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# **Integrating microclimatic variation in phenological responses to climate change: a 28-year study in a hibernating mammal.**

## **Running head: Phenology and microclimate**

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17 preparation: AT. All authors read and commented on the final manuscript.

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## 24 ABSTRACT

25           Phenological shifts associated with directional changes in climate, resulting in earlier  
26 spring activities, have been documented in several animal species. However, the extent to  
27 which species respond to overall climate change versus local climate variation is rarely  
28 studied. In addition, climate data are usually averaged over large spatial scales, even though  
29 local heterogeneity in habitats may be high, and species might be more susceptible to changes  
30 in local rather than global climate conditions. In this study, we examined the effects of spatio-  
31 temporal climate variation and climate change on the phenology of a hibernating mountain  
32 rodent, the Columbian ground squirrel (*Urocitellus columbianus*). Over 28 years of research  
33 (1992-2019), we studied the relationship between the microclimatic conditions experienced  
34 by adult and juvenile ground squirrels from four neighboring meadows, and their dates of  
35 emergence from hibernation. We used a microclimate model to calculate microclimate  
36 variables (local snow depth, soil temperature, air temperature, wind speed, and humidity) at  
37 an hourly scale, a 5-m spatial resolution, and at animal height on the study sites over 28 years.  
38 Emergence dates varied with age and sex, among years, as well as among and within  
39 meadows, with some areas averaging earlier emergence from hibernation than others (up to  
40 10 days of difference). While emergence dates tended to be delayed throughout the study  
41 period, long-term temporal changes and interannual variability in emergence dates differed  
42 among meadows and depended on individual age and sex. Dates of hibernation emergence  
43 were correlated with local climate variables considered either during hibernation or during the  
44 preceding summer. Ground squirrels emerged earlier in years or at locations when/where  
45 snow melted earlier (years: all individuals excluding 2-year-old males, locations: yearlings  
46 and older females), and when the previous summer was less windy ( $\geq 3$ -year-old individuals)  
47 and more humid (2-year-old males). Two-year-old male ground squirrels also emerged later  
48 in locations where snow depth during winter was higher. Using a microclimate model

49 provided more realistic predictions of phenological responses to climate, highlighting its  
50 potential for research on animal responses to abiotic change.

51 **Keywords:** *Phenology, climate variability, hibernation, exogenous effects, microclimate*  
52 *model, spatial variability, snow cover.*

## INTRODUCTION

53           The extent to which animals are able to adapt to current climate change (e.g. earlier  
54           springs in the temperate zones) and increasing fluctuations in extreme events (e.g. storms,  
55           droughts, late snow falls) is of major concern in terms of biodiversity loss and ecosystem  
56           function (Walther et al. 2002, Martay et al. 2017, Pires et al. 2018). In particular, variations in  
57           winter and spring onsets are occurring globally in seasonal ecosystems around the world  
58           (Menzel and Fabian 1999, Kunkel et al. 2004, Kreyling and Henry 2011, Pachauri et al.  
59           2014a, 2014b), affecting the annual timing, known as phenology, of life cycle events (e.g.  
60           reproduction) in many animal species (Charmantier et al., 2008; Cohen et al., 2018; Sparks &  
61           Yates, 1997). Phenological shifts are generally consistent with the direction of climate change  
62           in most animal species, such as earlier spring activities following earlier spring onsets  
63           (Parmesan and Yohe 2003, Radchuk et al. 2019). The strength of phenological shifts,  
64           however, varies greatly within and among species, between trophic levels, and between  
65           geographical locations, from little or no changes to marked changes in seasonal timing  
66           (Radchuk et al., 2019; Strobe, 2003; Visser & Holleman, 2001; Winder & Schindler, 2004;  
67           Chmura et al., 2019; Parmesan, 2007; Thackeray et al., 2016; see Parmesan & Yohe, 2003;  
68           Root et al., 2003 for a meta-analyses).

69           Because global climate change is altering phenological cycles (Menzel 2002, Cleland  
70           et al. 2007, Chmura et al. 2019), and because phenological shifts have marked consequences  
71           for individual reproduction (e.g. match-mismatch of reproduction and peak resource  
72           availability; Durant et al., 2007; Visser & Both, 2005) and population dynamics (Ozgul et al.,  
73           2010), it is critical to understand how species phenology responds to fluctuations in climate.  
74           The need to distinguish phenological responses to long-term climate change from responses to  
75           short-term climate variability complicates this understanding. While climate variability  
76           usually considers year-to-year variation in climate, climate change only refers to those

77 variations that persist for longer periods, usually greater than a decade (World Meteorological  
78 Organization, 2015). Another layer of complexity is added by the temporal and spatial scales  
79 over which inferences are drawn. Numerous studies rely on satellite or weather station data,  
80 often collected several kilometers or tens of kilometers from studied populations (Graae et al.  
81 2012, Potter et al. 2013). However, individuals are often more affected by local climate  
82 conditions, which are shaped by spatial heterogeneity in habitat topography, soil composition,  
83 or sun exposure (Suggitt et al. 2011, Maclean et al. 2017, Zellweger et al. 2019). This is  
84 especially true in rugged areas, such as mountain habitats, where heterogeneity is high over  
85 relatively small spatial scales (Huggett 1995, Nagy and Grabherr 2009, Gultepe 2015). Local  
86 contrasts in slope angles, sun exposure, soil composition, and vegetation cover can cause  
87 climate to vary, through variations in solar radiation, wind exposure or humidity, from scales  
88 of 1-10 kilometers (*i.e.*, mesoclimates) to scales of 0-100 meters (*i.e.*, microclimates) (Barry  
89 1992). Due to a lack of climate data at a fine resolution (<1 km), few studies have examined  
90 phenological responses to microclimatic conditions (James et al. 1984, Suggitt et al. 2011,  
91 Potter et al. 2013, Varner and Dearing 2014, Paruchuri et al. 2019).

92         In this study, we examined the relationship between the phenology of hibernation and  
93 climate in a mountain hibernator, the Columbian ground squirrel (*Urocitellus columbianus*).  
94 We focused on hibernation emergence dates (ED) for individual ground squirrels from four  
95 neighboring meadows monitored over a period ranging from 18-28 years, depending on the  
96 meadow. Our objectives were to (1) examine spatial (among and within the four meadows)  
97 and temporal (over the years) variation of ground squirrel ED and to (2) determine how this  
98 variation might be explained by local and temporal variation in microclimatic conditions  
99 (scale of tens of meters, as experienced by the animals). Columbian ground squirrels are  
100 colonial ground-dwelling sciurid rodents inhabiting burrow systems in subalpine meadows of  
101 the northern regions of the Rocky Mountains. Columbian ground squirrels are an interesting

102 model system to investigate changes in phenology in relation to microclimates. These  
103 relatively long-lived animals (the oldest squirrel in our data set lived up to 14-yo.) hibernate  
104 for ~8 months of the year, and are only active for a short summer period during which  
105 reproduction occurs (Murie and Harris 1982, Young 1990b, Dobson et al. 1992). Because of  
106 this short active season, phenological shifts may be important in determining animal  
107 reproduction or ability to fatten for winter. A long-term delay adult female ED, correlating  
108 with lower spring temperature and delayed snowmelt, has already been reported (9.4 days  
109 over a 20-year period) in one of our four populations (Lane et al., 2012). While this study  
110 suggested phenological plasticity in ground squirrel ED, likely due to climate change (see also  
111 Dobson et al., 2016), it only considered adult females from a single population and used wide-  
112 scale climate variables to test for their effects on ground squirrel ED (the weather data came  
113 from a meteorological station located in a prairie habitat, some 55km from the study site).  
114 Yet, although some emigration occurs (Wiggett et al., 1989), adult ground squirrels are  
115 largely highly philopatric and have a relatively small ranges over their lifetimes (e.g. female  
116 range rarely exceeds 1 km<sup>2</sup> and male range around 4.2km<sup>2</sup>; Arnaud et al., 2012; Festa-  
117 Bianchet & Boag, 1982; Harris & Murie, 1984; Murie & Harris, 1978). Thus, these animals  
118 are more likely to respond to very local climate conditions than to wide-scale climate  
119 variations. In addition, previous studies have shown that adult males emerge from hibernation  
120 first, followed by adult females, and lastly yearlings (Murie and Harris 1982, Dobson et al.  
121 1992). However, data was lacking on whether different age or sex-categories show similar or  
122 different phenological plasticity to local climate, both within and between neighboring  
123 populations (resolution of ~300m).

124         To study the relationship between emergence date and climate, we performed a three-  
125 step analysis. First, we analyzed how variable ED was both within and among four different  
126 meadows over a 28-year period. We analyzed variation in ED in relation to individual (sex

127 and age) and environmental characteristics (year, hibernation location) that were expected to  
128 affect hibernation emergence. Second, although our four study sites are located in the same  
129 valley, they present observable variability in slope, topography, and exposure to sun both  
130 within and among sites. Thus, we expected local climate variations to occur, affecting  
131 variation in ED both among meadows and within different parts of a given meadow. In the  
132 absence of local weather stations, we used a microclimate model (see Kearney, 2020; Kearney  
133 et al., 2020; Lembrechts & Lenoir, 2020; Maclean, 2020; Saleeba et al., 2020) to predict  
134 climate since 1992 on the four study sites, at a 5-m resolution, and at the height of the animal  
135 (10 cm above ground, or 1-m below ground, roughly the depth of a hibernaculum; Young,  
136 1990). We then analyzed climate variation and tested whether we could detect a directional  
137 change in local climate patterns over the past 28 years (viz. climate change). Finally, we  
138 tested whether variation in ED could be explained by the local climate conditions encountered  
139 by the animals. Because emergence from hibernation is strongly related to the energetic state  
140 of individuals at the end of the hibernation (Norquay and Willis 2014, Williams et al. 2014,  
141 Fietz et al. 2020), there are two theoretical ways that climate could affect ground squirrel  
142 emergence dates: 1) by modifying individual energy expenditure during hibernation  
143 (Humphries et al. 2002, Pretzlaff and Dausmann 2012, Geiser 2013), and 2) through carry-  
144 over effects from one active season to another (Norris 2005, Saino et al. 2017, Moore and  
145 Martin 2019). On one hand, the energy available and stored by individuals during the active  
146 period should affect their ability to fast during hibernation (as Columbian ground squirrels are  
147 “fat-storing” hibernators, Murie and Boag 1984, Humphries et al. 2003). On the other hand,  
148 harsh climate conditions during winter could also affect ground squirrel energy expenditure,  
149 and thus influence individual ability to fast and hibernate (Davis 1976, Humphries et al. 2004,  
150 Fietz et al. 2020).

151           As the environment is multifactorial by nature, our analyses included several climate  
152 variables that could affect either energy storage before hibernation or energy expenditure  
153 during hibernation (as recommended by McGuire et al. 2021). Specifically, we expected areas  
154 or years with earlier snowmelt and higher underground temperature to be associated with  
155 earlier ED (see Lane et al. 2012). The presence and depth of the snow cover directly impacts  
156 soil insulation and ground temperature, potential external cues for hibernating individuals. In  
157 addition, we expected carry-over effects of climate on ED to occur from one year to the next.  
158 During hibernation, ground squirrels rely almost exclusively on body fat (Shaw 1926).  
159 Overwinter survival depends on fat reserves accumulated during the previous season (e.g.  
160 Murie & Boag, 1984), and low fat deposition is likely to affect ED the subsequent year. We  
161 did not measure body mass before hibernation in our study, but we reasonably expected  
162 foraging conditions (length and quality of forage) during the previous summer to directly  
163 reflect the amount of fat accumulated and burned during winter (Dobson et al. 1992, Neuhaus  
164 2000). Thus, we expected unfavorable forage conditions – e.g. low rainfall (reflected by  
165 humidity) to be associated with low primary productivity (Dobson and Kjelgaard 1985,  
166 Neuhaus et al. 1999, Dobson et al. 2016), and strong winds to be associated with more time  
167 spent by animals in vigilance rather than foraging (Fairbanks & Dobson, 2007). Through the  
168 decrease of fur thermal insulation (McCafferty et al. 2017), humidity might also negatively  
169 affect the time foraging, which will have detrimental effects on the accumulation of fat stores  
170 and ultimately on hibernation duration. This may cause individuals to emerge earlier due to  
171 the early depletion of overwintering fat stores, or conversely to delay emergence by more  
172 pronounced hypometabolism and a longer torpor period until resource availability is high  
173 again (i.e. avoiding early arousals when resource availability is low). Juveniles, which are less  
174 able to mitigate the survival costs of low-fat energy stores during hibernation, might  
175 experience this more than adults (Murie & Boag, 1984). Alternately, more favorable

176 conditions during the previous summer could also allow for longer hibernation periods and  
177 later ED in juveniles, allowing them to avoid the period of high territorial aggression  
178 displayed by reproducing adults early in the season (Murie & Harris, 1978; Murie & Harris,  
179 2011). Taken together, the joint investigation of summer and winter condition effects on ED  
180 in different neighboring populations was expected to provide us with a comprehensive  
181 understanding of how these mountain-adapted rodents deal with local heterogeneity in  
182 weather conditions, and whether different populations respond differently to long-term  
183 changes in climate patterns.

## 184 MATERIALS AND METHODS

### 185 **Emergence date sampling**

#### 186 *Study site and population monitoring*

187       Columbian ground squirrels were monitored in the Sheep River Provincial Park in  
188 Alberta, Canada (50°38'N, 114°39'W), located in the foothills of the Rocky Mountains (Fig.  
189 1.A). This study area includes four different meadows surrounded by mixed forests (primarily  
190 lodgepole pine, white spruce, quacking aspen, and birch trees) and composed of vegetation  
191 that is representative of grasslands in montane sub-regions (Alberta Parks 2008). We  
192 monitored ground squirrel colonies on: Meadow A (3.6 ha, from 1510-1535m, monitored  
193 since 1994), Meadow B (2.6 ha, from 1500-1540m, monitored since 1992, meadow on which  
194 the Lane et al. 2012 study was done), Meadow C (1.7 ha, from 1540-1560m, monitored since  
195 1999) and Meadow DOT (5.7 ha, from 1527-1570m, monitored since 2001). Meadows A, B,  
196 and C slopes are southeast facing, whereas Meadow DOT slope is southwest facing.

197       We collected individual data with comparable methods on all four meadows.  
198 Individuals were trapped and permanently marked as pups, or when they first appeared in the

199 meadow as immigrant adults, with application of unique metal numbered ear tags (Model no.  
200 1, National Band & Tag Co.). Sex was determined based on visual inspection of genitalia  
201 (Murie & Harris, 1982). Each year, the meadows were monitored daily from before the first  
202 emergences from hibernation (early April each year) to the end of lactation for breeding  
203 females. Unfortunately, dates of entry into hibernation were not recorded and we were not  
204 able to follow the entire cycle of annual phenology. From mid-April to the end of May each  
205 year, ground squirrels were captured within a couple of days of emergence from hibernation  
206 (usually on the day of emergence or the following morning) using live-traps (National Live  
207 Traps; Tomahawk Co., WI, USA: 13 x 13 x 40 cm<sup>3</sup>) baited with peanut butter. The first day of  
208 observation or capture (usually the same) of a given squirrel was used as a proxy for  
209 hibernation emergence date (ED), typically confirmed by the squirrel's appearance and  
210 physical condition (large skin flakes from hibernation lost within few days, large abdominal  
211 flaps of skin where fat reserves were accumulated and lost, no defecation upon capture; Murie  
212 & Harris, 1982). Emergence was recorded as an ordinal date (i.e. number of days after 1<sup>st</sup>  
213 January each year). Emergence data were not collected in 2006 on Meadow DOT, in 2003-  
214 2006 on MA, and in 2002-2003 on MC. The location of each initial capture was recorded at a  
215  $\pm 1.0\text{m}$  resolution, on 10 x 10 m Cartesian grids of color-flagged wires at each meadow.  
216 Hibernacula are usually used by the animals during a few days after emergence until  
217 collective burrows were re-excavated for the active season. First capture locations should thus  
218 provide a reasonable approximation of the area where individuals hibernated.

219 Recorded Cartesian coordinates were converted to GPS coordinates using a database  
220 of GPS and Cartesian coordinates collected in 2018-2019. We estimated the error associated  
221 with the conversion of Cartesian to GPS coordinates at a median of  $5.5 \pm (\text{SD}) 3.4\text{m}$  ( $n = 225$   
222 coordinates). Coordinates were collected for 74% of the emergences, 4351/5873. The missing  
223 emergence sites were before 1994 on Meadow A, 1999 on Meadow B, 2006 on Meadow C,

224 and 2012 on Meadow DOT. Emergence locations were also not recorded in 2000-2007 on  
225 MA. Thus, sample sizes varied among years.

### 226 *Age classification*

227 Because male Columbian ground squirrels emigrate, and new individuals occasionally  
228 leave and arrive on meadows, some individuals on the Meadows A, B, C, and DOT were not  
229 known from birth (19% of the cases overall, 455/2436). For these individuals, recorded age  
230 resulted from estimates of physical characteristics mainly distinguishing between yearlings, 2-  
231 year-old, and older individuals. To establish meaningful age bins in further analyses we  
232 conducted a preliminary analysis investigating how emergence date varied according to age  
233 using individuals of known age (n = 4681 observations, N = 1981 individuals). We ran a  
234 linear mixed effects model (LMM) of emergence date (dependent variable) as a function of  
235 age (independent categorical variable), specifying individual identity as a random factor in the  
236 model to account for repeated measures of individuals among years. Tukey HSD tests were  
237 applied for post-hoc comparisons. Emergence date of one-year-old individuals (ordinal date  $\pm$   
238 SE =  $126.5 \pm 0.3$  days) was significantly later than all other age categories (Tukey HSD,  $p <$   
239 0.001). For 2-year-old individuals, emergence ordinal date ( $121.7 \pm 0.3$  days) was  
240 significantly earlier than yearlings ( $p < 0.001$ ) but significantly later than older age categories  
241 ( $116.7 \pm 0.2$  days;  $p < 0.001$ ). No other significant differences were found among older age  
242 categories (all  $p > 0.05$ ). Thus, individuals aged 3 and older were combined in a unique age  
243 category ( $\geq 3$ -year-old) for subsequent analyses allowing us to use all existing ED data (n =  
244 5873 observations in total: N = 2436 individuals). Sample sizes per meadow, year and age  
245 and sex classes are provided in Appendix S1 (Table S1).

