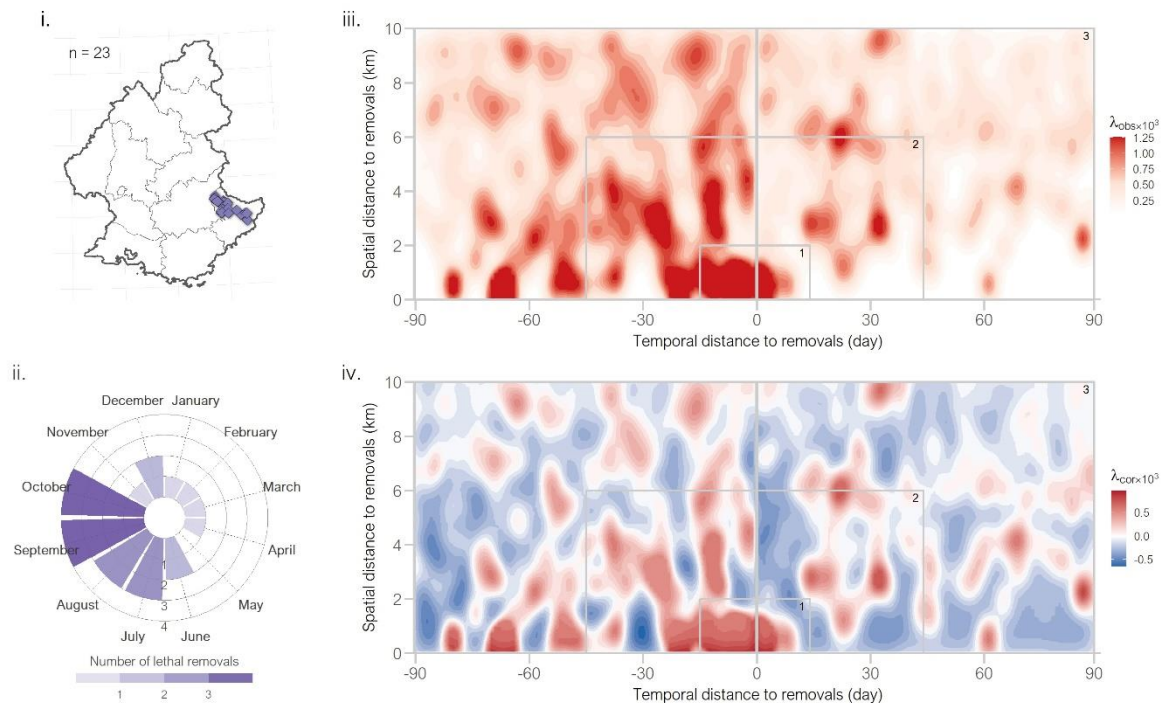
C. Les Trois Evêchés



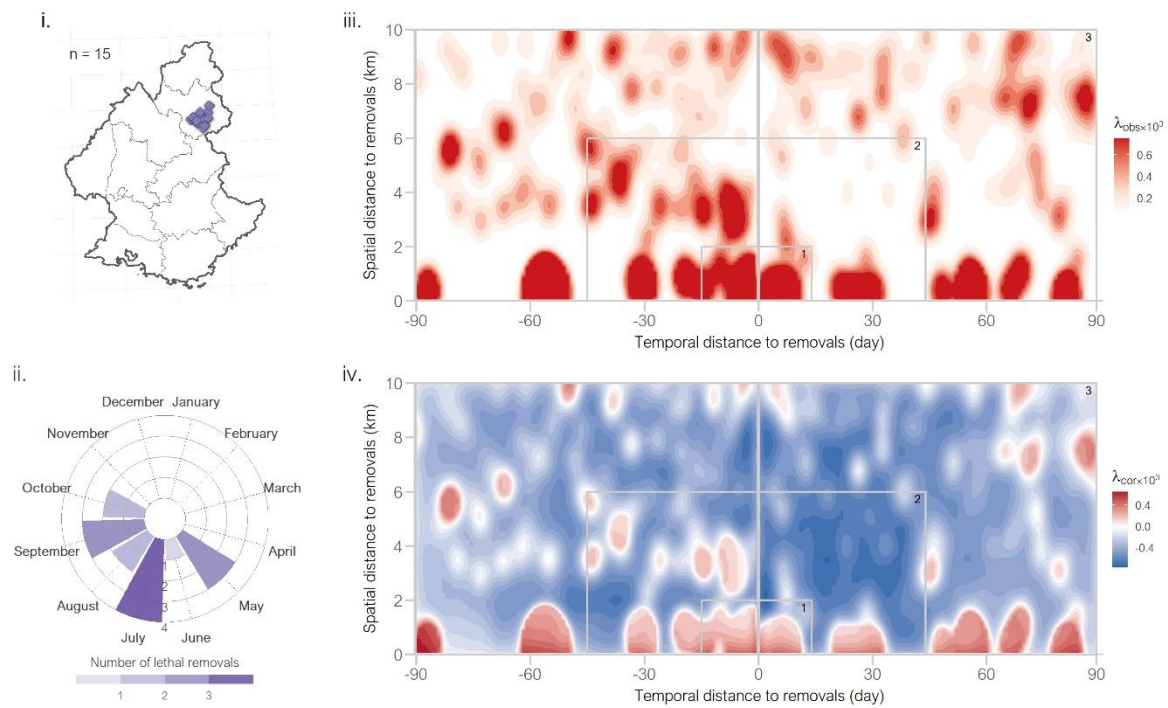
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784 *Figure S1. Results of kernel estimation of attack intensities surrounding lethal removals, detailed for each analyzed subset*
 785 *of removals. Each panel includes (i) the map of the removal locations with the annotated number of involved removals, (ii)*
 786 *the monthly distribution of the removal dates, (iii) the observed attack intensities λ_{obs} and (iv) the corrected attack*
 787 *intensities λ_{corr} . Intensities are given along the continuous temporal axis (x-axis) and spatial axis (y-axis). The coordinate*
 788 *(0,0) indicates the date and the location at which removals occurred. Grey rectangles of subpanels iii and iv delimit the*
 789 *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 λ_{corr} lower, equal or*
 790 *higher than zero indicated that the observed attack intensity was lower, equal or higher, respectively, than the attack*
 791 *intensity expected according pastoral use. (Part 1/4)*

D. Mercantour



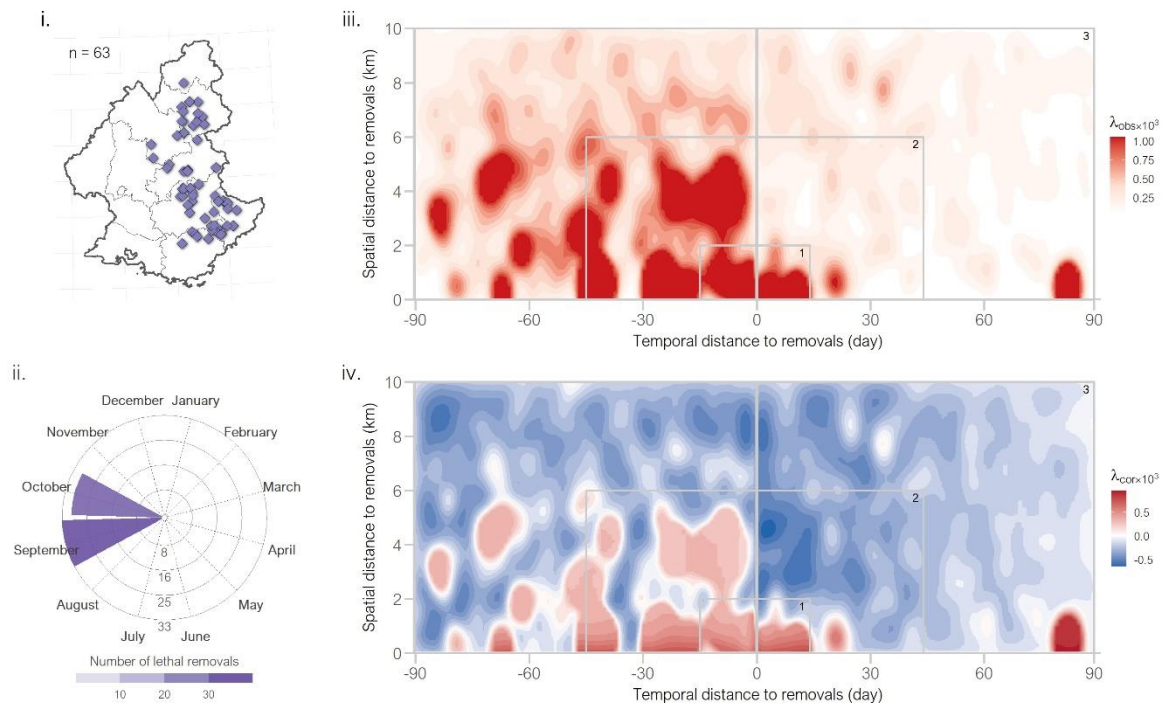
E. Vanoise



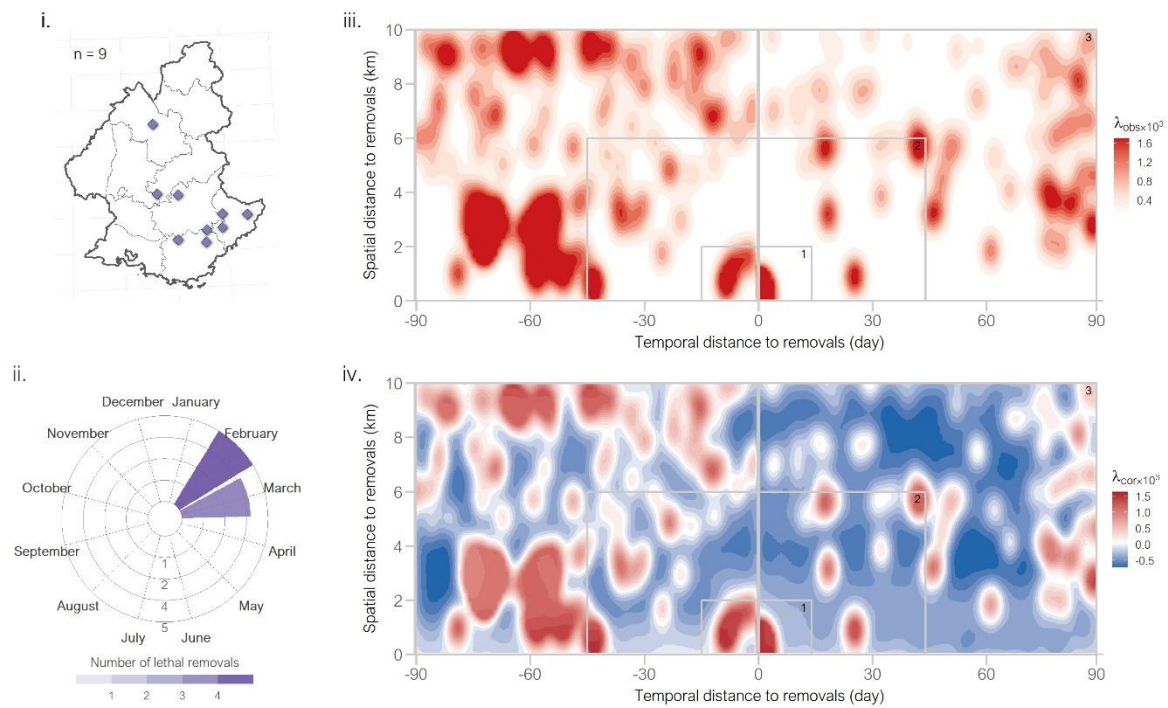
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793 *Figure S1. (Part 2/4)*

F. Fall



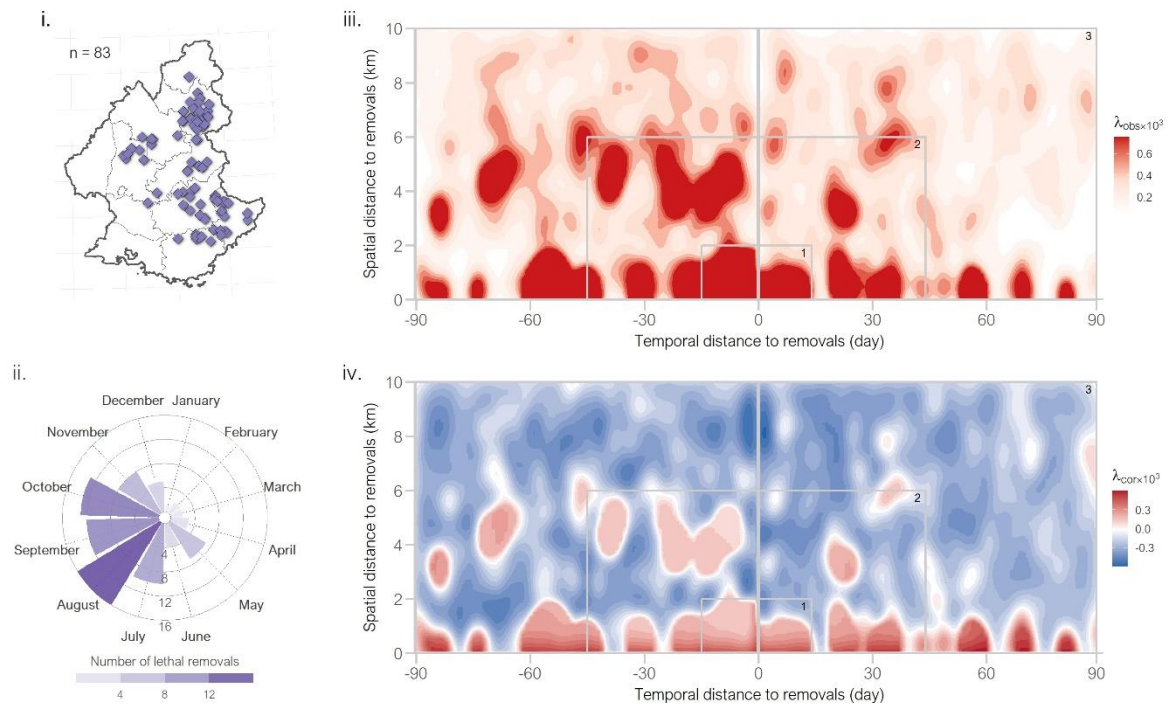
G. Reproduction



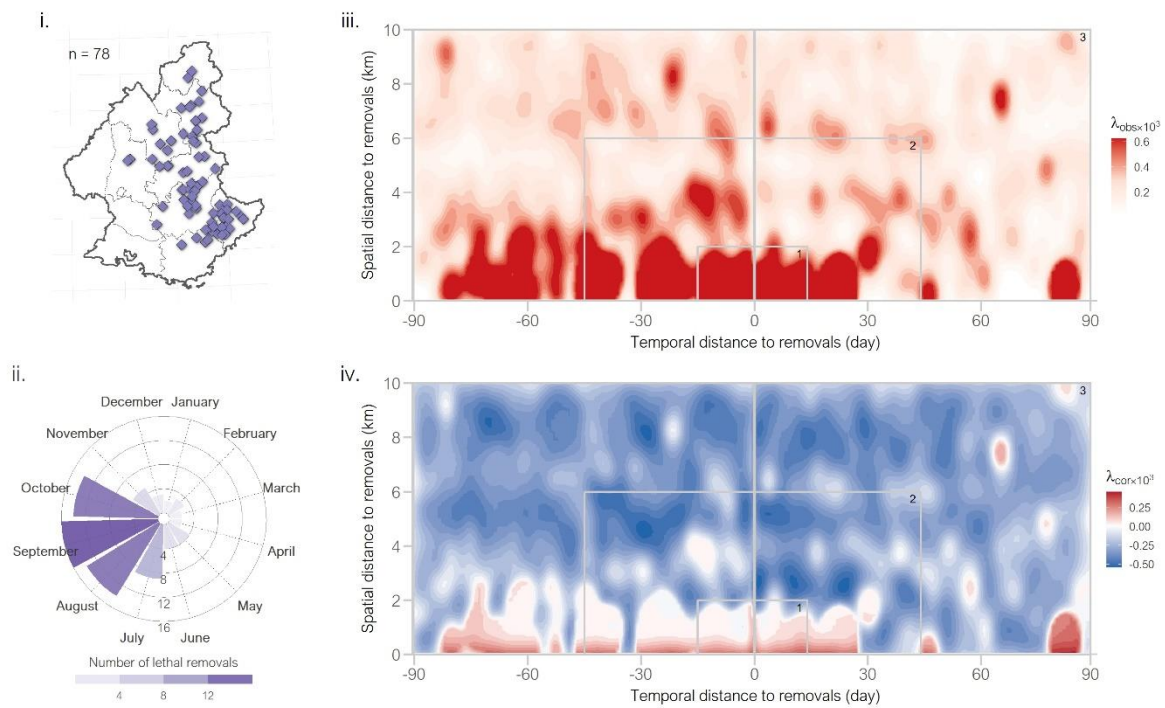
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795 *Figure S1. (Part 3/4)*

H. Lethal removal of male



I. Lethal removal of female



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797 *Figure S1. (Part 4/4)*

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

812 **Conflict of interest disclosure**

813 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in
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816 Ecology.

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821 **References**

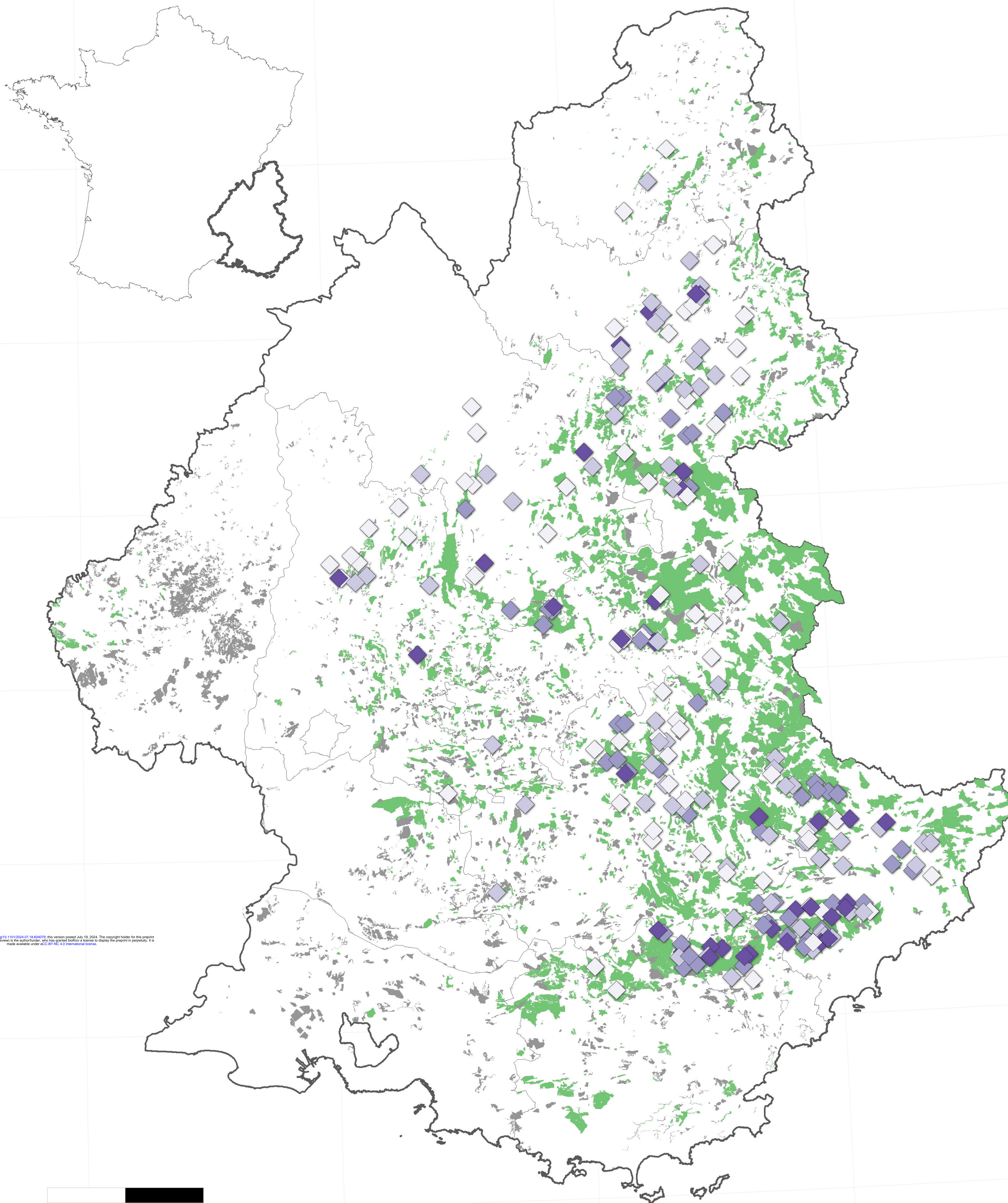
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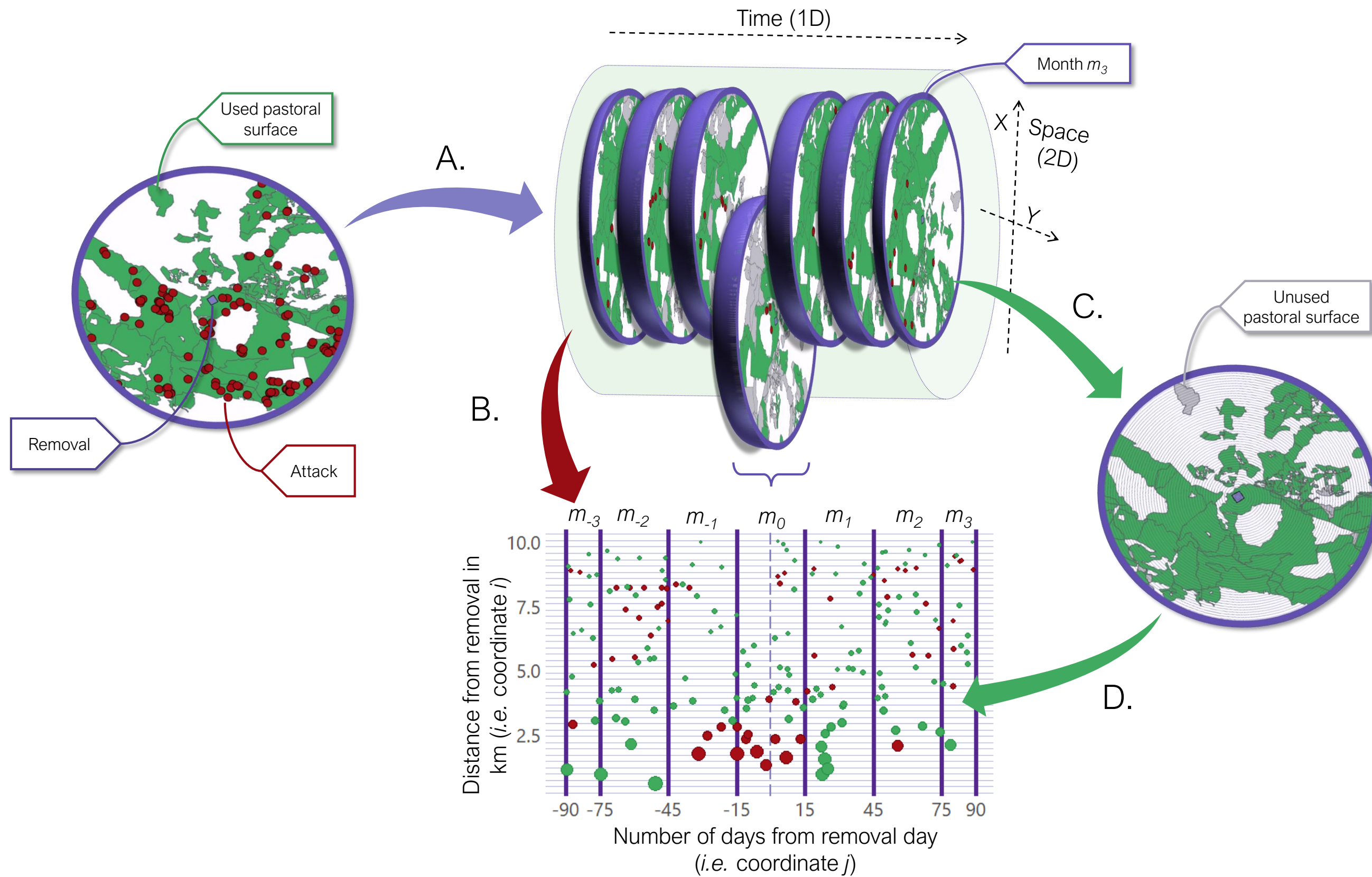


