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1 **Site-specific factors influence the richness and phenology of**
2 **snowbed plants in the Pyrenees**

3 Marta Domènech, Benjamin Komac, Josep Peñuelas and Josep Antoni Conesa.

4
5 **ABSTRACT**

6 Although the timing of snowmelt and growth temperatures appear to be the main
7 factors that influence the species richness and phenology of snowbed plants, site-
8 specific characteristics may also play a role in modifying the effects of the timing of
9 snowmelt and temperature. In this study, the effects of site-specific factors (micro-
10 topography and snow origin) on species richness and plant phenology were evaluated
11 in 72 plots in two snowbeds in the Andorran Pyrenees. Snowmelt patterns influenced
12 the spatial distribution of species richness and abundance. Site-specific factors had
13 significant effects on the responses of species (shortening or lengthening the duration
14 of the phenophase) and on the extent to which the timing of snowmelt influenced leaf
15 expansion and flowering. Notably, the highest rates of leaf expansion occurred on late
16 snowmelt isoclines, where, nevertheless, the time taken to reach peak flowering was
17 significantly longer than on the early snowmelt isoclines. The results of this study
18 highlight the fact that, in addition to the effects of inter-annual variability in climate, site-
19 specific factors have a significant effect on the phenology and reproductive success of
20 the commonest plants in the snowbed communities of the Pyrenees.

21 **Keywords:** phenology, Pyrenees, richness, site-specific, snowbed.

22

23 INTRODUCTION

24 Climate change is a threat to alpine plants (Theurillat and Guisan 2001, Grabherr 2003,
25 Hülber et al. 2006) and, above all, to those such as snowbed plants that depend on
26 snow cover for protection against harsh weather (Schöb et al. 2009, Björk and Molau
27 2007, Nagy 2006). Global circulation models forecast an increase in temperatures of
28 1.4–5.8°C (IPCC 2007) during the twenty-first century and in the Pyrenees the mean
29 annual temperature is expected to increase by 2.5–5°C (AEMET 2008). Ambient
30 temperature has a significant effect on the timing of snowmelt and most studies report
31 reductions in or the disappearance of snow cover in alpine habitats (EEA 2004,
32 Stanton et al 1994, Walker et al. 1993, Beniston et al. 2003, Muñoz et al. 2007). This
33 highlights the vulnerability of the flora and vegetation of snowbeds to climate change
34 (Lluent 2007, Schöb et al. 2009, Surina et al. 2010).

35 Numerous studies link the influence of the timing of snowmelt and temperature
36 with plant cover and species richness in snowbeds (Lluent 2007, Totland and Alatalo
37 2002, Hülber et al. 2011) and in the snowpack (Chen et al. 2011). The effects of
38 climate change (for example, the timing of snowmelt and temperature) will probably
39 modify the current physical conditions of snowbed habitats, thereby affecting species
40 richness and plant cover.

41 The timing of snowmelt (Galen and Stanton 1995, Körner 2003, Hülber et al. 2010,
42 Hülber et al. 2006, Totland and Alatalo 2002) and the temperature during the growing
43 season (Kudo and Hirao 2006, Molau et al. 2005, Hülber et al. 2006, Körner 2003)
44 have a significant effect on plant development and phenology in alpine snowbeds.
45 Numerous studies have demonstrated the influence of the timing of snowmelt and
46 temperature on species richness and plant cover in snowbeds (Lluent 2007, Hülber et
47 al. 2011) and have indicated the susceptibility of snowbed communities to climate
48 change effects. Although those factors appear to be the major drivers of the
49 development of snowbed plants, site-specific factors might modify (exacerbate or
50 diminish) the overall effects of the timing of snowmelt and temperature. However, few
51 studies to date have examined the influence of site-specific factors such as micro-
52 topography and snow origin on the phenology of alpine plants (Kudo and Hirao 2006,
53 Hülber et al. 2010, Lluent 2007).

54 To gain a more comprehensive understanding of the impacts of climate change on
55 the cover, richness and phenology of alpine plants in snowbed communities, it is
56 important to know whether changes in phenologies and variations in patterns of
57 species richness can be attributed to site-specific factors. These issues are particularly

58 important on the Iberian side of the Pyrenees, where global warming is predicted to
59 have an especially significant effect (Lluent 2007), and where snowbeds are being
60 reduced in size – or even disappearing altogether – as the cryo-Mediterranean belt
61 moves upward in altitude (Tomaselli 1991). Furthermore, the Pyrenees represent the
62 southern limit of most alpine snowbed plants and therefore the snowbed habitat of
63 these mountains is particularly vulnerable to the effects of climate change.

64 In this study, we addressed the following specific questions: How do site-specific
65 factors influence plant cover and species richness in snowbeds? Do site-specific
66 factors influence the date of snowmelt and the microclimate in snowbeds? Do the
67 effects of snowmelt on plant phenology (leaf expansion and flowering) differ between
68 early and late snowmelt sites? Do the phenologies of snowbed plant species differ in
69 their responses to the timing of snowmelt?

70

71 **METHODS**

72 **Study site**

73 The study was conducted in two snowbeds in the northwest of the alpine region of
74 Andorra: Cataperdis (1° 28' 48.1079"; 42° 37' 1.7774") at an elevation of 2,525 m a.s.l.
75 and Arbella (1° 29' 24.1448"; 42° 39' 3.2380") at an elevation of 2,475 m. a.s.l. (Fig. 1).
76 Acidic soils have developed on the gneiss, granodiorite and granite bedrocks of both
77 snowbeds. However, the origin of the snow is different: in Cataperdis snow
78 accumulates primarily because of the topography, while in Arbella the snowbed is fed
79 by snow from avalanches. These snowbeds have slope aspects of 15-22° and 20-30°,
80 respectively, and continuous snowmelt gradients varying from concave forms to
81 moderately exposed slopes. The area has a cold continental climate with
82 Mediterranean influences. In the Central Pyrenees (Andorra), 2009 was warm and dry,
83 2010 was cold and wet, and 2011 was warm and wet (Servei Meteorològic de
84 Catalunya, 2012).

85

86 **Data collection**

87 In 2009, we established 36 permanent plots (50x50 cm) in both of the two snowbeds,
88 12 each on the late-snowmelt (LSM), intermediate-snowmelt (ISM) and early-snowmelt
89 (ESM) isoclines. The 12 plots on one isocline were located within a 20-m² area. To
90 monitor snowmelt patterns the snowbeds were observed in June–August in 2009, 2010
91 and 2011 at weekly intervals. We defined the growing season as the period between
92 permanent snow release in spring and permanent snowfall in autumn.