246 *Spatial clustering*

247       To evaluate spatial heterogeneity in emergence dates within a meadow, we  
248 investigated the spatial autocorrelation of emergence dates. Specifically, we examined  
249 whether correlation between emergence dates at two locations depended on the distance  
250 between them. To do so, we used variograms (Matheron 1963) that measured the value of the  
251 spatial variance at different distance intervals. For any two data points, we measured their  
252 spatial distance and estimated the variance in ED. The variance was then averaged over bins  
253 of distance intervals. Empirical variograms were based on all emergence locations, but with  
254 pairs of points considered only if points were in the same year and within the same meadow.  
255 We modelled variograms using a least square method (Rivoirard et al. 2008). The empirical  
256 variogram of emergence date exhibited spatial structure (i.e., increasing variance when the  
257 distance between sampling points increased before levelling off; see Appendix S1, Figure  
258 S1), meaning that the emergence dates were not random, such that spatially close locations  
259 had closer emergence dates than more distant locations. Based on the modelled variogram, we  
260 found that variance in emergence date stabilized at a range of about 40 m. Thus, hibernation  
261 emergence locations were grouped into spatially relevant clusters according to their GPS  
262 coordinates to understand whether individuals on some parts of the meadow emerged earlier  
263 than others.

264       We built clusters by grouping emergence locations according to an iterative algorithm  
265 (adapted from Woillez et al., 2007, see also Saraux et al., 2014). The algorithm started with  
266 each location as its own cluster. Each iteration of the algorithm then: (1) calculated the  
267 distances between the center of gravity of all clusters on the meadow; (2) merged the two  
268 closest clusters if the shortest distance among all cluster distances was below a threshold  
269 distance of 40 m (according to above variogram results). The process was reiterated until  
270 none of the distances between clusters were lower than 40 m. In total, we defined eleven,

271 eight, seven, and twelve clusters for Meadows A, B, C, and DOT respectively (named  
272 differently depending on the meadow), which corresponded to hotspots of ground squirrel  
273 emergences in the habitat (compared to zones where ground squirrels were rarely seen  
274 emerging). Emergence locations and built clusters were imported into QGIS (3.10.12 long-  
275 term released version, QGIS.org, QGIS Geographic Information System, 2021) and presented  
276 on a Google satellite map © 2021 (see Fig. 1.B).

## 277 **Microclimate data**

278 We calculated hourly microclimatic conditions using the Kearney et al. (2020)  
279 microclimate model, at a fine-scale resolution (5 x 5 m grid) for each meadow during the  
280 entire monitoring period (from 1992-2019). The modelling function (*micro\_ncep* from  
281 NicheMapR package, Kearney et al., 2020) downscales global atmospheric climate-forcing  
282 data (NCEP Reanalysis, historical data from the National Centre for Environmental  
283 Predictions, Kalnay et al., 1996, provided by the NOAA/OAR/ESRL PSL, Boulder, Colorado,  
284 USA, from their Web site at <https://psl.noaa.gov/>), using terrain-specific corrections,  
285 including spatial variations in slopes (from the Mapzen elevation and Mapzen terrain service,  
286 via ‘elevatr’ package in R; Hollister et al., 2020), soil composition and hydrological properties  
287 (acquired from the ‘SoilGrids’ database in R; Hengl et al., 2017), orientation, and hill shade.  
288 The microclimate model increases the quality and resolution of large-scale weather data, and  
289 has been empirically validated (Kearney, 2020; Lembrechts & Lenoir, 2020; Maclean, 2020;  
290 Saleeba et al., 2020). Because Columbian ground squirrels live in open grass meadows with  
291 adjacent trees (see Fig. 1), we estimated climatic variables without specifying shade due to  
292 vegetation cover.

293 Our model estimated snow depths (cm) on the ground as well as temperatures (°C),  
294 wind speed (m/s), and relative humidity (%) at 10 cm above ground (roughly the height of a

295 ground squirrel). In addition, we estimated temperature at various soil depths below ground  
296 (0, 2.5, 5, 25, 50, 75, 100, 125, 150, and 200 cm). Hibernating burrows are usually around 70  
297 cm in depth and rarely exceed 1 m (Young, 1990). Soil temperatures at various depths were  
298 highly correlated (see Appendix S1, Figure S2). Thus, we used 1-meter-deep temperatures as  
299 representative of hibernaculum conditions.

300         There was no reasonably close weather station with records of climate data for the  
301 entire study period (the closest one being 58 km away at lower altitude in the plains). In  
302 addition, weather stations record temperature and precipitation variables, at a standard height  
303 of 2 m, which is not representative of what a ground-squirrel might experience a few  
304 centimeters above ground. Thus, using the microclimate model enabled us to obtain climate  
305 data over the entire study period at a high resolution and at the height of the animal, and  
306 further allowed us to measure snow cover (see Appendix S1, Figure S3 for a validation of the  
307 microclimate model).

308         To estimate spatial and temporal variation of climate, we averaged the model-  
309 generated time series at two different spatial scales for each meadow: i) over the entire  
310 meadow and ii) separately within each cluster. Hourly data were averaged over 24-hour  
311 periods. Based on the average ordinal day of first hibernation emergence (older males) across  
312 all years (15 April  $\pm$  2 days) and previous studies showing that emergence occurs close to  
313 the beginning of August (Young 1990b, Neuhaus 2000), we further divided the year in two  
314 phases: the active season (15 April – 1 August), and the inactive (hibernation) season for the  
315 remainder of the year. This allowed us to test for possible effects of climate conditions during  
316 the winter and the previous summer on individual emergence dates. Besides air temperature  
317 ( $^{\circ}$ C), soil temperature at 1m depth ( $^{\circ}$ C), relative humidity (%), wind speed (m/s), and snow  
318 depth (cm), we considered two additional climate variables: first day of the calendar year  
319 without snow cover on the ground (over the entire meadow or within each given spatial

320 cluster, in ordinal date), and number of days with snow falls during the active period for  
321 investigation of late snowstorms on ED.

## 322 **Data analyses**

### 323 *Quantifying variance in emergence date*

#### 324 *Emergence date variance partitioning*

325 To identify how much variance in ground squirrel emergence dates (ordinal days) was  
326 explained by endogenous (sex, age category, individual ID), spatial (meadow, emergence  
327 cluster within the meadow), and temporal (year) factors, we used a linear mixed effects model  
328 (LMM) with all variables specified as random terms (with  $1/\text{variable}$ ):

$$329 \text{Emergence date} \sim (1/\text{sex}) + (1/\text{age}_{\text{category}}) + (1/\text{ID}) + (1/\text{meadow}/\text{cluster}) + (1/\text{year}) \text{ [1]}$$

330 This model allowed us to partition variance components between the different random terms;  
331 (1|meadow/cluster) representing both the effect of the meadow, and the effect of the cluster  
332 nested within the meadow.

#### 333 *Effects of sex and age on emergence date*

334 Because sex and different age (especially sexually mature versus immature  
335 individuals) classes face different reproductive constraints, we tested the effects of individual  
336 endogenous characteristics (sex and age specified as independent variables) on emergence  
337 date, while controlling for spatial and temporal effects (set as random terms):

$$338 \text{Emergence date} \sim \text{sex} + \text{age}_{\text{category}} + \text{sex} * \text{age}_{\text{category}} + (1/\text{ID}) + (1/\text{meadow}/\text{cluster}) + (1/\text{year})$$

339 [2]

340 *Spatio-temporal variation in emergence date*

341 *Spatial variation in emergence date*

342 Because of differences in slope and exposure at different meadows, we expected  
343 emergence dates to vary spatially. To test for spatial variation in emergence date, we assessed  
344 among and within meadow differences using separate LMMs. Differences were tested by  
345 specifying emergence date as the dependent variable, meadow (or cluster) as an independent  
346 variable, and year and the sex-age category (determined based on sex and age results) as  
347 random terms:

348  $Emergence\ date \sim meadow_{[MA\ vs.\ MB\ vs.\ MC\ vs.\ DOT]} + (1/year) + (1/sex-age_{category}) + (1/ID)$  [3]

349  $Emergence\ date \sim cluster + (1/year) + (1/sex-age_{category}) + (1/ID)$  [4] (one LMM per  
350 meadow)

351 *Temporal variation in emergence date*

352 Individuals might be phenotypically plastic, and time their ED to interannual  
353 variations, including directional changes in climate variables. We differentiate between  
354 interannual variation in ED and long-term directional changes in ED. Because emergence  
355 locations were not always known (especially in the early years, see above), we did not include  
356 spatial clusters in the following models [5] and [6], enabling us to study potential changes in  
357 time over a larger data set (e.g. starting in 1992 instead of 1999).

358 **Interannual variation in EDs**

359 To explore interannual variation in hibernation emergence dates, we built generalized  
360 additive mixed models (GAMMs) with emergence date as the response variable, and year as  
361 the independent variable. This facilitated identification of changes between years, and  
362 detection of nonlinear temporal variation. Because temporal trends could differ among  
363 meadows or according to the individual sex-age category, we considered interactions

364 (specified with “by =”) between the continuous variable (year) and these factors by  
365 constructing separate GAMMs, keeping individual ID as a random variable:

366  $Emergence\ date \sim s(year, by = meadow) + s(year, by = sex\text{-}age_{category}) + sex\text{-}age_{category} +$   
367  $meadow + (1/ID)$  [5]

### 368 **Long-term directional changes in ED**

369 In a context of climate change, most phenological studies showed advanced spring  
370 season (Walther et al. 2002, Cleland et al. 2007, Dingemanse and Kalkman 2008). Yet, in  
371 Columbian ground squirrels, females older than 3 displayed a delay in emergence over a 20-  
372 year period (Lane et al. 2012). To test whether this long-term directional pattern was  
373 consistent over the 4 populations and over other sex/age categories, we ran the previous  
374 model (model [5]) as a LMM, and assessed interactions between continuous (year) and  
375 categorical (meadow or sex-age<sub>category</sub>) variables:

376  $Emergence\ date \sim year + sex\text{-}age_{category} + meadow + year*meadow + year*sex\text{-}age_{category} +$   
377  $(1/ID)$  [6]

### 378 *Spatio-temporal variation in climate*

#### 379 *Spatial variation in climate variables*

380 To investigate microclimates, we assessed correlations among the 11 previously  
381 defined climate variables (air temperature during the active and inactive period, soil  
382 temperature at 1m depth during the active and inactive period, relative humidity during the  
383 active and inactive period, wind speed during the active and inactive period, snow depth  
384 during inactive period, first day of calendar year without snow and number of days with snow  
385 during the active period), using a Principal Component Analysis (PCA) on data averaged by  
386 year and by cluster on each meadow. The objective was to identify principal variations related  
387 to spatial variables (clusters and meadows) given the large amount of climate data at a micro-

388 scale within the meadows. Spatial differences in climate were analyzed from resulting  
389 components (PCs), through LMs at two different scales:

390  $PCs \sim meadow$  [7]

391  $PCs \sim cluster$  [8]

392 Using our results (see below), only climate variables expected to affect emergence  
393 date were kept for subsequent analyses. These included (1) snow depth ( $depth_{snow}$ ) and soil  
394 temperature ( $temp_{soil}$ ) at a 1-meter depth during hibernation (inactive phase), and (2) air  
395 temperature ( $temp_{air}$ ), relative humidity and wind speed during the previous summer (active  
396 phase), in addition to the ordinal date of spring snowmelt ( $day_{snowmelt}$ ) and the number of days  
397 with snow during the active period ( $days_{snow}$ ).

398 *Temporal variation in climate variables*

399 Because interannual variability in climate often result from different processes: trend  
400 in climate (e.g., due to climate change), cyclic effects (e.g., El-Niño) and random year-to-year  
401 variation, we decided to use a 2-step approach. First, we focused on short-term variation using  
402 GAMs. Then we looked for directional trend in ED (as expected as a result of climate change)  
403 using LMs.

#### 404 **Climate variation**

405 To explore how climate varied, we ran GAMs for each climate variable as a function  
406 of year. This allowed identification of changes between years, and detection of nonlinear  
407 temporal variation. Because the interannual variability of climate could differ among  
408 meadows (or among clusters), we also considered interactions of years with these factors in  
409 the following GAMs:

410  $Climate\ variable \sim s(year, by = meadow) + meadow$  [9]

411  $Climate\ variable \sim s(year, by = cluster) + cluster$  [10] (one GAM per meadow)

412 **Climate change**

413 To test for long-term directional climate changes over 28 years, we ran the previous  
414 GAMs [9] & [10] as LMs [11] & [12], with each climate variable as a dependent variable and  
415 the year, meadow (or cluster) and their interaction as independent variables:

416 *Climate variable ~ year\*meadow + meadow* [11]

417 *Climate variable ~ year\*cluster + cluster* [12] (one LM per meadow)

418 *Climate – emergence date relationships*

419 We tested how climate might affect emergence date through two processes: energy  
420 expenditure and carry-over effects of energy stored before hibernation. Because Columbian  
421 ground squirrels start breeding at 2-years-old, the emergence date of  $\geq 2$ -year-old individuals  
422 may vary with climate differently between males and females. Thus, we considered five sex-  
423 age categories for these analyses: yearlings, 2-year-old females, 2-year-old males,  $\geq 3$ -year-  
424 old females, and  $\geq 3$ -year-old males.

425 *Mean relationships between climate and emergence date*

426 To test for overall relationships between microclimates and hibernation emergence  
427 dates, emergence dates were averaged by year, meadow, and sex-age category. We built  
428 separate LMMs for the different age-sex categories, with emergence date as the dependent  
429 variable and climate variables (averaged by meadow and year) as independent variables:

430 *Emergence date ~ depthsnow\_winter + tempsoil\_winter + tempair\_active n-1 +*

431 *humidityactive n-1 + windactive n-1 + daysnowmelt + daysnow\_active + (1/Year) +*

432 *(1/Meadow)* [13] (one LMM per age-sex category)

433 Individual responses in emergence date might differ due to different constraints  
434 between spatial heterogeneity (related to spatial living locations) and temporal heterogeneity  
435 (plasticity that matches interannual variation). To distinguish between temporal vs. spatial

436 effects of climate on hibernation emergence dates, we ran two further analyses, building  
437 separate models for different sex-age categories.

438 *Year-centered approach: are spatial differences in ED related to spatial variation in climate?*

439 To investigate spatial effects of climate variables on emergence date, we removed all  
440 temporal variation by centering emergence date and climate variables by year and sex-age  
441 category (mean of the years and category subtracted to each observation). During the active  
442 season, ground squirrels might visit most locations on the meadow in a single day. Because  
443 spatial clusters were defined from hibernation emergence locations and not the total active  
444 range of individuals, we included in the model only climate variables considered during  
445 hibernation (inactive phase). For each individual emergence date, we associated the climatic  
446 conditions of the given winter averaged over the spatial cluster in which the individual  
447 emerged. Thus, the linear mixed model was:

448  $Emergence\ date \sim depth_{snow\_winter} + temp_{soil\_winter} + day_{snowmelt} + day_{snow\_active} + (1|cluster) +$   
449  $(1|ID)$  [14]

450 *Spatial-centered approach: are interannual differences in ED related to interannual variation*  
451 *in climate?*

452 To investigate temporal effects of climate variables on emergence date, we centered  
453 emergence date and all climate variables (including those considered during the active phase)  
454 by cluster and sex-age category. This way, spatial variations in climate were entirely removed  
455 from the data, and we tested whether yearly differences in climate could explain differences in  
456 emergence date among years.

457  $Emergence\ date \sim depth_{snow\_winter} + temp_{soil\_winter} + temp_{air\_activen-1} + humidity_{activen-1} +$   
458  $wind_{activen-1} + day_{snowmelt} + day_{snow\_active} + (1|year) + (1|ID)$  [15]

460 Statistical analyses were done in R v 4.0.3 (R Core Team, 2019). All tests were  
461 conducted with a probability error threshold of 5%. Results presented are means  $\pm$  SE, along  
462 with the number of observations (n) and the number of individuals (N). Where appropriate  
463 (i.e. for LMMs and LMs), we ensured model residuals were normally distributed by visual  
464 inspection of density distributions, Q-Q plots, cumulative distribution functions, and P-P plots  
465 using the “fitdistrplus” package in R (Delignette-Muller and Dutang 2015). When the  
466 assumptions of a normal distribution of residuals were not met, we applied a Box-Cox  
467 transformation (from MASS R package, Box & Cox, 1964) to the data (monotonous  
468 transformation), or removed extreme values from the data (i.e., emergence dates later than the  
469 22<sup>nd</sup> of May for which we likely missed the actual emergence date, representing 2.7%  
470 (116/4351) of observations). Results with and without transformation or extreme values  
471 yielded similar results, and we present results obtained from complete and untransformed data  
472 sets for clarity (exceptions are specified in the results). Post-hoc multiple comparisons were  
473 run to compare all factor levels of categorical variables, using the Least Square Means (LSM)  
474 test, to account for multiple testing (Lenth 2016). GAM(M)s were run using the ‘gam’ and  
475 ‘gamm’ function in R (‘mgcv’ package, Wood, 2017). Principal Component Analysis was run  
476 using the ‘PCA’ function, and components accounting for a meaningful amount of variance  
477 (i.e. from 75%, O’Rourke & Hatcher, 2013) were then considered in the models [7] and [8]  
478 (‘FactoMineR’ package, Lê et al., 2008). Whenever interaction effects between independent  
479 variables were included in LMs and LMMs, we compared the models with and without the  
480 interactions, and chose the final model according to Akaike’s Information Criterion (AIC)  
481 (lowest AIC and for  $\Delta$ AIC < 2, we chose the most parsimonious model, Burnham &  
482 Anderson, 2004). However, we also analyzed meadows separately to assess difference in  
483 trends between populations. The results on the link between climate and emergence date are

484 presented from the full models (i.e. with all tested variables included). Multicollinearity was  
485 checked and when variables were collinear, the one with the highest variance inflation factor  
486 (VIF) was removed, meaning that only variables with variance inflation factors below three  
487 remained in the models (Zuur et al. 2010). Finally, to allow comparisons of effect sizes in the  
488 last models [13], [14], and [15], we standardized (by subtracting the mean and dividing by the  
489 standard deviation) all explanatory climate factors.