Removal type
◇ Simple defense
◇ Reinforced defense
◇ Hunting
◇ Interacting

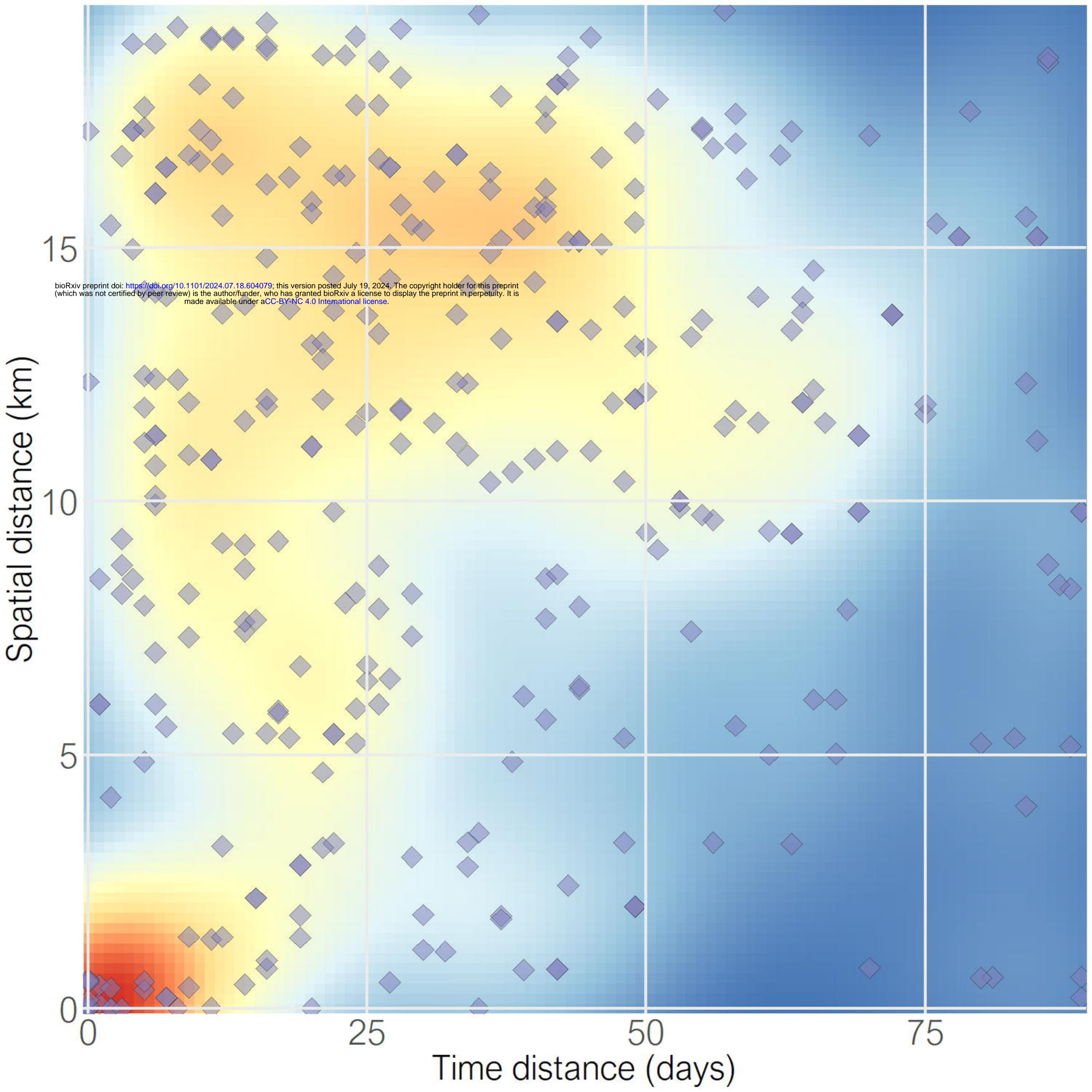
Pastoral surfaces
■ Attacked
■ Unattacked

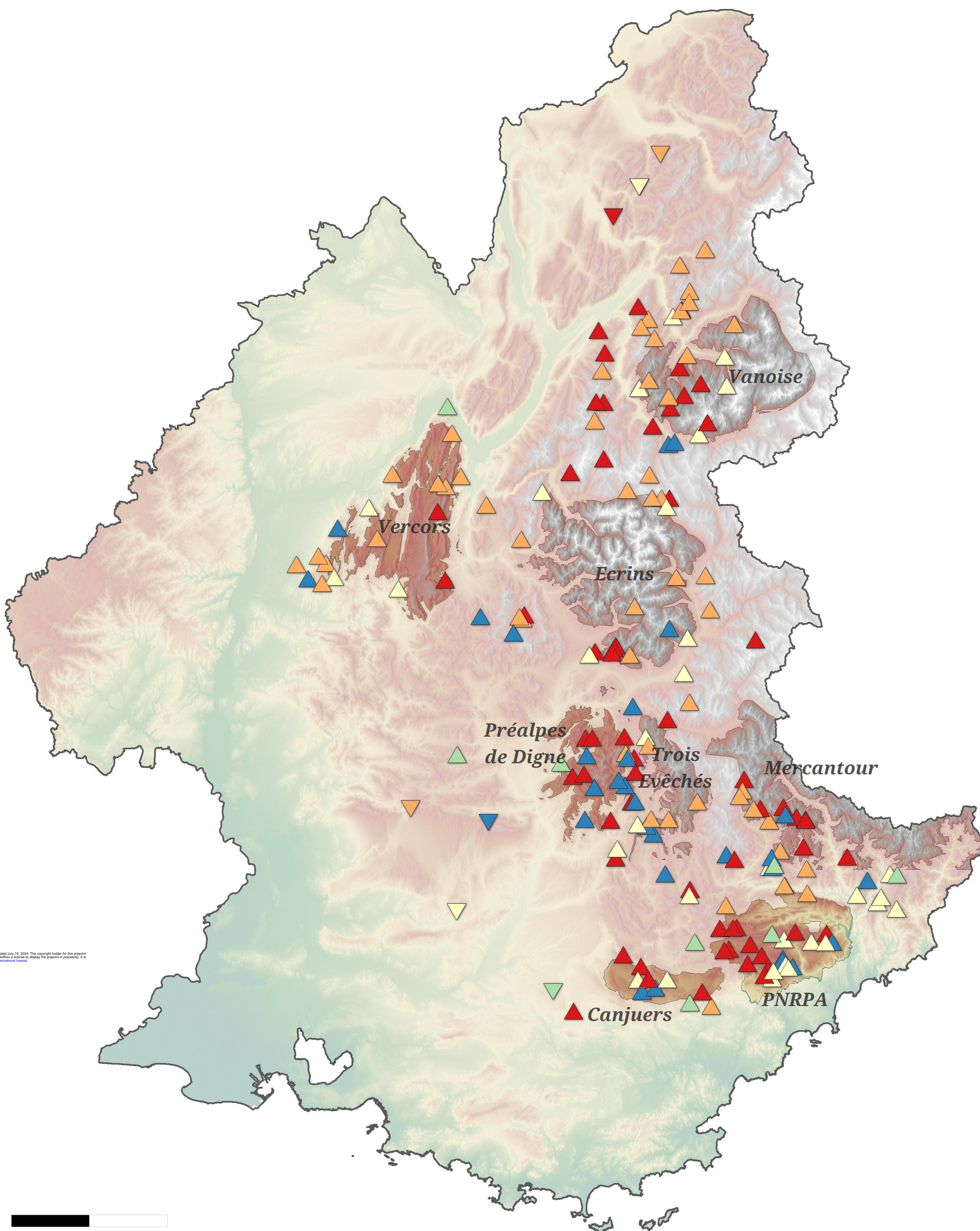
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0 25 50km

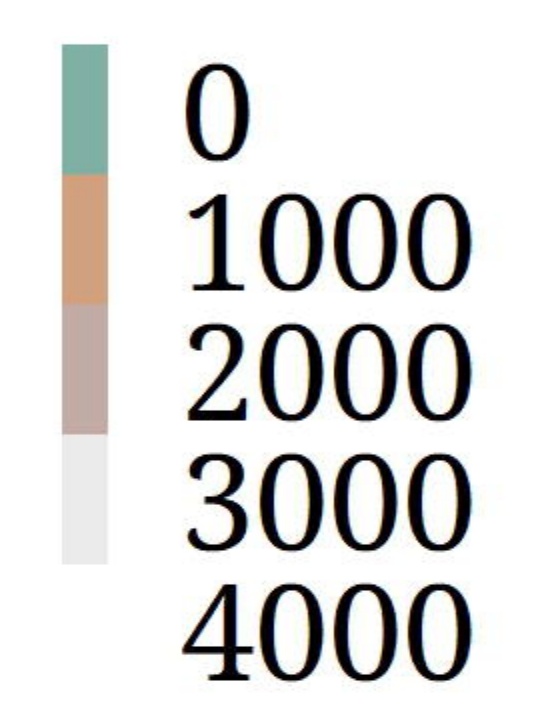


	First day of m_3	...	Last day of m_3
Ring r	$pa_{r,m_3,75}$	$pa_{r,m_3,\dots}$	$pa_{r,m_3,90}$
1	$pa_{1,m_3,75}$	$pa_{1,m_3,\dots}$	$pa_{1,m_3,90}$
2	$pa_{2,m_3,75}$	$pa_{2,m_3,\dots}$	$pa_{2,m_3,90}$
...	$pa_{\dots,m_3,75}$	$pa_{\dots,m_3,\dots}$	$pa_{\dots,m_3,90}$
199	$pa_{199,m_3,75}$	$pa_{199,m_3,\dots}$	$pa_{199,m_3,90}$
200	$pa_{200,m_3,75}$	$pa_{200,m_3,\dots}$	$pa_{200,m_3,90}$





Altitude (m)



Season

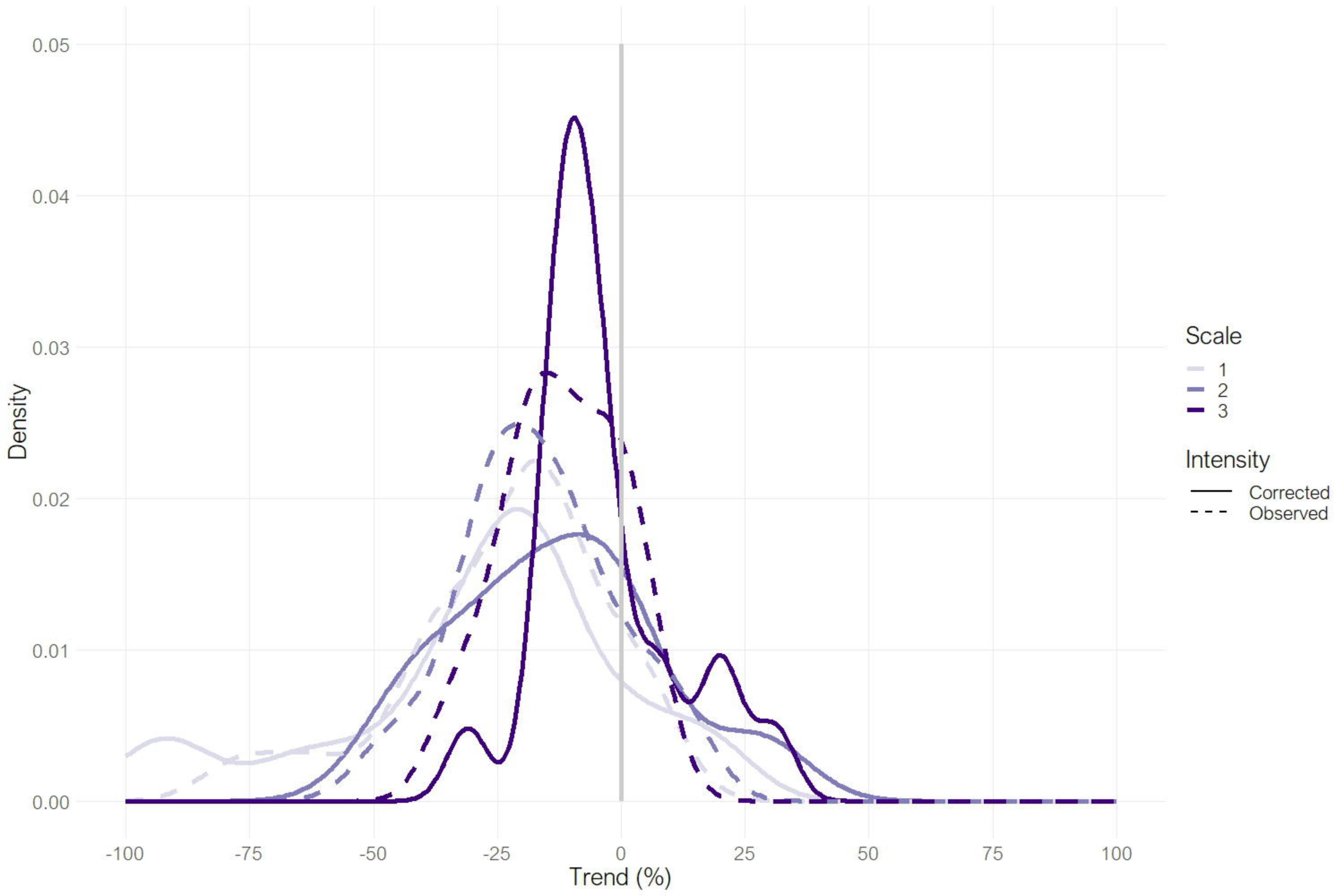
- ▲ Winter
- ▲ Reproduction
- ▲ Deñ
- ▲ Rendez-vous
- ▲ Fall