93 Six temperature data loggers (Temperature logger i-button-Maxim Integrated
94 Products, Sunnyvale, USA, range -40° to +85°) were placed on each of the three
95 isoclines in each snowbed. From June 2010 to October 2011, soil surface
96 temperatures were recorded at 3-hour intervals

97

98 **Species and plant cover**

99 During the growing season (early July–early October) the number of species and the
100 plant cover of all vascular plants and bryophytes in each plot were recorded at weekly
101 intervals (14 times per year). The main phenological sequences of each plant species
102 were recorded weekly during the growing season, which included the two following
103 phenophases: cessation of leaf expansion and peak flower opening. We determined
104 the main peak flower opening to have occurred when more than 70% of the species
105 had entered the flowering phenophase or when more than 70% of individuals of each
106 species were in the flowering phenophase. In addition, we documented the abundance
107 of the four most common species in both of the snowbeds; viz., *Sedum alpestre*,
108 *Mucizonia sedoides*, *Gnaphalium supinum* and *Poa alpina*. Plant identification and
109 nomenclature follows Bolòs et al. (2005).

110

111 **Data analysis**

112 The factors affecting the timing of snowmelt (days elapsed since the end of the
113 snowmelt) and accumulated temperature during the growth period (°C) were evaluated
114 separately using a General Linear Model, with year (2010 and 2011), site (Cataperdis
115 and Arbella snowbeds) and the snowmelt isoclines (LSM, ISM and ESM) as the
116 explanatory variables. To test for normality, data were subjected to a Kolmogorov-
117 Smirnov Test. To estimate the independent explanatory power of each predictor
118 variable, we used hierarchical partitioning (Chevan and Sutherland 1991), specifically,
119 the “hier.part” procedure of the “hier.part” package (Mac Nally and Walsh 2005) in R, to
120 obtain a measure of the independent contribution of each variable as a proportion (%)
121 of the total explained variance (Mac Nally and Walsh 2005). The statistical significance
122 of the amount of variance explained by each variable was tested using a
123 Randomization Test based on 100 randomizations of each of the independent
124 variables. To test for significant differences in the timing of snowmelt and accumulated
125 temperature between the different levels of the environmental factors, Tukey-HSD
126 Tests were performed, while to assess the co-linearity between the timing of snowmelt
127 and accumulated temperature, a Pearson Chi-squared Test was performed.

128

129 Species richness and total plant cover were subjected to an analysis of variance
130 that included the following explanatory factors: snowmelt isocline (LSM, ISM and ESM),
131 site (Cataperdis and Arbella snowbeds), year (2010 and 2011), and the plot nested
132 within the isocline in a General Linear Model. To test for normality, the data were
133 subjected to a Kolmogorov-Smirnov Test. To test for significant differences in species
134 richness and plant cover, we used Tukey's Post-hoc Multiple Comparisons Test.

135

136 The effects of snowmelt isocline, site, year and plot on the number of days
137 before each phenophase was reached were evaluated collectively for all of the species
138 and individually for *Mucizonia sedoides*, *Sedum alpestre*, *Gnaphalium supinum* and
139 *Poa alpina*. To quantify the explanatory power of each variable (site, year and
140 snowmelt isocline) on the response variables (the timing of snowmelt and accumulated
141 temperature), we used hierarchical partitioning.

142

143 The effects of the time taken to reach each phenophase on the three snowmelt
144 isoclines in the two snowbeds were performed using the non-parametric Kruskal-Wallis
145 Test (non-parametric one-way ANOVA).

146

147 All of the analyses were performed using the SAS statistical package (SAS 9.0,
148 SAS Institute, 2003) and the R (version 2.12.1 (R Development Word Team, 2010)).

149

150

151 **RESULTS**

152 **Timing of snowmelt and accumulated temperature**

153 The earliest snowmelt on ESM isoclines occurred at Cataperdis on 6 July 2010, while
154 the latest on LSM isoclines began at Arbella on 24 August 2010; thus, the difference
155 between the extreme dates for snowmelt was substantial (49 days) (Table I). The mean
156 length of the growing season differed significantly between the snowmelt isoclines
157 (ESM sites = 77.5 d, ISM sites = 61.75 d and LSM sites = 47.75 d). The timing of
158 snowmelt did not vary significantly between years ($F= 2.59$; $p=0.15$); however, the
159 timing differed significantly between snowbeds ($F= 23.28$; $p=0.002$) and snowmelt
160 isoclines ($F= 22.66$; $p<0.001$). Snowmelt occurred 18 days later at Arbella than at
161 Cataperdis. On average, the snow melted 30 days later on LSM isoclines than on ESM
162 isoclines; on the other hand, the timing of snowmelt did not differ significantly between
163 the ISM and the LSM sites.

164 Accumulated temperature ranged from 188°C (desv=3.77°C) at an LSM site to
165 1150 °C (desv=7.01°C) at an LSM site (Table 2), but did not vary significantly between
166 years ($F= 1.10$; $p=0.330$) or snowbeds ($F= 0.62$; $p=0.460$); however, the accumulated
167 temperatures of the snowmelt isoclines did differ significantly ($F= 56.18$; $p<0.0001$).

168 The timing of snowmelt and accumulated temperature during the growing period
169 were significantly correlated ($r=0.965$; $p<0.001$). Snowmelt isocline and site explained
170 much of the variance in the timing of the snowmelt, while the snowmelt isocline
171 explained a substantial amount of the variance in accumulated temperature over the
172 growing season (Table II).

173

174 **Species richness and plant cover**

175 Thirty-four plant species were found in the two snowbeds (28 species at
176 Cataperdis and 33 at Arbella) (Table III). The species richness of vascular plants
177 (mainly forbs) was much higher than the richness of bryophytes (Table IV). Overall,
178 mean plant cover was 87.54%, ranging from 14% at the LSM site at Arbella to 100% at
179 the ESM site at Cataperdis. Plant cover varied significantly between years ($F=16.12$;
180 $p<0.001$), sites ($F=39.11$; $p<0.001$) and snowmelt isoclines ($F=22.59$; $p<0.001$), but did
181 not vary significantly within plots ($F=0.14$; $p<0.867$). Species richness varied
182 significantly between years ($F=18.13$; $p<0.001$), sites ($F=111.46$; $p<0.001$) and
183 snowmelt isoclines ($F=80.84$; $p<0.001$), but not within plots ($F=0.51$; $p<0.581$). Plant
184 cover and species richness were highest on the ESM isocline (mean richness per plot=
185 9.64 ± 2.06 species, mean plant cover per plot= $84.04\%\pm 38.72$) and were lowest on the
186 LSM isocline (mean richness per plot= 4.77 ± 1.70 species, mean plant cover per
187 plot= $57.59\%\pm 28.12$).