## 490 RESULTS

### 491 *Quantifying variance in emergence date*

#### 492 *Emergence date variance partitioning*

493 Across all individuals, meadows, and years, mean emergence date from hibernation  
494 was 2 May  $\pm$  4 days (ordinal date 122  $\pm$  4) and ranged from 6 April to the 30 May (ordinal  
495 date 96-150). The model [1] with age, sex, meadow, cluster within meadow, year, and  
496 individual as random effects explained 65.7% of the total variance in emergence date (LMM,  
497 n = 4351 data points). Variables contributing most were age (26.3%), year (16.1%), and  
498 individual identity (14.6%). Within-meadow cluster, sex, and meadow explained fairly trivial  
499 amounts of variation, 3.9%, 3.1%, and 1.7% of the variance in ED, respectively.

#### 500 *Effects of sex and age on emergence date*

501 Age, sex, and their interaction, were all retained in the best model explaining  
502 emergence date (LMM [2], n = 4351, N = 1950 individuals, 26 years). We found differences  
503 in emergence date between males and females only in individuals  $\geq$ 3 years old, with males  
504 emerging around 7.3  $\pm$  0.4 days earlier than females (post-hoc LSM, z = -18.3, p < 0.001).  
505 Post-hoc comparisons revealed significant differences in emergence dates between four  
506 categories: yearlings, 2-year-old individuals,  $\geq$ 3-year-old females and  $\geq$ 3-year-old males  
507 (LSM, all p < 0.001). On average, older males ( $\geq$ 3-year-old) emerged first around 21 April

508 (111.2 ± 0.2 days), followed by older females (≥3-year-old) around 28 April (118.5 ± 0.2  
509 days), 2-year-old individuals around 2 May (121.8 ± 0.3 days), and finally one-year old  
510 individuals around 6 May (125.5 ± 0.2 days).

#### 511 *Spatio-temporal variation in emergence date*

##### 512 *Spatial variation in emergence date*

513 Analyses on spatial differences in hibernation emergence dates showed that  
514 individuals on Meadow DOT emerged 2.2 ± 0.5 days and 1.8 ± 0.4 days earlier than  
515 individuals on Meadow C and Meadow B, respectively. Meadow C and Meadow B  
516 individuals emerged 3.3 ± 0.4 days and 3.6 ± 0.3 days earlier than Meadow A individuals  
517 (LMM [3], post-hoc LSM: all  $p < 0.001$ ,  $n = 5873$ ,  $N = 2436$  individuals, 28 years). Similarly,  
518 within-meadow differences in emergence dates were found between different clusters (see  
519 cluster colors on Fig. 1.B). As an example, on Meadow B, individuals in “bottom-west”  
520 cluster emerged between 1.9 ± 0.5 and 8.8 ± 2.5 days earlier than individuals from other  
521 clusters (LMM [4], post-hoc LSM:  $p < 0.001$ ,  $n = 1315$ ,  $N = 579$  individuals, 21 years). In  
522 contrast, individuals from the “top” cluster emerged between 4.6 ± 0.9 and 8.1 ± 0.8 days  
523 after individuals from other clusters (post-hoc LSM:  $p < 0.001$ ,  $n = 1315$ ,  $N = 579$   
524 individuals, 21 years) (see Fig. 1.B and Appendix S1, Table S2).

##### 525 *Temporal variation in emergence date*

#### 526 **Interannual variability in ED**

527 Emergence date exhibited marked interannual variations over the course of the study  
528 on all meadows and for each age-sex category (GAMMs [5]; 2.09 < edf < 8.73, 3.43 < F <  
529 31.61,  $p < 0.001$ , Fig. 2), except for older males (≥3-year-old) on Meadow B and C ( $p =$   
530 0.158 and  $p = 0.652$ , respectively). Cyclic patterns over time were observed with a period  
531 varying from 6-10 years, depending on the period or the meadow considered. Older males

532 ( $\geq 3$ -year-old) showed less variation in emergence date over time on Meadow A than on  
533 Meadow DOT. Emergence date of yearlings and older females on Meadow A was especially  
534 delayed between 1995-97 as compared to 1999, as well as in 2011 compared to 2014-17. On  
535 Meadow B, yearlings' and  $\geq 3$ -year-old females' emergence date exhibited shorter  
536 fluctuations at the start of the monitoring period (1992-2002) than in recent years (2005-  
537 2019). Emergence date appeared to be delayed from 2005 to 2009, then advanced from 2009-  
538 2016, and delayed again from 2016-2019. On Meadow DOT, emergence date for yearlings  
539 and older individuals showed lower variation than on other meadows, with fluctuations of  
540 smaller amplitude. Meadow C individuals exhibited the greatest variation during the most  
541 recent years, emergence dates being advanced between 2013 and 2015 and delayed between  
542 2016 and 2018. In general, the emergence date of 2-year-old individuals showed slightly  
543 lower fluctuations and a more stable pattern. On all meadows, individual emergence dates  
544 appeared to be earlier in 2015 and 2016 when compared with other years. Whereas the  
545 emergence date of Meadow A and Meadow B individuals was later in 2010 than other years,  
546 it was earlier on Meadow C and Meadow DOT.

#### 547 **Long-term directional changes in ED**

548       When testing for long-term directional linear changes in emergence dates, the  
549 interaction between year and meadow was retained in the best model (LMM [6],  $\Delta AIC = 35$ ,  
550  $n = 5873$ ,  $N = 2436$  individuals). On Meadow DOT, emergence dates of individuals did not  
551 significantly change in a directional manner through time for any of the sex-age categories  
552 (LMM, interaction year\*sex-age not retained,  $\Delta AIC = 5$ ,  $t = 1.094$ ,  $p = 0.274$ ,  $n = 1303$   
553 observations,  $N = 503$  individuals) (see Appendix S1, Figure S4). On Meadow C, regardless  
554 of sex and age (interaction year\*sex-age not retained,  $\Delta AIC = 2$ ), emergence from hibernation  
555 was significantly delayed over time, averaging a 4-day later emergence over an 18-year  
556 period (LMM,  $+0.22 \pm 0.06$  day/year,  $t = 3.769$ ,  $p = 0.001$ ,  $n = 704$  observations,  $N = 385$

557 individuals). On other meadows, temporal trends differed according to the sex-age category  
558 ( $\Delta AIC = 17$  and  $22$  for meadow A and B, respectively). On Meadow A, over a 22-year  
559 period, emergence was advanced by 2 days for 2-year-olds (LM,  $-0.11 \pm 0.05$  day/year,  $t = -$   
560  $2.290$ ,  $p = 0.023$ ,  $n = 399$  observations,  $N = 399$  individuals), delayed by 3 days for  $\geq 3$ -year-  
561 old individuals (LMMs,  $\geq 3$ -year-old Females:  $+0.14 \pm 0.04$  day/year,  $t = 3.254$ ,  $p = 0.001$ ,  $n$   
562  $= 767$  observations,  $N = 290$  individuals;  $\geq 3$ -year-old Males:  $+0.13 \pm 0.04$  day/year,  $t =$   
563  $3.058$ ,  $p = 0.003$ ,  $n = 368$  observations,  $N = 155$  individuals) and stable in yearlings (LM:  $p =$   
564  $0.053$ ,  $t = -1.936$ ,  $n = 625$  observations,  $N = 625$  individuals). On Meadow B, the hibernation  
565 emergence of yearlings, 2-year-old individuals and  $\geq 3$ -year-old females was delayed by 11, 7  
566 and 5 days, respectively over 28 years (LMs; yearlings:  $+0.40 \pm 0.04$  day/year,  $t = 9.110$ ,  $p <$   
567  $0.001$ ,  $n = 631$  observations,  $N = 631$  individuals; 2-year-old:  $+0.26 \pm 0.06$  day/year,  $t =$   
568  $4.678$ ,  $p < 0.001$ ,  $n = 318$  observations,  $N = 318$  individuals; LMM:  $\geq 3$ -year-old Females:  
569  $+0.17 \pm 0.05$  day/year,  $t = 3.455$ ,  $p < 0.001$ ,  $n = 531$  observations,  $N = 164$  individuals),  
570 whereas the emergence date of  $\geq 3$ -year-old males did not significantly change through time  
571 (LMM;  $p = 0.379$ ,  $n = 227$ ,  $N = 83$ ).

## 572 *Spatio-temporal variation in climate*

### 573 *Spatial variation in climate variables*

574 The three most influential components of the PCA explained 78.3% of the variance in  
575 climate variables and each generated an eigenvalue higher than one. The first component  
576 (PC1), explaining 39.4% of the variance, primarily reflected air and soil temperature during  
577 the summer (active period), soil temperature during the winter (inactive period), and  
578 negatively correlated to wind speed and humidity during the summer (see Fig. 3 and  
579 Appendix S1, Table S3). Winter air temperature and humidity were positively correlated with  
580 the second component (PC2, explaining 24.5% of the variance), whereas snow depth during  
581 winter negatively loaded on PC2. The third component (PC3, explaining 14.4% of the

582 variance), was mainly related to wind speed during the winter. The three principal  
583 components varied depending on the meadow (LMs [7],  $p < 0.001$ ), and depending on the  
584 cluster (LMs [8],  $p < 0.001$ , see Appendix S1, Figure S5).

585 As presented on Fig. 3.B and 3.D, clusters on Meadow A were between 9.9% and  
586 29.2% windier during the inactive period, between 16.3% and 26.4% windier during active  
587 periods, and between 0.6% and 2.7% more humid during the active period than clusters from  
588 other meadows. Conversely, soil temperatures of clusters on Meadow B were higher, during  
589 both winter (between 1.7% and 4.5%) and summer (between 2.4% and 6.6%), and the air  
590 during summer was between 1.4% and 4.3% warmer than on other meadows. Despite those  
591 general patterns, within-meadow variability was also quite high among clusters, especially on  
592 Meadow B, which displayed both very positive and negative PCs clusters (Fig. 3 B & D and  
593 Appendix S1, Figure S5).

#### 594 *Temporal variation in climate variables*

#### 595 **Climate variation**

596 As predicted, all climate variables exhibited temporal variability (GAMs [9] and [10];  
597  $6.51 < \text{edf} < 8.78$ ,  $2.79 < F < 15.33$ , all  $p < 0.01$ , Fig. 4). Interannual variation in these  
598 variables was similar among meadows (no year\*meadow interactions retained,  $N = 28$  years),  
599 although the absolute values in wind speed and relative humidity varied across meadows. This  
600 confirmed previous results that Meadow A was the windiest and most humid meadow, while  
601 Meadow B was the least humid and windy, Meadows C and DOT being intermediate.  
602 Summer air temperature exhibited particularly high interannual variation, increasing and  
603 decreasing from 1 to 4°C from one year to the next (e. g. between 1997 and 1998), fluctuating  
604 on average between 7-13°C. During 2006-2007, air temperature was particularly high, and  
605 much warmer than the next four years. Conversely, the relative humidity during summer was  
606 particularly low in 2006-2007 compared to the next four years, staying relatively stable over

607 the rest of the study period. Wind speed during the active period showed regular cycles  
608 oscillating between 0.8-1.2 m/s every five years. During the inactive period, soil temperature  
609 varied between 2-5 °C within approximately five-year periods. Winter snow depth showed  
610 interannual variation as well, with especially low values in 2018 and 2019. Similarly, the  
611 ordinal day of snowmelt varied between mid-February and 10 April, depending on the year.  
612 Number of days with snow during the active period contrasted between years of no late  
613 snowstorms (1992-1995, 1997-1998, 2004-2006, 2012, 2015-2016) and years of late snow  
614 falls (between 2000-2003, and between 2008-2013).

### 615 **Climate change**

616 Temporal trends in climate did not differ between meadows (LMs: no year\*meadow  
617 interactions retained, N = 28 years, see Appendix S1, Figure S6). Over 28 years, air  
618 temperature increased by 1.40°C during the active season (LM [11], Active:  $0.05 \pm$   
619  $0.01^\circ\text{C}/\text{year}$ ,  $t = 3.510$ ,  $p < 0.001$ ). Winter (inactive period) soil temperature at a 1-m depth  
620 increased at a slower rate of  $0.03 \pm 0.01^\circ\text{C}/\text{year}$  (i.e. 0.84°C over 28 years, LM,  $t = 5.642$ ,  $p <$   
621  $0.001$ ). Conversely, the snow depth during the inactive period (winter) decreased by  $-0.13 \pm$   
622  $0.06$  cm per year, or 3.64 cm over the 28 years of study. During the active period, relative  
623 humidity increased by  $0.08 \pm 0.03$  % points per year (LM,  $t = 2.818$ ,  $p = 0.006$ ). Moreover,  
624 the first ordinal day of complete snowmelt increased through time (delay of 13 days within 28  
625 years, i.e.  $0.45 \pm 0.18$  day/year, LM,  $t = 2.509$ ,  $p = 0.014$ ). The only climatic variable that  
626 appeared to remain relatively invariant over the study period were wind speed and the number  
627 of snow days during the active period (LMs, wind:  $t = 0.070$ ,  $p = 0.944$ , nbdays:  $t = 0.207$ ,  $p =$   
628  $0.836$ ). In summary, the climate tended to be warmer, more humid and with a smaller snow  
629 cover during winter. Yet, this snow cover disappeared later in the spring.

630 *Climate – emergence date relationships*

631 *Mean relationships between climate and emergence date*

632         Among the different climate variables considered during winter (inactive phase) or the  
633 previous summer (active phase), only the air temperature during previous summer had a VIF  
634 greater than three (between 5.244 and 5.460 according to the sex-age category considered)  
635 and was removed from the model (probably due to its high correlation with soil temperature;  
636 see Appendix S1, Figure S7). The ordinal day of snowmelt and wind during summer were  
637 positively related with annual mean emergence date (Fig. 5). Emergence dates were delayed  
638 with a delay in the first day of snow melt for all individual categories, apart from 2-year-old  
639 individuals (LMMs [13], yearlings:  $t = 2.211$ ,  $p = 0.036$ ,  $n = 84$  observations, 2-year-old  
640 females:  $t = 1.713$ ,  $p = 0.099$ ,  $n = 82$  observations, 2-year-old males:  $t = 0.424$ ,  $p = 0.676$ ,  $n =$   
641  $77$  observations,  $\geq 3$ -year-old females:  $t = 2.994$ ,  $p = 0.007$ ,  $n = 83$  observations,  $\geq 3$ -year-old  
642 males:  $t = 3.958$ ,  $p < 0.001$ ,  $n = 83$  observations). Ground squirrels therefore emerged earlier  
643 when (or/and where) snow melted earlier; emergence date being delayed by approximately  
644 0.25 day for a day of delayed snowmelt. Similarly, the summers with higher wind speed  
645 correlated with later emergences, but only for older females ( $\geq 3$ -year-old, LMM,  $t = 2.230$ ,  $p$   
646  $= 0.037$ ,  $n = 83$  observations). Indeed, older females emerged around 13 days later per 1 m/s  
647 increase in wind speed.

648 *Year-centered approach: are spatial differences in ED related to spatial variation in climate?*

649         Once centered per year, no strong correlations were highlighted between climate  
650 variables, and we included all four of them in the model (VIFs  $< 1.308$ , see Appendix S1,  
651 Figure S8). Day of snowmelt was related positively to emergence date, but only in yearlings  
652 and older ( $\geq 3$ -year-old) females; individuals emerged later when they emerged from locations  
653 where snow melted later (Fig. 6; ED around 0.2 day later for a day of delayed snowmelt, ED  
654 and climate variables centered by year, LMMs [14], yearlings:  $t = 2.253$ ,  $p = 0.024$ ,  $n = 1450$

655 observations,  $N = 1450$  individuals,  $\geq 3$ -year-old females:  $t = 2.389$ ,  $p = 0.017$ ,  $n = 1392$   
656 observations,  $N = 559$  individuals). Males of 2-year-old and  $\geq 3$ -year-old seemed to emerge  
657 around 2 days later in locations where the snow depth was 1cm higher during hibernation  
658 (LMMs, 2-year-old males:  $t = 2.303$ ,  $p = 0.023$ ,  $n = 280$  observations,  $N = 280$  individuals,  
659  $\geq 3$ -year-old males:  $t = 2.085$ ,  $p = 0.039$ ,  $n = 693$  observations,  $N = 300$  individuals, effect  
660 only marginally significant after transforming the data, Box-Cox transformation,  $p = 0.058$ ).  
661 Soil temperature during winter tended to have an effect on the emergence date of yearlings  
662 and older males, with individuals emerging earlier from warmer hibernacula (Fig. 6, LMMs,  
663 yearlings:  $t = -1.625$ ,  $p = 0.105$ ,  $n = 1450$  observations,  $N = 1450$  individuals,  $\geq 3$ -year-old  
664 males:  $t = -1.498$ ,  $p = 0.137$ ,  $n = 693$  observations,  $N = 300$  individuals).