Zone

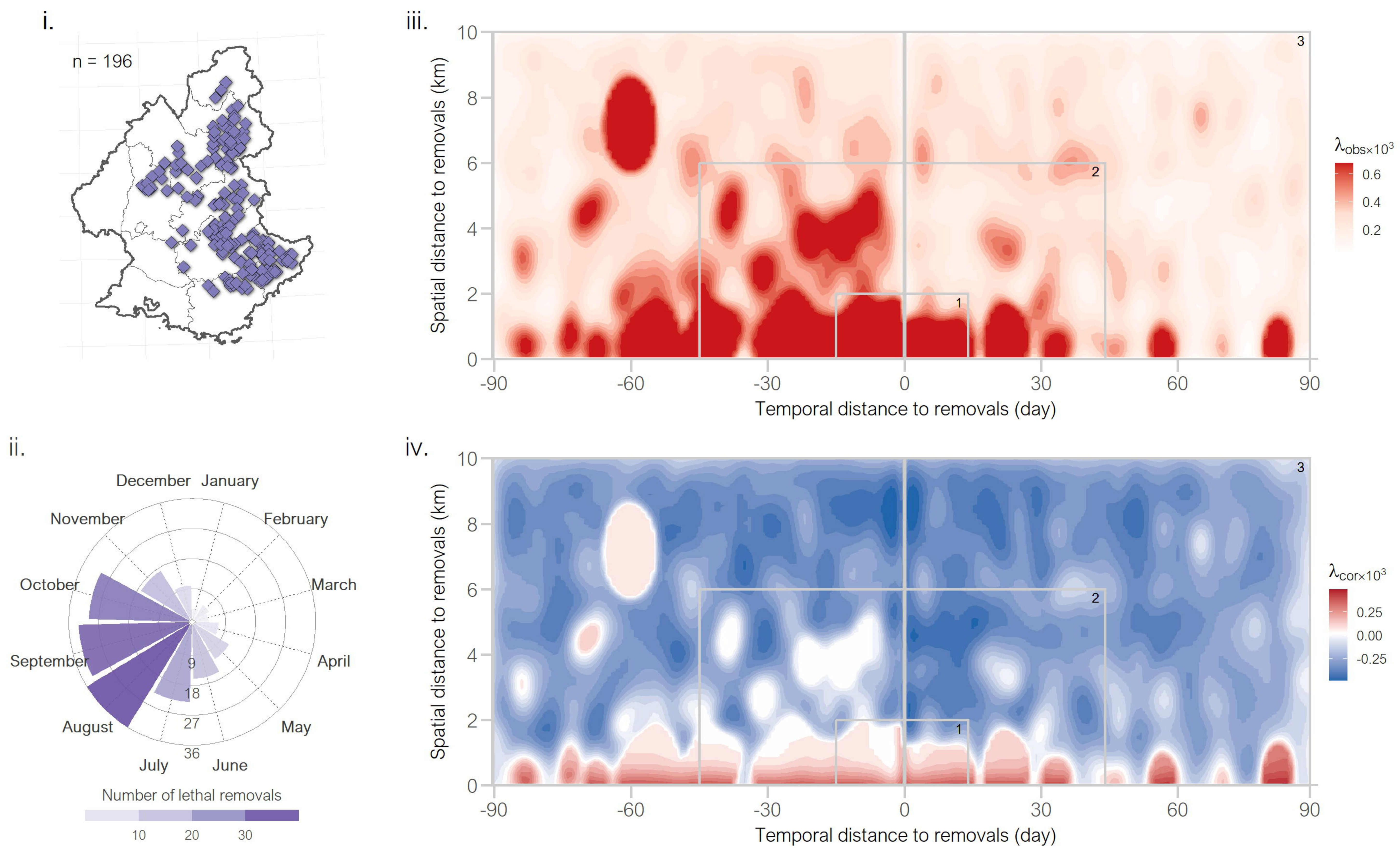
- ▲ Attributed
- ▼ Not attributed



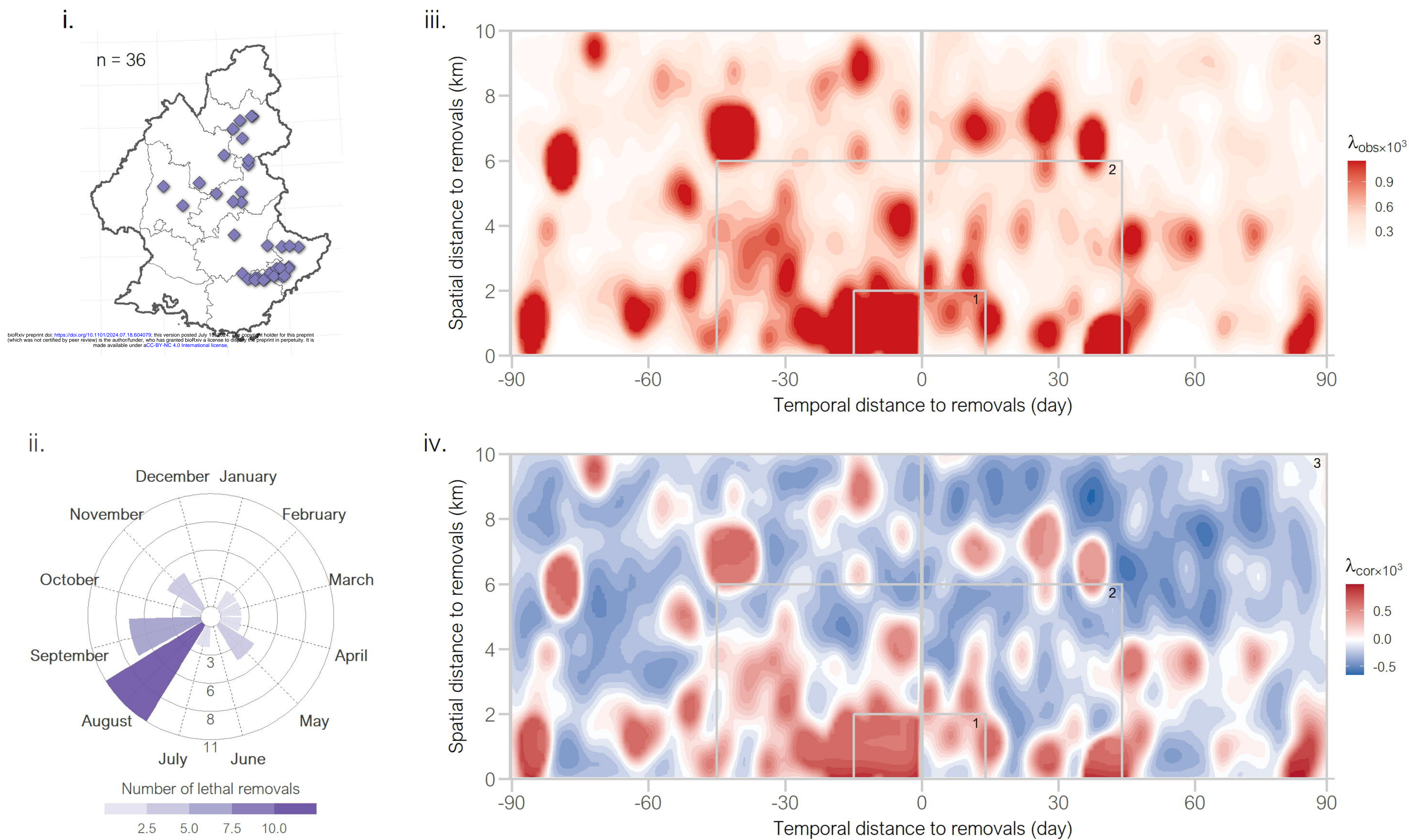
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A. Non-interacting lethal removals

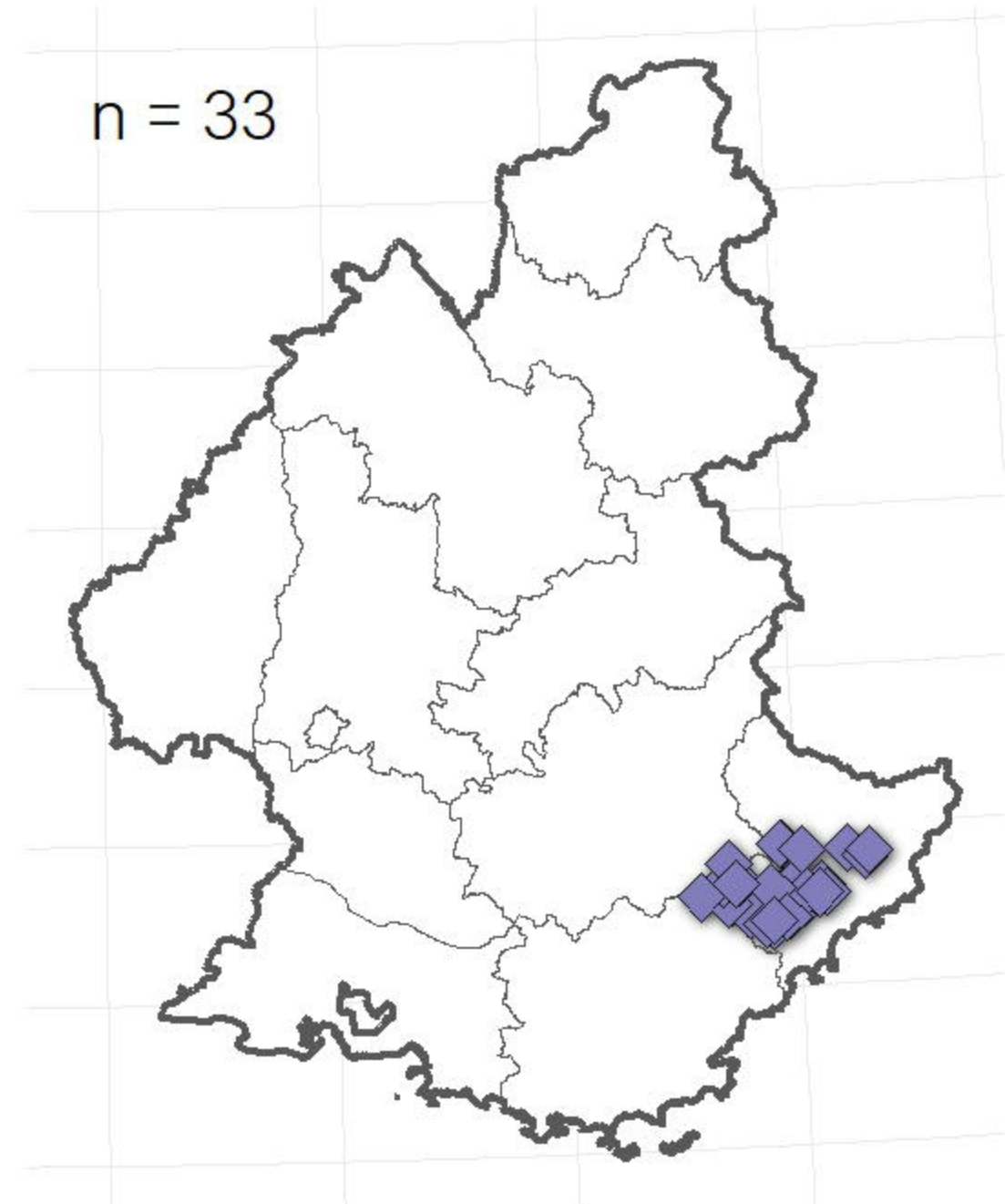


B. Interacting lethal removals

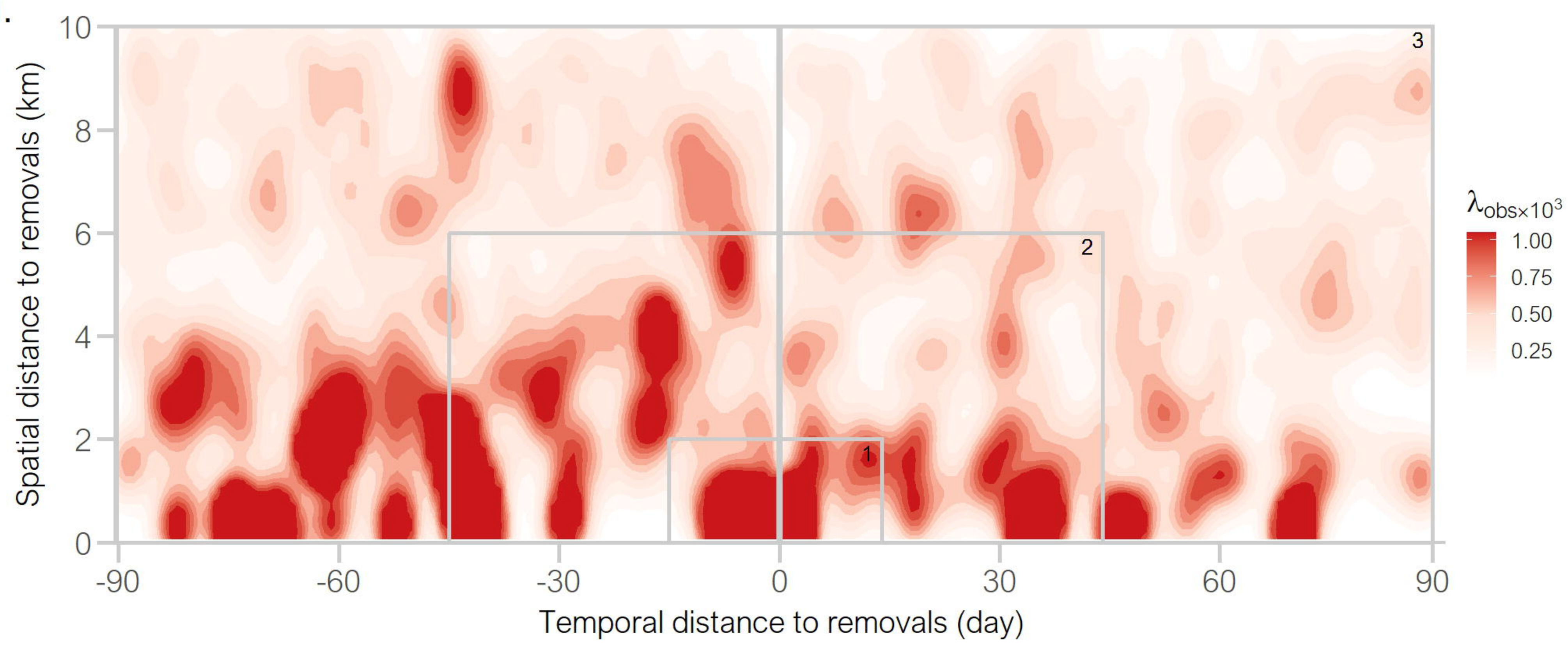


C. PNRPA

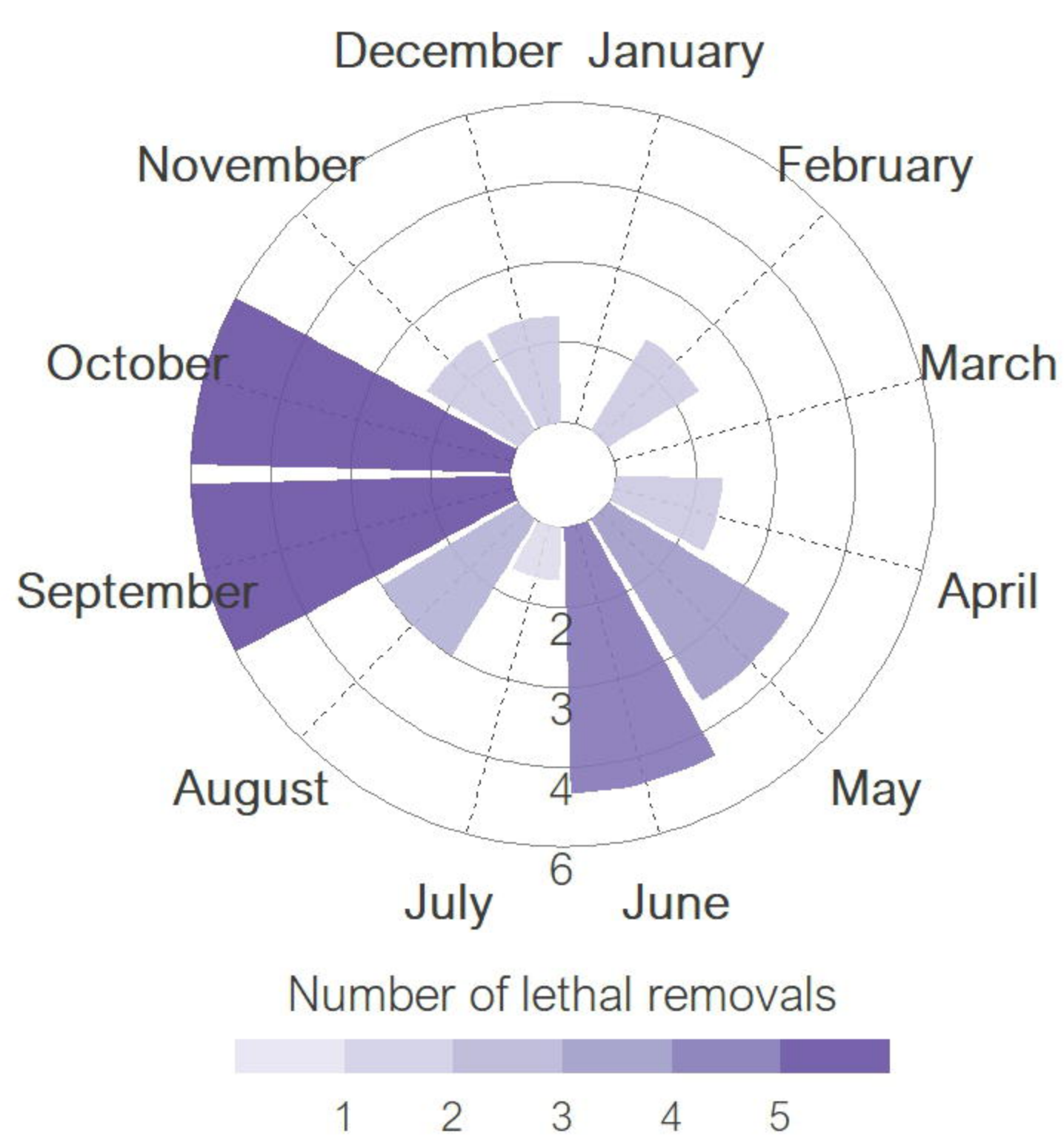
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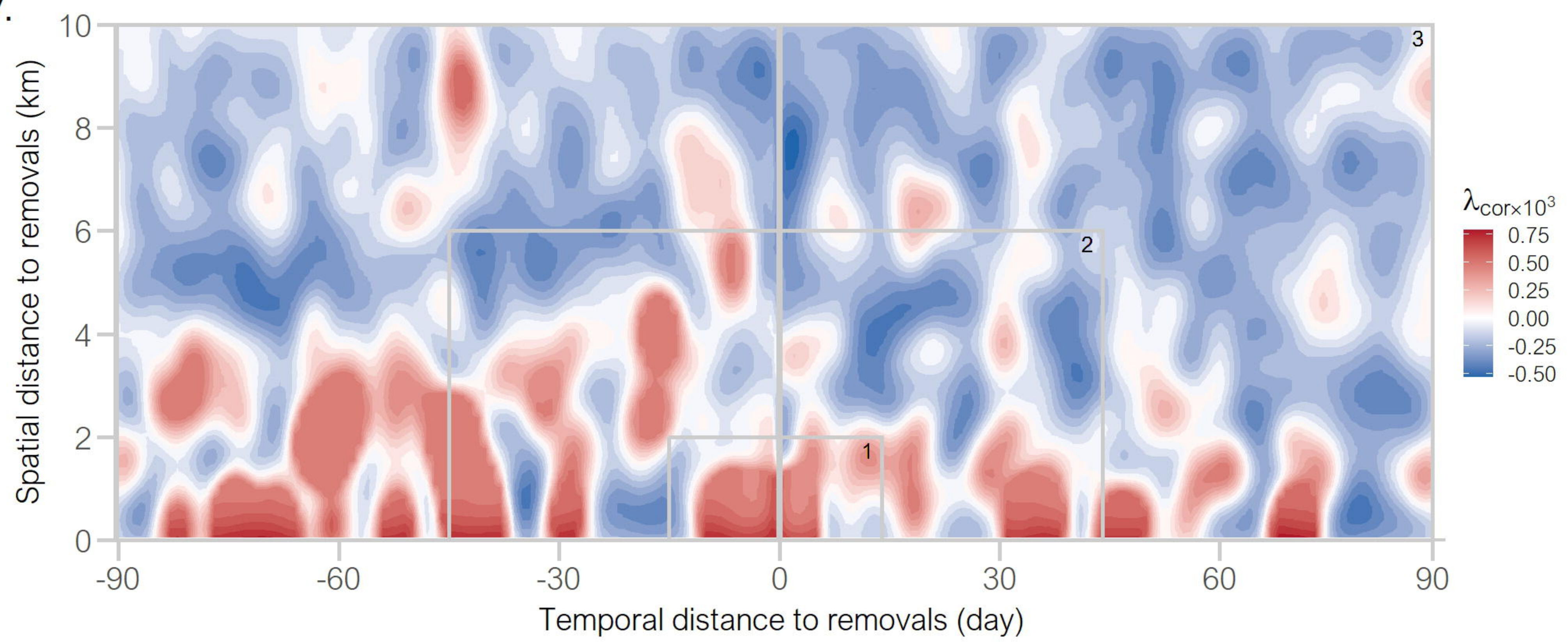
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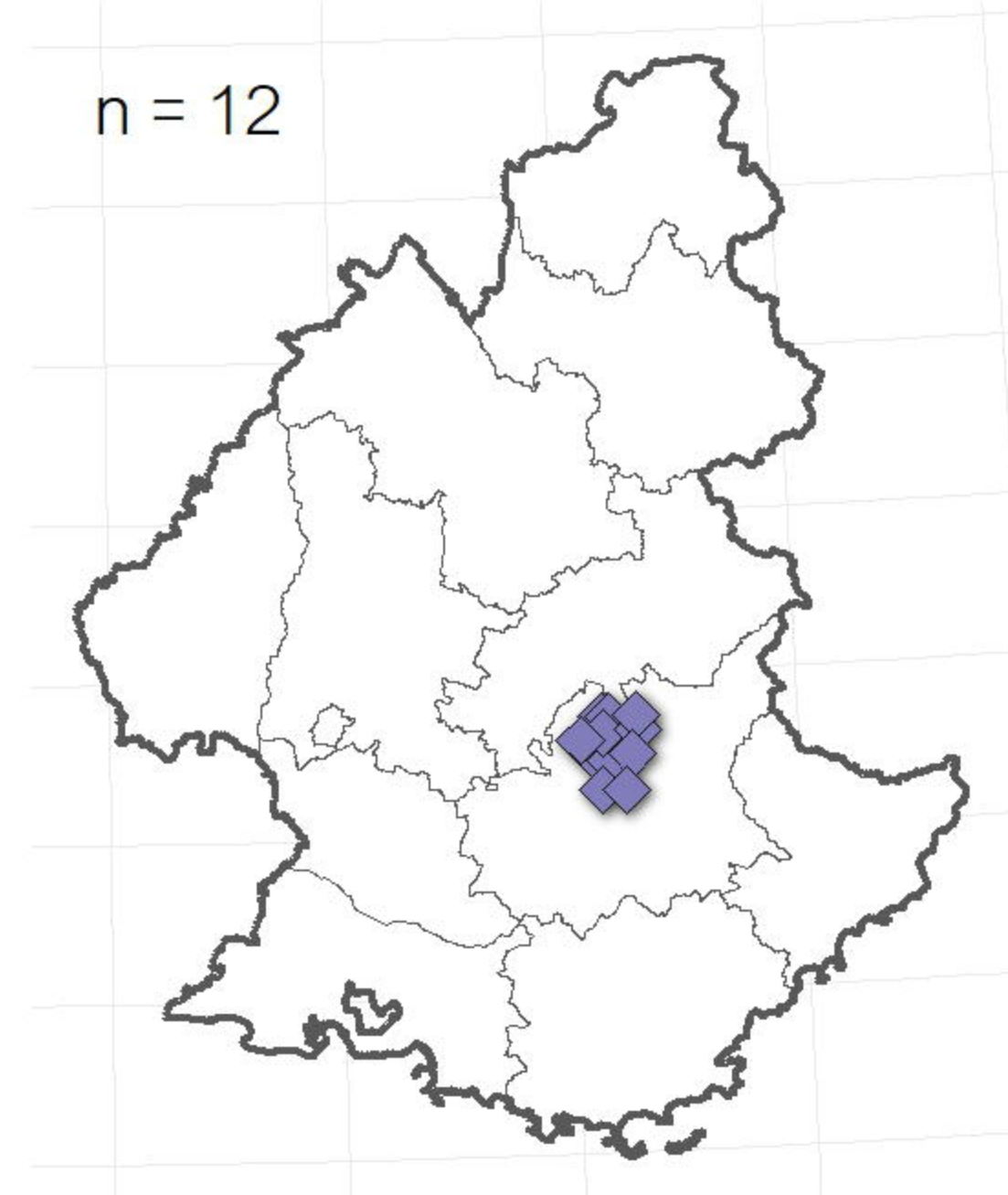