188 The species richness of vascular plants, especially grasses (e.g. *Poa alpina*,
189 *Agrostis rupestris* and *Nardus stricta*), was significantly higher on ESM isoclines (mean
190 richness per plot= $2.10\pm \text{desv}=1.10$) than on LSM isoclines (mean richness per
191 plot= $0.37\pm \text{desv}=0.60$); nonetheless, bryophytes species richness was significantly
192 higher on LSM isoclines than on the other isoclines.

193 On average, at Cataperdis there were significantly higher plant richness per
194 plot (8.83 species) and greater plant cover (94.29%) than at Arbella (5.52 species,
195 66.80% plant cover). Mean richness per plot and mean plant cover were significantly
196 higher in 2010 (7.84 species, 86% plant cover) than in 2011 (6.51 species and 64.22%
197 plant cover).

198 **Growth and flowering phenology**

199 All the plots on ESM isoclines reached the cessation of leaf expansion and flowering
200 phenophases. On ISM isoclines, plants in 96% and 85% of the plots reached the
201 cessation of leaf expansion phenophase and the flowering phenophase, respectively;
202 however, the corresponding figures for the LSM isoclines were only 68% and 50% of
203 plots, respectively.

204 The period from the end of snowmelt to the cessation of leaf expansion differed
205 significantly between snowmelt isoclines (Chi=12.16; $p<0.002$), between years (Chi=
206 29.38; $p<0.001$) and between sites (Chi=4.19; $p=0.040$). This period was significantly
207 shorter on LSM isoclines than on either ESM (4.87 d) or ISM isoclines (6.64 d). In
208 2010, this period lasted 6.34 d longer than in 2011 and, on average, was 2.49 d longer
209 at Cataperdis than at Arbella.

210 The period from the cessation of leaf expansion to peak flowering differed
211 significantly between snowmelt isoclines (Chi= 8.03; $p<0.010$) and between years
212 (Chi= 15.64; $p<0.001$), but not between sites (Chi= 0.77; $p=0.370$). This period was
213 significantly longer on LSM isoclines than on either ESM (8.82 d) or ISM isoclines (6.84
214 d), and was 4.37 d longer in 2011 than in 2010.

215 The period from the end of snowmelt to peak flowering differed significantly
216 between sites (Chi=5.43; $p<0.010$) but not between years (Chi=1.49; $p=0.220$) or
217 snowmelt isoclines (Chi=1.85; $p=0.390$), and was significantly shorter (4.06 d) in the
218 plots at Arbella than at Cataperdis.

219 The mean accumulated temperature at the cessation of leaf expansion in ESM
220 plots (131 °C) was significantly ($F = 4.55$; $p<0.010$) higher than in LSM plots (85°C).
221 The mean accumulated temperature at peak flowering in the plots on ESM isoclines
222 (212 °C) was significantly higher than on ISM isoclines (148 °C), but did not differ
223 significantly from the plots on LSM isoclines, possibly because only 50% of plots on
224 LSM isoclines reached the flowering phenophase.

225 Peak flowering occurred earlier (Fig. 2) and the number of flowering species
226 was greater on ESM than on LSM isoclines. The flowering period was, respectively,
227 17.5 d and 38 d shorter at the LSM sites than at ESM sites, which left very little time for
228 the later phenophases including fructification. Peak flowering always occurred later at
229 Arbella than at Cataperdis.

230

231 **Species-specific phenological responses**

232 The amount of variance in the time needed to reach the two phenophases explained by
233 site-specific factors was very high (>36.9%) for all species in the flowering phenophase
234 except *Mucizonia sedoides* (18.7%) and *Gnaphalium supinum* (20%) (Table V).
235 Snowmelt isoclines and year had the greatest effect on the phenologies of most of the
236 snowbed species; however, the cessation of the leaf expansion phenophase in *Sedum*
237 *alpestre* was much more influenced by site than by year. As was expected, the
238 proportion of plots in which all species reached the flowering phase was lower than the
239 proportion of the plots in which the plants reached the cessation of leaf expansion.

240 In *Sedum alpestre*, *Mucizonia sedoides* and *Gnaphalium supinum*, but not *Poa alpina*,
241 the time needed to reach the flowering phenophase differed significantly between
242 snowmelt isoclines (Table VI). *G. supinum* (mean = 11 d) and *S. alpestre* and *M.*
243 *sedoides* (14 d and 21 d, respectively) required more time from the end of snowmelt to
244 reach the flowering phase on ESM than on LSM isoclines.

245

246 **DISCUSSION**

247 **Timing of snowmelt and accumulated temperature**

248 In the two studied snowbeds in the Andorran Pyrenees, the timing of snowmelt, but not
249 accumulated temperature, differed significantly, which suggests that site-specific
250 factors may have had a significant effect on accumulated temperature through their
251 localized effects on the microclimate of the snowbeds. At the Arbella snowbed,
252 avalanches are the main source of accumulated snow, whereas at Cataperdis, micro-
253 topography is responsible for the accumulated snow. Consequently, the volume of
254 accumulated snow is greater and snowmelt occurs later in the former than in the latter.
255 At the ESM site at Arbella, snowmelt occurred 7 d later in 2010 than in 2011;
256 consequently, the accumulated temperature was higher in 2011. At the ESM site at
257 Cataperdis, snowmelt occurred 7 d later in 2011 than in 2010, and so the accumulated
258 temperature was higher. When snowmelt occurs early in the summer, the effective
259 accumulated temperature increases gradually, initially, but the rate of increase
260 accelerates quickly. However, when the snow cover on a snowbed is removed after
261 mid-summer, the effective accumulated temperature increases at a constant rate,
262 initially, but then decreases (Kudo and Hirao 2006). At LSM sites in the Andorran
263 Pyrenees, accumulated temperatures were similar between sites and years, even
264 when there were differences in the date of snowmelt. Thus, at ESM sites, the snowmelt
265 date might have had a greater effect on phenologies than on accumulated temperature
266 (see also Kudo and Hirao 2006).

267

268 **Species richness and plant cover**

269 In the snowbeds in the Andorran Pyrenees, the diversity of vascular plants and the
270 amount of plant cover were correlated with the snowmelt isocline gradient; specifically,
271 diversity and plant cover decreased between early and late snowmelt isoclines, a
272 finding that has been observed elsewhere (Totland and Alatalo 2002, Lluent 2007).
273 Abiotic factors such as water content, nutrient fixation capacity and the C/N ratio differ
274 between snowmelt isoclines (Retzer 1956, Billings and Bliss 1959, Hülber et al. 2011)
275 and Galen and Stanton (1995), for example, reported strong correlations between the
276 timing of snowmelt, soil quality and structure, and the productivity of alpine plants.