665 *Spatial-centered approach: are interannual differences in ED related to interannual variation*  
666 *in climate?*

667 When conducting the analysis, air temperature during the previous summer had a VIF  
668 greater than three (between 4.154 and 5.249) and was removed from the model (probably due  
669 to its high positive correlation with soil temperature, see Appendix S1, Figure S9). Regarding  
670 temporal effects of climate on emergence date, the ordinal day of snow melt was positively  
671 correlated to emergence date for all individuals excepting 2-year-old males (emergence dates  
672 and climate variables centered by cluster, LMMs [15], yearlings:  $t = 3.015$ ,  $p = 0.003$ ,  $n =$   
673  $1450$  observations,  $N = 1450$  individuals; 2-year-old females:  $t = 2.821$ ,  $p = 0.006$ ,  $n = 525$   
674 observations,  $N = 525$  individuals; 2-year-old males:  $t = 1.275$ ,  $p = 0.211$ ,  $n = 280$   
675 observations,  $N = 280$  individuals;  $\geq 3$ -year-old females:  $t = 3.246$ ,  $p = 0.002$ ,  $n = 1392$   
676 observations,  $N = 559$  individuals;  $\geq 3$ -year-old males:  $t = 3.610$ ,  $p < 0.001$ ,  $n = 693$   
677 observations,  $N = 300$  individuals). Thus, individuals emerged later in years when snow  
678 melted later (around 0.1 day later for a day of delayed of snowmelt, see Fig. 7). Similarly,  
679 active periods with high wind speed correlated positively with delayed emergence dates of

680 older individuals the next year (between 13 and 17 days delay per m/s increase, LMMs,  $\geq 3$ -  
681 year-old females:  $t = 3.357$ ,  $p = 0.001$ ,  $n = 1392$  observations,  $N = 559$  individuals;  $\geq 3$ -year-  
682 old males:  $t = 2.803$ ,  $p = 0.006$ ,  $n = 693$  observations,  $N = 300$  individuals). Earlier emergence  
683 date of 2-year-old males correlated with higher summer humidity (LMMs, 2-year-old males:  $t$   
684  $= -2.197$ ,  $p = 0.036$ ,  $n = 280$  observations,  $N = 280$  individuals), although this effect was only  
685 marginally significant after transforming the data (Box-Cox transformation,  $p = 0.054$ ). Depth  
686 of snow during winter may have a positive effect on the ED of older individuals, and the  
687 emergence date of 2-year-old males seems to be negatively associated with the hibernation  
688 soil temperature (ED around 3 days earlier per degree increase of soil temperature at one-  
689 meter depth).

## 690 DISCUSSION

691 Consistent with previous studies (Dobson et al., 1992; Murie & Harris, 1982), ground  
692 squirrel age and sex accounted for a substantial amount of variation (29.4%) in ED. Older  
693 males emerged first from hibernation, followed by older females, 2-year-old individuals, and  
694 finally yearlings. Individual identity had a significant effect in the overall pattern of  
695 emergence date. This is consistent with previous knowledge on the heritability of emergence  
696 date of Columbian ground squirrels ( $h^2 = 0.22$  in females and  $0.34$  in males, Lane et al. 2011).  
697 The magnitude of the individual effect (14.6% of variance) was similar to the temporal  
698 variance in ED (16.1% of variance), in spite of the strong individual plasticity in ED from  
699 year to year (Lane et al. 2012). These results confirm the importance of including among-  
700 individuals heterogeneity in understanding population dynamics (Hamel et al. 2018).

701 ED varied over space and time (21.7% of variance), suggesting that this trait is plastic  
702 and capable of responding to climate variation (see also Dobson, 1988; Dobson & Kjelgaard,  
703 1985; Lane et al., 2019). Also, separating the temporal and spatial effects of climate on the

704 emergence, either by centering by cluster or by year, enabled us to compare different  
705 mechanisms. Indeed, philopatric individuals (such as adult Columbian ground squirrels) are  
706 adapted to the environmental conditions in which they live. Oppositely, interannual variations  
707 in climate are more stochastic and might trigger plastic responses of animals. Whereas the  
708 years effects (16.1% of variance) are consistent with previous observations that ED was  
709 delayed through time in some populations (Lane et al., 2012; Neuhaus et al., 1999), our  
710 results importantly show that part of the variance (5.6%) in ED was also explained by spatial  
711 variation both within and among meadows. Such spatial heterogeneities were unlikely  
712 explained by variations in altitude (Dobson et al. 1992), since the four study populations are  
713 less than 70-m apart in terms of elevation. Interestingly, the variation in ED among  
714 individuals from different locations was even higher within than among meadows, ground  
715 squirrels from some parts of the meadows emerging earlier than others. This suggests that  
716 local heterogeneities occur at a micro-scale (~40 m; see Results) rather than meso-scale (1-10  
717 km). These results add to the growing literature showing that several animal and plant species  
718 are more sensitive to microscale than wider environmental variations (Lampe et al. 2019,  
719 Lundblad and Conway 2021, Wang and Hou 2021). Concurrently, spatial microclimate  
720 differences were found between clusters, suggesting a potential link between ED and local  
721 habitat conditions.

## 722 **Emergence date relationship to climate**

723 Our analyses of microclimate effects on ED focused on two distinct temporal phases:  
724 the climate conditions during the previous summer (active period) and those during  
725 hibernation (inactive period). First, our results showed the importance of carry-over effects of  
726 the period preceding hibernation on ground squirrel emergence dates the subsequent year. In  
727 particular, we found that delayed emergence occurred in older individuals when the preceding  
728 summer was windier and associated with lower humidity (see Appendix S1, Figure S9 for

729 temporal correlations between climate variables). Carry-over climatic effects on animal  
730 phenology have mainly been documented in birds (Finch et al., 2014; but see Ockendon et al.,  
731 2013), fish (Wilson et al. 2021), and insects (Dingemanse and Kalkman 2008, McCauley et  
732 al. 2018). Yet, carry-over effects are widespread, including in mammals, and are thought to be  
733 primarily mediated through macronutrient supply (reviewed by Harrison et al. 2011). Climate  
734 directly affects food availability/quality or/and foraging patterns (Levy et al., 2016), which  
735 may have direct consequences on individual mass gain before hibernation. In particular,  
736 strong wind conditions may have decreased the time spent foraging for ground squirrels  
737 (Fairbanks and Dobson 2007), while low humidity associated with decreased precipitation  
738 may have resulted in reduced primary productivity and inadequate forage quantity/quality,  
739 also affecting the accumulation of fat stores (Dobson and Kjelgaard 1985, Neuhaus et al.  
740 1999, Dobson et al. 2016). In turn, lower fat stores might have resulted in longer hibernation  
741 to avoid emerging when resources were scarce, explaining tardier emergence dates. Whereas  
742 our study suggests climatic carry-over effects on phenology, such effects are largely  
743 understudied, and yet likely widespread. For instance carry-over effects of food availability  
744 on the relationship between temperature and hibernation emergence were shown in edible  
745 dormice (Fietz et al., 2020).

746         Similarly, climate conditions during hibernation had marked effects on the timing of  
747 emergence of ground squirrels, either by affecting the quality of hibernation and animal  
748 energy expenditure, or acting as cues indicating the end of the winter period. Years with later  
749 snow melt resulted in later emergences for one-year-old individuals, 2-year-old females, and  
750  $\geq 3$ -year-old individuals. Similarly, spatial clusters where snow melted later resulted in  
751 yearlings and  $\geq 3$ -year-old females emerging later than in other areas. This was true both at  
752 the spatial and temporal scales, and for almost all individual categories, suggesting the  
753 necessity for snow to melt and uncover growing vegetation resources before ground squirrels

754 emerge. In addition, a melting and wet snow pack makes it hard for the animals to easily  
755 move around the meadow (VAV, FSD, PN; personal observations) and likely increases the  
756 costs of thermoregulation, increasing overall energy expenditure at a time where their  
757 remaining fat stores are likely depleted. Local climate may thus act as a strong cue on the  
758 timing of ground squirrel emergence, though the question of the immediate mechanism that  
759 stimulates emergence remains for future research.

760         We found a positive spatial correlation between snow depth and emergence of 2-year-  
761 old and  $\geq 3$ -year-old males, suggesting that males of 2-year-old and older emerged later in  
762 locations where snow depth was higher during the inactive period. Higher snowpack or  
763 delayed snowmelt during the inactive period may also insulate and stabilize soil temperatures  
764 and hibernation conditions, decreasing fat reserve consumption, and thus allowing a longer  
765 hibernation or emergence in better condition (the latter important for reproduction; Rubach et  
766 al., 2016). Snowpack thickness is an important variable influencing hibernating species, such  
767 as alpine marmots (Canale et al. 2016), hoary marmots (Patil et al. 2013), or northern Idaho  
768 ground squirrels (Goldberg and Conway 2021). A negative correlation between the soil  
769 temperature during inactive period (at one-meter depth) and the emergence date of yearlings  
770 and  $\geq 3$ -year-old males also seemed to apply. As for northern Idaho ground squirrels  
771 (Goldberg and Conway 2021), this result possibly indicates that unfavorable hibernating  
772 conditions lead to earlier emergence. For example, elevated soil temperatures prevent animals  
773 from lowering their body temperature sufficiently for efficient energy conservation during  
774 hibernation. In short, fat-storing and hibernating species might be sensitive to local  
775 environmental conditions and especially elevated temperatures, which are directly influencing  
776 energy expenditure during this period of fast.

777         Climatic variables correlating with ED differed between sex-age categories.  
778 Explanations for such diverging responses may be both ecological and physiological. Young

779 (1990a) reported the existence of long post-hibernation euthermic phases only in adult males,  
780 remaining several days underground before emerging despite favorable aboveground  
781 conditions, possibly to allow for gonadal maturation (Williams et al. 2017). Physiological and  
782 phenological differences in sex and age categories might therefore reflect distinct constraints  
783 between reproductively mature individuals and non-mature individuals. Yearlings and 2-year-  
784 olds that emerge later in the spring likely do so when resources become more abundant and  
785 perhaps to avoid predator exposure or the social aggression related to reproduction (Murie  
786 and Harris 1982, Constant et al. 2020). By contrast, mature individuals may optimize their  
787 emergence date according to the trade-off between energy resources (remaining fat stores,  
788 food availability) and the advantages of an early reproduction (Neuhaus 2000). Furthermore,  
789 reproductive strategies might differ between males and females, with males taking advantage  
790 of earlier hibernation emergence to seek more breeding opportunities (Richardson's ground  
791 squirrels, Michener, 1983) and establish their territories (Manno and Dobson 2008). Thus,  
792 environmental influence on a population might differ importantly between individuals with  
793 different life history constraints (*e.g.* age classes; Bonamour et al., 2020; Pardo et al., 2013).

#### 794 **Long-term changes in climate in relationship to emergence date**

795 Previous studies have reported shifts in animal phenology linked to changes in  
796 climate, species especially responding to temperature (more so at high latitudes) and  
797 precipitations (Cohen et al. 2018). In the context of climate change, advancements in spring  
798 phenology have been found in the vast majority of cases (Parmesan & Yohe, 2003; but see  
799 Radchuk et al., 2019). However, in studying long-term effects of climate change on animal  
800 phenology, mammals are poorly represented (Parmesan & Yohe, 2003; but see Radchuk et  
801 al. 2019). Among those studied, *Marmotini* species appear to respond differently to  
802 directional changes in climate. The phenology of Uinta ground squirrels did not change over  
803 time, despite a locally changing climate (Falvo et al. 2019). Yellow-bellied marmot have been

804 found to emerge earlier in response to warming air temperatures (Inouye et al. 2000), while  
805 Columbian ground squirrels had been shown to display a trend toward later emergence,  
806 related to late spring snowstorms (Lane et al., 2012).

807         Interestingly, our results are only partially consistent with previous findings on  
808 Columbian ground squirrels. We found evidence for delayed snowmelt (13 days) over the 28  
809 years of study despite a general warming trend (air temperature increased by 1.40°C during  
810 the active season), and a positive effect of the first day without snow on emergence date  
811 (except for 2-year-old individuals). Despite such a climatic trend, different phenological  
812 responses were observed in Columbian ground squirrels of different age categories and  
813 meadows. As an example, on Meadows C and B, all individuals (except older males on MB)  
814 delayed emergences by 4 to 11 days over the 18 to 28 year period. Yet, no changes in  
815 emergences were observed on DOT for any age category, and long-term temporal trends in  
816 ED differed substantially depending on individual age and sex on Meadow A. Two-year-old  
817 individuals advanced their emergence by 2 days over 22 years, whereas older individuals  
818 delayed their emergence by 3 days in the same period, and no change in ED was found for  
819 yearlings. Differences in ED trends between closely located meadows may be related to the  
820 spatial heterogeneity of field, slope, or sun and wind exposure, with different effects of  
821 microclimates. Similar results were found in a recent study on the North American deer  
822 mouse (*Peromyscus maniculatus*), where temperature and photoperiod were positive cues of  
823 breeding phenology, the relationship varying among regions (McLean and Guralnick 2021).  
824 Whether variation in ground squirrel phenology is linked to behavioral plasticity versus long-  
825 term adaptation remains to be seen. The small spatial scales tested here, and the diverging  
826 responses among nearby populations might suggest phenological plasticity, as recently  
827 suggested (Lane et al. 2019).

828 Many species responses to climate are likely to occur at micro-scale, rather than meso-  
829 or macro-scale (e.g. sockeye salmon; *Onchorhynchus nerka*; Martins et al., 2012). As  
830 highlighted here, the relationships between phenology and climate variables are likely to  
831 differ between neighboring populations of the same species, in response to contrasting  
832 microclimate conditions, even over small spatial scales. Thus, studies focusing on climate-  
833 phenology relationships in animals would benefit by integrating fine local scale information  
834 on habitat.

### 835 **Conclusion and further perspectives**

836 Taken together, our results point to important differences in microclimate effects on  
837 animal phenology in neighboring populations. Of course, phenology may be linked to  
838 individual fitness, and thereby the dynamics of the populations. Thus, we might also expect  
839 variation in these variables over small spatial scales. Integrating microclimatic variation in the  
840 study of climate change is likely to provide more accurate predictions of a variety of animal  
841 responses to a changing world.