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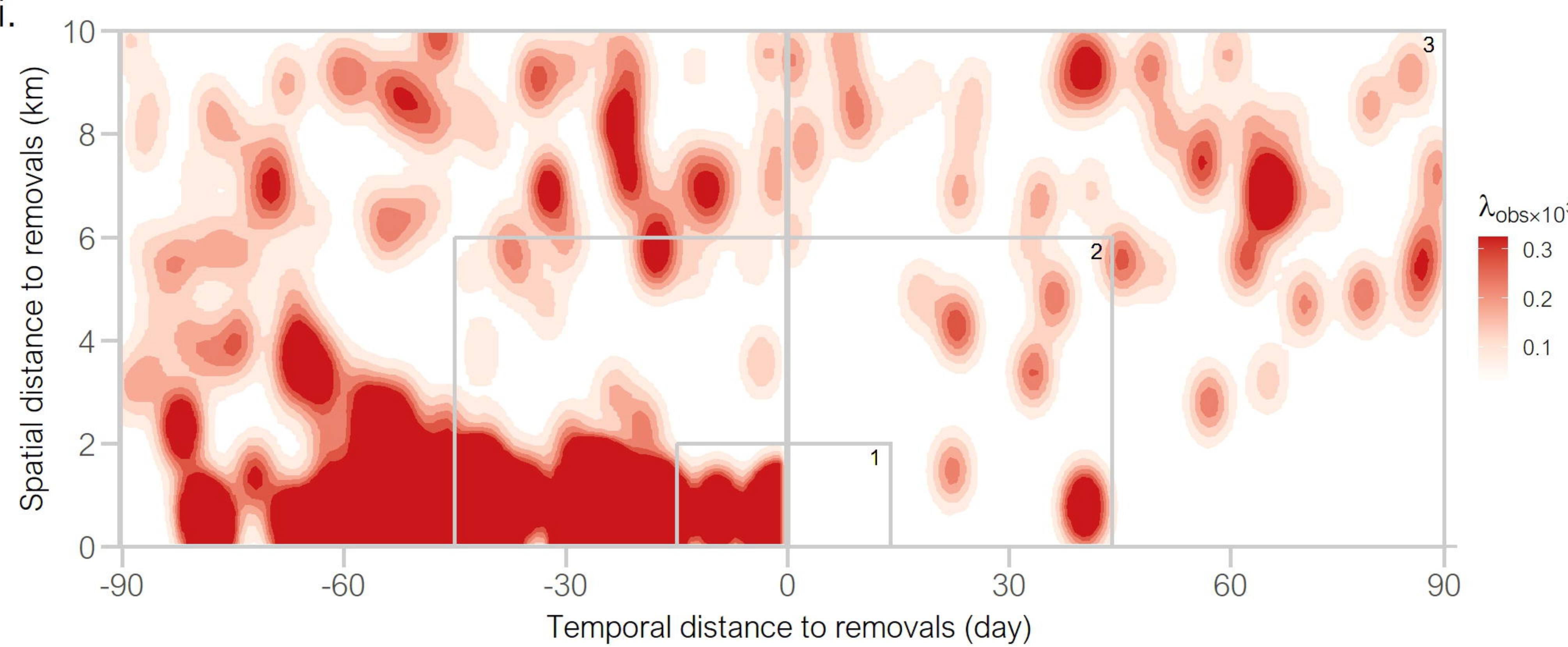


D. Préalpes de Digne

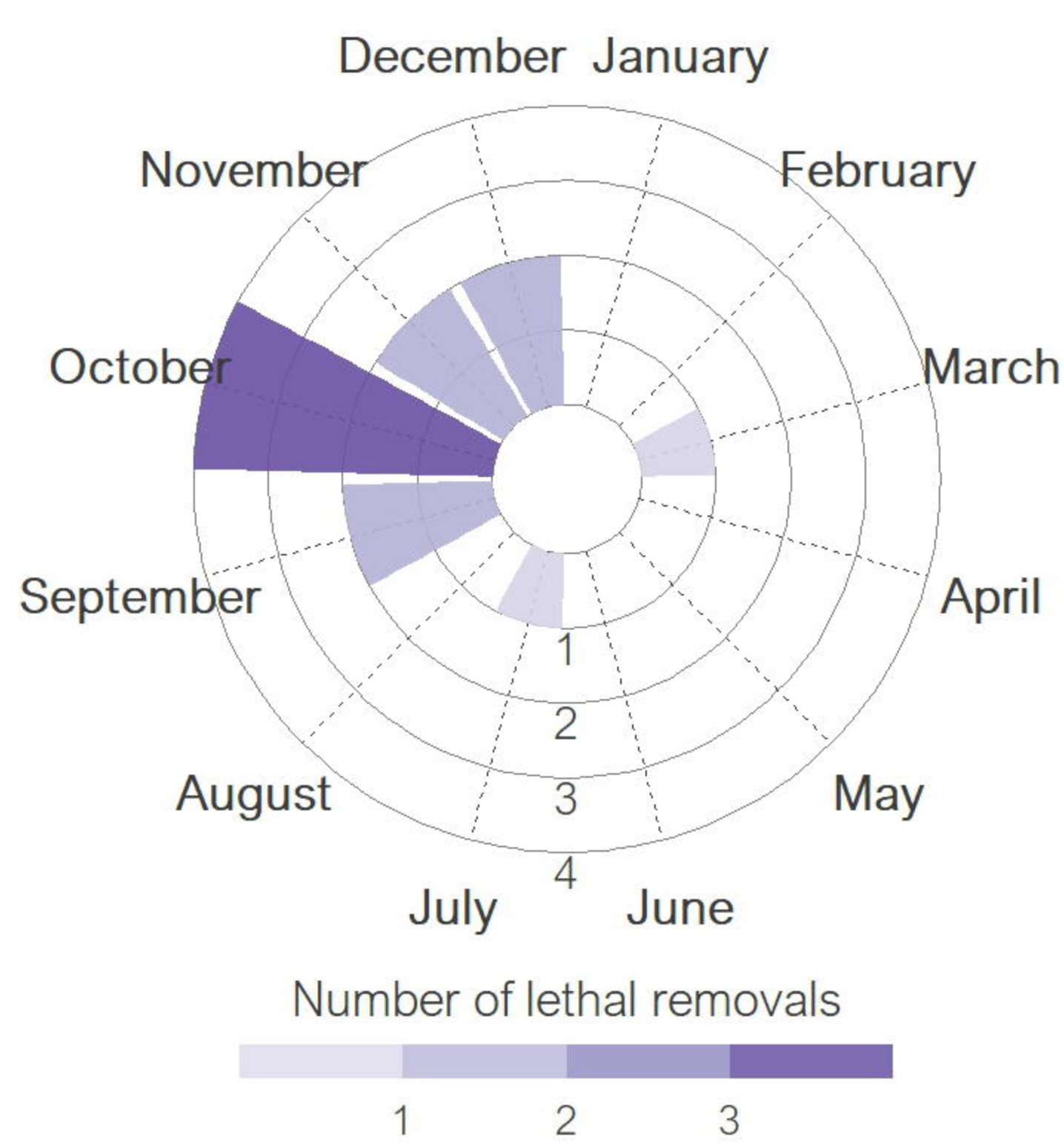
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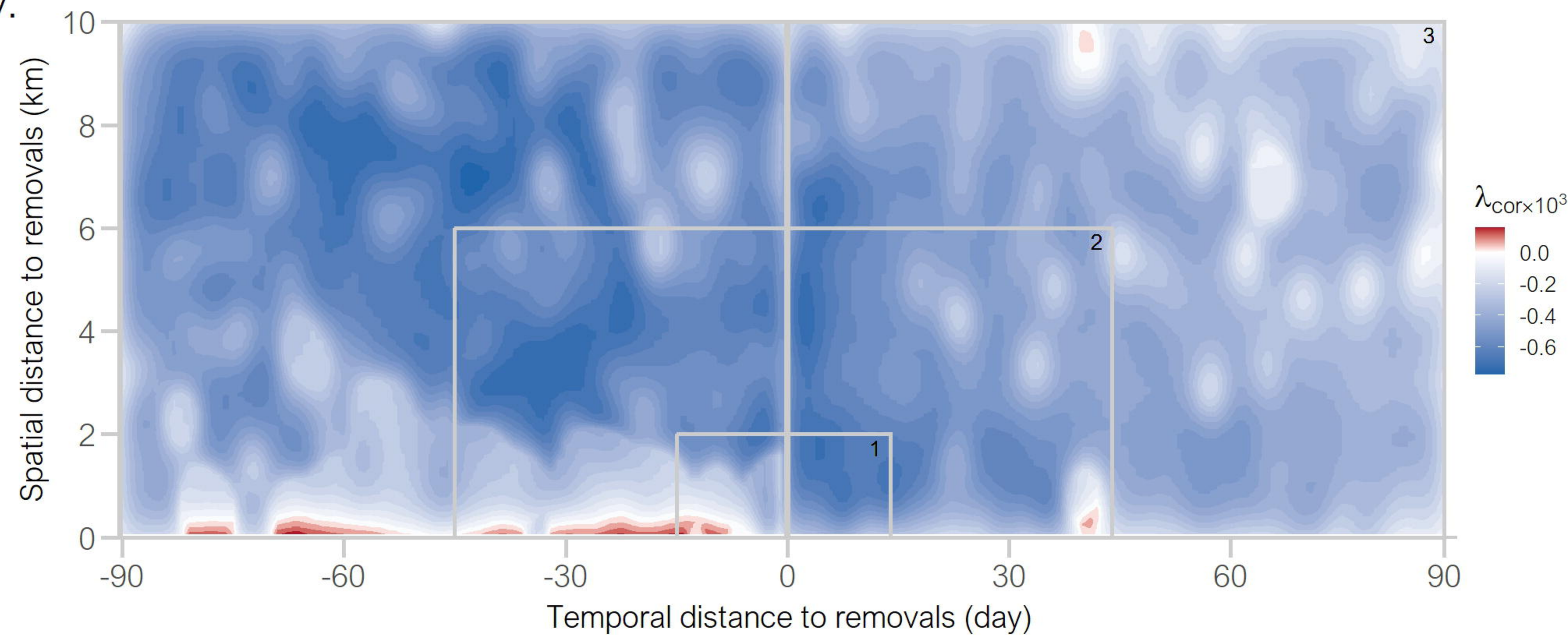
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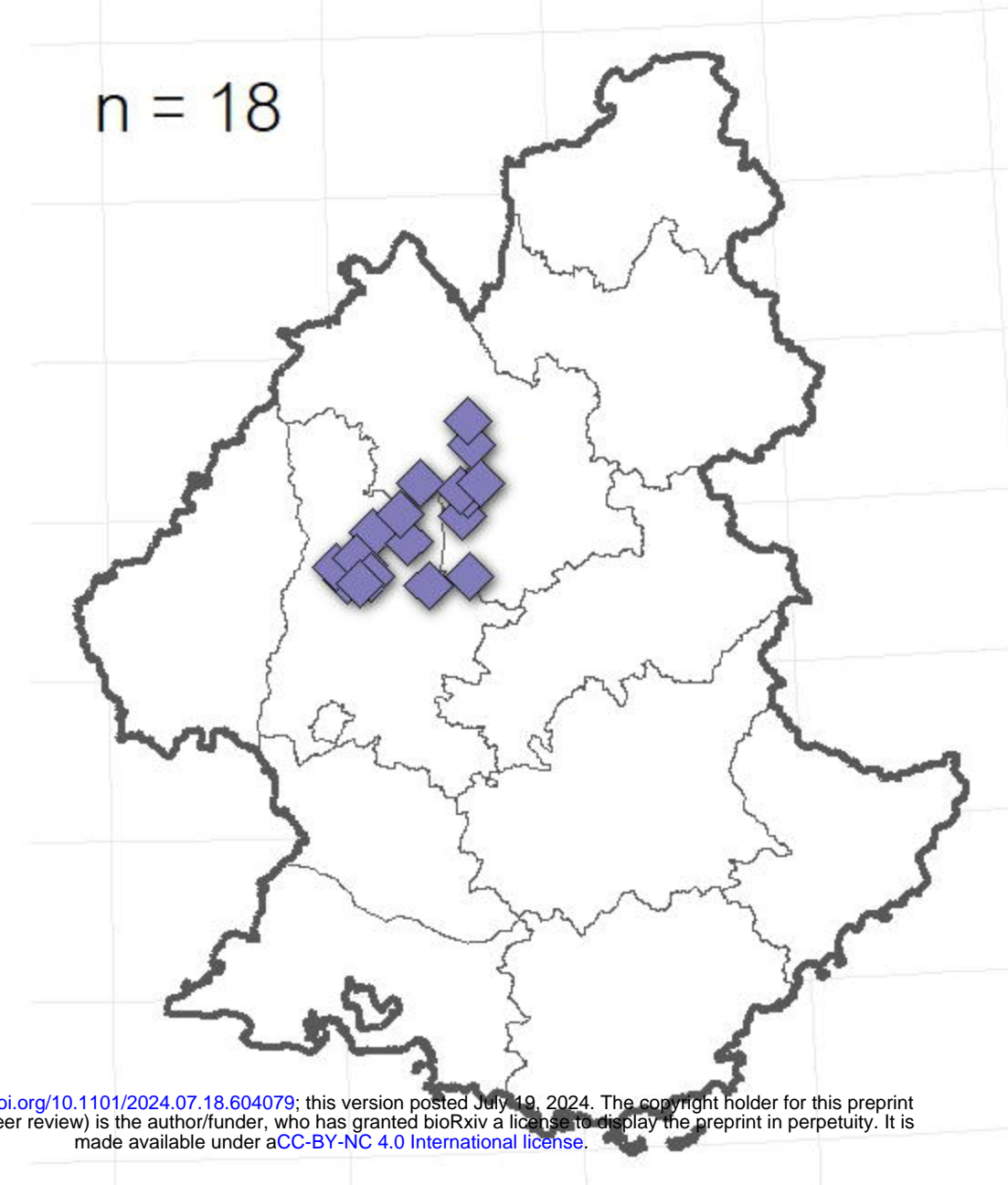


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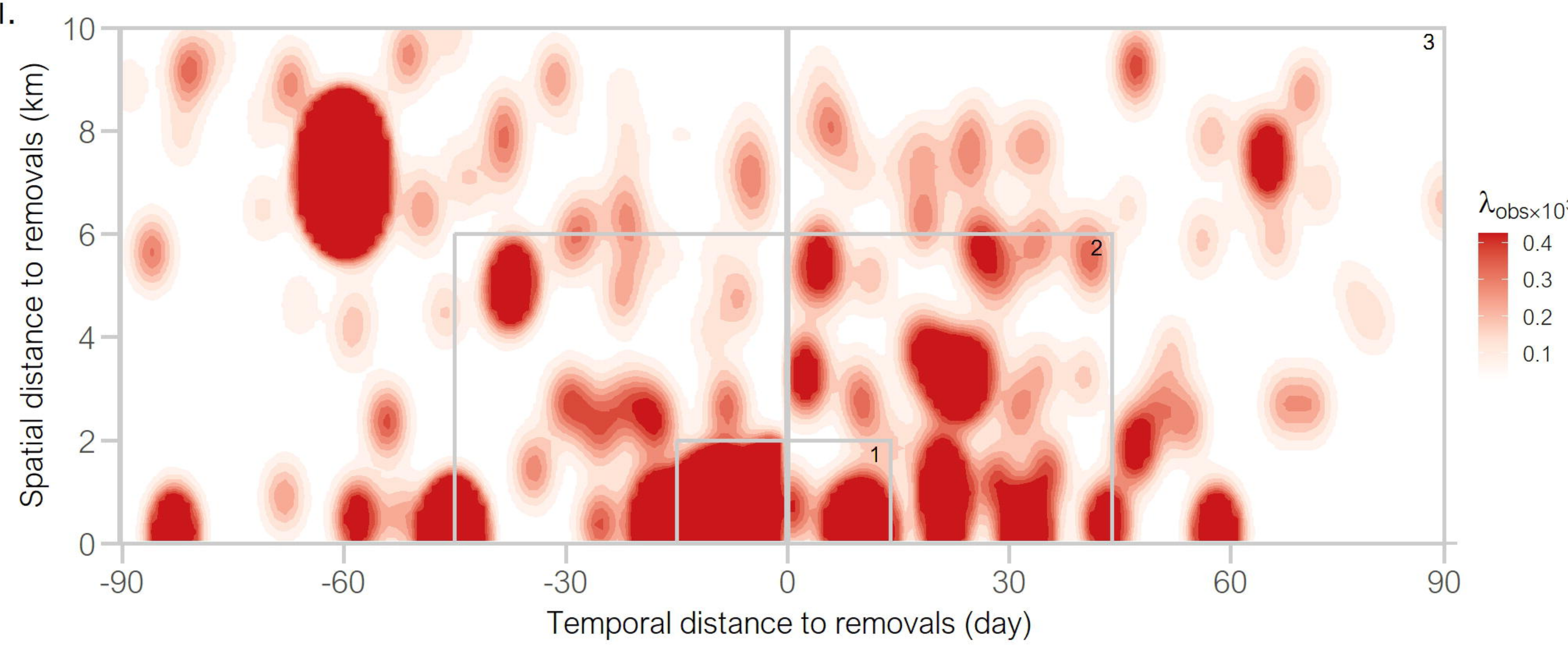