277 In the present study, overall plant diversity was highest at ESM sites at both
278 snowbeds. However, the relatively low diversity at LSM sites, where bryophytes
279 predominated, was associated with snowbed specialists and in these sites we failed to
280 find many of the species that occur in adjacent habitats and at ESM sites (mainly
281 grasses) (see also Stanton et al. 1994, Schöb et al. 2009). Thus, snowmelt isoclines
282 (i.e. the gradient of micro-variations) influence and help maintain the floral diversity of
283 snowbeds. We found that the diversity per plot was higher at Cataperdis than at
284 Arbella, probably because, at the former, the snow melted earlier and plants had a
285 longer growing season. Even so, the total number of species (Table III) shows higher
286 global diversity in the Arbella snowbed.

287 Species richness and plant cover were greater in 2010, a colder and more
288 humid year, than in 2011; however, this was probably a carry-over effect from 2009,
289 warmer and drier, and with an earlier snowmelt than in 2010. Presumably, the flowering
290 season in 2009 influenced seed success and phenology in 2010 (Kudo and Hirao
291 2006) and, consequently, may well have increased species richness and plant cover in
292 2010.

293

294

295 **Plant growth and flowering phenology**

296 As expected, in the Andorran snowbeds accumulated temperatures were lower at LSM
297 sites than at ESM sites, even though the highest rates of leaf expansion were found at
298 LSM sites. The contrary occurred with the flowering phenophases: the time taken to
299 reach peak flowering was significantly longer on LSM than on ESM isoclines. Other
300 studies have noted this (Wipf 2010, Hülber et al. 2006, Galen and Stanton 1995) and,

301 for example, Wipf (2010) reported that early season phenophases are more affected by
302 the timing of snowmelt than by temperature. Nevertheless, in later phenophases
303 temperature has a stronger effect on both Alpine and Andorran snowbeds.

304 The time between snowmelt and peak flowering did not differ significantly
305 between the snowmelt isoclines in the studied snowbeds, although the time elapsed
306 between the cessation of leaf expansion and flowering was longer at LSM than ESM
307 sites. Plants at LSM sites flowered in late summer when the air temperatures were
308 decreasing and accumulated temperatures were lower than at ESM sites. It is likely
309 that the low input of thermal energy at LSM sites was responsible for this delay in the
310 flowering phenophases, which negatively affected the success of sexual reproduction,
311 because fructification and fruit dispersal occurred just before the new snowfall (onset of
312 winter). Thus, it appears that the onset of winter (a stochastic event) dictates the sexual
313 reproductive success of plants at LSM sites. Furthermore, Kudo and Hirao (2006) have
314 demonstrated the importance of the minimum temperature for the onset of flowering,
315 which might explain why only 50% of the plots at LSM sites in these two Andorran
316 snowbeds reached the flowering phenophase.

317 Given that the growing season was longer at ESM than at LSM sites, it is
318 plausible that increases in global temperatures – thereby causing an earlier retreat of
319 the snow – led to a lengthening of the growing season at LSM sites and therefore
320 greater sexual reproductive success. Nevertheless, in most alpine species,
321 reproduction is generally clonal rather than sexual (Bliss 1960, Lluent 2007) and
322 therefore vegetative growth phenophases may be more important than flowering
323 phenophases (Wipf 2010).

324 In our study, the differences in the durations of the phenophases (cessation of
325 leaf expansion and flowering) between the three snowmelt isoclines were probably the
326 product of the phenotypic plasticity of the plants and their adaptive responses to
327 environmental variability (Post et al. 2008). At LSM sites, species have to adapt to
328 having relatively less time to reach leaf expansion but cannot reduce the amount of
329 time needed to reach flowering because of the fall in temperatures in late summer.

330 As already commented, in these two Pyrenean snowbeds the timing of
331 snowmelt differed between snowmelt isoclines (ESM sites vs. LSM sites), which
332 affected the number of species that flowered and the timing of the peak flowering
333 period. Despite this, there were differences between the two snowbeds: the
334 temperature and the timing of snowmelt had a significant influence on phenologies and

335 site-specific factors (probably, the micro-topography and snow origin) were important
336 due to their influence on the timing of snowmelt and accumulated temperature.

337

338 **Species-specific phenology responses**

339 We found that *Poa alpine* – but not *Mucizonia sedoides*, *Sedum alpestre* or
340 *Gnaphalium supinum* – was highly conservative in its phenological responses to
341 differences in snowmelt isoclines in these snowbeds. Probably, these three other
342 species are better adapted to variations in the timing of snowmelt than this grass. Many
343 studies have demonstrated the strong phenotypic responses of plant species to
344 changes in their environment (Arft et al. 1999, Hülber et al. 2006, Peñuelas and Filella
345 2001, Peñuelas et al. 2002) and, typically, such phenological responses are highly
346 species-specific, even among closely related taxa (Miller-Rushing and Primack 2008).

347 In two of the snowbed species (*Mucizonia sedoides* and *Sedum alpestre*) the
348 flowering period was shortest at LSM sites, which enabled them to maximize the period
349 for seed maturation and conferred an advantage on the sites where snowmelt occurs
350 later in the season. Thus, site-specific factors such as the effects of isocline or climate
351 in a given year on the timing of snowmelt can influence the competitive advantage of
352 some species.

353 In our study, the year had a significant effect on the phenologies of all of the
354 snowbed plants evaluated and on the duration of the growing season, which indicates
355 that inter-annual variation in climate has a significant effect on the phenology of these
356 plants. Domènech et al. (submitted) found a close relationship between annual climate
357 and the number and extent of snowbeds in the Pyrenees and suggested that changes
358 in climate will have a strong influence in the future on Pyrenean snowbeds. Inter-
359 annual variation in climate is common in the Pyrenees (López Moreno et al. 2009) and
360 in many other mountainous areas such as the Alps (Hülber et al. 2011) and will
361 probably increase in the near future. Changes in climate (above all, temperature and
362 precipitation) will affect the snowpack (Johnson and Billings 1962, Scott and Billings
363 1964, Tieszen 1975, Evans and Fonda 1990, Auerbach and Halfpenny 1991, Cess et
364 al. 1991, Walker et al. 1993, Stanton et al. 1994) and the rate of snowmelt (affected by
365 air temperature), which, in turn, will modify the timing of snowmelt and, consequently,
366 the nature of the growing season.