842

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## 863 ETHICAL APPROVAL

864 All applicable international, national, and/or institutional guidelines for the care and  
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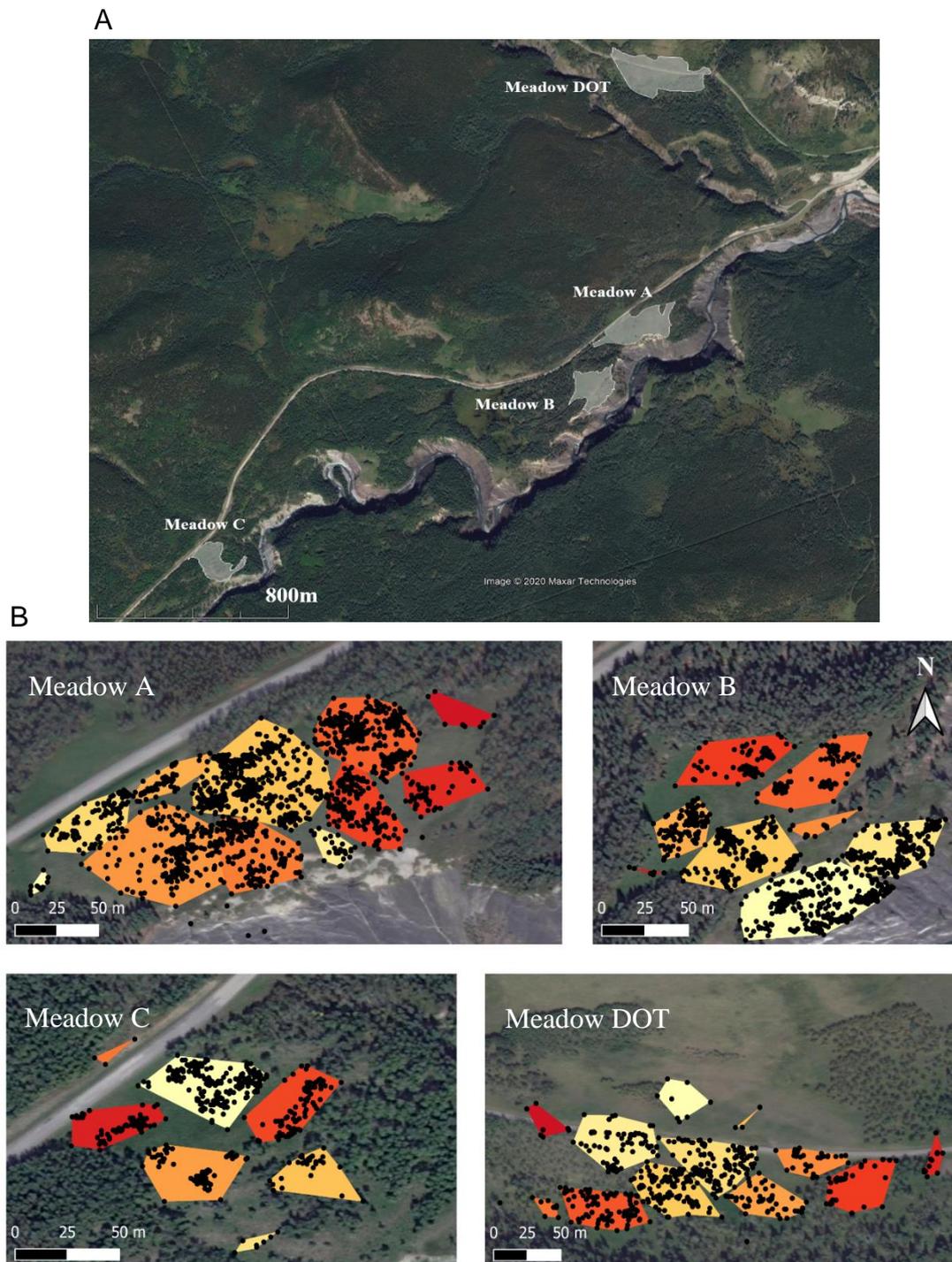
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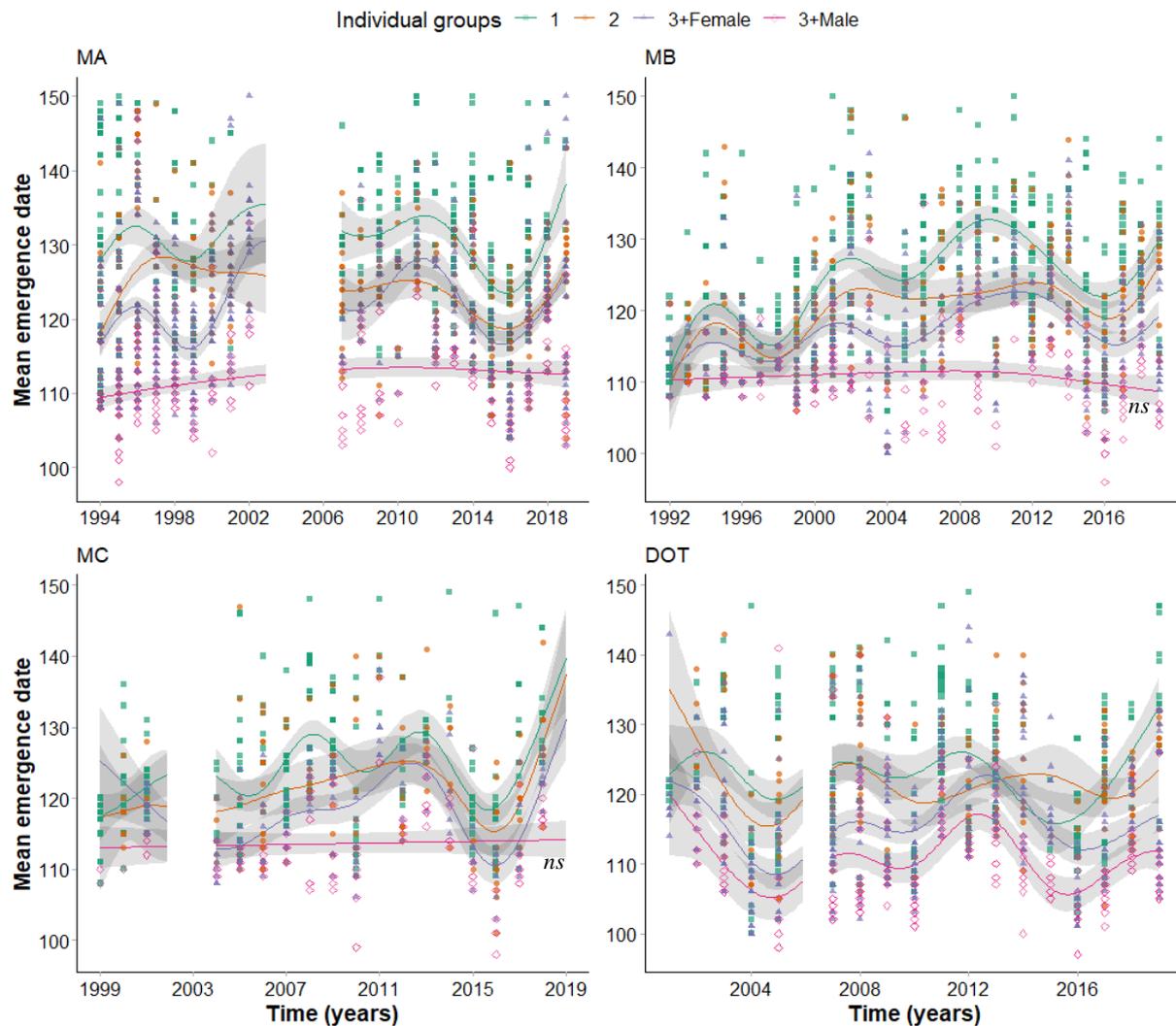
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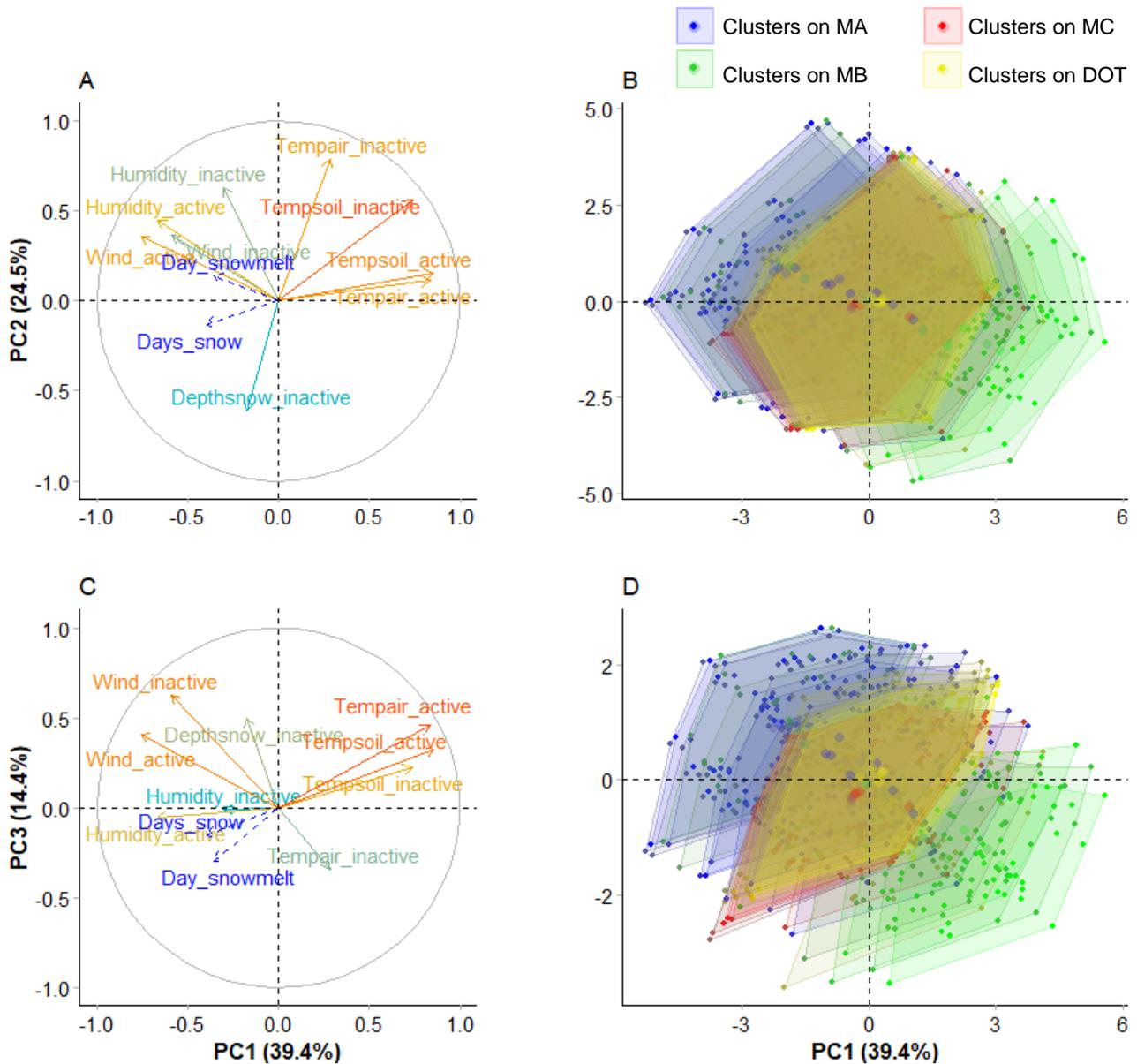
## Figures



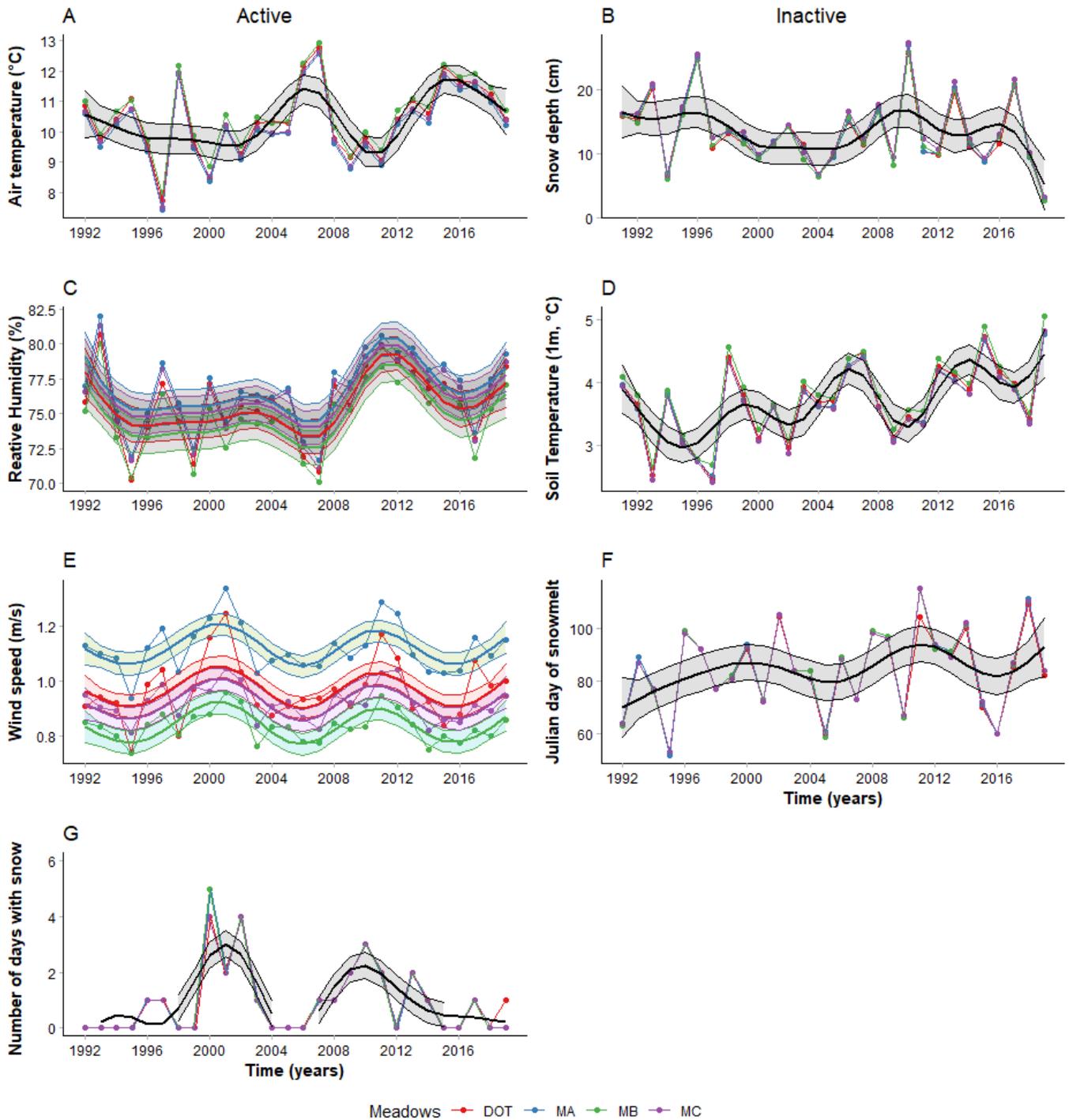
**Fig. 1. Study site composed of meadows and clusters within meadows.** (A) The four different meadows where populations were monitored (grey areas on the map). (B) Emergence locations (black dots) grouped into spatial clusters on each meadow. Clusters are represented by minimum convex polygons and colored according to their mean emergence date. Lighter colors correspond to earlier mean emergence date of the cluster (yellow and light orange) and darker colors correspond to later mean emergence date of the cluster (dark orange and red). Mean ordinal emergence date on clusters ranged from 118 to 127 on MA, from 118 to 130 on MB, from 120 to 124 on MC and from 114 to 124 on DOT.



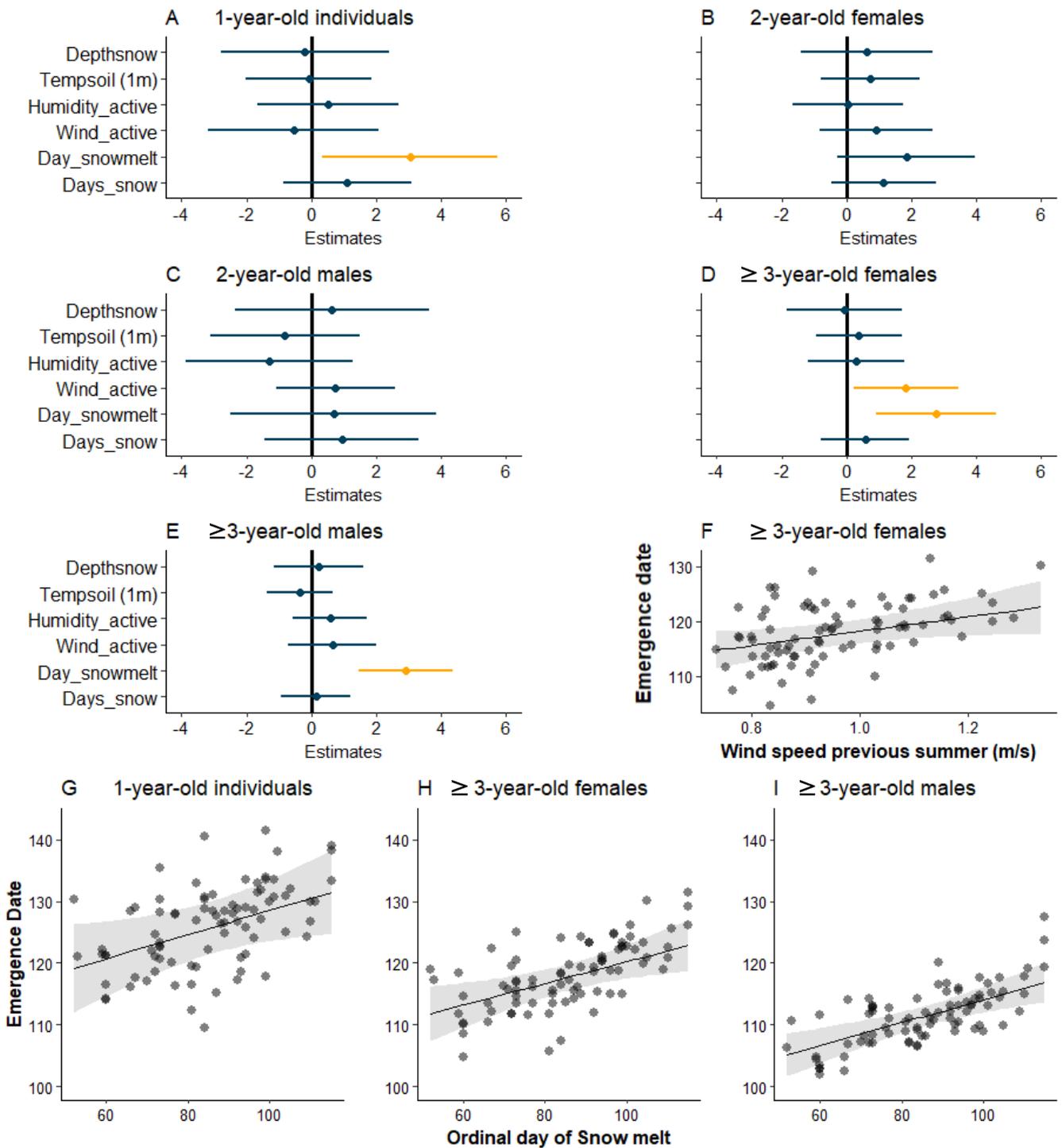
**Fig. 2. Interannual variability in emergence date.** Temporal patterns of emergence dates (in ordinal day) on each meadow (MA, MB, MC, DOT) and for different individual categories. Yearlings (green squares, 1), 2-year-old individuals (orange circles, 2), older females (blue triangles, 3+ Female), and older males (pink diamonds, 3+ Male) are represented. Plotted lines correspond to significant temporal trends and their 95% confidence interval according to GAMs [5], excepting the temporal pattern of older males on MB and MC which is non-significant (*ns*).



**Fig. 3. Spatial variation of climate conditions.** Left side: Climate variables, considered either during the active or inactive period, included in the Principal Component Analysis along dimensions 1 and 2 (A) and dimensions 1 and 3 (C). The number of days with snowfalls during the active period (Days\_snow) and the ordinal day of snowmelt (Day\_snowmelt) were not used to estimate the PCA but projected on it. Right side: Annual mean values of climate conditions for each cluster of the four meadows. Clusters are represented by minimum convex polygons colored by meadows (MA in shades of blue, MB in shades of green, MC in shades of red and DOT in shades of yellow), with their center of gravity represented by larger dots.