E. Vercors

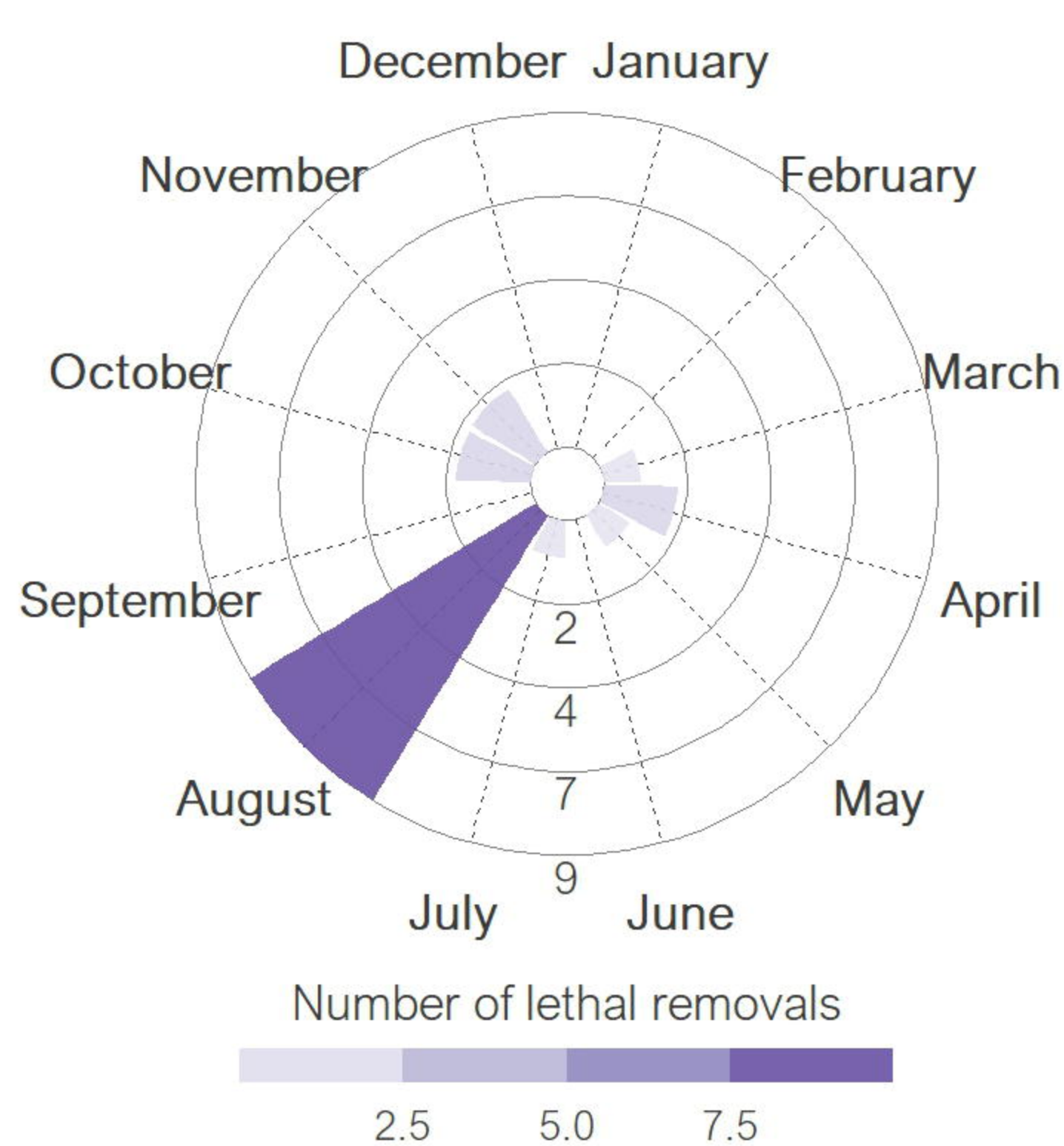
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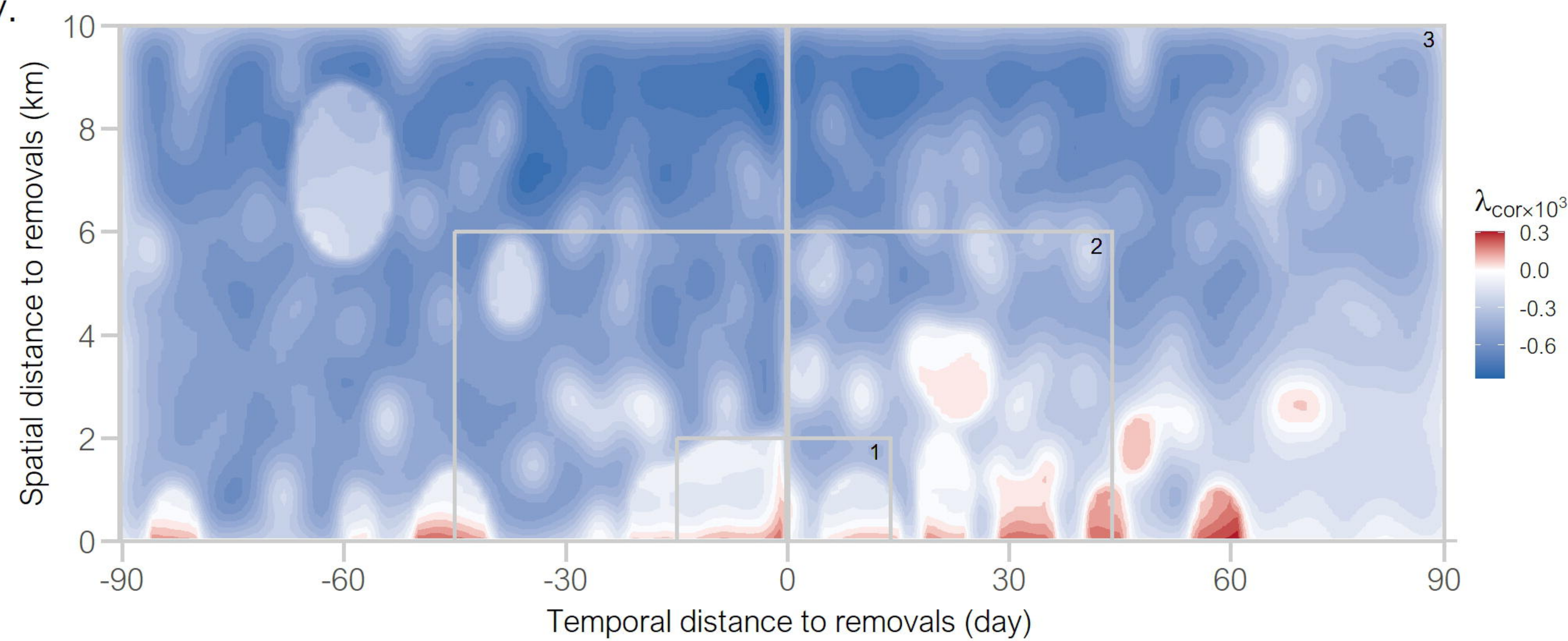
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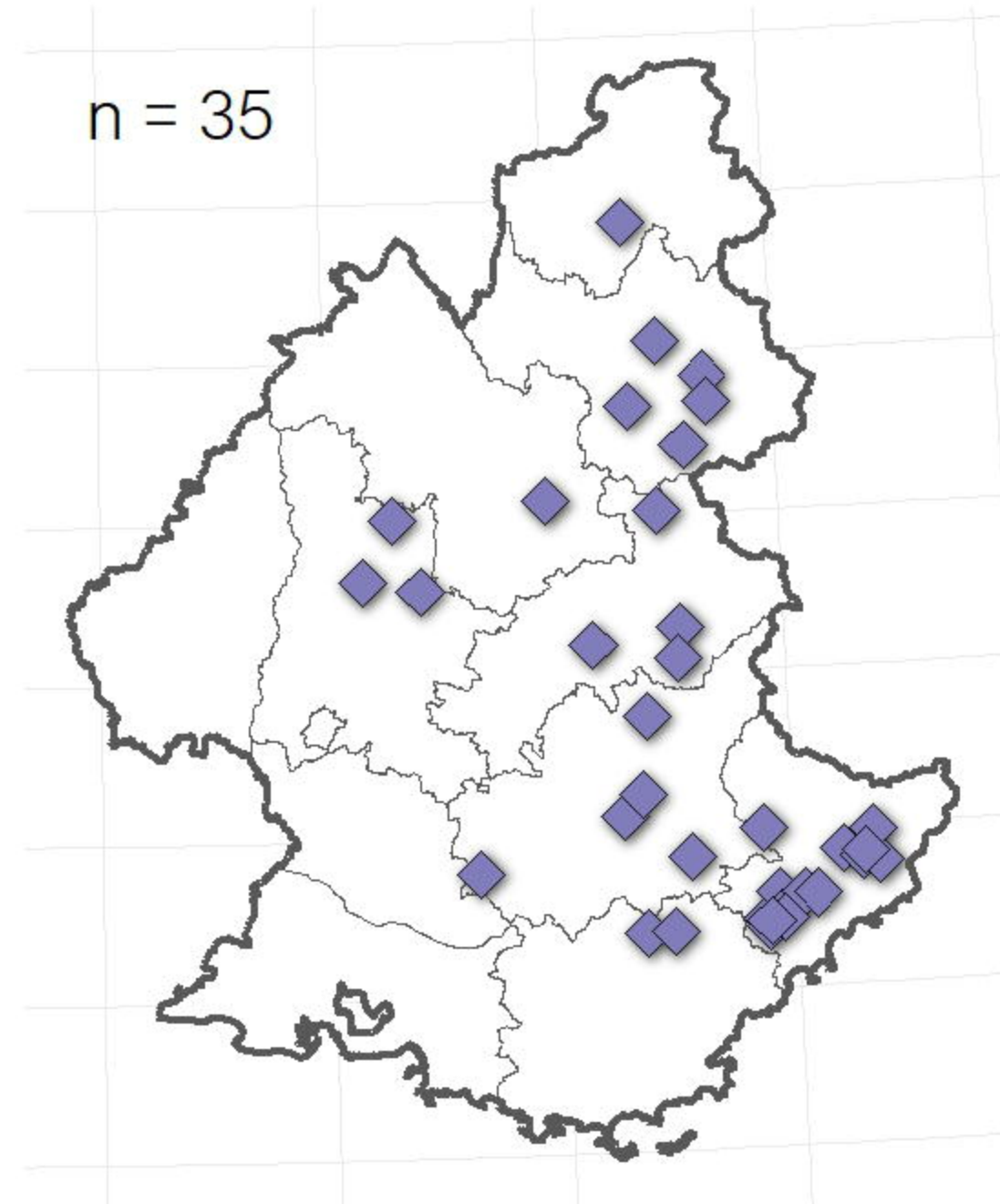


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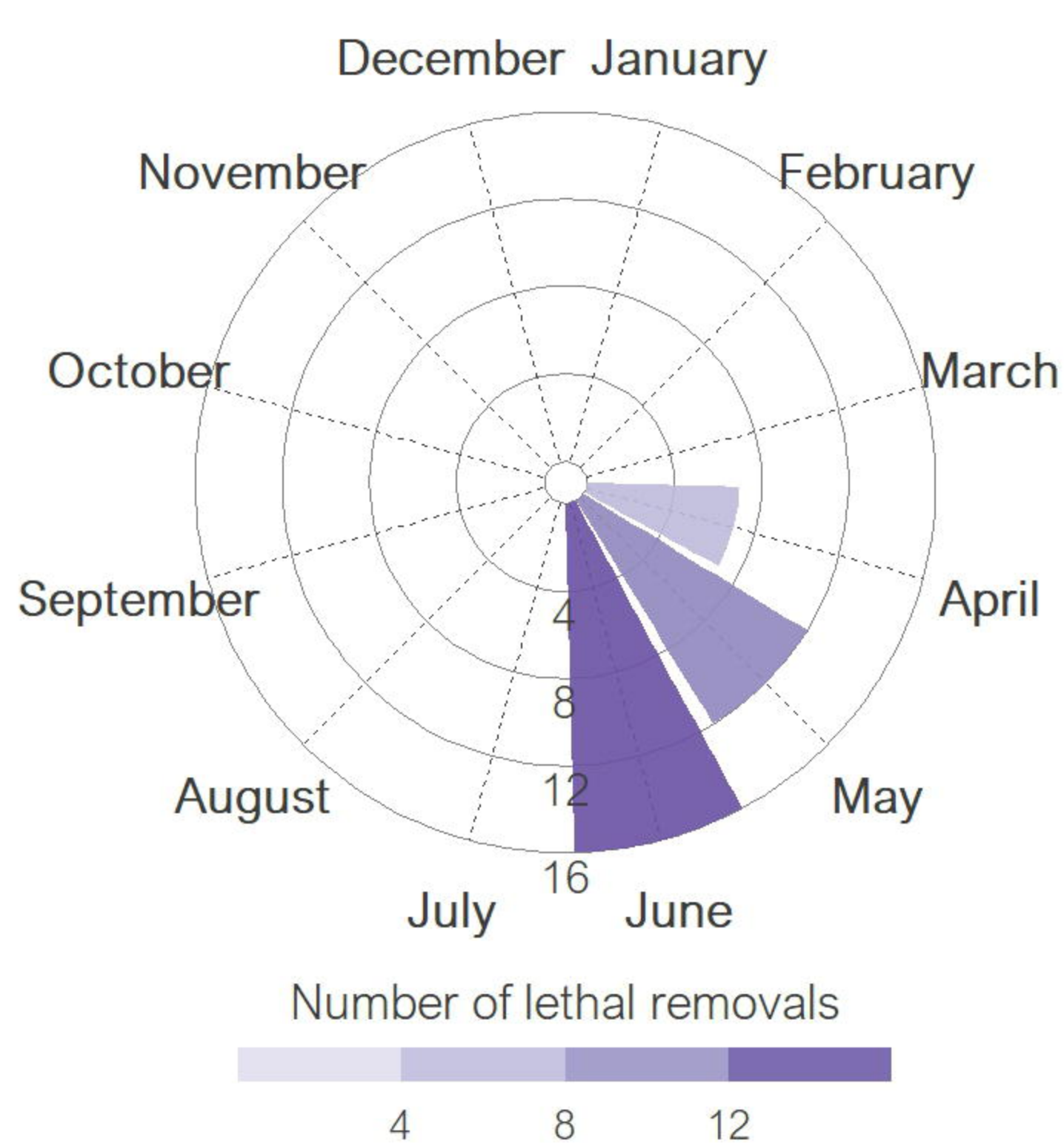


F. Den

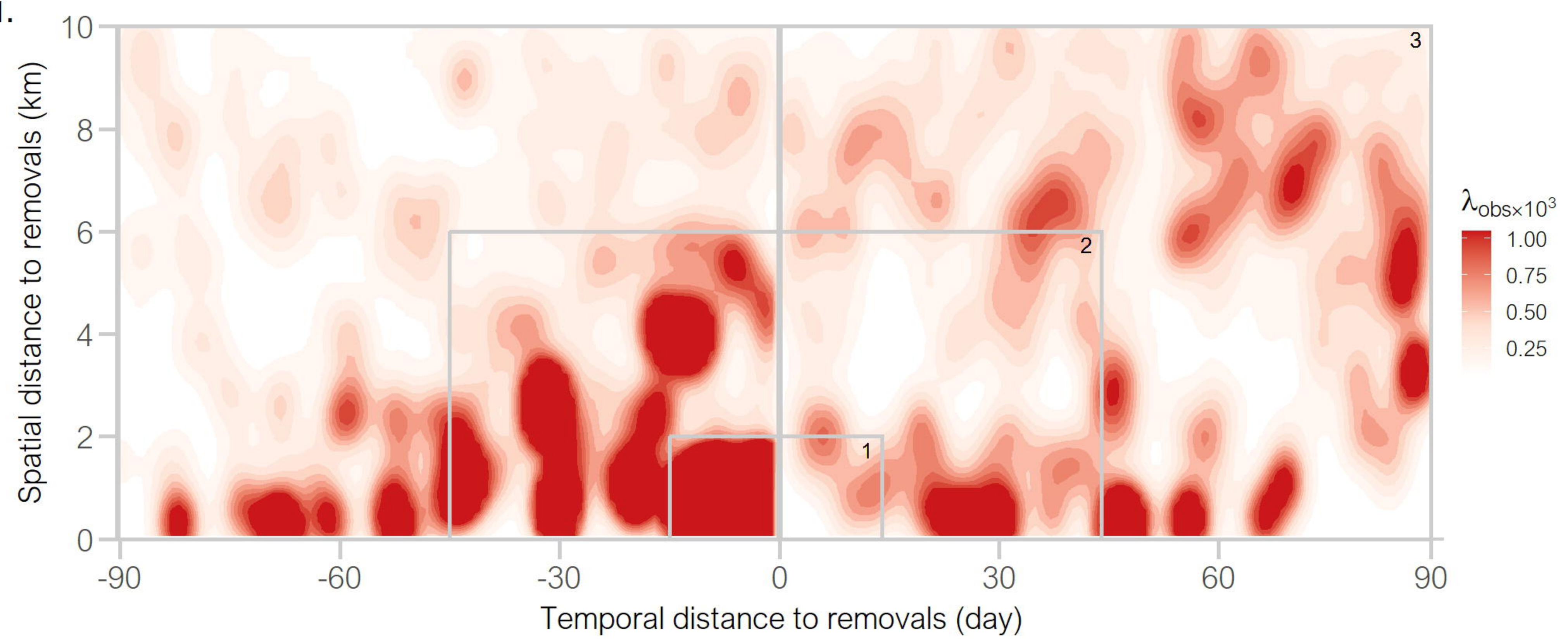
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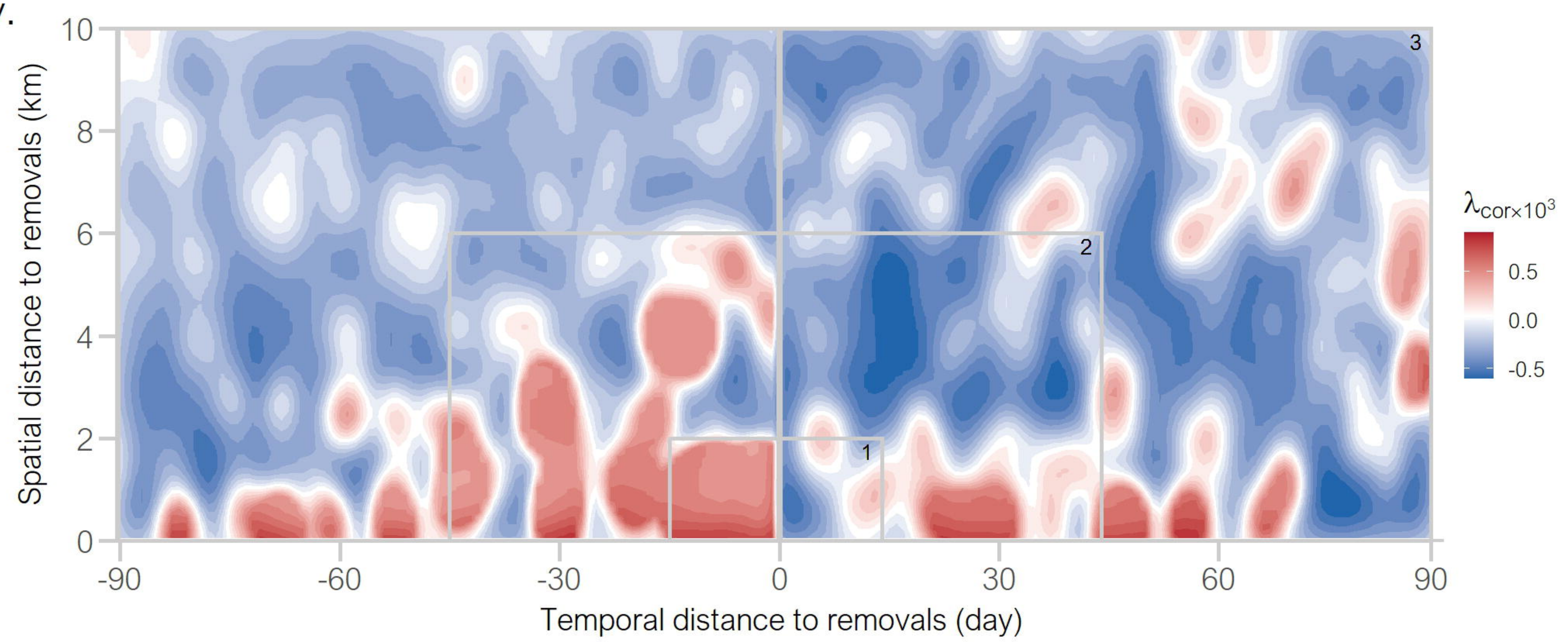
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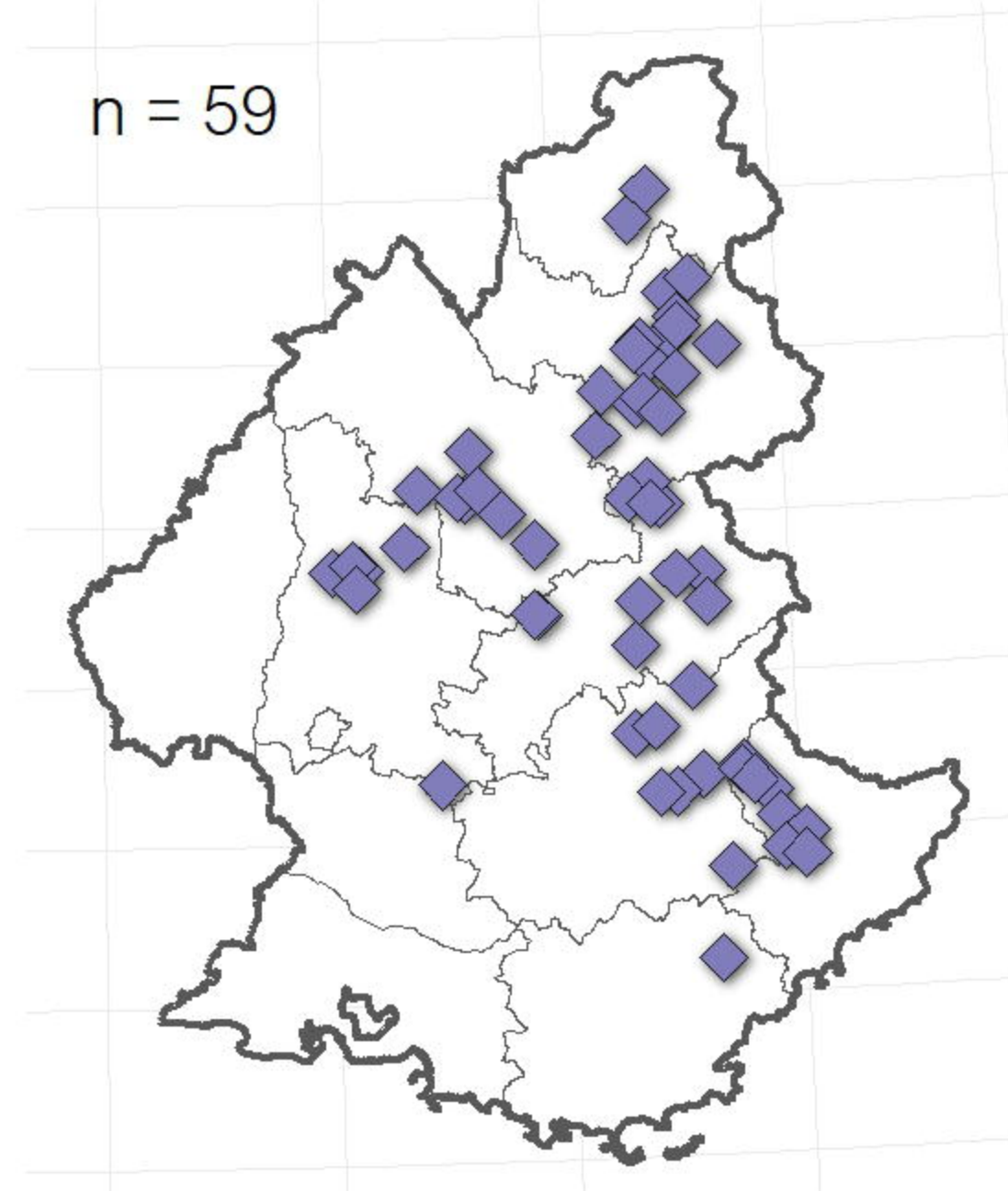