367

368

369 **CONCLUSIONS**

370 In two snowbeds in the Andorran Pyrenees, (1) site-specific factors (micro-topography
371 and snow origin) had significant effects on the timing of snowmelt, (2) the timing of
372 snowmelt had a greater effect on plant phenologies than accumulated temperature at
373 early snowmelting sites, (3) the timing of snowmelt had a significant effect on leaf
374 expansion and flowering schedules, (4) species richness and abundance were greater
375 at early snowmelt isoclines, and (5) species differed in their reactions (shortening or
376 lengthening the duration of the phenophases) to differences in the timing of snowmelt,
377 probably, because of differences in their phenotypic responses.

378 In summary, this study showed that, in addition to the effects of inter-annual
379 variation in climate, site-specific factors had a significant effect on snowbed plant
380 diversity and on the phenology and reproduction of the commonest plants in snowbed
381 communities in the Pyrenees. Hence, site-specific factors may influence – and
382 accentuate – the effects of climate change on alpine plants given that they encourage a
383 diversity of environmental micro-variations. Thus, these environmental micro-variations
384 could act as a source of survival possibilities for plant snowbeds in the future.

385

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391

392

393 **REFERENCES**

- 394 Agencia Estatal de Meteorología (AEMET) 2008. Generación de escenarios
395 regionalizados de cambio climático para España. Ministerio de Medio Ambiente.
396 Madrid. pp 157.
- 397 Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M,
398 Gugerli F, Henry GHR, Jones MH, Hollister R, Jónsdóttir IS, Laine K, Lévesque E,
399 Marion GM, Molau U, Molgaard P, Nordenhäll U, Rasvhizin V, Robinson CH, Starr G,
400 Stenström A, Stenström M, Totland O, Turner L, Walker L, Webber P, Welker JM,
401 Wookey PA. 1999. Responses of tundra plants to experimental warming: a meta-
402 analysis of the international tundra experiment. *Ecological Monographs*, 69, pp. 491-
403 511.
- 404 Auerbach NA, Halfpenny JC. 1991. Snowpack and the subnivean environment for
405 different aspects of an open meadow in Jackson Hole, Wyoming, USA. *Arctic and*
406 *Alpine Research* 23: 41-44.
- 407 Beniston M, Keller F, Goyette S. 2003. Snowpack in the Swiss Alps under changing
408 climatic conditions: an empirical approach for climate impact studies. *Theoretical and*
409 *Applied Climatology* 74: 19-31.
- 410 Billings WD, Bliss LC. 1959. An alpine snowbank environment and its effects on
411 vegetation, plant development, and productivity. *Ecology* 40: 388-397.
- 412 Björk RG and Molau U. 2007. Ecology of alpine snowbeds and the impact of global
413 change. *Arctic and Antarctic Alpine Research* 39: 34-43.
- 414 Bliss LC. 1960. Adaptations of arctic and alpine plants to environmental conditions.
415 *Symposium Life Under Extreme Conditions*; 1960 December 9-10; New York. United
416 States of America. p 144.
- 417 Bolòs O, Vigo O, Carreres J, Ninot JM. 2005. *Flora Manual dels Països Catalans*, third
418 ed. Pòrtic Barcelona. p 419.
- 419 Cess RD, Potter GL, Zhang M-H, Blanchet J-P, Chalita S, Colman R, Dazlich DA, Del
420 Genio AD, Dymnikov V, Galin V, Jerrett D, Keup E, Lacis AA, Le Treut H, Liang X-Z,
421 Mahfouf JF, McAvaney BJ, Meleshko VP, Mitchell JFB, Morcrette J-J, Norris PM,
422 Randall DA, Rikus L, Roeckner E, Royer J-F, Schlese U, Sheinin DA, Slingo JM,
423 Sokolov AP, Taylor KE, Washington WM, Wetherald RT, Yagai I. 1991. Interpretation of

424 snow-climate feedback as produced by 17 general circulation models. *Science* 253:
425 888-892.

426 Chen MN, Wu Y, Wu N, Wang Q. 2011. Effect of snowmelt time on growth and
427 reproduction of *Pedicularis davidii* var. *pentodon* in the eastern Tibetan Plateau. *Plant*
428 *Biosystems* 145 (4): 802-808.

429

430 Chevan A, Sutherland M. 1991. Hierarchical partitioning. *The American Statistician* 45:
431 90-96.

432 Domènech M, Esteban P, Conesa JA, Peñuelas J. (in press). Change in Andorran
433 (Pyrenees) snowbeds patterns: 1948-2003. *Arctic, Antarctic and Alpine Research*.
434 Submitted.

435 European Environmental Agency (EEA). 2004. Impacts of Europe's Changing Climate.
436 An indicator-based assessment. Copenhagen p 100.

437 Evans RD, Fonda RW. 1990. The influence of snow on subalpine meadow community
438 pattern, North cascades, Washington. *Canadian Journal of Botany* 68: 212-220.

439 Galen C, Stanton M. 1995. Responses of snowbed plant species to changes in growing
440 season length. *Ecology* 76: 1546-1557.

441 Grabherr G. 2003. Alpine vegetation dynamics and climate change - a synthesis of
442 long-term studies and observation. In: Nagy L, Grabherr G, Körner C, Thompson DBA
443 (eds) *Alpine Biodiversity in Europe*. Springer, Berlin, p. 399-409.

444 Hülber K, Bardy K, Dullinger S. 2011. Effects of snowmelt timing and competition on
445 the performance of alpine snowbed plants. *Perspectives in Plant Ecology, Evolution*
446 *and Systematics* 13: 15-26.

447 Hülber K, Winkler M, Grabherr G. 2010. Intraseasonal climate and habitat-specific
448 variability controls the flowering of high alpine species. *Functional Ecology* 24: 245-
449 252.

450 Hülber K, Gottfried M, Pauli H, Reiter K, Winkler M, Grabherr G. 2006. Phenological
451 responses of snowbed species to snow removal dates in the Central Alps: Implications
452 for climate warming. *Arctic, Antarctic and Alpine Research* 38: 99-103.

453 IPCC Fourth Assessment Report: Climate Change 2007. Contribution of Working
454 Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel of

455 Climate Change. Ore Writing Team, Pachauri, RK and Reisinger, A. (eds.). IPCC,
456 Geneva, Switzerland. p 104.

457 Johnson PL, Billings WD. 1962. The alpine vegetation of the Beartooth Plateau in
458 relation to cryopedogenic processes and patterns. *Ecological Monographs* 32: 105-
459 135.