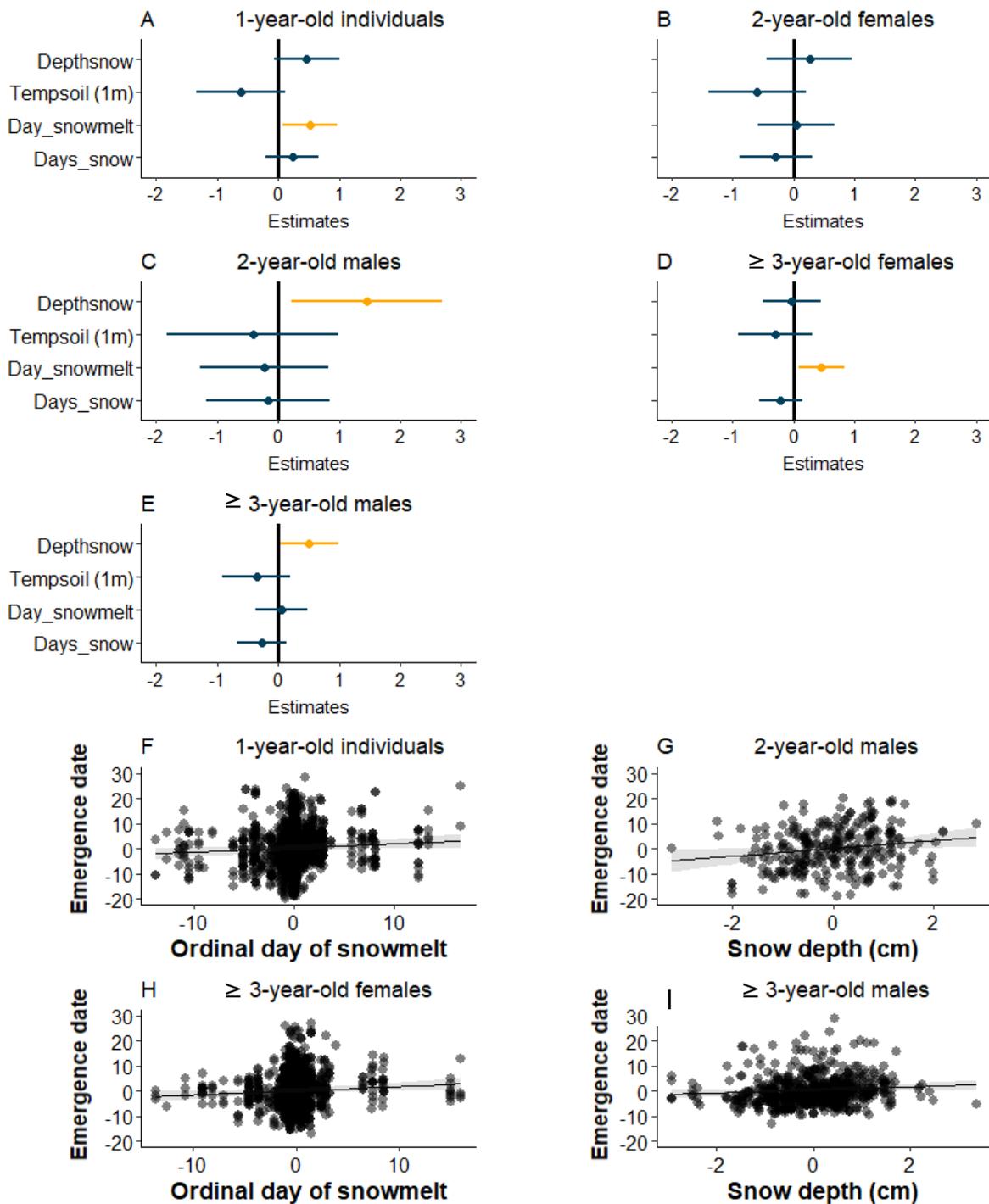


**Fig. 4. Climate interannual variability.** Annual mean values of climate variables averaged by meadow. The lines correspond to temporal patterns of climate variables estimated by the GAM [9] on the four meadows (MA in blue, MB in green, MC in purple, and DOT in red) between 1992 and 2019. Climate time series were divided into two periods: inactive from the 1<sup>st</sup> of August to the 15<sup>th</sup> of April (right column) and then active the rest of the year (left column) and averaged by year. Where no difference was found between meadows (all variables except wind and humidity), a single prediction line was plotted for all locations (in black) with its 95% confidence interval (shaded area).

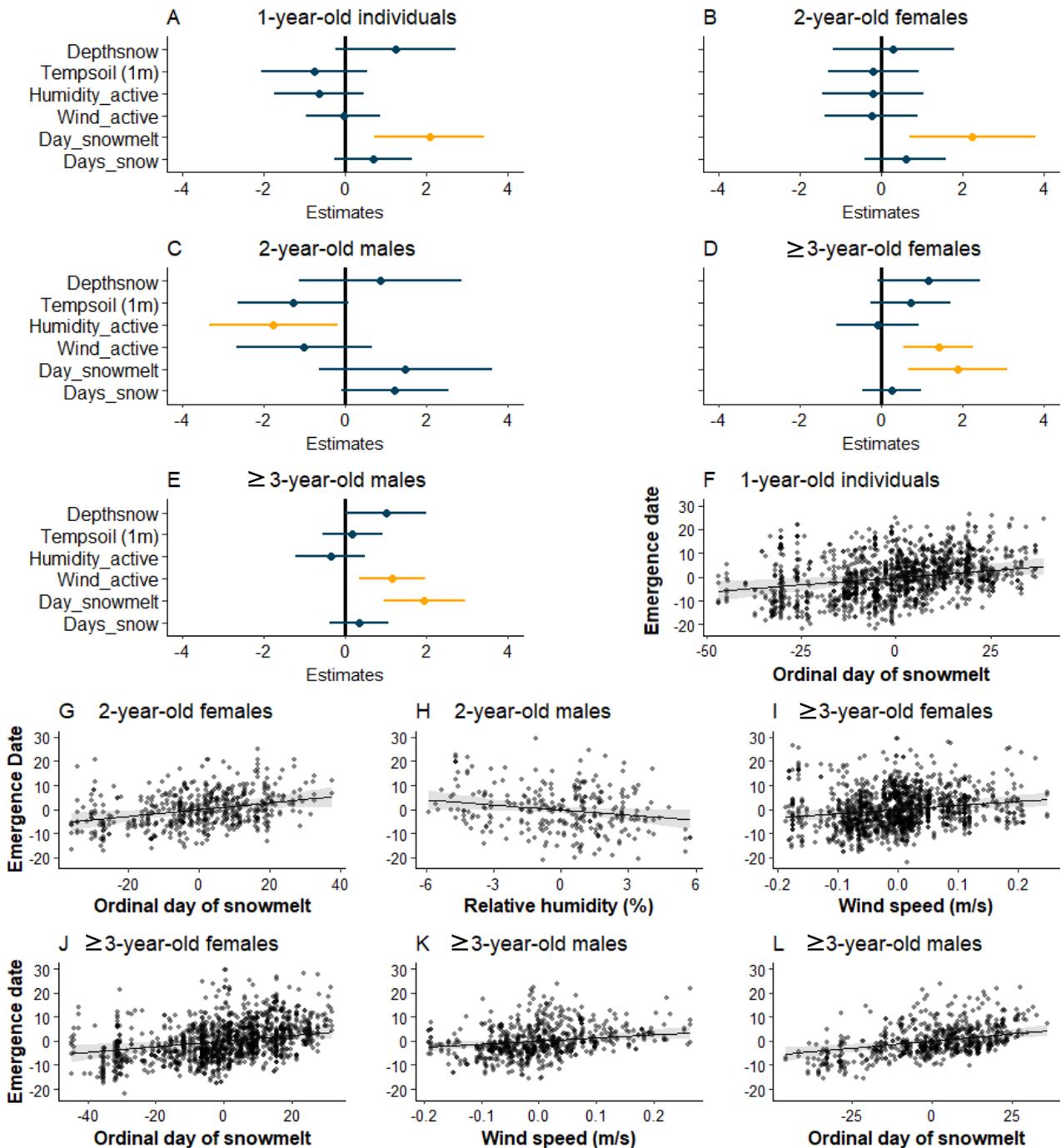


**Fig. 5. Climate effects on hibernation emergence date of different individual categories.**

From (A) to (E): Estimates and 95% confidence intervals from the full LMM [13] explaining annual mean emergence dates per meadow are presented. Significant effects are presented in orange while non-significant ones are blue. (F) Annual mean emergence date as a function of the wind speed during the previous active period for  $\geq 3$ -year-old females and model predictions (predicted line and 95% CI around). From (G) to (I): Annual mean emergence date as a function of the ordinal day of snow melt and model predictions for one-year-old individuals (G),  $\geq 3$ -year-old females (H) and  $\geq 3$ -year-old males (I).



**Fig. 6. Spatial climate effects on centered emergence dates of different individual categories.** From (A) to (E): Estimates and 95% confidence intervals from the full LMMs [14] are presented with significant effects in orange. From (F) to (I): Spatial effect of climate on emergence date (year-centered observations to remove temporal variance). Model predictions are indicated along with their 95% confidence intervals (shaded area) on top of observations. Significant spatial effect of the ordinal day of snowmelt on emergence date of (F) yearlings and (H) older females ( $\geq 3$ -year-old and more). Significant spatial effect of the winter snow depth on the emergence date of (G) 2-year-old males and (I)  $\geq 3$ -year-old males.



**Fig. 7. Temporal climate effects on centered emergence dates of different individual categories.** From (A) to (E): Estimates and 95% confidence intervals from the full LMMs [15] are presented with significant effects in orange. From (F) to (L): Temporal effect of climate on emergence date (all cluster-centered to remove the spatial variance). Model predictions are indicated along with their 95% confidence intervals (shaded area) on top of observations. Significant temporal effects of the ordinal day of snowmelt on the ED of (F) yearlings, (G) 2-year-old females, (J) ≥3-year-old females, and (L) ≥3-year-old males. Significant temporal effects of (H) relative humidity during preceding summer on the ED of 2-year-old males, and of wind speed on the ED of ≥3-year-old (I) females and (K) males.

## *Appendix S1: Supplementary Figures and Tables*

**Journal Name:** Ecosphere

**Article Title:** Integrating microclimatic variation in phenological responses to climate change: a 28-year study in a hibernating mammal

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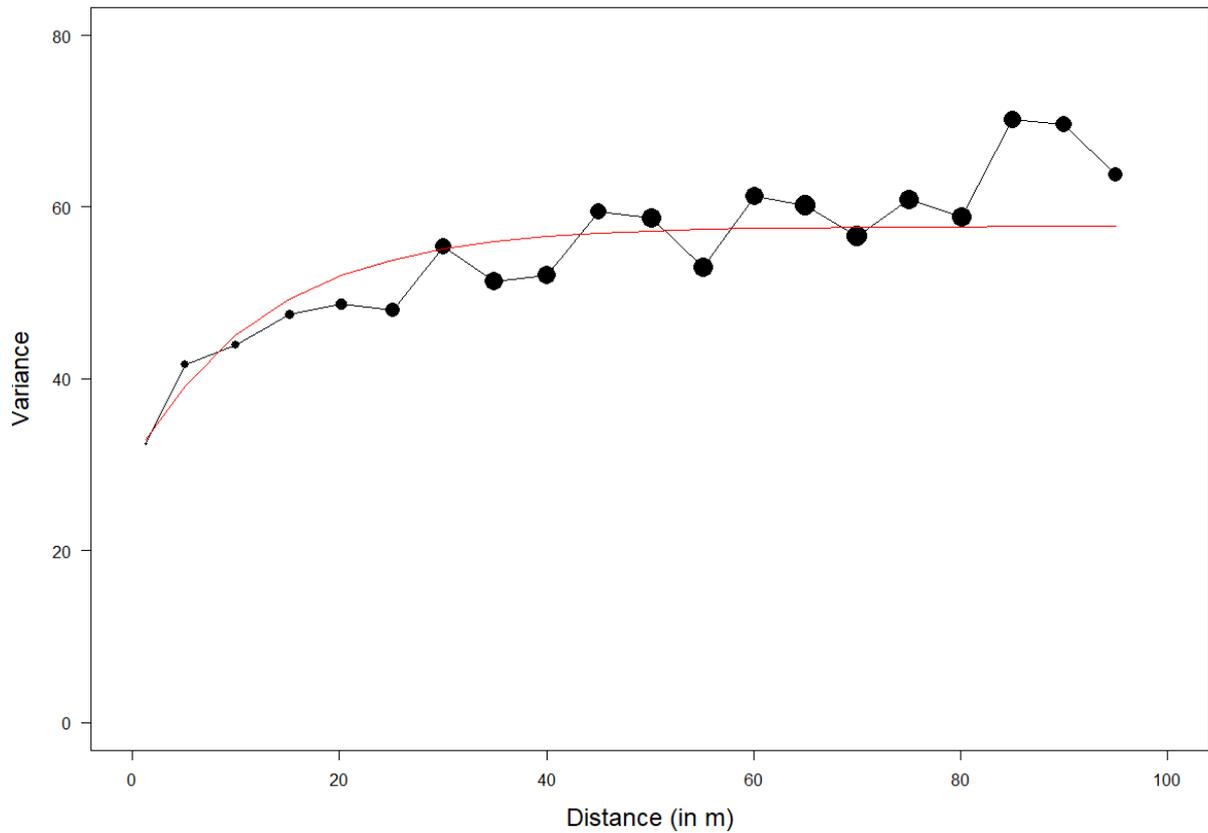
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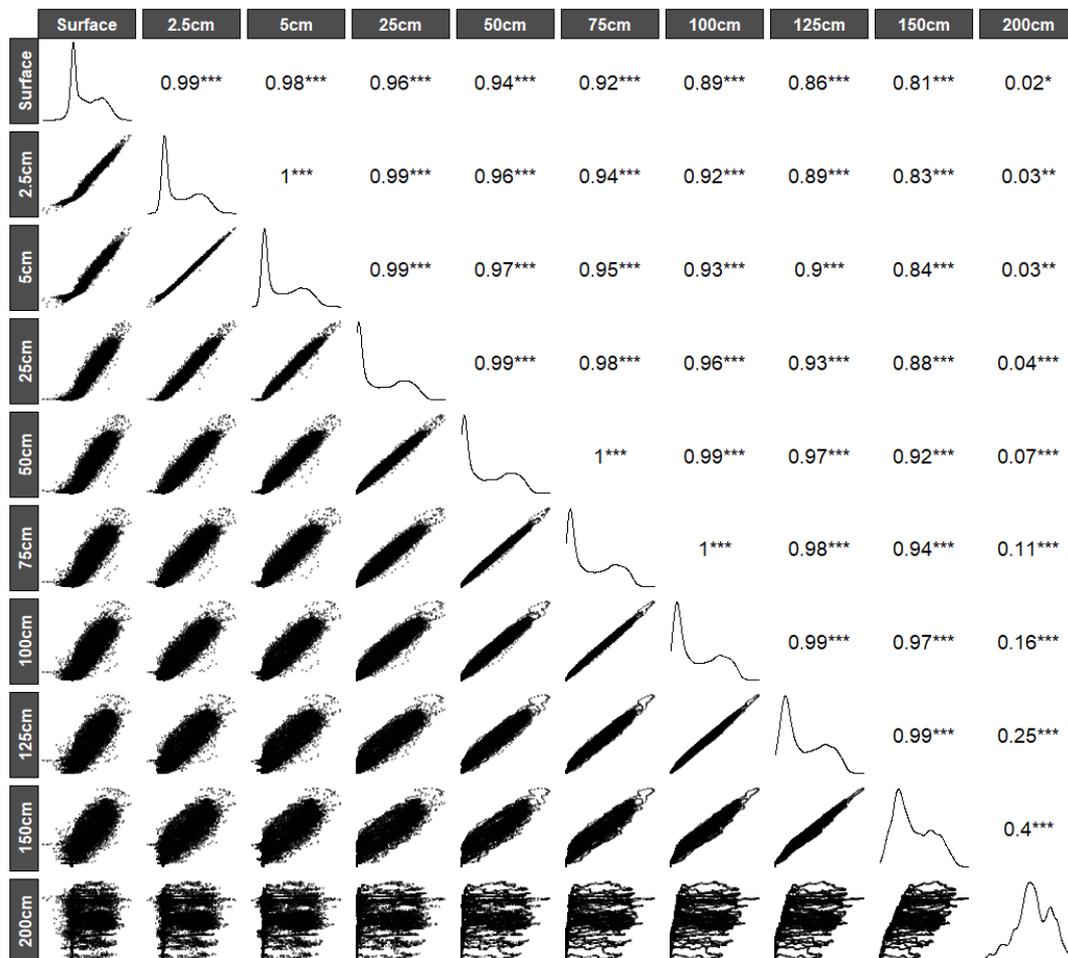
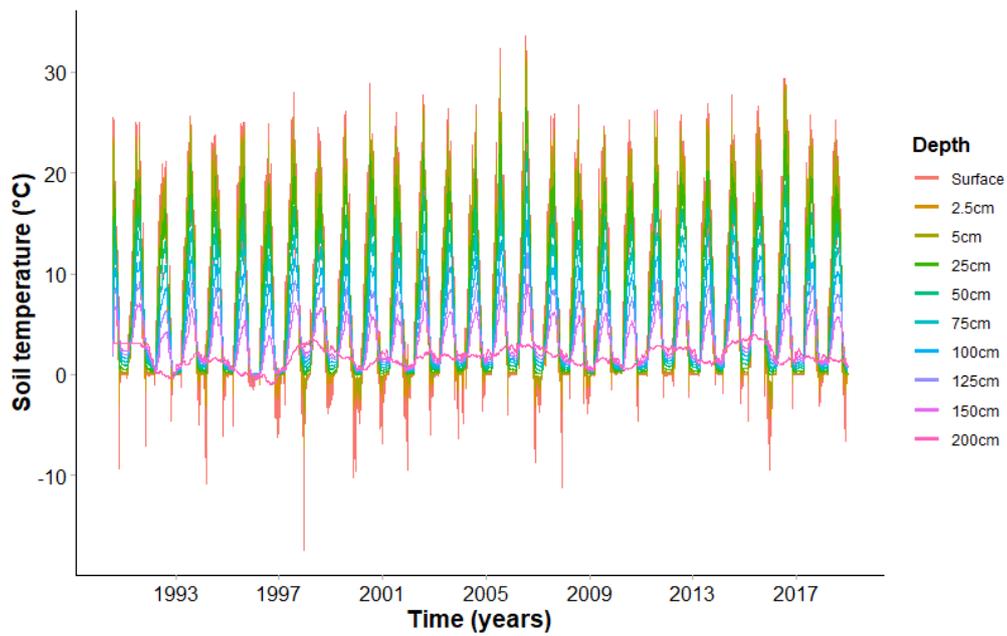
<sup>a</sup>Corresponding author: [anouch.tamian@iphc.cnrs.fr](mailto:anouch.tamian@iphc.cnrs.fr)

**Table S1.** Table of emergence date observations per year on the four different meadows. The number of observations is presented for each individual (sex-age) category: 1-year-old individuals (*1*), 2-year-old individuals (*2*),  $\geq 3$ -year-old females (*3+Fem*), and  $\geq 3$ -year-old males (*3+Mal*).