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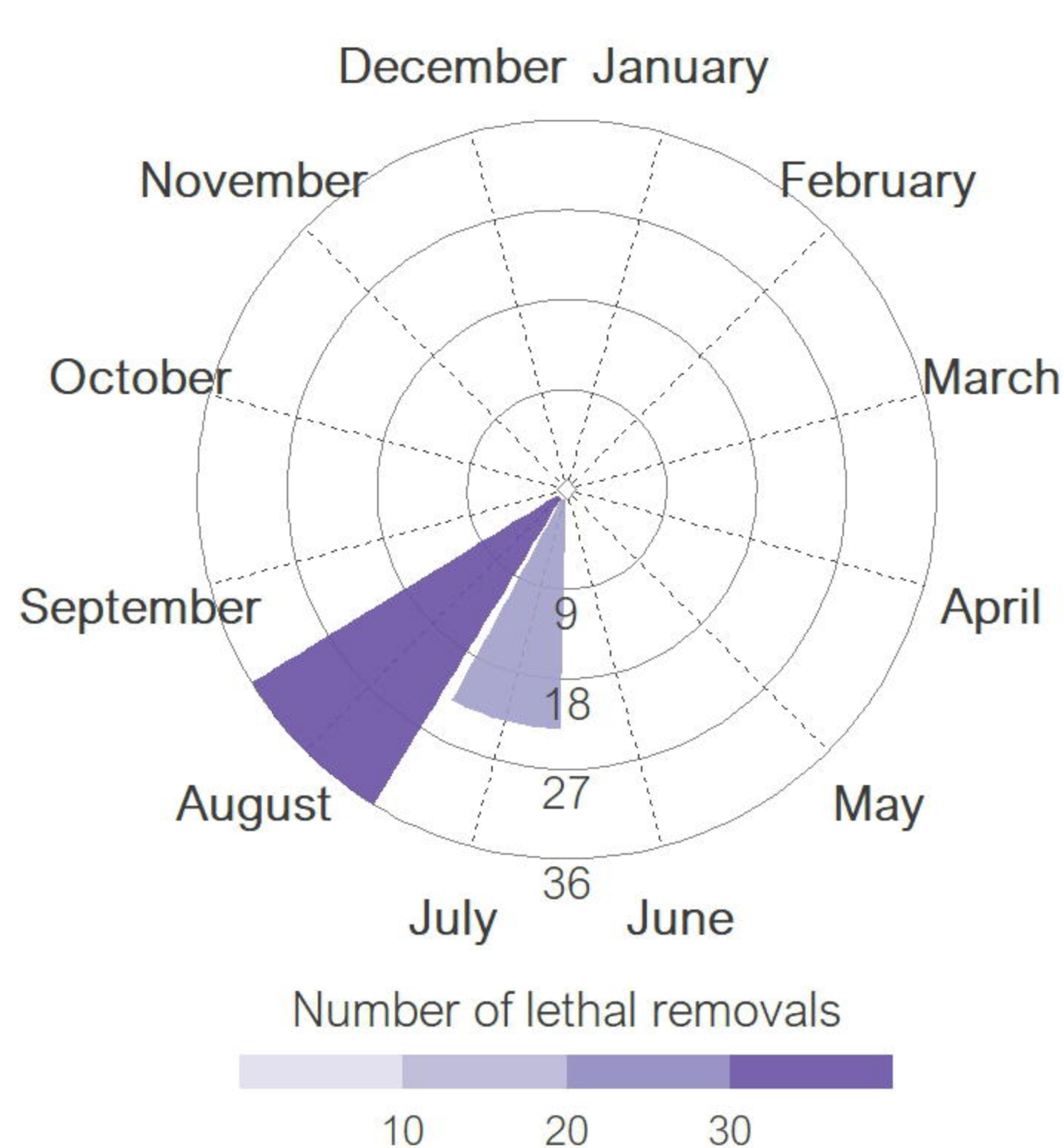


G. Rendez-vous

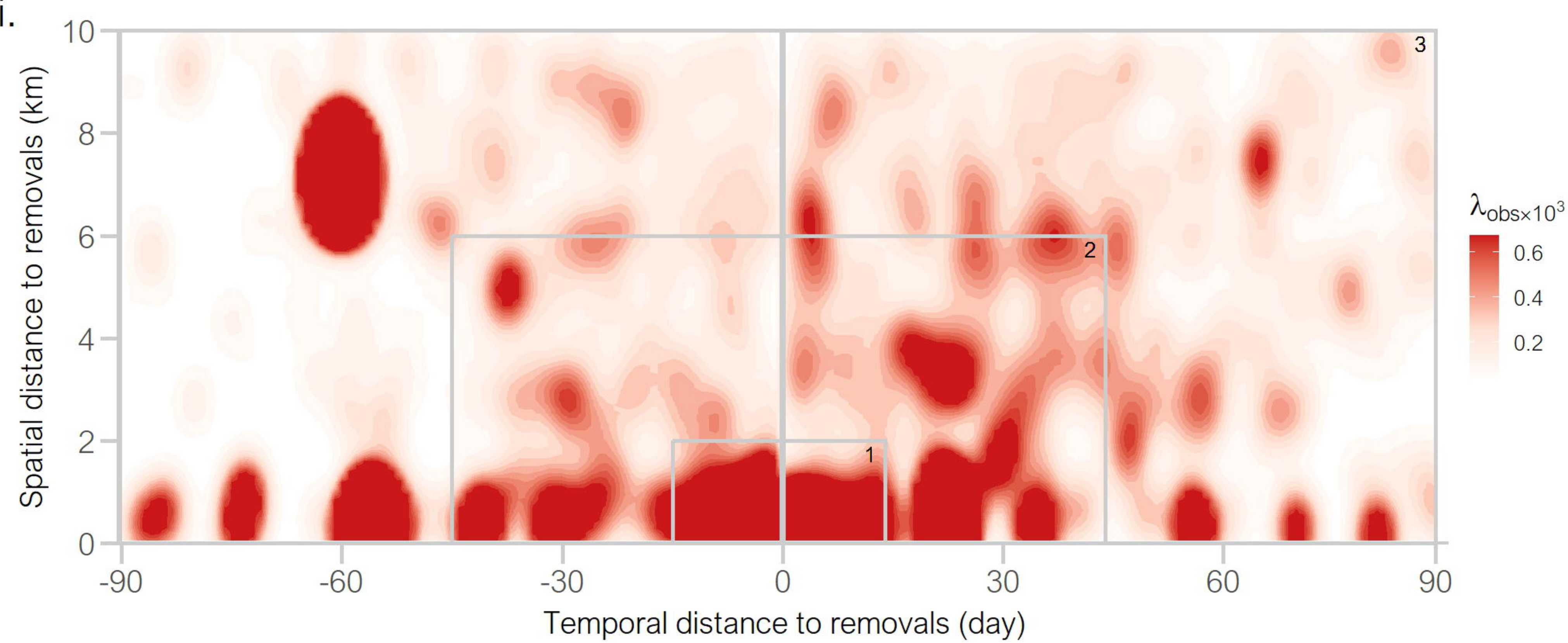
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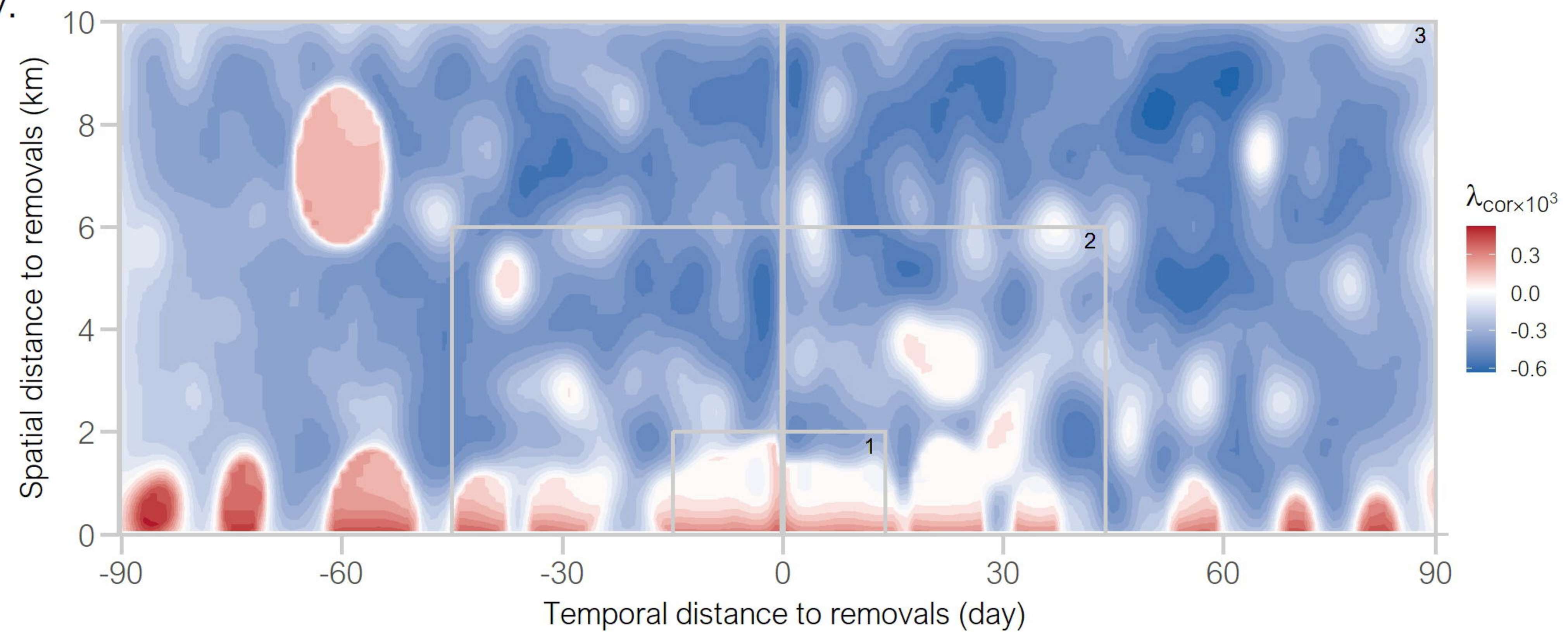
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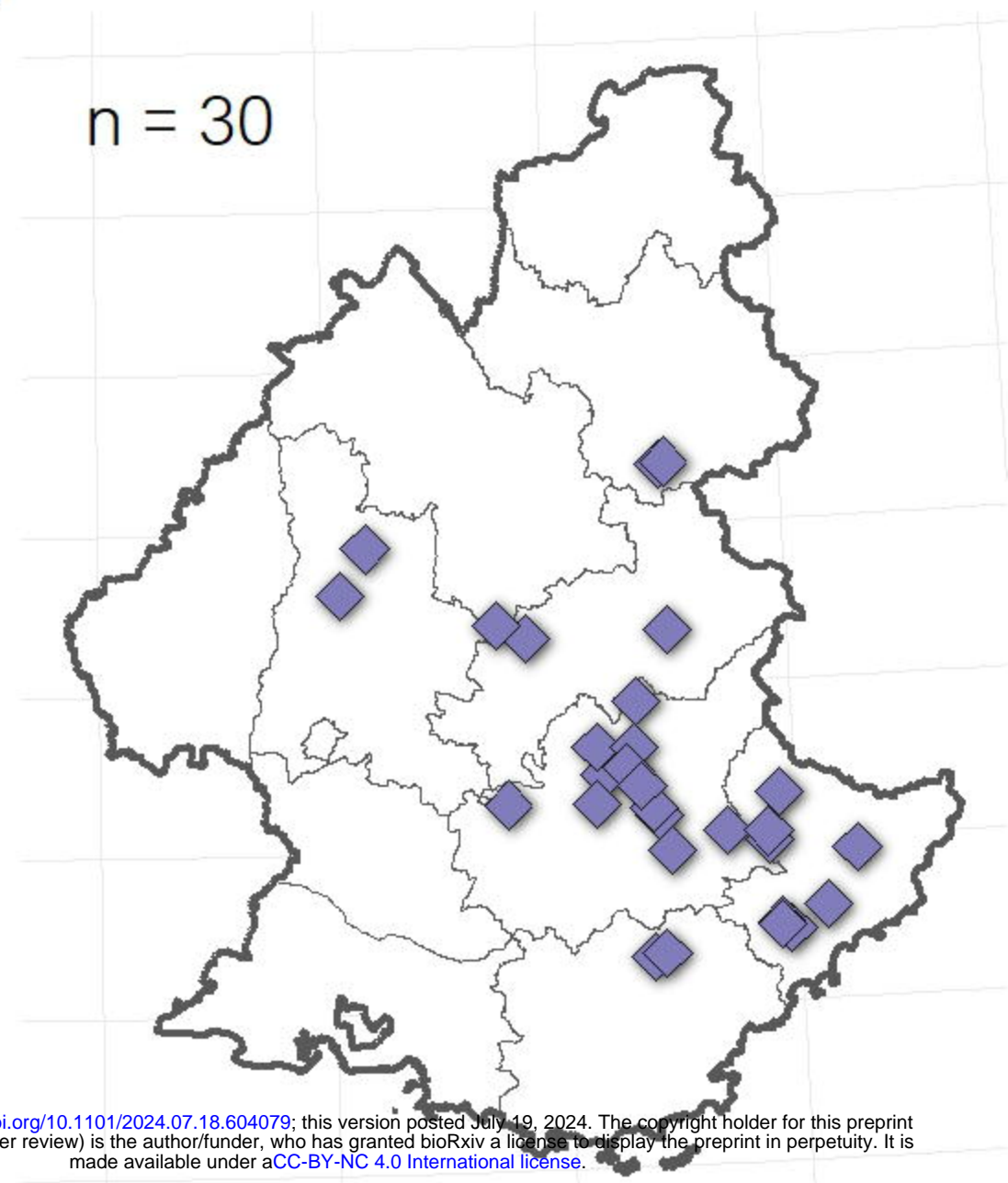


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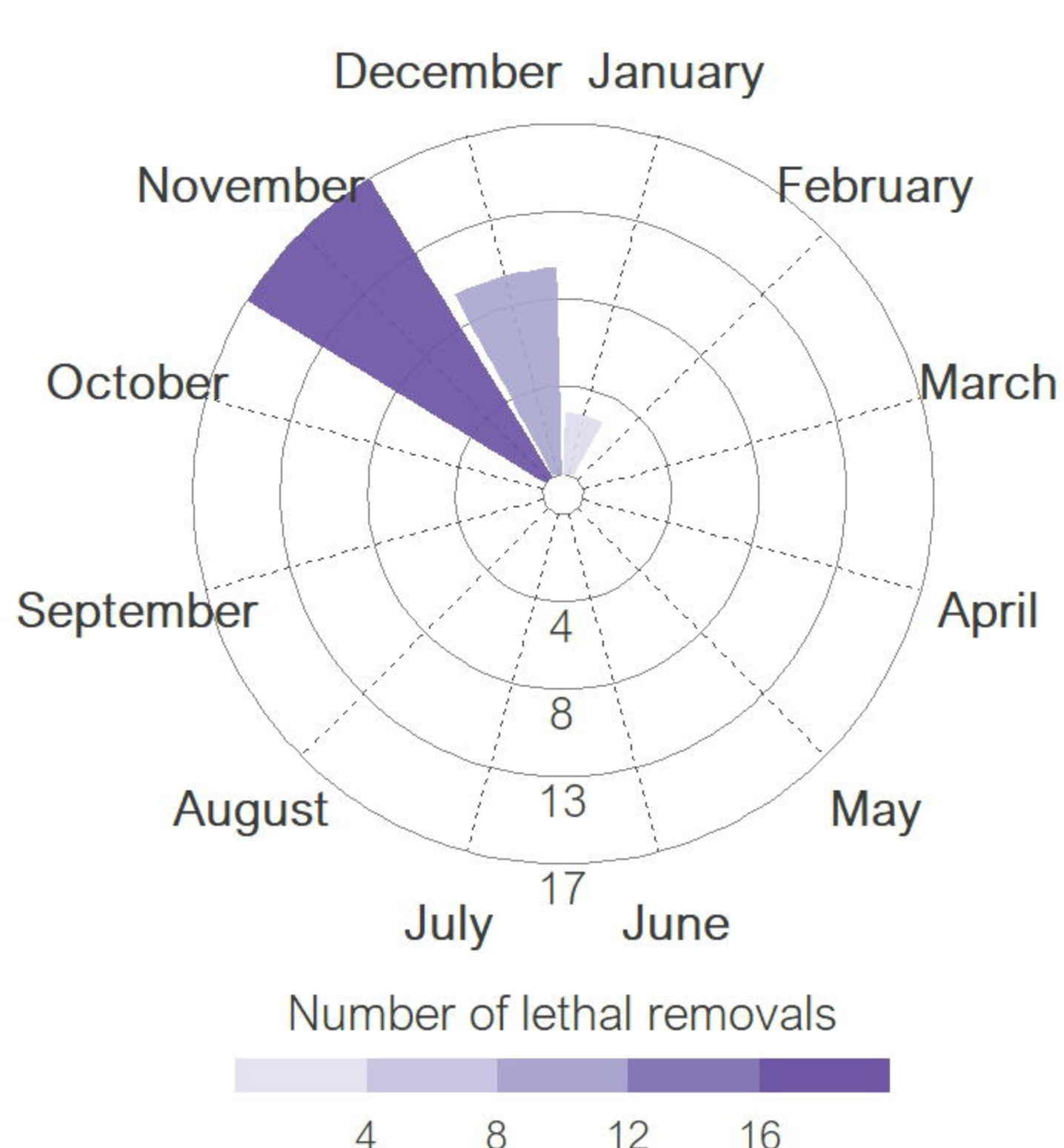