460 Körner C. 2003. *Alpine Plant Life. Functional Plant Ecology of High Mountain*
461 *Ecosystems. Second Edition Springer-Verlag. Germany. p 344.*

462 Kudo G, Hirao AS. 2006. Habitat-specific responses in the flowering phenology and
463 seed set of alpine plants to climate variation: implications for global-change impacts.
464 *Population ecology* 48:49-58.

465 Lluent A. 2007. *Estudi de l'estructura i funcionament de les comunitats quionòfiles als*
466 *Pirineus en relació a la variació dels factors ambientals. Located at: Barcelona*
467 *University (UB). Barcelona, Espanya. p 243.*

468 López-Moreno JI, Goyett, S, Beniston M. 2009. Impact of climate change on snowpack
469 in the Pyrenees: Horizontal spatial variability and vertical gradients. *Journal of*
470 *Hydrology* 374: 384-396.

471 Mac Nally R, Walsh C. 2005. hier.part:variance partition of a multivariate data set. R
472 package version 2.3. [http:// www.r-project.org](http://www.r-project.org)

473 Miller-Rushing AJ, Primack RB. 2008. Global warming and flowering times in Thoreau's
474 concord: a community perspective. *Ecology* 89: 332-341.

475 Molau U, Nordenhäll U, Eriksen B. 2005. Onset of flowering and climate variability in an
476 alpine landscape: a 10-year study from Swedish Lapland. *American Journal of Botany*
477 92: 422-431.

478 Muñoz J, García A, Andrés N, Palacios D. 2007. La vegetación del ventisquero de la
479 condesa (Sierra de Guadarrama, Madrid) y sus condicionantes termo-nivales. *Boletín*
480 *de la Asociación Española Geografía* 44: 29-52.

481 Nagy L. 2006. European High Mountain (Alpine) vegetation and its suitability for
482 indicating climate change impacts. *Biology and environment: proceedings of the Royal*
483 *Academy. Royal Irish. Academy. 106B, (3), pp. 335-341.*

484 Peñuelas J, Filella I. 2001. Phenology: Responses to a warming world. *Science* 294:
485 793-795.

486 Peñuelas J, Filella I, Comas P 2002. Change plant and animal life cycles from 1952 to
487 2000 in the Mediterranean region. *Global Change Biology* 8: 531-544.

488 Post ES, Pedersen C, Wilmers CC, Forchhammer MC. 2008. Phenological sequences
489 reveal aggregate life history response to climate warming. *Ecology* 89: 363-370.

490 R Development Core Team 2010. R Foundation for Statistical Computing, Vienna,
491 Austria.

492 Retzer JL. 1956. Alpine soils of the Rocky Mountains. *European Journal of Soil*
493 *Sciences* 7: 22-32.

494 SAS Institute, 2003. SAS for Windows. Version 9.1. SAS. Institute, Cary, North
495 Carolina, USA.

496

497 Schöb C, Kammer PM, Choler P, Veit H. 2009. Small-scale plant species distribution in
498 snowbeds and its sensibility to climate change. *Plant Ecology* 200: 91-104.

499 Scott D, Billings WD. 1964. Effects of environmental factors on standing crop and
500 productivity of an alpine tundra. *Ecological Monographs* 34: 243-270.

501 Servei Meteorològic de Catalunya (Meteocat). 2012. Butlletins Climàtics dels anys
502 2009, 2010 i 2011. Departament de Territori i Sostenibilitat. Generalitat de Catalunya.
503 [Http://www.meteocat.com](http://www.meteocat.com). Accessed 21 March 2012.

504 Stanton ML, Rejmanek M, Galen C. 1994. Changes in vegetation and soil fertility along
505 a predictable snowmelt gradient in the Mosquito range, Colorado, USA. *Arctic and*
506 *Alpine Research* 26: 364-374.

507 Surina Modric Z, Surina B. 2010. Snowbed vegetation in Croatia: Phytosociology,
508 ecology and conservation status. *Plant Biosystems*, 144 (4): 747-768.

509 Theurillat JP, Guisan A. 2001. Potential impact of climate change on vegetation in the
510 European Alps: a review. *Clim. Change* 50: 77-109.

511 Tieszen LL. 1975. CO₂ exchange in the Alaskan arctic tundra: seasonal changes in the
512 rate of photosynthesis of four species. *Photosynthetica* 9: 376-390.

513 Tomaselli M. 1991. The snow-bed vegetation in the Northern Apennines. *Vegetatio* 94:
514 177-189.

- 515 Totland O, Alatalo JM. 2002. Effects of temperature and date of snowmelt on growth,
516 reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*.
517 *Oecologia* 133: 168-175.
- 518 Walker DA, Halfpenny JC, Walker MD, Wessman CA. 1993. Long-term studies of
519 snow-vegetation interactions. *BioSciences* 43: 287-301.
- 520 Wipf S. 2010. Phenology, growth, and fecundity of eight subarctic tundra species in
521 response to snowmelt manipulations. *Plant Ecology* 201: 53-66.
- 522

523 **Tables**

524 Table I. Timing of snowmelt (Julian date) and accumulated temperature (°C) on three snowmelt
 525 isoclines [late snowmelt (LSM), intermediate snowmelt (ISM) and early snowmelt (ESM)] in two
 526 snowbeds in the Andorran Pyrenees.

| Site | Year | Snowmelt isocline | Timing of snowmelt (day of year) | Accumulated temperature (°C) |
|------------|------|-------------------|----------------------------------|------------------------------|
| Cataperdis | 2010 | ESM | 188 | 1150 |
| Cataperdis | 2010 | ISM | 209 | 572 |
| Cataperdis | 2010 | LSM | 230 | 184 |
| Cataperdis | 2011 | ESM | 195 | 978 |
| Cataperdis | 2011 | ISM | 202 | 668 |
| Cataperdis | 2011 | LSM | 209 | 336 |
| Arbella | 2010 | ESM | 209 | 941 |
| Arbella | 2010 | ISM | 230 | 513 |
| Arbella | 2010 | LSM | 237 | 212 |
| Arbella | 2011 | ESM | 202 | 923 |
| Arbella | 2011 | ISM | 223 | 744 |
| Arbella | 2011 | LSM | 237 | 284 |

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530 Table II. Hierarchical partitioning analysis of the factors considered (year, site and snowmelt
531 isocline explaining the variance (%) in snowmelt date and accumulated temperature in two
532 snowbeds in the Andorran Pyrenees. Values represent a measure of importance that adds up to
533 100. Significant factors ($p < 0.05$) are given in bold.