Year	Meadow A				Meadow B				Meadow C				Meadow DOT			
	<i>1</i>	<i>2</i>	<i>3+Fem</i>	<i>3+Mal</i>												
1992					17	1	4	6								
1993					12	13	4	2								
1994	74	22	65	31	22	9	11	6								
1995	73	39	66	33	33	10	15	10								
1996	10	43	68	32	22	13	18	9								
1997	8	9	71	22	5	5	24	9								
1998	25	6	58	24	32	3	25	10								
1999	23	13	43	20	43	17	26	8	17			2				
2000	5	14	27	17	28	22	25	10	19	10		1				
2001	3	11	26	16	35	21	39	13	26	2	8	11	5		10	
2002		1	24	12	53	15	41	11					8	6	22	9
2003					4	6	21	6					18	9	32	13
2004					7	4	17	4	5	5	10	5	16	7	29	
2005					19	2	14	5	26	7	11	5	34	15	24	15
2006					28	14	10	6	11	17	8	6				
2007	13	16	6	9	7	18	12	9	39	6	12	9	35	16	39	16
2008	12	8	9	15	16	4	18	9	28	7	9	13	14	22	28	32
2009	34	10	13	15	29	11	19	12	30	7	14	12	10	6	39	27
2010	17	8	8	5	12	9	13	2	15	8	7	7	19	6	35	21
2011	25	16	12	5	24	5	15	3	5	2	7	5	34	11	30	17
2012	16	21	18	10	31	14	13	5	12	10	5	4	32	17	25	11
2013	39	11	27	14	24	17	17	8	11	9	6	9	30	16	28	22
2014	41	20	31	11	13	17	18	11	3	6	6	8	1	19	27	16
2015	50	23	26	9	25	7	19	11	16	2	7	6	2	1	23	15
2016	49	25	35	15	28	15	21	12	21	11	5	6	20	3	17	21
2017	59	28	43	16	17	21	19	13	14	10	10	8	35	17	12	18
2018	45	31	45	21	25	13	28	10	14	9	14	8	12	24	20	22
2019	4	24	46	16	20	12	25	7					15	8	27	18
<b>Total</b>	<b>625</b>	<b>399</b>	<b>767</b>	<b>368</b>	<b>631</b>	<b>318</b>	<b>531</b>	<b>227</b>	<b>312</b>	<b>128</b>	<b>139</b>	<b>125</b>	<b>340</b>	<b>203</b>	<b>467</b>	<b>293</b>

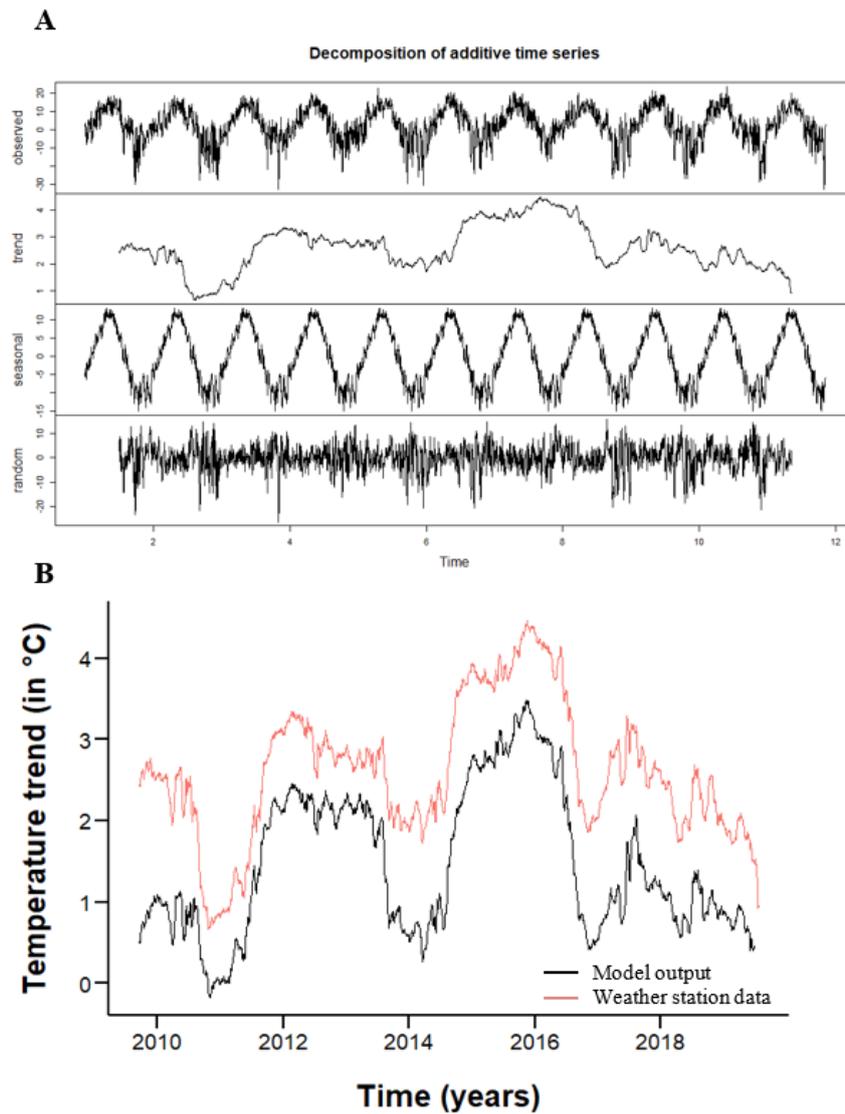


**Figure S1.** Variance of emergence date as a function of the distance between emergence locations, all meadow and individual categories considered. The black dots and line represent the empirical variogram, the size of the point representing the number of pairs of points considered in each distance bin. The red line represents the modelled variogram. The variance stabilized around 40 meters distance between two emergence locations.



1184 **Figure S2.** Correlations between soil temperatures at different depths. Upper part: Daily mean  
 1185 of soil temperatures at various depth (different colors) over the 28 years of study. Lower part:  
 1186 Pearson correlation matrix between soil temperature at depths between surface and two-meter  
 1187 depth (\* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ ).

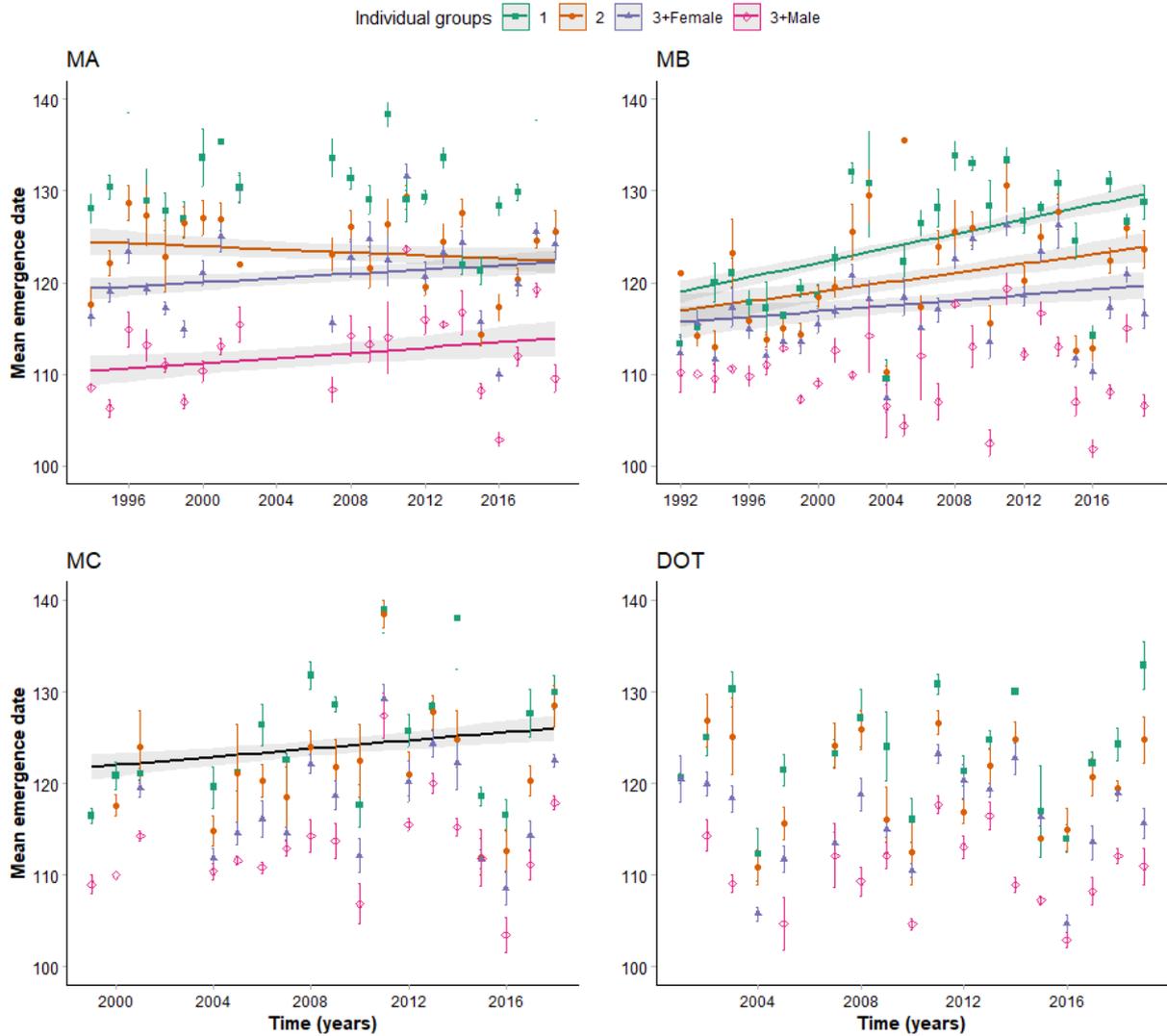
1188 From 2008 to 2019, we were able to acquire air temperatures from the Sheep River  
 1189 weather station (the closest weather station from the study site, with records starting in  
 1190 September 2008, <https://acis.alberta.ca/weather-data-viewer.jsp>) and compare it to our model  
 1191 estimations at the same location. This was a first validation of the model, in one location not  
 1192 far away from the study site (see figure S3 below), where the microclimate model outputs were  
 1193 highly correlated with empirical data when ran in the place of the weather station. Besides the  
 1194 good predictive ability of the model in other places, this further validated the use of the  
 1195 microclimate model in our study.  
 1196



1197  
 1198  
 1199 **Figure S3.** (A) Example of decomposition of a time series of temperature (in °C) recorded at  
 1200 the weather station sheep river between 2008 and 2019. The upper part is the observed signal,  
 1201 and below the trend without the seasonal and random patterns, which can be extracted and  
 1202 analyzed. (B) Correlation of two temperature trends (°C) at sheep river location, between  
 1203 2008 and 2019 ( $r = 0.94$ , Pearson correlation test,  $p < 0.001$ ). The trends, extracted from  
 1204 decompositions from model estimations (black line) and empirical data (red line), had  
 1205 variations closely related.

**Table S2.** Summary table of spatial variation in emergence date. The mean emergence date (in ordinal day) of each cluster within each meadow (MA, MB, MC, DOT) is presented along with standard errors.

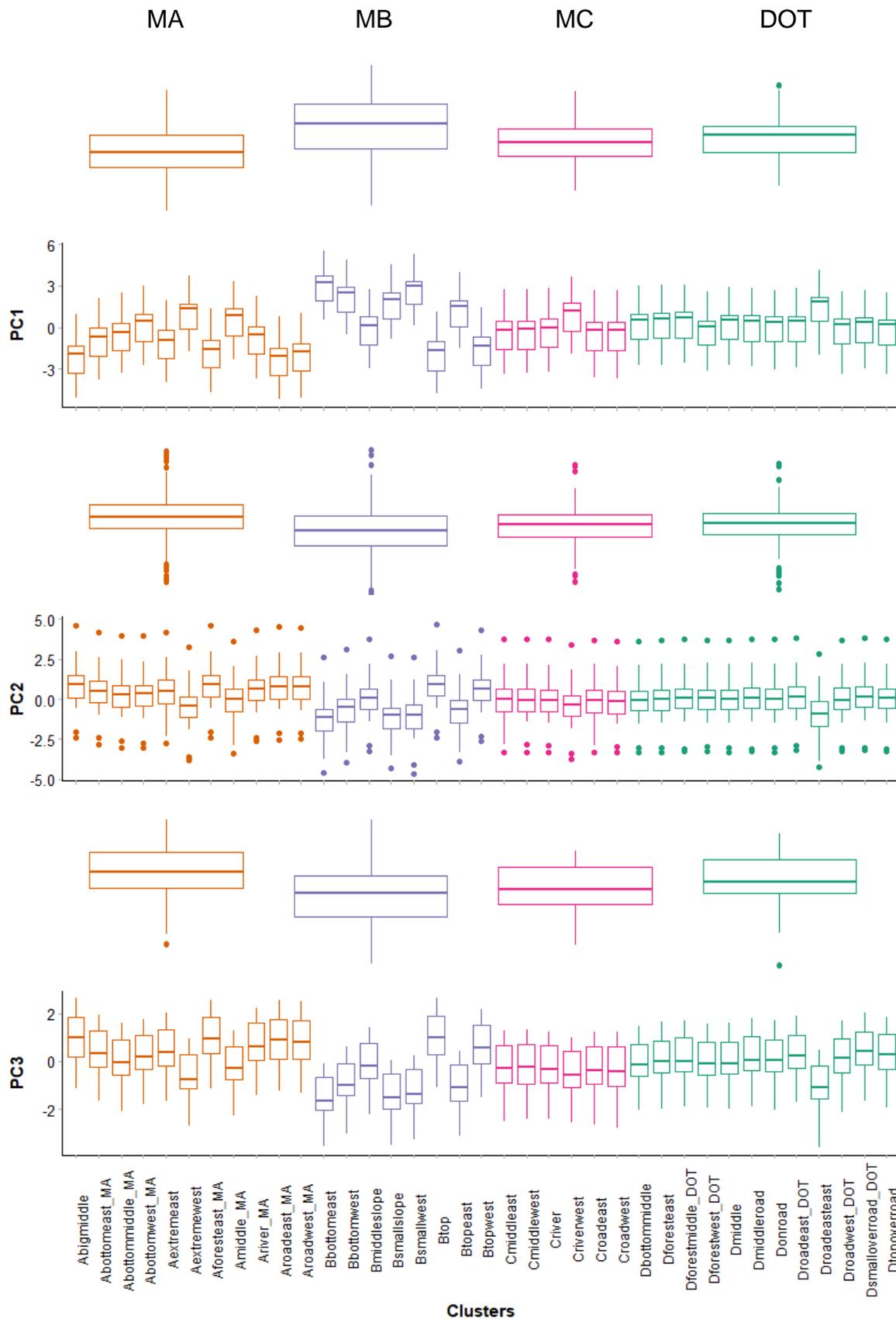
Cluster	Meadow	Emergence date	Cluster	Meadow	Emergence date
bigmiddle	MA	120 ± 0.4	middleeast	MC	123 ± 0.9
bottomeast	MA	126 ± 1.2	middlewest	MC	121 ± 0.8
bottommiddle	MA	124 ± 0.7	overroad	MC	122 ± 6.3
bottomwest	MA	122 ± 0.6	river	MC	121 ± 1.4
extremeast	MA	127 ± 3.7	riverwest	MC	120 ± 2.6
extremewest	MA	118 ± 2.6	roadeast	MC	120 ± 0.5
foresteast	MA	124 ± 0.5	roadwest	MC	124 ± 1.1
middle	MA	122 ± 0.6	bottommiddle	DOT	121 ± 0.9
river	MA	119 ± 1.5	foresteast	DOT	123 ± 1.5
roadeast	MA	122 ± 1.1	forestmiddle	DOT	118 ± 1.3
roadwest	MA	120 ± 0.9	forestwest	DOT	121 ± 4.2
bottomeast	MB	118 ± 0.5	middle	DOT	118 ± 0.7
bottomwest	MB	118 ± 0.4	middleroad	DOT	117 ± 0.7
middleslope	MB	121 ± 0.5	onroad	DOT	117 ± 0.9
smallslope	MB	122 ± 2.9	roadeast	DOT	118 ± 1.5
smallwest	MB	130 ± 4.2	roadeasteast	DOT	123 ± 3.2
top	MB	127 ± 1.2	roadwest	DOT	124 ± 1.3
topeast	MB	126 ± 0.9	smalloverroad	DOT	118 ± 5.9
topwest	MB	122 ± 0.7	topoverroad	DOT	114 ± 0.7