H. Winter

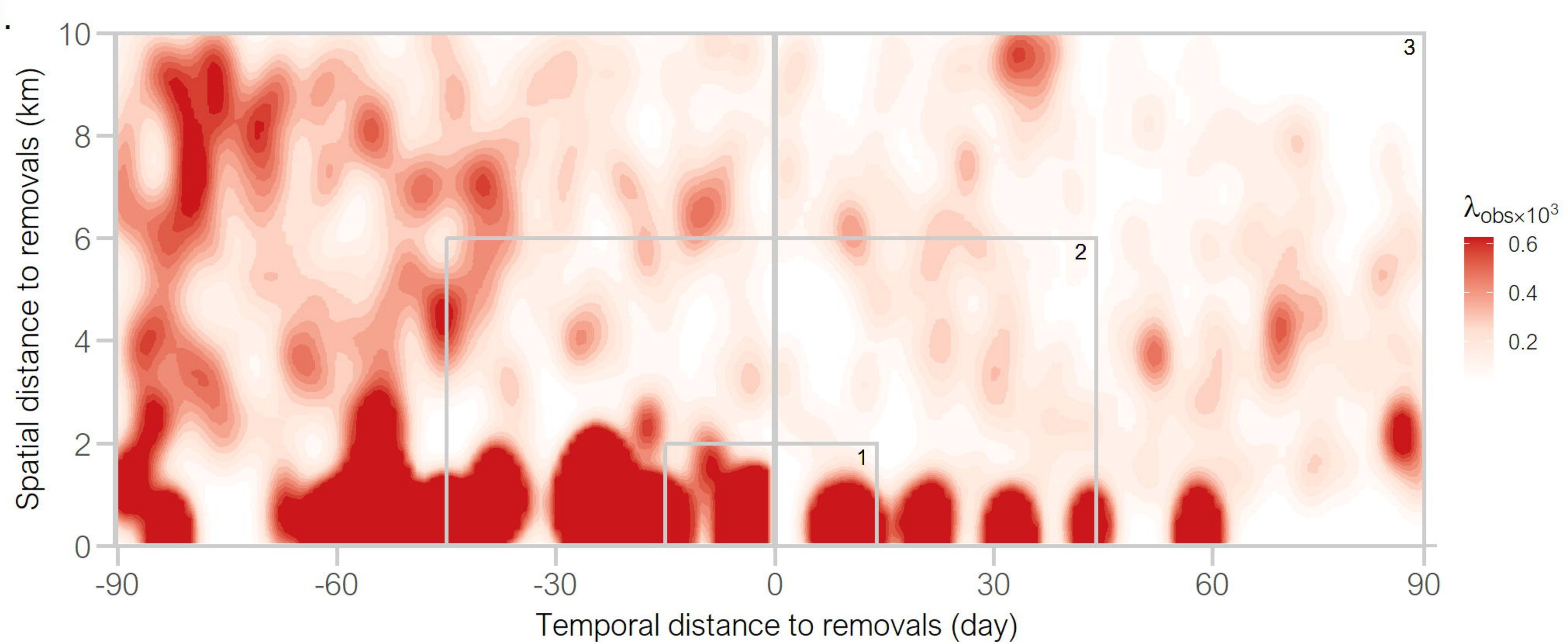
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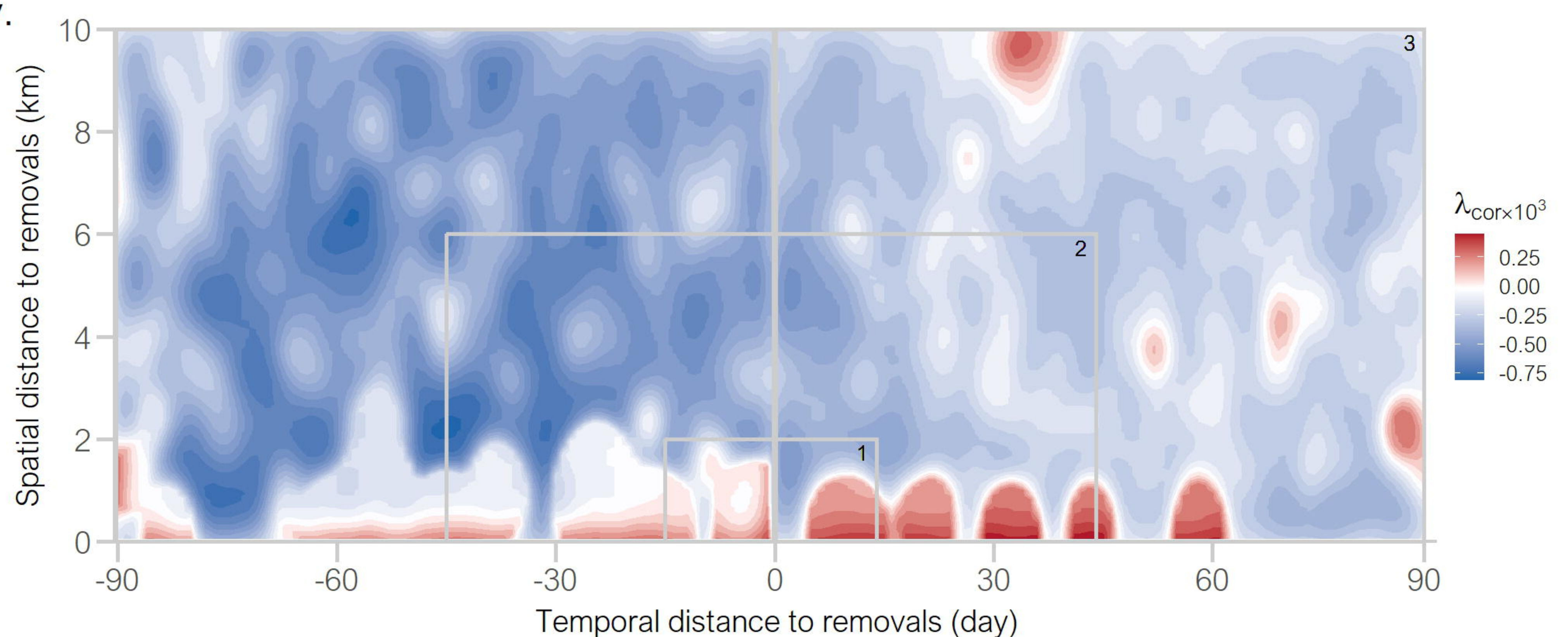
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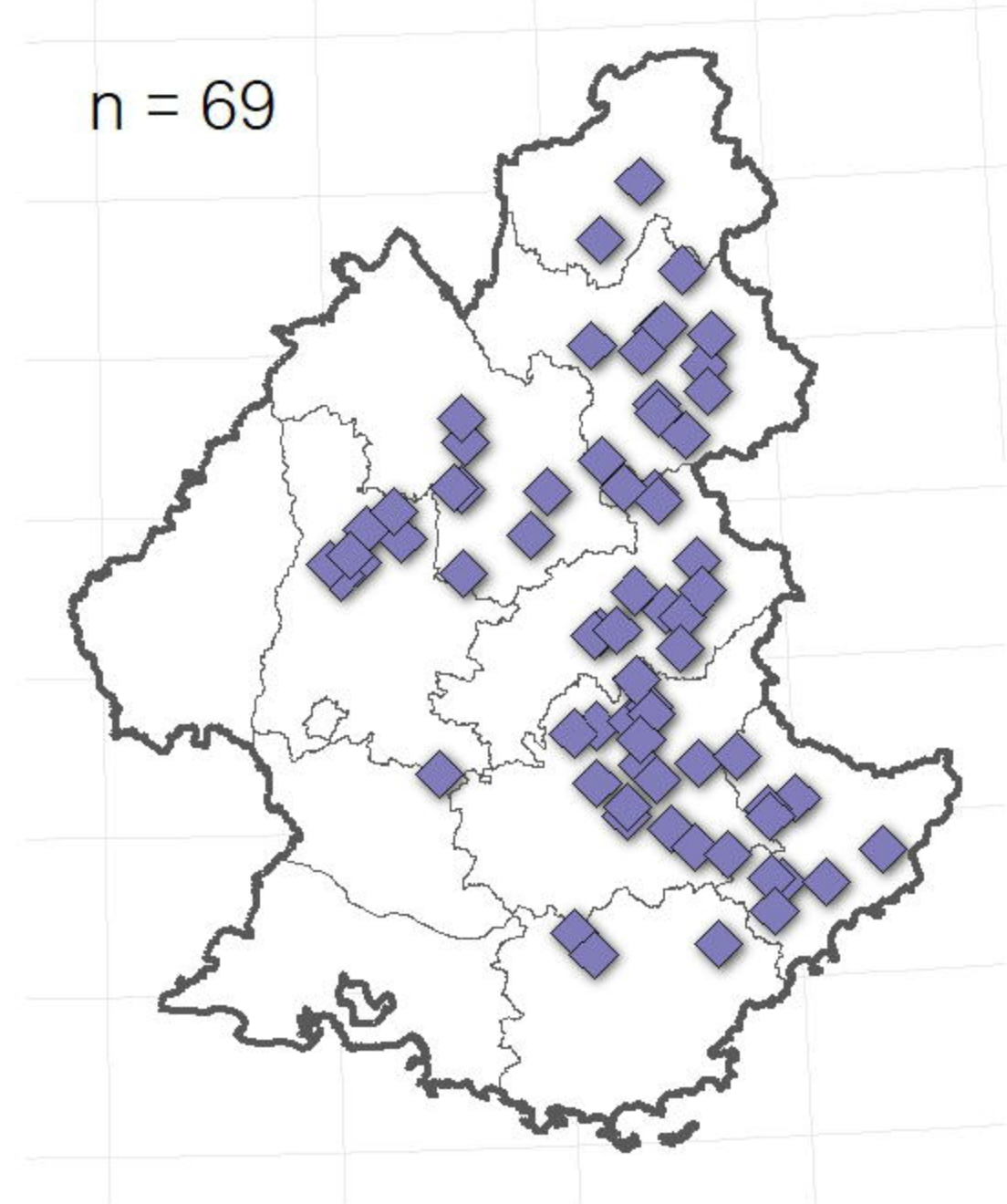


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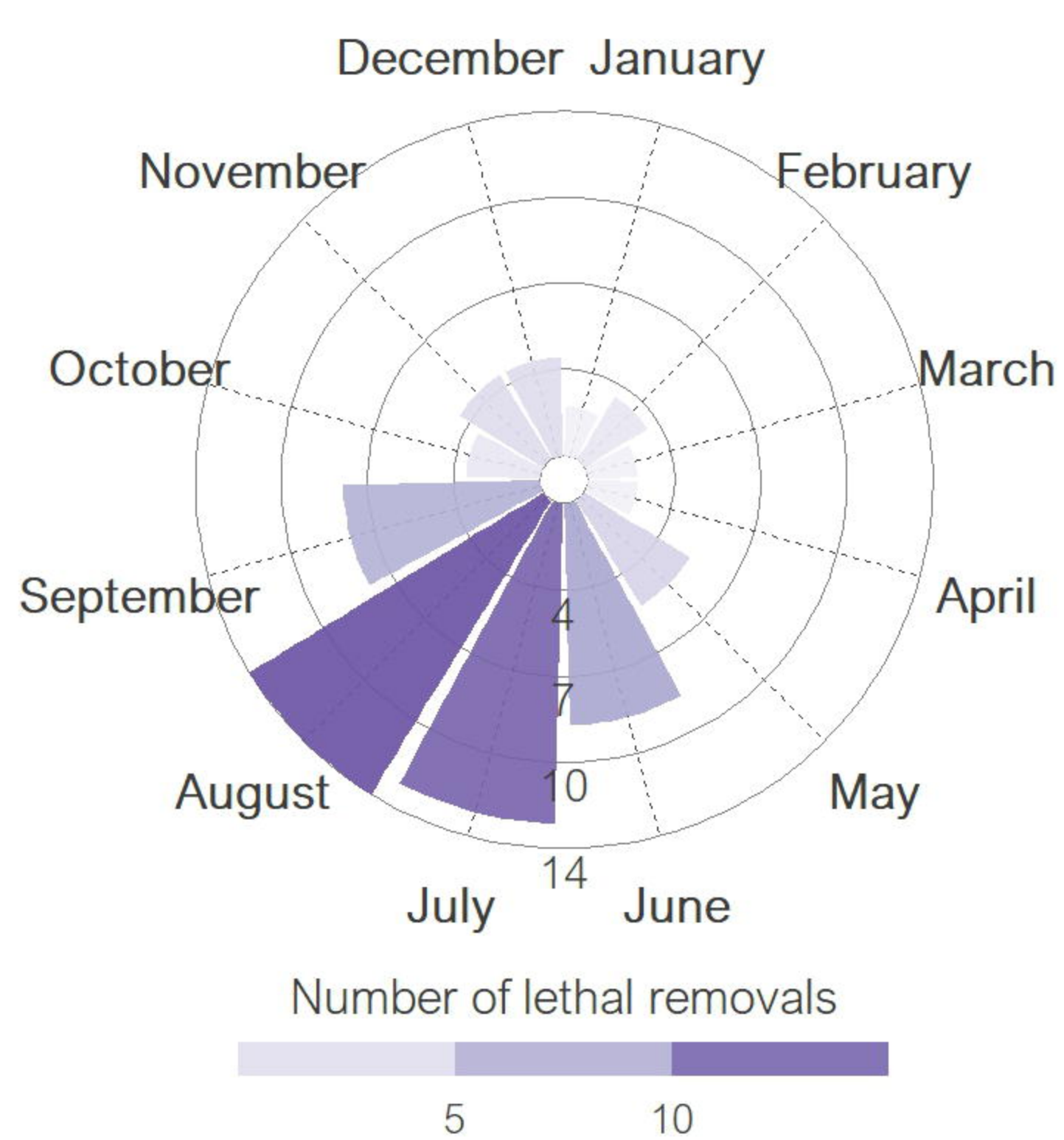


I. Simple defense

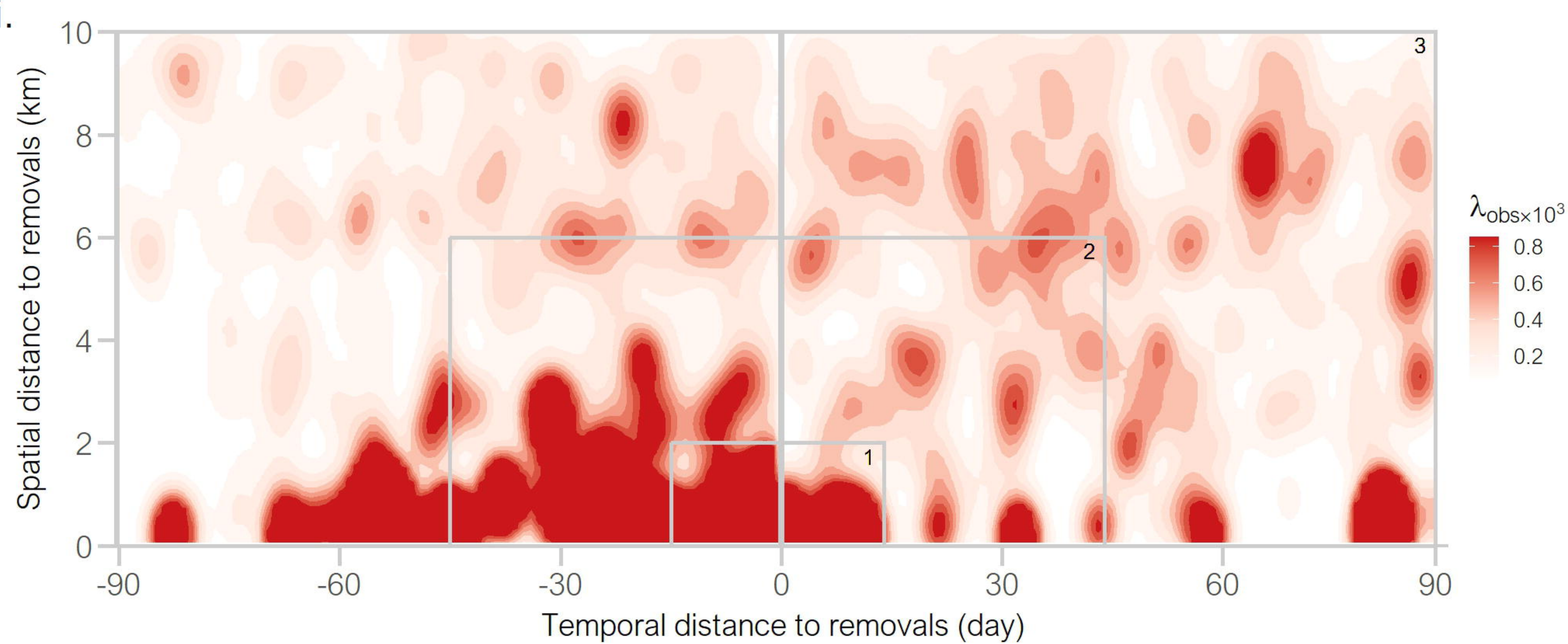
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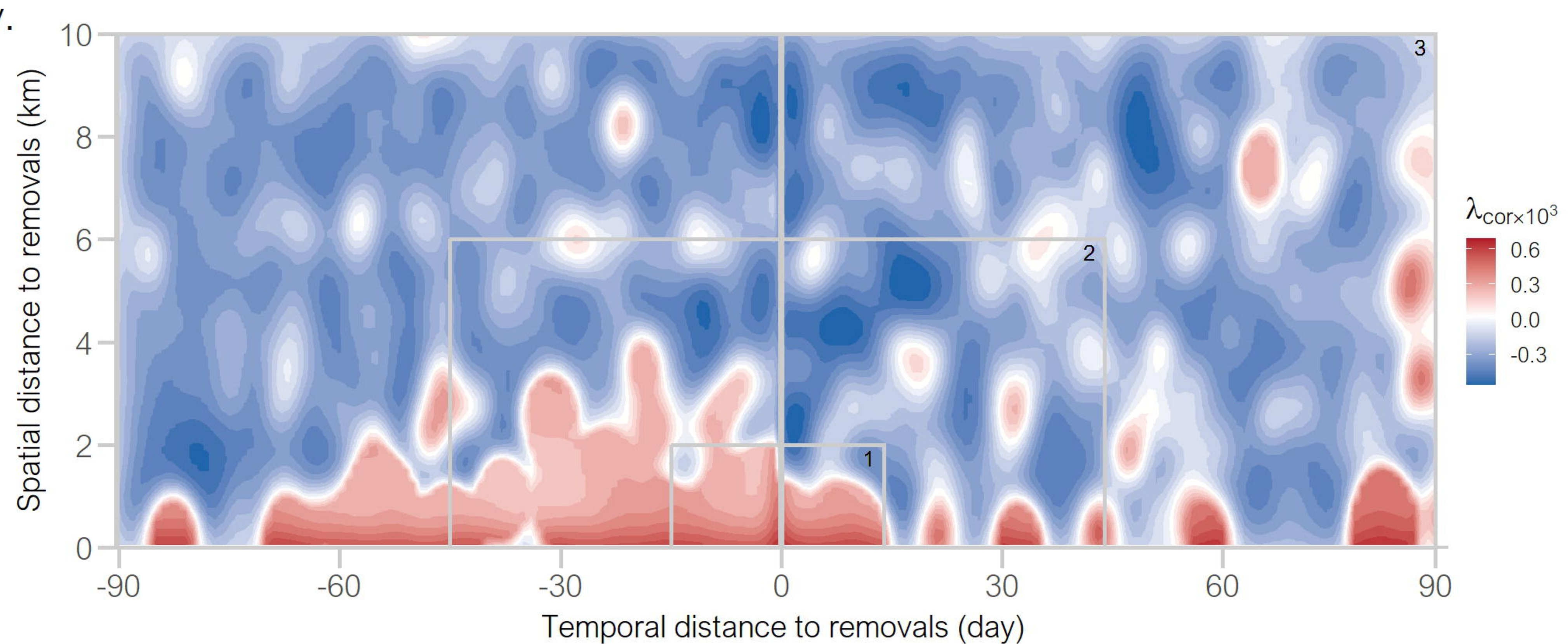
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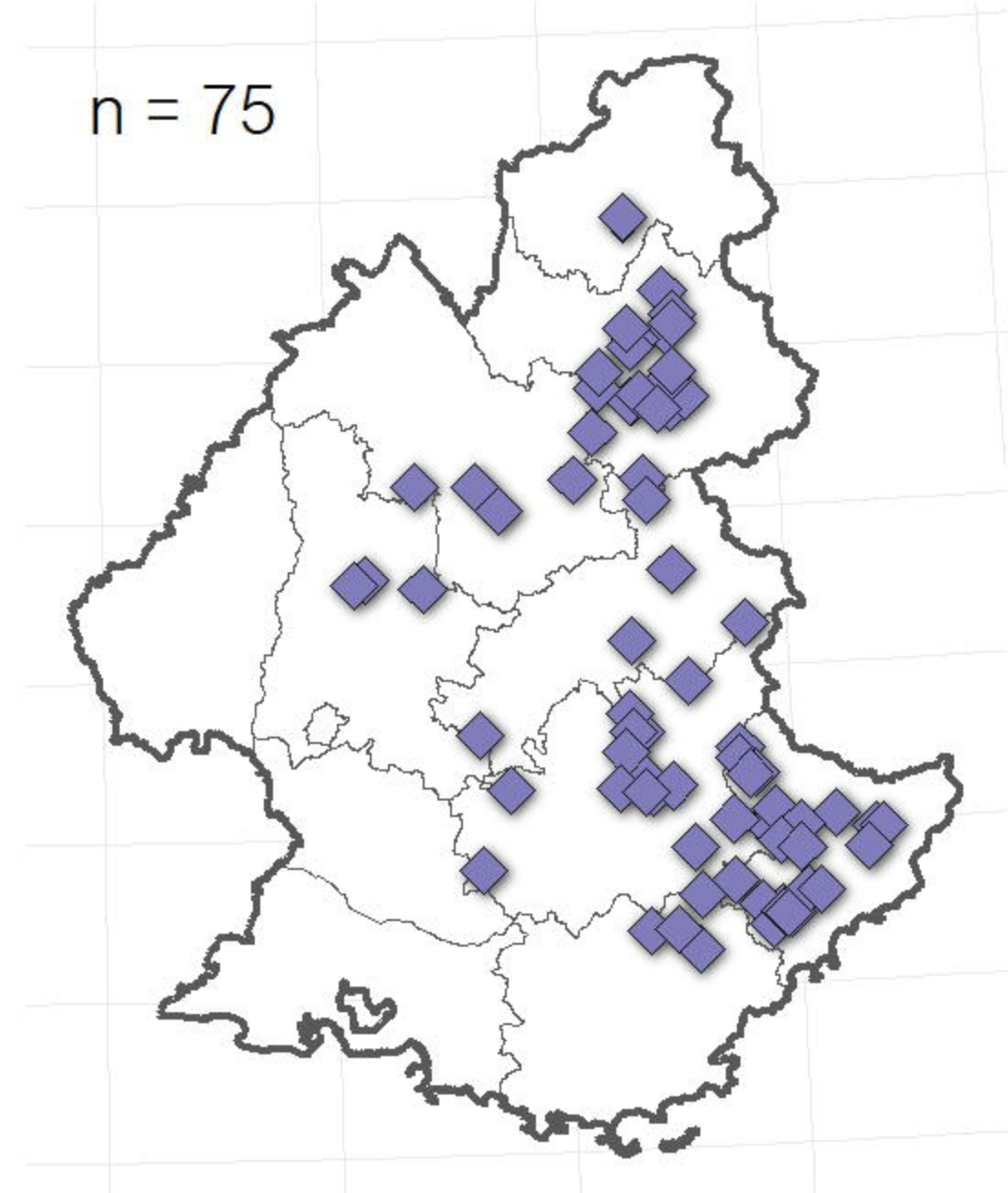


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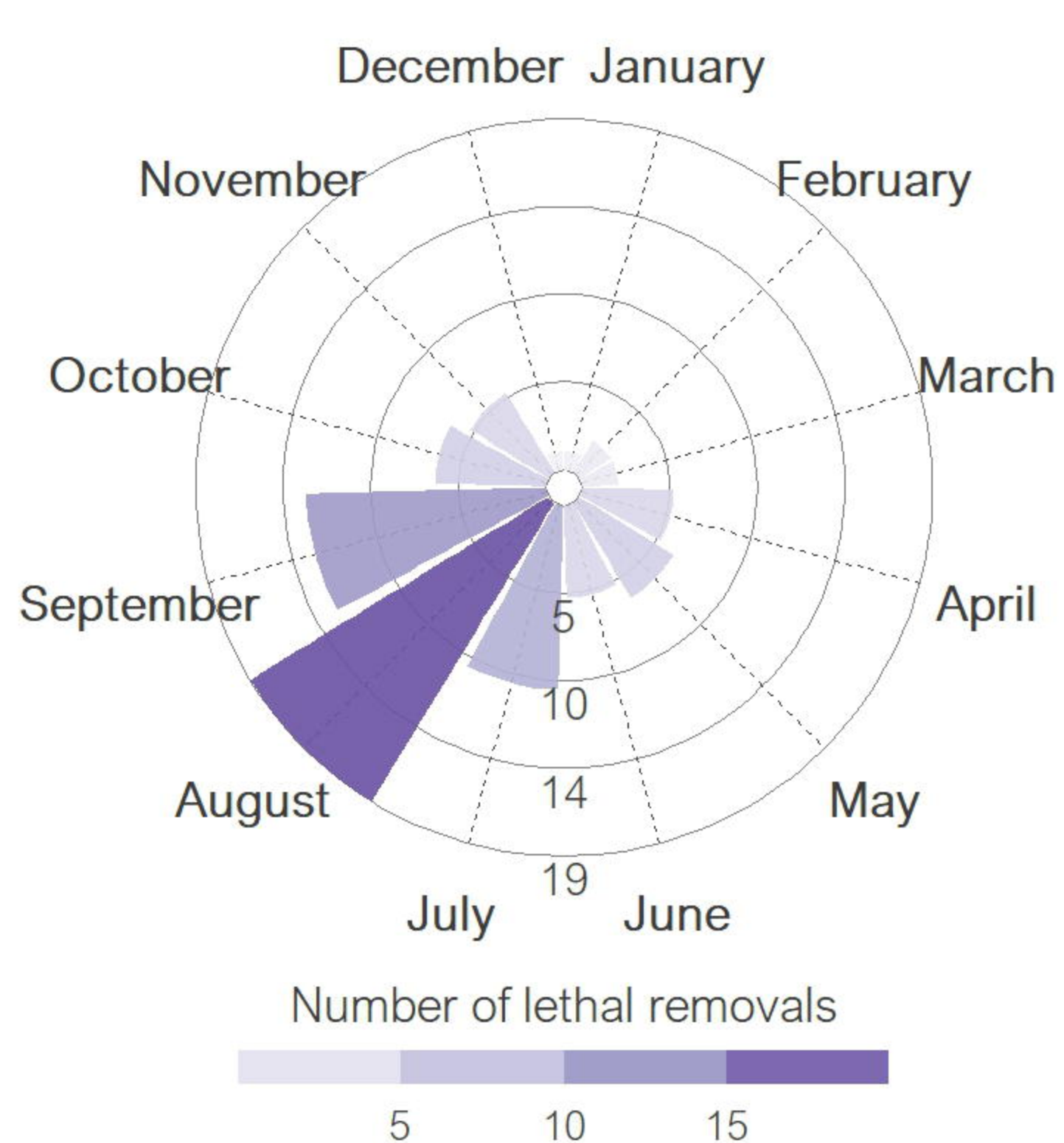


J. Reinforced defense

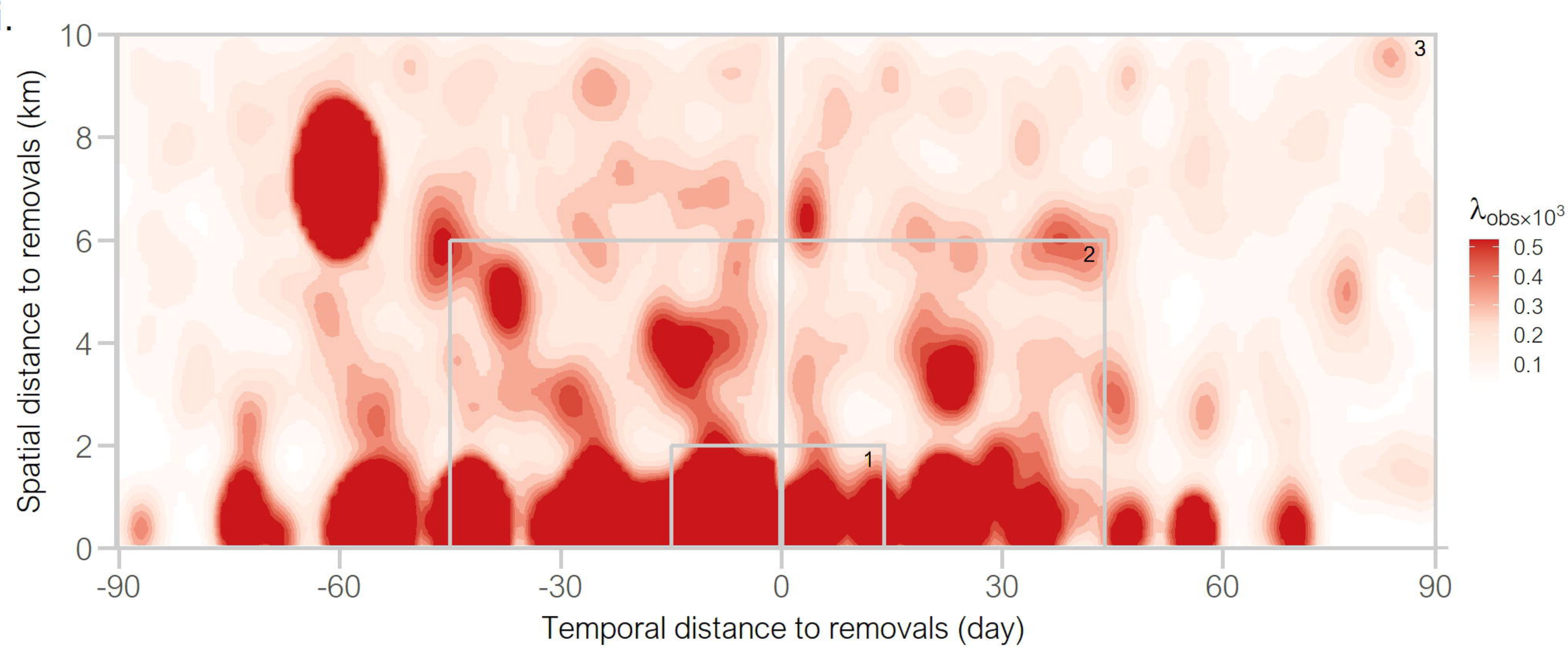
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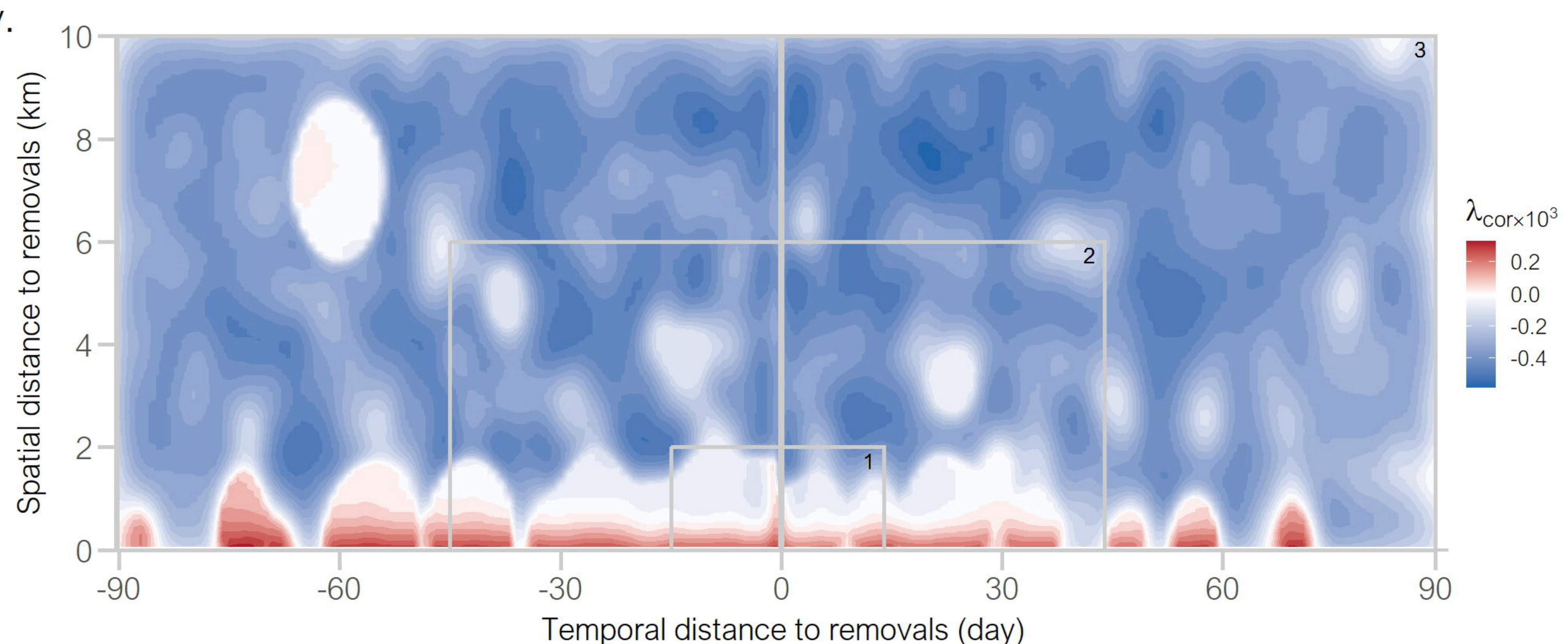
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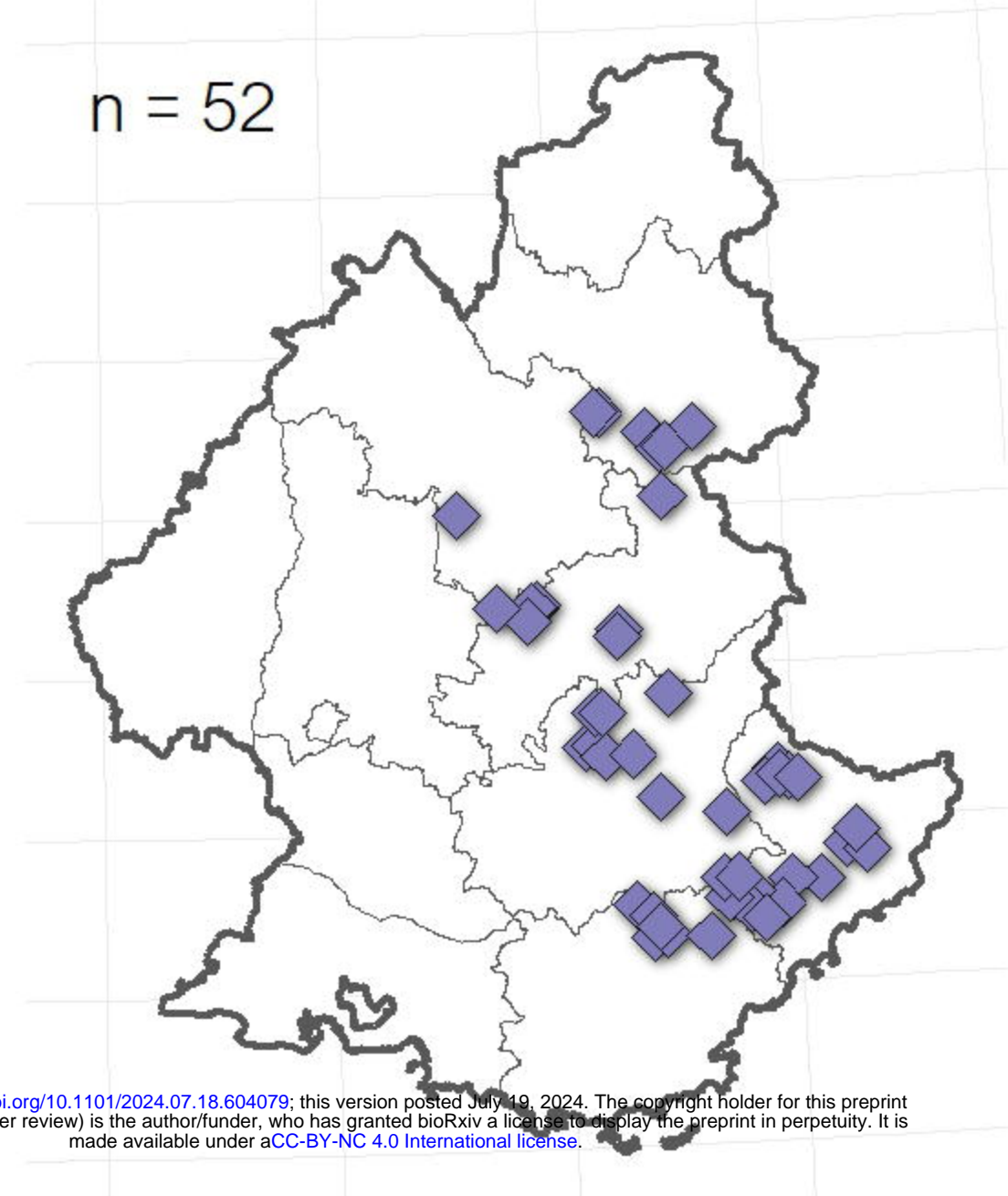


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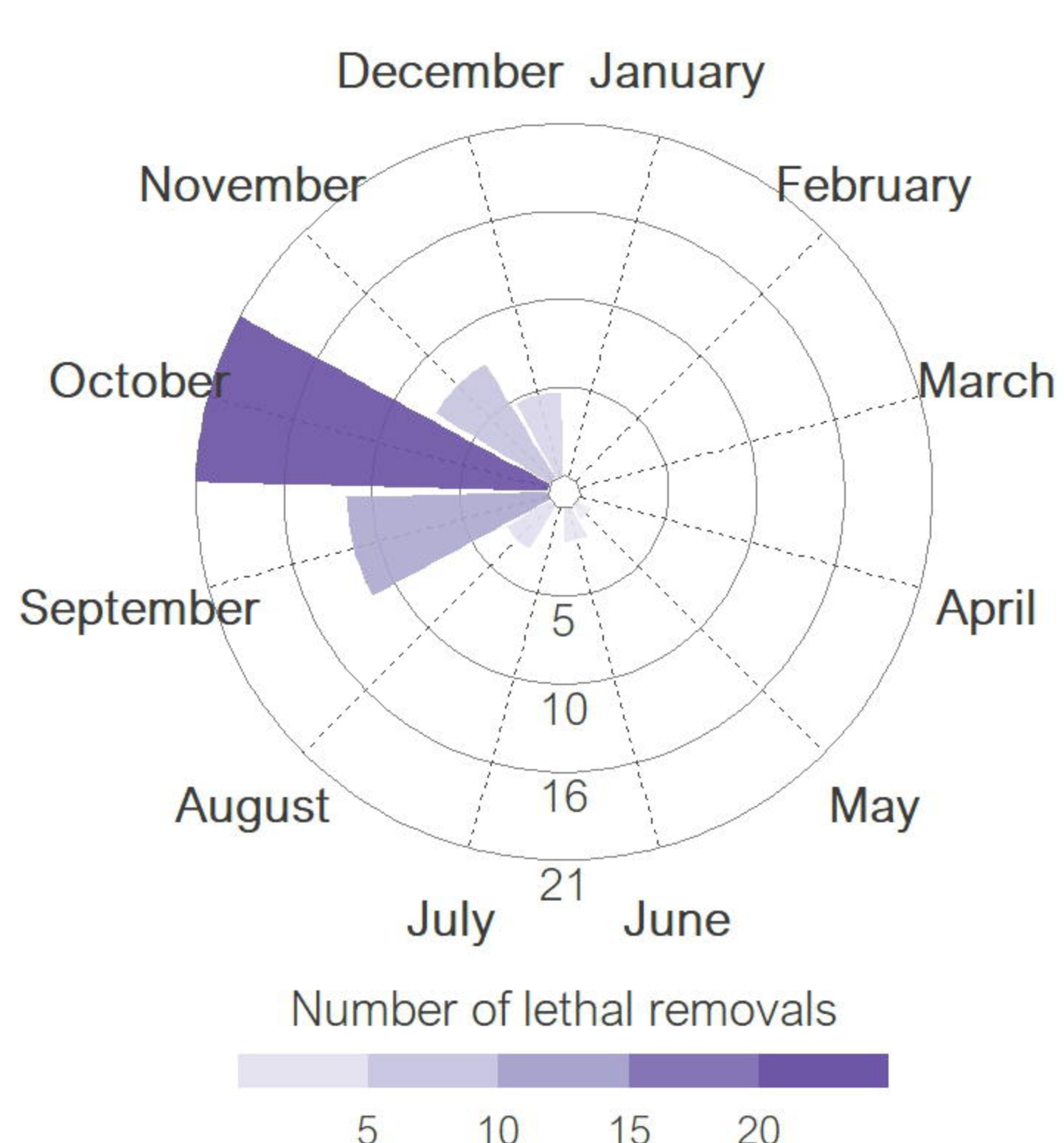


K. Hunting

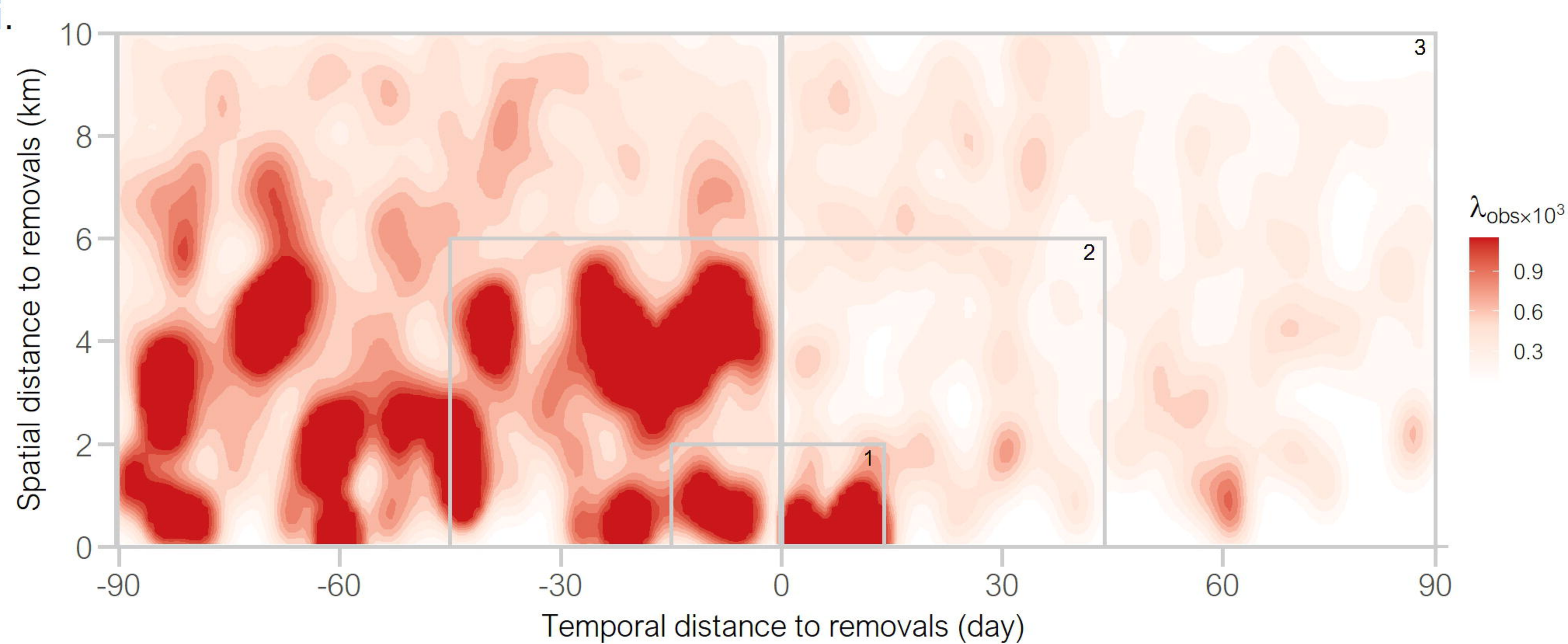
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ii.



iii.



iv.