| | Hierarchical partitioning | | | |
|-------------------------|---------------------------|------|-------------|-------------------|
| | Variance explained (%) | Year | Site | Snowmelt isocline |
| Snowmelt date | 15.2 | 6.0 | 36.3 | 57.7 |
| Accumulated temperature | 16.6 | 1.5 | 2.5 | 96.0 |

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542 Table III. Species recorded in the two snowbeds studied in the Andorran Pyrenees in 2010 and
 543 2011. The species present only in the Cataperdis or Arbella snowbeds are indicated by a
 544 superscript C and A, respectively.

| Species | |
|---|---|
| <i>Agrostis rupestris</i> | <i>Mucizonia sedoides</i> |
| <i>Arabis alpina</i> | <i>Murbeckiella pinnatifida</i> |
| <i>Armeria maritima</i> | <i>Nardus stricta</i> |
| <i>Androsace carnea</i> | <i>Polytrichum sexangulare</i> |
| <i>Alopecurus gerardii</i> ^A | <i>Polytrichum piliferum</i> |
| <i>Anthelia juratzkana</i> | <i>Pohlia drumondi</i> |
| <i>Cardamine bellidifolia</i> | <i>Kiaeria starkei</i> ^A |
| <i>Carex pyrenaica</i> | <i>Oreochloa disticha</i> ^A |
| <i>Cerastium cerastoides</i> | <i>Poa alpina</i> |
| <i>Cryptogama crispa</i> ^A | <i>Polytrichum piliferum</i> |
| <i>Epilobium anagalifolium</i> | <i>Polytrichum sexangulare</i> |
| <i>Festuca glacialis</i> ^C | <i>Sedum alpestre</i> |
| <i>Gnaphalium supinum</i> | <i>Sagina saginoides</i> |
| <i>Hieracium gr. pilosella</i> | <i>Saxifraga stellaris</i> ^A |
| <i>Leucanthemopsis alpina</i> | <i>Sibbaldia procumbens</i> |
| <i>Luzula alpinopilosa</i> ^A | <i>Veronica alpina</i> |
| <i>Minuartia recurva</i> | <i>Veronica nummularia</i> |

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547 Table IV. Species richness (mean richness and standard deviation per plot of all species,
548 vascular plants, bryophytes and grasses) at Cataperdis, at Arbella and at both snowbeds in the
549 Andorran Pyrenees.

| | Both snowbeds | Cataperdis | Arbella |
|-----------------|----------------------|-------------------|----------------|
| All species | 7.19±3.25 | 8.83±2.97 | 5.52±2.64 |
| Vascular plants | 5.34±3.09 | 6.56±2.61 | 4.12±3.08 |
| Bryophytes | 1.85±1.03 | 2.33±0.95 | 1.37±0.87 |
| Grasses | 1.43±1.28 | 1.81±0.93 | 1.06±1.48 |

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557 Table V. Hierarchical partitioning analysis of the factors considered (year, site, snowmelt isocline
 558 and plot) explaining the variance (%) in the time required to reach phenophases (cessation of
 559 leaf expansion and flowering) in the four commonest species (*Gnaphalium supinum*, *Mucizonia*
 560 *sedoides*, *Poa alpina* and *Sedum alpestre*) occurring in two snowbeds in the Andorran
 561 Pyrenees Significant terms ($p < 0.05$) are given in bold.

| Species | Phenophase | n | Variance Explained (in %) | Hierarchical partitioning | | | |
|---------------------------|-----------------------------|----|---------------------------|---------------------------|-------------|-------------------|------------|
| | | | | Year | Site | Snowmelt isocline | Plot |
| <i>Gnaphalium supinum</i> | Cessation of leaf expansion | 80 | 37.1 | 42.1 | 9.7 | 47.6 | 0.6 |
| | Flowering | 57 | 20.0 | 43.0 | 7.9 | 47.0 | 2.1 |
| <i>Mucizonia sedoides</i> | Cessation of leaf expansion | 72 | 71.0 | 66.2 | 7.0 | 26.7 | 0.1 |
| | Flowering | 52 | 18.7 | 59.6 | 22.4 | 9.7 | 8.3 |
| <i>Poa alpina</i> | Cessation of leaf expansion | 42 | 40.1 | 27.4 | 27.4 | 44.4 | 0.8 |
| | Flowering | 38 | 36.9 | 46.6 | 28.5 | 27.1 | 2.8 |
| <i>Sedum alpestre</i> | Cessation of leaf expansion | 91 | 92.7 | 12.9 | 48.0 | 38.9 | 0.2 |
| | Flowering | 46 | 58.2 | 56.0 | 26.8 | 16.7 | 0.5 |

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564 Table VI. Non-parametric one-way ANOVA of the time taken to reach each phenophase on
 565 three snowmelt isoclines in two snowbeds in the Andorran Pyrenees. P-values for significant
 566 terms are indicated in bold. SA *Sedum alpestre*; MS *Mucizonia sedoides*; GS *Gnaphalium*
 567 *supinum* and PA *Poa alpina*.

| Species | Phenology (days) | n | Chi ² value | P value |
|---------|---|----|------------------------|--------------|
| | Snowmelt to the cessation of leaf expansion | 94 | 36.42 | 0.001 |
| SA | Leaf expansion to flowering | 48 | 3.55 | 0.168 |
| | Snowmelt to flowering | 48 | 8.78 | 0.012 |
| | Snowmelt to the cessation of leaf expansion | 69 | 5.89 | 0.052 |
| MS | Leaf expansion to flowering | 54 | 12.79 | 0.001 |
| | Snowmelt to flowering | 54 | 14.63 | 0.001 |
| | Snowmelt to the cessation of leaf expansion | 79 | 1.22 | 0.542 |
| GS | Leaf expansion to flowering | 61 | 1.47 | 0.478 |
| | Snowmelt to flowering | 61 | 10.62 | 0.004 |
| | Snowmelt to the cessation of leaf expansion | 48 | 0.16 | 0.923 |
| PA | Leaf expansion to flowering | 39 | 5.83 | 0.054 |
| | Snowmelt to flowering | 39 | 2.63 | 0.268 |

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570 **Figure captions**

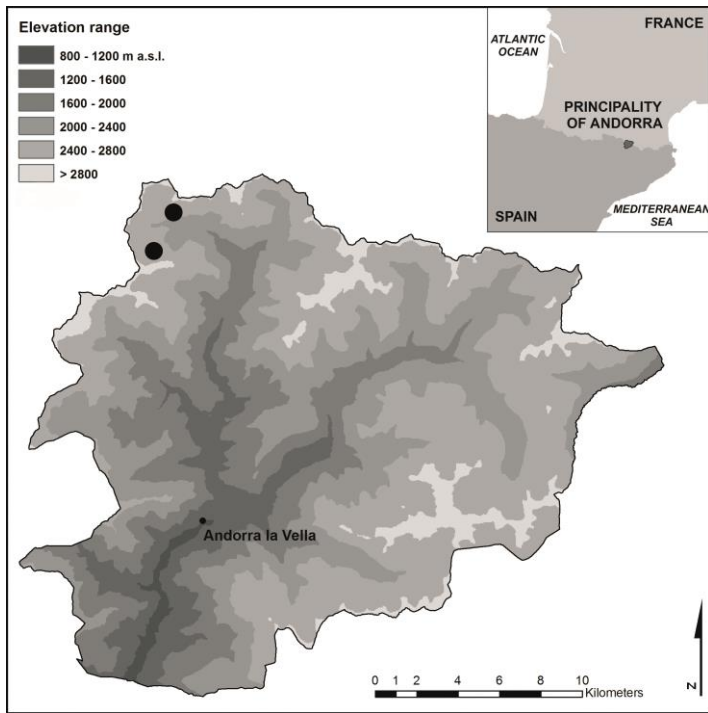
571 Figure 1. Location of the two snowbeds in the Andorran Pyrenees (black dots).

572 Figure 2. Peak flowering at early (ESM isoclines) and late (LSM isoclines) snowmelt plots in two
573 snowbeds (Cataperdis and Arbella) in the Andorran Pyrenees in 2010 and 2011. Flowering
574 duration at Cataperdis in 2010 and at ESM sites was 7 weeks, 4 in 2011. Flowering duration at
575 Cataperdis in 2010 and at LSM sites was 2 weeks, 3 in 2011. Flowering duration at Arbella in
576 2010 and at ESM sites was 7 weeks, 7 in 2011. Flowering duration at Arbella in 2010 and at
577 LSM sites was 3 weeks, 2 in 2011.

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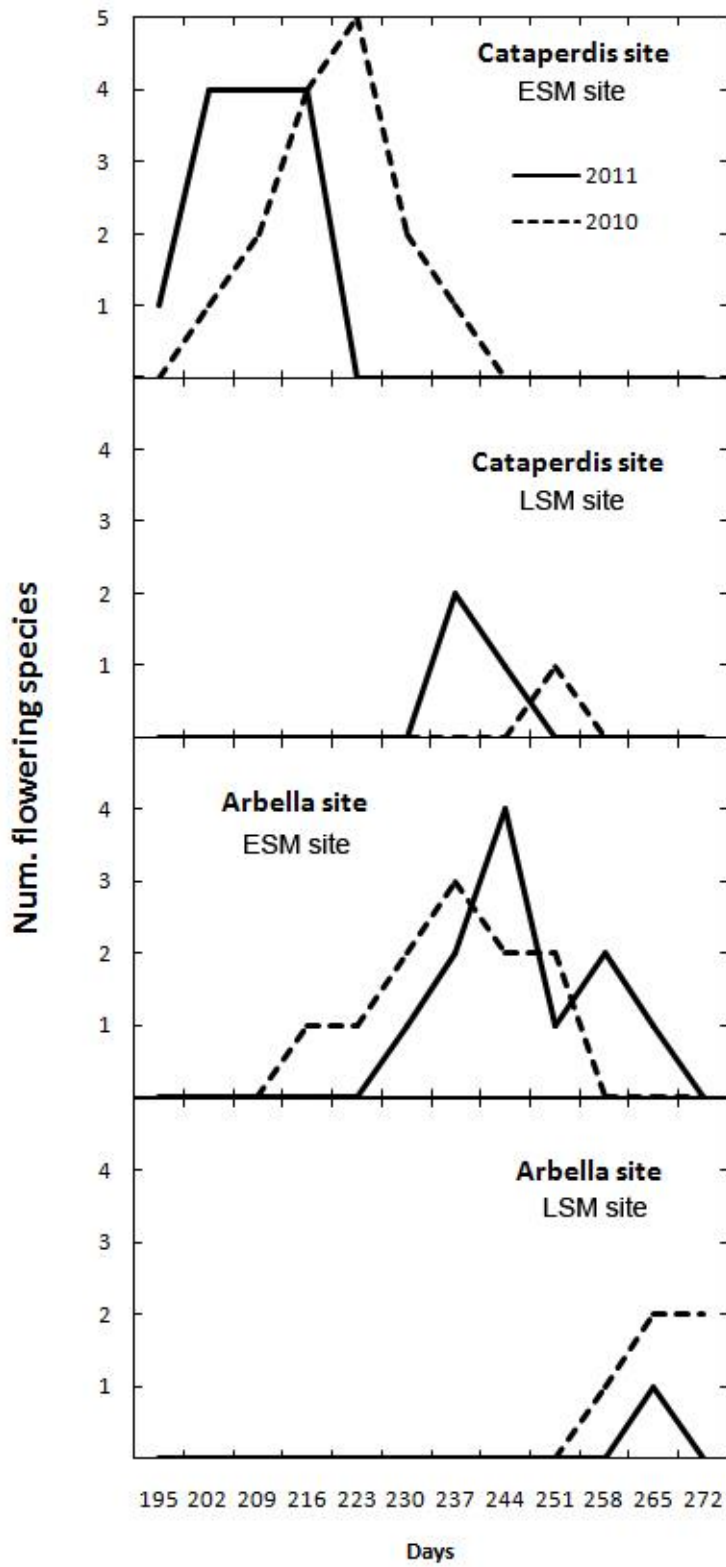
579 Figure 1.

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582 Figure 2.



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586 **Marta Domenèch and Benjamin Komac:** Centre d'Estudis de la Neu i la Muntanya d'Andorra
587 (CENMA) de l'Institut d'Estudis Andorrans (IEA); Av. Rocafort, 21-23, AD600 Sant Julià de
588 Lòria, Andorra;

589 **Josep Peñuelas:**

590 1. CSIC, Global Ecology Unit CREAF-CSIC-UAB, Cerdanyola del Vallès, 08913 Catalonia, Spain

591 2. CREAF, Cerdanyola del Vallès, 08913 Catalonia, Spain

592

593 **Josep Antoni Conesa:** Departament de Hortofructicultura, Botànica i Jardineria de l'Escola
594 Tècnica Superior d'Enginyeria Agrària de la Universitat de Lleida (UdL); Rovira Roure 191,
595 25198 Lleida, Spain.