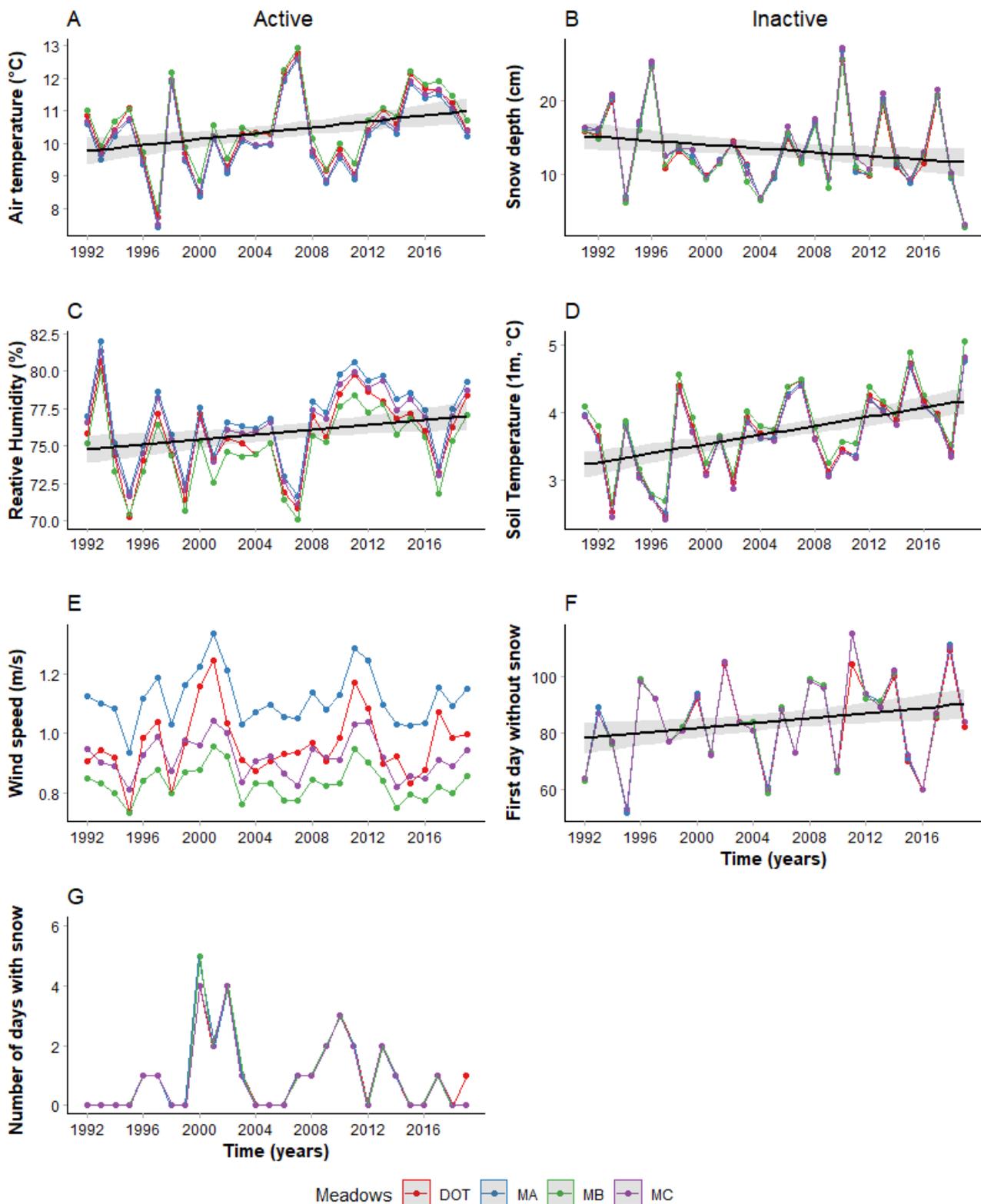
**Figure S4.** Long-term directional changes in emergence date. Linear temporal trends of annual mean emergence dates (in ordinal day) on the four different meadows (MA, MB, MC, DOT) and for each individual category. Points represent annual means  $\pm$  standard error in emergence dates of yearlings (green squares), 2-year-old individuals (orange circles), older females (blue triangles), and older males (pink diamonds). Plotted lines correspond to significant temporal trends and their 95% confidence interval.

**Table S3.** Table of the contribution of the 11 climate variables to the principal component analysis performed on annual time series of climate variables per cluster. Loadings of climate factors on the three first components of the principal component analysis (cumulative explained variance: 78.3%).

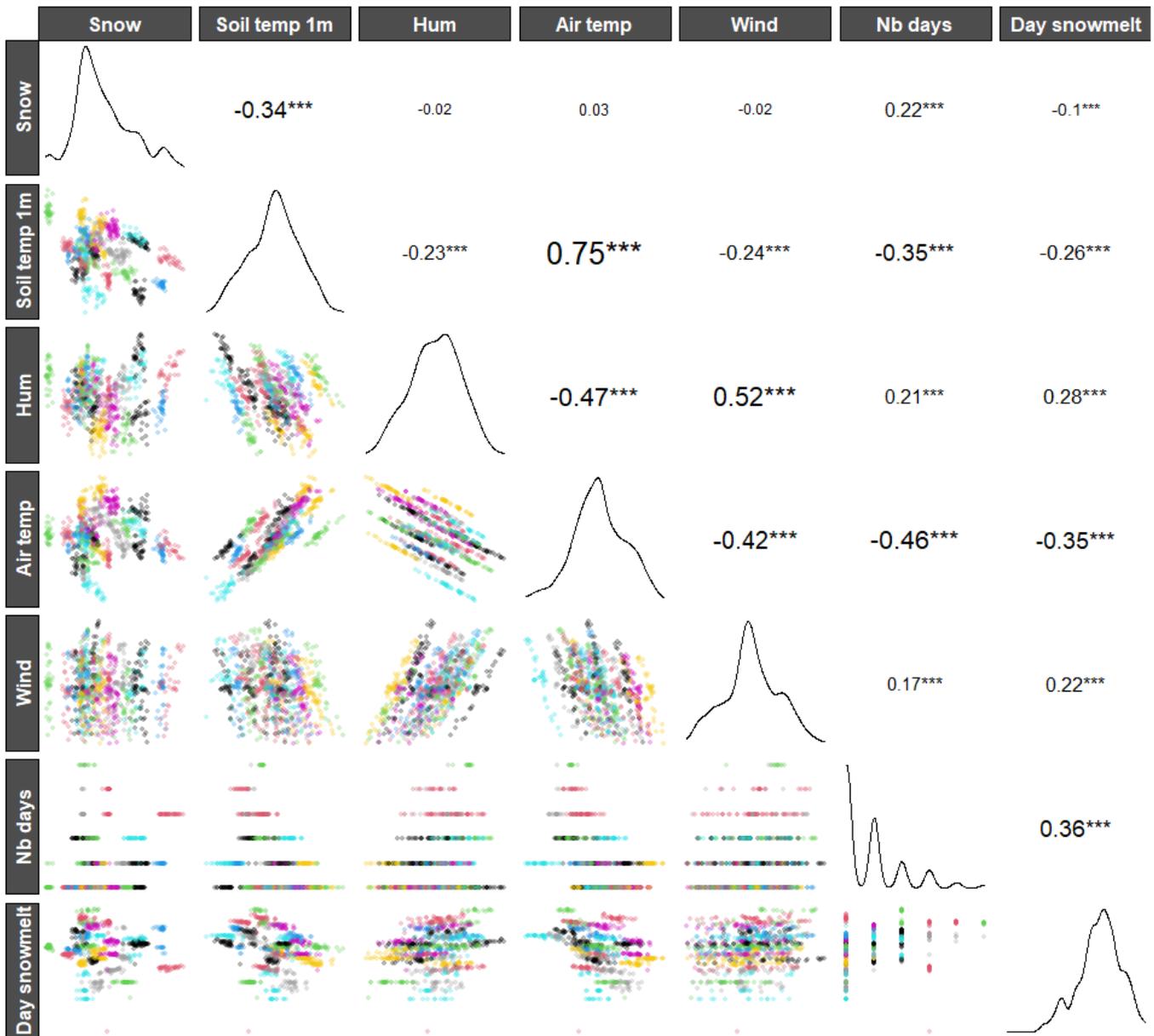
<b>Factor</b>	<b>Dim.1</b>	<b>Dim.2</b>	<b>Dim.3</b>
<i>Humidity_inactive</i>	-0.3	<b>0.6</b>	-0.0
<i>Depthsnow_inactive</i>	-0.2	<b>-0.6</b>	0.5
<i>Tempair_inactive</i>	0.3	<b>0.8</b>	-0.3
<i>Wind_inactive</i>	<b>-0.6</b>	0.4	<b>0.6</b>
<i>Tempsoil_inactive</i>	<b>0.7</b>	<b>0.6</b>	0.2
<i>Humidity_active</i>	<b>-0.7</b>	0.4	-0.1
<i>Tempair_active</i>	<b>0.8</b>	0.1	0.5
<i>Wind_active</i>	<b>-0.8</b>	0.4	0.4
<i>Tempsoil_active</i>	<b>0.9</b>	0.2	0.3
<i>Days_snow</i>	<b>-0.4</b>	-0.1	-0.1
<i>Day_snowmelt</i>	<b>-0.4</b>	0.1	-0.3



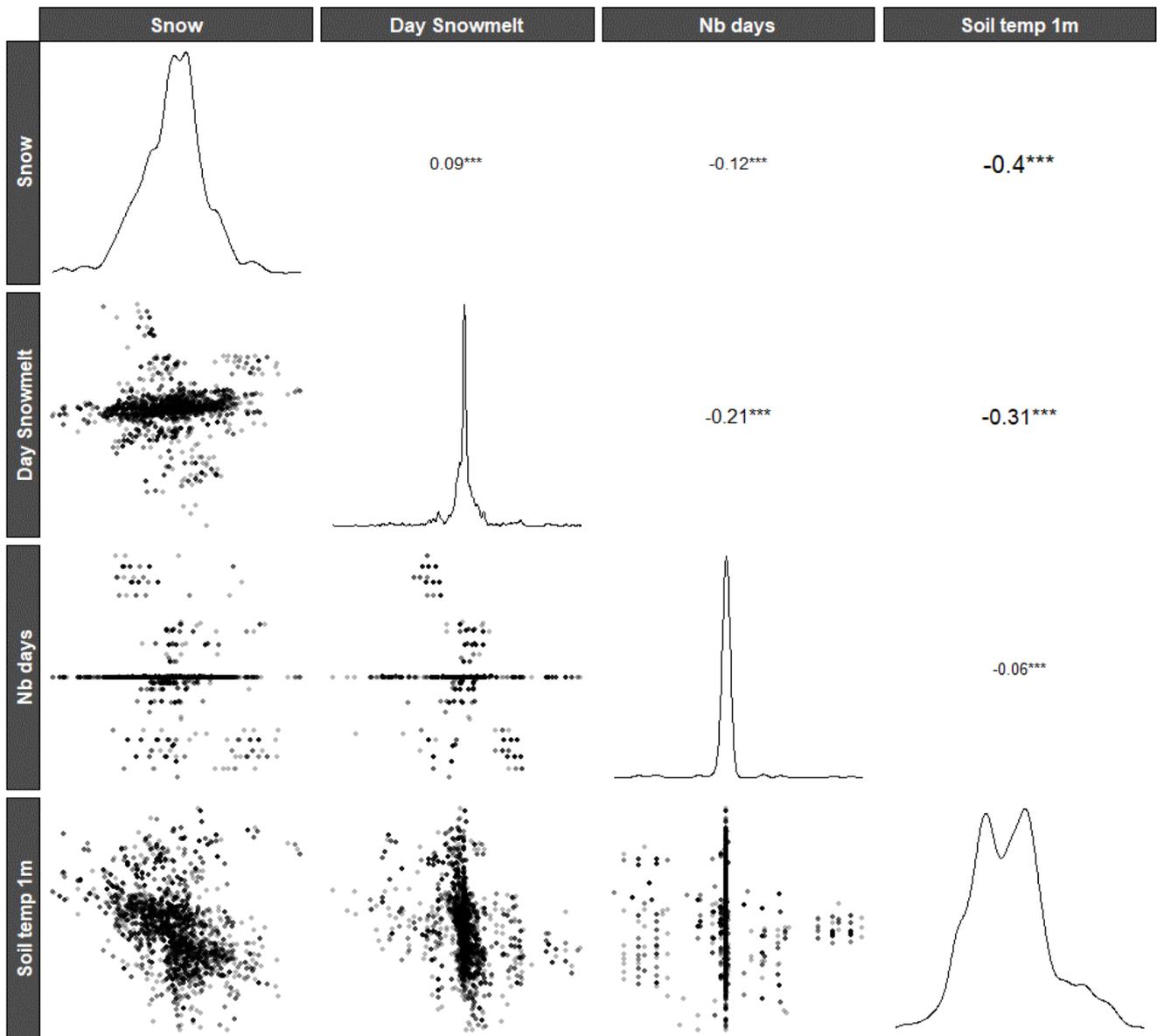
**Figure S5.** Spatial variability of climate. Principal components, built from climate variables, compared between meadows (highest boxplots of each panel) and clusters of the different meadows (lowest boxplots of each panels).



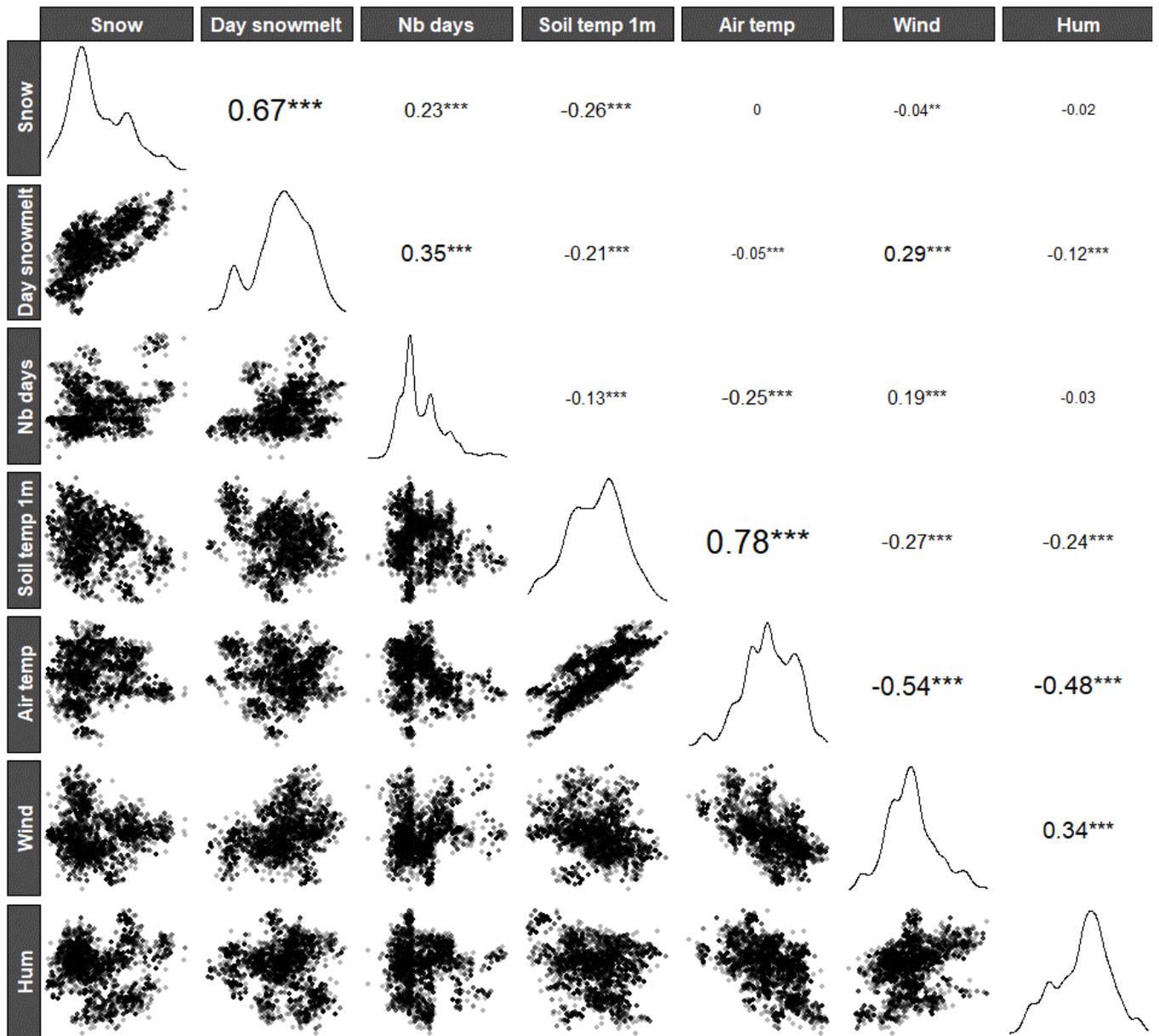
**Figure S6.** Long-term directional changes in climate. Linear temporal trends of annual mean values of climate variables averaged by meadow on the four different meadows (MA, MB, MC, DOT). Plotted lines correspond to significant temporal trends and their 95% confidence interval (shaded area).



**Figure S7.** Correlations between the different climate variables. The correlation matrix was established from climate variables used in the analyses on the link between climate and emergence date, averaged by year and cluster. Colors correspond to the different clusters (\* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ ).



**Figure S8.** Spatial correlations between the different climate variables. The correlation matrix was established from climate variables used in climate – ED analyses and centered by year (\* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ ).



**Figure S9.** Temporal correlations between the different climate variables. The correlation matrix was established from climate variables used in climate – ED analyses and centered by cluster (\* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ ).