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Moss survival through *in situ* cryptobiosis after six centuries of glacier burial

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Cryptobiosis is a reversible ametabolic state of life characterized by the ceasing of all metabolic processes, allowing survival of periods of intense adverse conditions. Here we show that 1) entire moss individuals, dated by ^{14}C, survived through cryptobiosis during six centuries of cold-based glacier burial in Antarctica, 2) after re-exposure due to glacier retreat, instead of dying (due to high rates of respiration supporting repair processes), at least some of these mosses were able to return to a metabolically active state and remain alive. Moss survival was assessed through growth experiments and, for the first time, through vitality measurements. Future investigations on the genetic pathways involved in cryptobiosis and the subsequent recovery mechanisms will provide key information on their applicability to other systematic groups, with implications for fields as divergent as medicine, biodiversity conservation, agriculture and space exploration.

Cryptobiosis is a reversible ametabolic state of life that has been considered as a third state between life and death[1]. It is characterized by the ceasing of all metabolic processes and allows survival of periods of intense adverse environmental conditions such as desiccation, freezing or oxygen deficiency, or combinations of these[1,2]. The occurrence of cryptobiosis is documented in several invertebrate groups including rotifers, chironomid midges, nematodes and tardigrades[1,3], as well as in many microbial groups occurring in polar and other extreme environments[4,5]. Cryptobiosis differs from dormancy (hibernation, aestivation, diapause or quiescence), which is associated with a low but still measurable level of metabolism (or hypometabolism), albeit with the temporary cessation of growth, development and (in animals) physical activity[2]. Dormancy is well documented in the invertebrates, plants and microbes of extreme environments[6], allowing their survival during inclement periods through different mechanisms (e.g. tolerance of freezing, desiccation).

Cryptobiosis is a survival strategy that appears particularly suited to the permafrost environment. Several different microbial groups are known to remain viable in permafrost, surviving under the permanently frozen habitat conditions possibly from the point of their formation, in some cases up to 30,000 years[4,7]. At subzero temperatures the rates of biochemical reactions and processes become extremely low, and ensure the preservation of the biological system[4].

Survival under frozen or anhydrobiotic conditions in nematodes, rotifers and tardigrades, widely acknowledged to be three of the most resistant invertebrate groups, has likewise been demonstrated over periods of only a decade or two at most[7,8]. Survival through cryptobiosis in mosses and lichens has been reported for laboratory experiments by Keilin[2]: fragments of mosses and lichens previously desiccated and cooled at −273 °C revived after being kept for about 2 hours at −272 °C. Direct regeneration after cryptobiosis has been demonstrated in mosses in laboratory experiments from herbarium (dried) and frozen material preserved for 20 years at most[9,10] and over shorter periods (five years) for ferns and angiosperms[11]. Long-term cryoptobiosis lasting for centuries has been described for angiosperm seeds, although seed germination was obtained only in the laboratory through cloning and *in vitro* culturing approaches[4,12,13]. Regeneration, suggested by *in vivo* field observations, was recently demonstrated through *in vitro* growth from exhumed mosses re-exposed by glacier retreat after 400 years of burial by a cold-based glacier in Canada, demonstrating the totipotent capacity of bryophytes[14]. Millennial scale viability has been described from a core of an *in situ* moss bank in Antarctica preserved within permafrost that,

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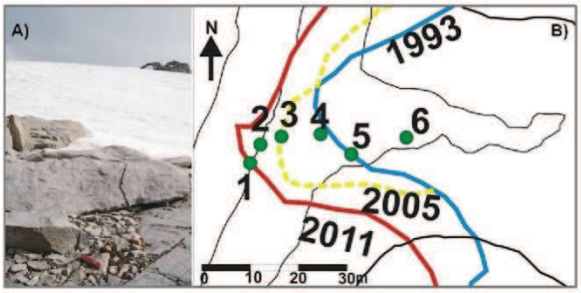

Figure 1. (**A**) View of the glacial margin of the Wormald Ice Piedmont (Rothera Point, Antarctic Peninsula, taken in 2009). The occurrence of exhumed patches of the moss *Bryum pseudotriquetrum* can be seen in the foreground. (**B**) Map showing the location of the moss samples (see Table 1) with the position of the glacier boundary in 1993 (blue line), 2005 (yellow line) and 2011 (red line) (map created by CorelDraw 6.0).

after thawing in the laboratory, showed regeneration of moss shoots[15]. These studies were interpreted as cases of cryptobiosis, but did not involve direct measurements of moss metabolic vitality.

Mosses are major components of plant communities in terms of diversity and biomass in high latitude ecosystems in the High Arctic and in Antarctica, where macroscopic vegetation is dominated by cryptogams[16,17]. Mosses are poikilohydric organisms with high degree of phenotypic plasticity[18] and have well-developed features allowing them to tolerate stress[15] and thrive in environments subject to change and disturbance[16]. Among the key traits allowing mosses to persist in harsh environments, one of the most important is tolerance to desiccation and drought[18], also contributing to their ability to resist freezing (as during the Antarctic winter)[19].

In this study, measurements of metabolic activity through chlorophyll *a* fluorescence (as indicators of vitality and survival) and growth chamber experiments applied to mosses exposed by recent glacier retreat at Rothera Point (maritime Antarctica) present evidence of: a) *in situ* moss survival for over more than 600 y in the natural habitat through cryptobiosis, and their subsequent spontaneous recovery to active metabolism after glacier retreat, b) persistence of active metabolism and growth in surviving exhumed mosses, c) regeneration with development of green stem apices from moribund stems of exhumed mosses.

Results

Direct Observations and Radiocarbon Dating. Two moss species, *Bryum pseudotriquetrum* (Hedw.) P. Gaertn. and *Sanionia uncinata* (Hedw.) Loeske, were collected from six sites in the glacier front (Fig. 1A,B) and foreland: five samples of exhumed mosses (n. 1–5), plus an extant moss (n. 6, located at 16.8 m from the ice margin in 2011) used for comparison (Table 1). The sample n. 1 was emergent during the week of the collection, and the sample n. 2 was located less than 1 m from the glacier front and likely exhumed less than one year previously (Table 1). The remaining three samples (n. 3–5, Table 1) were located close to the glacier front (between <1 m and 10.1 m from the ice margin in 2011) and exhumed between six and 18 years ago (Table 1). All exhumed samples were from *in situ* habitats in the field, with exceptional preservation and no damage apparent to the gametophytes which exhibited intact rhizoids, stems and leaves. No sporophyte tissue was present. All samples lacked any sign of regrowth, with green lateral branches and stem apices being absent. The calibrated age (see methods) of three of the most recently exhumed moss (n. 1, 3, 4) was determined by radiocarbon dating and ranged between 640–526 and 626–510 cal years BP (Table 1).

Based on field observations and examination in the laboratory with a dissecting microscope (after sample collection, and prior to the growth experiment), two exhumed mosses (n. 1, 2) and the extant sample (n. 6) showed persistence of visibly greenish material with green leaves (Fig. 2A,B) lacking any decomposition processes and/or development of moulds. The other three exhumed samples (n. 3–5) were characterized by blackish leaves, and/or their desiccation (Table 1). From these observations, we suggest the two recently exhumed and extant mosses were biologically active populations whereas the other three exhumed mosses were moribund (Table 1).

Vitality Measurements. Moss vitality was tested by analyzing the metabolic activity of the gametophores using Chlorophyll *a* fluorescence with reference to a) the values of Fv/Fm (variable fluorescence/maximum fluorescence maximum) (Table 1), and b) the shape of the induction curve (Fig. 3). We considered the gametophytes to be metabolically active when Fv/Fm >0.2[20,21]. Applying this threshold, metabolic activity (compatible with life/vitality) was detected for all the three mosses suggested to be biologically active based on visual inspection (n. 1, 2, 6). The three mosses suggested to be moribund (n. 3–5) exhibited values of Fv/Fm slightly higher than the threshold of 0.2, also indicating metabolic activity, but at a poor level.

Analyzing the fluorescence induction curve shape, the progressive flattening observed comparing the extant moss specimen with the two recently exposed moss clumps indicated a progressive decrease of activity. Conversely, the flattened shape of the fluorescence induction curve of the three mosses suggested them to be moribund (samples n. 3–5) and indicated a lack of activity.

Growth Experiment. During the growth experiment, the three metabolically active samples (based on their Fv/Fm values; n. 1, 2, 6) remained alive (sample n. 2, Fig. 2A,B), with the extant moss (n. 6) and the recently

Sample #	Lab code for 14 C dating (Beta)	Conventional Age BP	Calibrated age 2σ range (cal y BP)	Maximum time since exhumation (yr); DIM (m)	Species name	Visual Observations	Chlorophyll *a* measurement of metabolic activity (Fv/Fm)	Induction curve shape	Response during growth experiment
1	356172	580 ± 30	626–510	0 y; at ice margin	SU	Active	0.39 ± 0.10	Active	Alive+Growth
2			626–510	1 y; <1 m	BP	Active	0.49 ± 0.13	Active	Alive
3	457644	600 ± 30	631–519	6 y; 6 m	BP	Moribund	0.28 ± 0.07	Inactive	Moribund
4	457643	620 ± 30	640–526	18 y; 9.7 m	BP	Moribund	0.28 ± 0.10	Inactive	Regeneration
5				18 y; 10.1 m	BP	Moribund	0.29 ± 0.04	Inactive	Regeneration
6			Extant	Never glacier covered; 16.8 m	BP	Active	0.53 ± 0.11	Active	Alive+Growth

Table 1. Moss samples collected along the boundary of the Wormald Ice Piedmont from the ice/glacier foreland, presenting conventional and calibrated age 2σ range (cal y BP); maximum time since exhumation after glacier retreat (see Fig. 1B); minimum distance from the ice margin (m) (DIM); species name; visual observations (field and dissecting microscope prior the 2014 regrowth experiment); value of Fv/Fm (variable fluorescence/maximum fluorescence) of the chlorophyll *a* fluorescence measurements; shape of the induction curve obtained during chlorophyll *a* fluorescence measurements; response during the growth experiment. Legend: BP = *Bryum pseudotriquetrum*; SU = *Sanionia uncinata*.

exposed sample of *S. uncinata* (n. 1) exhibiting growth (Table 1, Fig. 2F,H), and growth occurred from the stem apex in both the latter cases (without any protonemal or rhizoid initial growth). Among the moribund mosses, sample n. 3 became marcescent and covered by fungal hyphae, and did not show any regeneration (Table 1), whereas the other two moribund samples (n. 4, 5) exhibited regeneration (Fig. 2C–E,G), with growth of leaves at the branch apices in existing gametophyte shoots (Table 1).

Discussion

Cryptobiosis has already been demonstrated for mosses in polar environments, based on *in vivo* observations[14] and *in vitro* regeneration experiments[14,15]. Our data, based on fluorescence measurements, corroborate these previous studies. Cryptobiosis in our study is indicated by long-term survival for six centuries, but the study's true novelty is the demonstration, based on vitality measurements as well as on growth experiments, of the ability of entire moss individuals to withstand six centuries of cryptobiosis and, at its cessation, to spontaneously recover to active metabolism and survive *in situ* following glacier retreat. Indeed, the chlorophyll *a* fluorescence measurements indicated the occurrence of metabolic activity (compatible with life) for all the three mosses hypothesized to be active based on visual inspection (n. 1, 2, 6). Their Fv/Fm values were lower than would typically be recorded from extant field samples (ranging between 0.6 and 0.8)[21]. However, it is well known that repeated freeze-thaw cycles decrease Fv/Fm, especially when mosses are exposed to light[22], as would be the case for these mosses re-exposed by the glacier retreat during the austral summer (with 24 hours of light per day). These results are confirmed by the fluorescence induction curve (Fig. 3), that shows a decrease of activity from the extant moss and the two recently exposed mosses. This is similar to the report of Rutten and Santarius[23] when testing age-related differences in frost tolerance of mosses subject to experimental freezing, in particular, the data obtained from the extant moss (sample n. 6, Fig. 3 curve M6) with young leaves (cf. Rutten and Santarius, Fig. 3 curve 11), the most recently exhumed moss (sample n. 1, Fig. 3 curve M1) with mature leaves (cf. Rutten and Santarius, Fig. 3 curve 10), and the 1 y exhumed moss (sample n. 2, Fig. 3 curve M2) with old leaves (cf. Rutten and Santarius, Fig. 3 curve 6).

All vitality analyses indicated, at best, poor metabolic activity for the mosses with longer re-exposure times and suggested to be moribund on the basis of visual observations (n. 3–5). Using the extant moss specimen for comparison, our data indicated the persistence of active metabolism and capacity for regrowth of the very recently re-exposed mosses (n. 1), whereas survival and active metabolism were observed for the less recently exhumed moss clumps (≤1 y) (sample n. 2). The mosses that had been exposed for longer intervals were considered moribund as indicated by poor or lack of metabolic activity, but showed regeneration in the growth experiment, as noted in some previous studies[14,15].

Recovery processes leading to resumption of normal metabolic activity after cryptobiosis are often characterized by high rates of respiration repair processes that, in some cases, can be lethal[24], especially if mosses are exposed to light, due to photoinhibitory damage[22]. The intensity and frequency of these recovery processes may explain the different ability of mosses to survive and grow after different periods of re-exposure. As time progresses (>1 y) after re-exposure, the mosses will face repeated seasonal dormancy and adverse conditions[25]. Therefore, accumulated damage with the recovery processes will increase with time, explaining why longer re-exposure time may be associated with the observed lower vitality.

Future perspectives may concern investigations on the genetic mechanisms involved in cryptobiosis and the subsequent recovery mechanisms, which would also provide information on the potential exportability and applicability of these mechanisms to other systematic groups (including humans), with potential relevance for medicine (e.g. organ banking through the cryopreservation of complex tissues[26]), biodiversity conservation (germplasm, embryogenic cells of both gymnosperms and angiosperms[27]), agriculture (cultivars of major food crops[28]) and space exploration (dormancy during space travel[29], use of anhydrobiosis and cryobiosis to protect organisms exposed to space and exoplanetary environments[30]).

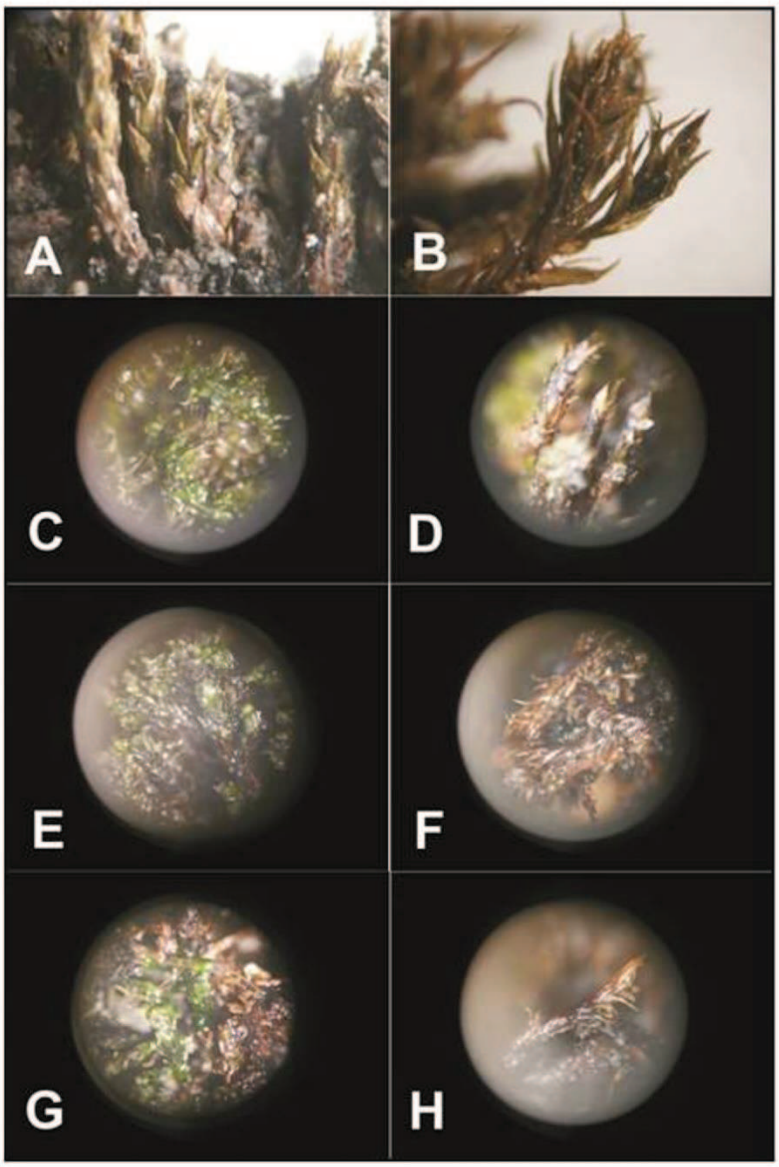

Figure 2. Moss samples of *Bryum pseudotriquetrum* (Hedw.) P. Gaertn. (**A**–**E**,**G**) and *Sanionia uncinata* (Hedw.) Loeske (**F**,**H**) that were assessed as active in the field ((**A**,**B**) sample n. 2), remained alive and exhibited regeneration during the growth experiment ((**C**–**E**,**G**) samples n. 4, 5 (**F**,**H**) sample n. 1).

Materials and Methods

Study area. The study area was located at Rothera Point (67°34′S; 68°07′W) on Adelaide Island, Marguerite Bay, southern Maritime Antarctic. The climate is a cold dry maritime climate, with mean annual air temperature of −4.2 °C and mean annual precipitation of about 500 mm, of which 20% occurs as rain. Permafrost is continuous and exceeds 100 m in depth with an active layer ranging between 0.76 and 1.40 m. Vegetation on Rothera Point is scattered and mainly composed of epilithic lichens (dominated by *Usnea sphacelata* and *Umbilicaria decussata*), and sporadic mosses.

The study site was located at the southern limit of the Wormald Ice Piedmont Glacier, locally known as the "ice ramp", and located between 10 and 110 m a.s.l. This glacier front has been monitored since 1989 and has receded rapidly in recent decades, with ablation rates (surface lowering) of 0.32 m water equivalent between 1989 and 1997, and a frontal retreat that increased from 0.85 m/y (period 1997–2005) to 1 m/y (2005–2011).

Field sampling. In February 2009 some scattered moss patches with 1–2 cm of underlying organic matter were observed among the boulders at 1.5 m from the 2009 ice/glacier front. These were sampled for radiocarbon

The kinetics of the light reaction provides an assessment of the recovery of the electron transport in PSII by analyzing the shape of the fluorescence induction curve[35]. To identify all steps in the induction curve a logarithmic presentation of the time axis was used[34]. According to the standard procedure adopted when using PEA fluorometers, the time axis of the induction curve started from 50 μs[34]. Normally the induction curve is characterized by four steps (named O, J, I, P), however samples subject to freezing exhibited different sensitivity of young vs. mature vs. old leaves, with resultant changes of the induction curve shape[23]. To achieve further confirmation of the vitality of the samples analyzed, and to test for differences linked to their different exposure ages, the induction curves for each assay were recorded and logged.

Growth experiment. The growth experiment utilized the natural substrate from beneath moss populations at Anchorage Island (close to Rothera Point) mixed with high quality commercial litter (Tercomposti s.r.l. Brescia). Twelve glass cups were filled each with 9 g of this soil substrate. The 12 filled cups were sterilized at 120 °C for 15 min, transferred into sterilized Petri dishes, sealed with parafilm and placed in a growth chamber (CV-36L5, Percival Scientifics Series 101) from 17 January 2014 to 17 March 2014. In the growth chamber they were kept under controlled conditions at a fixed temperature of 15 °C, with 16 h of light (17 W cool-white fluorescence lamps, light intensity of 64 μmoles/m^2/s) and 8 h of darkness[14,15]. After two months in the growth chamber all 12 Petri dishes with soil substratum were completely sterile. Six were then used for the moss samples and 6 as controls. On 18 March 2014 the moss samples were transferred into the Petri dishes with the soil substratum: in each Petri dish each moss sample was divided into three sub-samples. Then the 12 Petri dishes were returned to the growth chamber and maintained under the same controlled conditions[14,15]. Once per week each Petri dish received 5 ml of deionized water (misting each specimen with a handheld spray bottle), which had previously been sterilized for 15 min at 120 °C[14]. All samples were placed in shallow trays and repositioned every 15 d to minimize effects of any variations in light intensity within the chamber[14]. The contents of the Petri dishes were inspected visually (including both the moss samples and the six soil control plots) and regularly observed under a dissecting microscope[15] between 19 May and 2 December 2014.

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Author Contributions
N.C. planned the project; N.C. and F.M. performed the field sampling; N.C., F.M., P.G., T.C., A.V., P.C., I.V., S.Z., M.G. performed the sample preparation and laboratory analyses; M.G. created the map of Figure 1B with CorelDraw 6.0; all authors discussed the results and interpretation; N.C. wrote the manuscript with input from all authors.

Additional Information
Competing Interests: The authors declare that they have no competing interests.

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VI. CONCLUSIONS AND FINAL REMARKS

In conclusion, we started the assessment of expected impacts of climate change on terrestrial ecosystems within two case studies in regions geographically and evolutionary remote and distinct, but both already affected by recent climate changes: European Alps and Maritime Antarctica.

In the Alps, the *in-situ* manipulation experiments confirmed to be a valuable and relatively easy way to perform studies on climate change impacts. The deployment of Open Top Chambers (OTCs) and Snow Fence (SF) confirmed their influences on ground surface temperature and snowmelt respectively. The deployment of the Precipitation Shields (PS) confirm to affect the soil moisture, but with some unexpected pattern, due to the influence of wind during the rain events, and also an associated warming effect.

The warming effect generated by open top chambers and precipitation shields were within the expected increase of the global mean surface temperature by the end of the 21sr century (**IPCC, 2014**). Therefore, Biological responses to such a warming were those we could expect in that scenario.

The experiment design allowed us to identify already after 4 years of study the first responses of vegetation to climate forcing drivers, underlining once again the sensibility of the tundra ecosystems to a changing environment.

Ingression of new species (even still localised and scattered) and changes in coverages of the main vegetation layers and main growth forms, indicated the possible future direction of vegetation structure and, therefore, of ecosystem and landscape properties. Temperature resulted as the most limiting factors, but we reported evidences of growing season length and soil moisture limitations as well.

The phenology under changing environmental factors indicated species-specific differences, but also plant communities and local conditions (topography) played an important role and therefore they must be considered in the evaluation of the phenological plasticity of the alpine plants. It is remarkable that the same species responded differently to the same manipulation treatment depending on its community type and ecological requirement showing better performances or reduced damage within its optimal community and with larger stress and/or damage when within a sub-optimal community (***h4***).

Among all, it is of relevant interest the main effect of soil warming in determining the advancement of most of the phenological stages, from flowering, to seed development and dispersal but not of the leaf senescence, thus showing that the possible benefit of an extended growing season in response to a future Autumn warming will depend not only on the temperature change but also on the soil moisture. Even more relevant was the findings of the drought ability to buffer and counteract the biological answer to soil warming (***h1***), again with species-specific differences due to community types and ecological niches.
Moreover, plant size and the reproductive investment and success of the selected species have been found to be extremely sensitive to the environmental changes, but with different responses among species. This finding underlines once again the need and importance to analyse the species-specific responses, for each phenological stages, in order to identify “winner” and “looser” species in a climate change scenario, depending on their plasticity and conservative/adaptive strategies. Similarly, the

comparison of the same species between different communities could help to quantify the degree of species plasticity.

The phenological results supported also the hypothesis of a snowmelt effect on the late phenological stages (***h2***), particularly visible in the snowbeds species, and the strong sensitivity of the alpine species to extreme years (particular warm and dry or particularly cold) (***h5***), that exceed the biological answer under a constant environmental change.
Differently, an agreement between vegetative and reproductive phenology and changes in species abundance has been found only for some species and treatments, supporting only in part the third hypothesis (***h3***) and underlining the need of further years of monitoring to clarify this point.

The data that we collected at the Stelvio pass area could be used for adaptation strategies and management plans, which have to be implemented in a protected area such the Stelvio National Park.

In northern maritime Antarctica (Signy Island) we installed manipulation experiments similar to those set up in the Alps. The assessment of any vegetation changes was not possible, because of the logistical constrain and of the short period of manipulation (2 years). However the experiments could thus help to disentangle which are the main drivers of vegetation colonization and stabilization, in order to create models on the evolution of Antarctic terrestrial ecosystems under different future climate change scenario, which could enforce the management strategies of these peculiar environments

In southern maritime Antarctica (Rothera Point), we investigated the past climate changes and climate change impacts on the abiotic component of this ecosystems (**Guglielmin et al.,2016**) and how similar changes are reactivating moribund mosses (**Cannone et al.,2017**) with future perspective in medicine, biodiversity conservation, agriculture and space exploration.

Future perspectives

The maintenance and prosecution (from mid to, possibly, long term) of the monitoring and manipulation of both the environmental and the biological components are recommended to achieve a more accurate knowledge on the alpine plant plasticity to climate change. Moreover, it allows to detect the occurrence of any threshold above which the environmental conditions induce a change in the biological answer or otherwise to find species for which several years are required before a response can be detected (**Hoffmann et al., 2010**).

Several points of these experiments and data elaboration could improve our knowledge on the plasticity of alpine plants. We based our analysis on the first days of observation of each phenological stages, combined with some semi-quantitative data, such as the day of maximum amount of each stages. However, for further extending our analysis it will be interesting to consider all the distributional curve of each phenological stages, in order to assess how communities respond in a spatio-temporal dimension in each growing season. .

We observed the responses only on the above-ground tissues of the vegetation, but it would be important to analyse and assess the below ground tissues as well, in order to understand the occurrence of an increased or decreased below ground allocation under different climate change scenarios. This would be useful in the evaluation of the growth forms and species changes that could lie in an increased competitiveness in water and nutrients absorption.

Moreover, the monitoring of the photosynthetically activity of different species and growth forms, would be useful in the assessment of the metabolic adaptation to a changing climate in alpine species.

Tab. S 1 - Topographic characterization of permanent plots. Experiment: OTC = Open Top Chamber; SF = Snowfence; PS = Precipitation shield. Community: CC = *Caricetum curvulae*; SH = *Salicetum herbaceae*.

Plot ID	site	experiment	treatment	community	altitude (m asl)	slope (°)	aspect	Size (m2)	Plot ID	site	experiment	treatment	community	altitude (m asl)	slope (°)	aspect	Size (m2)
OTC-CC1	1	OTC	OTC	CC	2605	11	NW	2	SF2N07	1	SF	SFN07	CC	2612	9	N	1
OTC-CC1c	1	OTC	OTCc	CC	2608	10	NW	1	SF2N08	1	SF	SFN08	CC	2612	5	N	1
OTC-CC2	1	OTC	OTC	CC	2607	11	NW	2	SF2N09	1	SF	SFN09	CC	2609	16	N	1
OTC-CC2c	1	OTC	OTCc	CC	2609	11	NW	1	SF2N10	1	SF	SFN10	CC	2609	4	N	1
OTC-CC3	1	OTC	OTC	CC	2612	22	NW	2	SF2S01	1	SF	SFS01	CC	2612	4	NW	1
OTC-CC3c	1	OTC	OTCc	CC	2612	18	NW	1	SF2S02	1	SF	SFS02	CC	2612	6	W	1
OTC-SH1	1	OTC	OTC	SH	2632	5	N	2	SF2S03	1	SF	SFS03	CC	2612	32	W	1
OTC-SH1c	1	OTC	OTCc	SH	2634	5	N	1	SF2S04	1	SF	SFS04	CC	2612	12	SE	1
OTC-SH2	1	OTC	OTC	SH	2633	7	NW	2	SF2S05	1	SF	SFS05	CC	2612	6	NW	1
OTC-SH2c	1	OTC	OTCc	SH	2635	5	NW	1	SF2S06	1	SF	SFS06	CC	2611	18	NW	1
OTC-SH3	1	OTC	OTC	SH	2633	7	NW	2	SF2S07	1	SF	SFS07	CC	2610	16	W	1
OTC-SH3c	1	OTC	OTCc	SH	2632	7	NW	1	SF2S08	1	SF	SFS08	CC	2611	5	W	1
PS-CC1	1	PS	PS	CC	2619	11	NW	2	SF2S09	1	SF	SFS09	CC	2611	10	W	1
PS-CC1m	1	PS	PSc	CC	2618	16	NW	1	SF2S10	1	SF	SFS10	CC	2611	10	W	1
PS-CC1v1	1	PS	PSv1	CC	2618	9	NW	1	SF3N01	1	SF	SFN01	CC	2607	17	N	1
PS-CC1v2	1	PS	PSv2	CC	2618	10	NW	1	SF3N02	1	SF	SFN02	CC	2607	5	N	1
PS-CC2	1	PS	PS	CC	2617	11	NW	2	SF3N03	1	SF	SFN03	CC	2607	26	N	1
PS-CC2m	1	PS	PSc	CC	2619	12	NW	1	SF3N04	1	SF	SFN04	CC	2607	10	N	1
PS-CC2v1	1	PS	PSv1	CC	2620	10	NW	1	SF3N05	1	SF	SFN05	CC	2607	13	N	1
PS-CC2v2	1	PS	PSv2	CC	2620	22	NW	1	SF3N06	1	SF	SFN06	CC	2604	9	NE	1
PS-SH1	1	PS	PS	SH	2628	7	NW	2	SF3N07	1	SF	SFN07	CC	2604	11	NE	1
PS-SH1m	1	PS	PSc	SH	2629	8	N	1	SF3N08	1	SF	SFN08	CC	2604	16	NE	1
PS-SH1v1	1	PS	PSv1	SH	2629	7	N	1	SF3N09	1	SF	SFN09	CC	2603	4	N	1
PS-SH1v2	1	PS	PSv2	SH	2627	8	NW	1	SF3N10	1	SF	SFN10	CC	2603	6	N	1
PS-SH2	1	PS	PS	SH	2628	6	NW	2	SF3S01	1	SF	SFS01	CC	2608	16	NW	1
PS-SH2m	1	PS	PSc	SH	2629	7	N	1	SF3S02	1	SF	SFS02	CC	2608	6	NW	1
PS-SH2v1	1	PS	PSv1	SH	2629	7	NW	1	SF3S03	1	SF	SFS03	CC	2608	16	NW	1
PS-SH2v2	1	PS	PSv2	SH	2629	7	NW	1	SF3S04	1	SF	SFS04	CC	2608	16	NW	1
SF1N01	1	SF	SFN01	CC	2612	18	N	1	SF3S05	1	SF	SFS05	CC	2607	12	W	1
SF1N02	1	SF	SFN02	CC	2613	11	N	1	SF3S06	1	SF	SFS06	CC	2607	6	W	1
SF1N03	1	SF	SFN03	CC	2614	12	N	1	SF3S07	1	SF	SFS07	CC	2607	1	W	1
SF1N04	1	SF	SFN04	CC	2612	10	N	1	SF3S08	1	SF	SFS08	CC	2604	18	W	1
SF1N05	1	SF	SFN05	CC	2612	12	N	1	SF3S09	1	SF	SFS09	CC	2604	6	W	1
SF1N06	1	SF	SFN06	CC	2612	10	NE	1	SF3S10	1	SF	SFS10	CC	2604	8	W	1
SF1N07	1	SF	SFN07	CC	2611	9	NE	1	OTCs-CC1	2	OTC	OTC	CC	2630	9	S	2
SF1N08	1	SF	SFN08	CC	2611	11	N	1	OTCs-CC1c	2	OTC	OTCc	CC	2630	9	S	1
SF1N09	1	SF	SFN09	CC	2610	4	NE	1	OTCs-CC2	2	OTC	OTC	CC	2630	12	S	2
SF1N10	1	SF	SFN10	CC	2609	6	NE	1	OTCs-CC2c	2	OTC	OTCc	CC	2629	10	W	1
SF1S01	1	SF	SFS01	CC	2614	8	NW	1	OTCs-CC3	2	OTC	OTC	CC	2629	13	W	2
SF1S02	1	SF	SFS02	CC	2615	2	NW	1	OTCs-CC3c	2	OTC	OTCc	CC	2629	12	W	1
SF1S03	1	SF	SFS03	CC	2614	2	NW	1	OTCs-SH1	2	OTC	OTC	SH	2626	10	W	2
SF1S04	1	SF	SFS04	CC	2614	12	NW	1	OTCs-SH1c	2	OTC	OTCc	SH	2626	10	W	1
SF1S05	1	SF	SFS05	CC	2613	6	NW	1	OTCs-SH2	2	OTC	OTC	SH	2627	10	W	2
SF1S06	1	SF	SFS06	CC	2613	1	NW	1	OTCs-SH2c	2	OTC	OTCc	SH	2627	8	W	1
SF1S07	1	SF	SFS07	CC	2613	10	NW	1	OTCs-SH3	2	OTC	OTC	SH	2626	11	W	2
SF1S08	1	SF	SFS08	CC	2612	12	W	1	OTCs-SH3c	2	OTC	OTCc	SH	2627	10	W	1
SF1S09	1	SF	SFS09	CC	2612	8	W	1	PSs-CC1	2	PS	PS	CC	2628	12	W	2
SF1S10	1	SF	SFS10	CC	2611	11	SW	1	PSs-CC1m	2	PS	PSc	CC	2628	10	W	1
SF2N01	1	SF	SFN01	CC	2615	6	N	1	PSs-CC1v1	2	PS	PSv1	CC	2628	11	W	1
SF2N02	1	SF	SFN02	CC	2618	6	N	1	PSs-CC1v2	2	PS	PSv2	CC	2628	18	W	1
SF2N03	1	SF	SFN03	CC	2615	6	N	1	PSs-SH1	2	PS	PS	SH	2629	15	SW	2
SF2N04	1	SF	SFN04	CC	2615	16	N	1	PSs-SH1m	2	PS	PSc	SH	2629	10	SW	1
SF2N05	1	SF	SFN05	CC	2614	10	NE	1	PSs-SH1v1	2	PS	PSv1	SH	2629	12	SW	1
SF2N06	1	SF	SFN06	CC	2614	12	N	1	PSs-SH1v2	2	PS	PSv2	SH	2629	16	SW	1

Tab. S 2 - List of the species recorded in the manipulation experiments plots (nomenclature according to *Conti et al., 2005*; growth form according to *Elmendrof et al.,2012*). Legend: x = species selected for phenology monitoring during the study period (2014-2015).

species name	family name	elevation range	chorology	growth form	raunkier	monitored
Agrostis alpina Scop.	Poaceae	1700-2750	Orof. SW-European	graminoids_grass	H caesp	-
Agrostis rupestris All.	Poaceae	1700-2800	Orof. S-European	graminoids_grass	H caesp	x
Agrostis schraderiana Bech.	Poaceae	1500-2800	Orof. SW-European	graminoids_grass	H caesp	-
Alchemilla pentaphyllea L.	Poaceae	2200-3100	Alpine endemic	forbs	H ros	x
Anthoxanthum odoratum L. subsp. nipponicum (Honda) Tzvelev	Poaceae	1200-2800	Arctic-Alpine (Eurasiatic)	graminoids_grass	H caesp	-
Arenaria biflora L.	Caryophyllaceae	2300-2800	Arctic-Alpine (European)	forbs	Ch suff	-
Arenaria ciliata L. s.l.	Caryophyllaceae	2200-2800	Circumboreal Arctic-Alpine	forbs	Ch suff	-
Avenula versicolor (Vill.) Laínz	Poaceae	1800-2950	Orof. S-European	graminoids_grass	H caesp	-
Bistorta vivipara (L.) Delarbre	Polygonaceae	1600-2800	Circumboreal Arctic-Alpine	forbs	G rhiz	-
Campanula scheuchzeri Vill. s.l.	Campanulaceae	1400-2600 (3200)	Orof. S-European	forbs	H scap	-
Cardamine bellidifolia L. subsp. alpina (Willd.) B.M.G. Jones	Brassicaceae	2000-3080	Arctic-Alpine (Euromediterranean)	forbs	H scap	-
Cardamine resedifolia L.	Brassicaceae	1500-2600	Orof. S-European	forbs	H scap	-
Carex curvula All. s.l.	Cyperaceae	1900-2800 (3400)	Orof. S-European	graminoids_sedge	H caesp	x
Cirsium spinosissimum (L.) Scop.	Asteraceae	1500-2400 (3000)	Orof. S-European	forbs	H scap	x
Euphrasia minima Jacq. ex DC.	Scrophulariaceae	1500-2800	Orof. Central-European	forbs	T scap	-
Festuca halleri All. s.l.	Poaceae	2000-3000 (3400)	Orof. S-European	graminoids_grass	H caesp	-
Gentiana punctata L.	Gentianaceae	1500-2600 (3050)	Orof. Central-European	forbs	H scap	-
Gentiana sp.	Gentianaceae	2000-3000		forbs	H ros	-
Geum montanum L.	Rosaceae	1800-2600 (2800)	Orof. S-European	forbs	H ros	-
Gnaphalium supinum L.	Asteraceae	2400-3000 (3400)	Circumboreal Arctic-Alpine	forbs	H scap	x
Hieracium piliferum Hoppe	Asteraceae	1800-3000	Orof. S-European	forbs	H ros	-
Homogyne alpina (L.) Cass.	Asteraceae	800-2200	Orof. Central-European	forbs	H ros	x
Kalmia procumbens (L.) Gift, Kron & Stevens ex Galasso, Banfi & F. Conti	Ericaceae	1600-2400 (3000)	Circumboreal Arctic-Alpine	evergreen dwarf shrubs	Ch rept	x
Leontodon helveticus Mérat emend. Widder	Asteraceae	1800-2600	Orof. SW-European	forbs	H ros	x
Leucanthemopsis alpina (L.) Heywood	Asteraceae	2000-3600	Orof. SW-European	forbs	H scap	x
Ligusticum mutellina (L.) Crantz	Apiaceae	2100-2800	Orof. S-European	forbs	H scap	x
Luzula alpinopilosa (Chaix) Breistr. subsp. alpinopilosa	Cyperaceae	1800-3100	Orof. S-European	graminoids_rush	H scap	x

Tab. S2 - continued

species name	family name	elevation range	chorology	growth form	raunkier	monitored
Luzula spicata (L.) DC. s.l.	Cyperaceae	1500-3000	Circumboreal Arctic-Alpine	graminoids_rush	H caesp	-
Minuartia sedoides (L.) Hiern	Caryophyllaceae	1800-3825	Arctic-Alpine (European)	cushion plants	Ch pulv	-
Nardus stricta L.	Paceae	1200-2600	Eurosiberian	graminoids_grass	H caesp	-
Oreochloa disticha (Wulfen) Link	Poaceae	2000-2800 (3300)	Orof. SE-European	graminoids_grass	H caesp	-
Phyteuma hemisphaericum L.	Campanulaceae	1900-2600 (3600)	Orof. SW-European	forbs	H scap	x
Poa alpina L. subsp. Alpina	Poaceae	1500-2700 (3600)	Circumboreal	graminoids_grass	H caesp	x
Potentilla aurea L. subsp. Aurea	Rosaceae	1800-2900	Orof. S-European	forbs	H scap	-
Primula sp.	Primulaceae	-		forbs	H ros	-
Primula glutinosa Wulfen	Primulaceae	1800-3100	Alpine endemic	forbs	H ros	-
Primula minima L.	Primulaceae	1300-2700	Orof. SE-European	forbs	H ros	-
Ranunculus montanus Willd.	Ranunculaceae	1500-2800	Alpine endemic	forbs	H scap	-
Sagina saginoides (L.) H. Karst. subsp. Saginoides	Caryophyllaceae	1700-2900	Circumboreal Arctic-Alpine	forbs	H caesp	-
Salix herbacea L.	Salicaceae	2000-3000	Circumboreal Arctic-Alpine	deciduous dwarf shrubs	Ch frut	x
Sedum alpestre Vill.	Crassulaceae	1800-2800	Orof. S-European	forbs	Ch succ	-
Senecio incanus L. subsp. carniolicus (Willd.) Braun-Blanq.	Asteraceae	1800-2600	Alpine endemic	forbs	H scap	-
Sibbaldia procumbens L.	Rosaceae	2000-2800	Arctic-Alpine(European)	forbs	H scap	-
Soldanella pusilla Baumg. subsp. alpicola (F.K. Mey.) Chrtek	Primulaceae	1000-2500 (2800)	Orof. SE-European	forbs	H ros	x
Trifolium alpinum L.	Fabaceae	1500-2500	Orof. S-European	forbs	H ros	-
Vaccinium uliginosum L. subsp. microphyllum (Lange) Tolm.	Ericaceae	1000-2200 (2450)	Circumboreal	deciduous shrubs	Ch frut	-
Veronica alpina L.	Scrophulariaceae	1500-3000	Arctic-Alpine (Eurasiatic)	forbs	H scap	-

Tab. S 3 - Number of replicates of each monitored species in the whole study period (2014-2017) for each sites, plant community and treatment type.

	Site 1																
	CC								SH						CC	SH	all
treatment	OTC	OTCc	PS	PSv1	PSv2	PSc	SFN-lines	SFS-lines	OTC	OTCc	PS	PSv1	PSv2	PSc	all	all	all
species name	129	121	87	82	77	85	350	322	125	120	94	83	82	95	1253	599	1852
Agrostis rupestris	6	3	2	4		1	27	10	12	12	8	4	8	8	53	52	105
Alchemilla pentaphyllea	12	12	8	8	8	8	30	30	9	8	8	8	8	8	116	49	165
Carex curvula	12	12	8	8	8	8	28	30	4	4	7	8	4	8	114	35	149
Euphrasia minima	11	12	8	8	6	8	30	26	12	12	8	7	8	8	109	55	164
Gnaphalium supinum	12	12	8	8	8	8	30	25	12	12	8	8	8	8	111	56	167
Homogyne alpina	12	9			4	2	4	21	1		3	1		4	52	9	61
Leontodon helveticus	12	12	8	8	8	8	30	30	11	12	8	8	8	8	116	55	171
Leucanthemopsis alpina	10	10	8	8	8	7	24	21	12	12	8	8	8	8	96	56	152
Ligusticum mutellina	6	3						23	1						32	1	33
Luzula alpino-pilosa	4	4	1		5	4	22	13	12	12	8	7	4	8	53	51	104
Phyteuma hemisphaericum	12	12	7	4		1	28	20	3		4		2	3	84	12	96
Poa alpina	4	4	8	8	8	8	30	27	12	12	8	8	8	8	97	56	153
Salix herbacea	4	4	8	8	3	8	26	17	12	12	8	8	8	8	78	56	134
Soldanella pusilla	12	12	8	8	8	8	30	26	12	12	8	8	8	8	112	56	168

	Site 2																
	CC								SH						CC	SH	all
treatment	OTC	OTCc	PS	PSv1	PSv2	PSc	SFN-lines	SFS-lines	OTC	OTCc	PS	PSv1	PSv2	PSc	all	all	all
species name	109	109	34	37	37	38			70	70	34	38	35	35	364	282	646
Agrostis rupestris	9	9	3	3	3	3			9	9	3	3	3	3	30	30	60
Alchemilla pentaphyllea	9	9	3	3	3	3			9	9	3	3	3	3	30	30	60
Carex curvula	9	9	3	3	3	3			9	9	3	3	3	3	30	30	60
Euphrasia minima	9	8	2	3	3	2			2	2	2	3	2	2	27	13	40
Gnaphalium supinum	9	9	3	3	3	3			9	9	3	3	3	3	30	30	60
Homogyne alpina	8	8													16		16
Leontodon helveticus	9	9	3	3	3	3					3	3	3	3	30	12	42
Leucanthemopsis alpina	9	9	2	3	3	3			3	2	3	3	3	3	29	17	46
Ligusticum mutellina	9	9	3	3	3	3					3	3	3	3	30	12	42
Luzula alpino-pilosa			3	3	3	3			2	3	2	3	3	3	12	16	28
Phyteuma hemisphaericum	5	6		1	1	3						2			16	2	18
Poa alpina	6	6	3	3	3	3			9	9	3	3	3	3	24	30	54
Salix herbacea	9	9	3	3	3	3			9	9	3	3	3	3	30	30	60
Soldanella pusilla	9	9	3	3	3	3			9	9	3	3	3	3	30	30	60
all species	238	230	121	119	114	123	350	322	195	190	128	121	117	130	1617	881	2498

Tab. S 4 - Topographic characterization of permanent plots and environmental data recording devices installed at Signy Island. Experiment: OTC = Open Top Chamber; SF = Snowfence; PS = Precipitation shield. Community: M = mosses dominated community; L = lichens dominated community; MP = mosses dominated with patterned ground; LP = lichens dominated, with patterned ground. GST = Groung Surface Temperature (°C); VWC = Volumetric Water Content (m^3/m^3).

Plot ID	site	experiment	treatment	community	altitude (m asl)	slope (°)	Aspect (°N)	GST	VWC	rain gauge
OTCcb-M	1a	OTC	OTC	M	39	8	290			
OTCcb-Mc	1a	OTC	OTCc	M	39	8	290			
OTCcb-L	1a	OTC	OTC	L	39	10	290			
OTCcb-Lc	1a	OTC	OTCc	L	39	10	290			
PScb-M	1a	PS	PS	M	40	7	300			
PScb-Mv1	1a	PS	PSv1	M	40	10	300			
PScb-Mv2	1a	PS	PSv2	M	40	10	300			
PScb-Mc	1a	PS	PSc	M	40	10	300			
PScb-M2	1a	PS	PS	M	41	10	320			
PScb-M2v1	1a	PS	PSv1	M	41	10	320			
PScb-M2v2	1a	PS	PSv2	M	40	10	320			
PScb-M2c	1a	PS	PSc	M	40	10	320			
OTCca-M	1b	OTC	OTC	M	91	5	320	x		
OTCca-Mc	1b	OTC	OTCc	M	91	3	320	x		
OTCca-MP	1b	OTC	OTC	MP	91	5	320	x		
OTCca-MPc	1b	OTC	OTCc	MP	91	5	315	x		
OTCca-L	1b	OTC	OTC	L	88	8	320			
OTCca-Lc	1b	OTC	OTCc	L	88	8	310			
OTCca-LP	1b	OTC	OTC	LP	90	7	320			
OTCca-LPc	1b	OTC	OTCc	LP	90	5	320			
PSca-M	1b	PS	PS	M	89	5	325	x	x	
PSca-Mv1	1b	PS	PSv1	M	89	5	325	x	x	
PSca-Mv2	1b	PS	PSv2	M	89	5	325	x	x	x
PSca-Mc	1b	PS	PSc	M	89	5	325	x	x	
CALM_SFv1	1b	SF	SFv	M	89	5	110			
CALM_SFv2	1b	SF	SFv	M	89	5	120	x		
CALM_SFv3	1b	SF	SFv	M	89	5	120	x		
CALM_SFv4	1b	SF	SFv	M	89	5	120			
CALM_SFv5	1b	SF	SFv	M	89	5	115			
CALM_SFm1	1b	SF	SFm	M	89	5	120			
CALM_SFm2	1b	SF	SFm	M	89	5	115	x		
CALM_SFm3	1b	SF	SFm	M	89	5	120	x		
CALM_SFm4	1b	SF	SFm	M	89	5	115			
CALM_SFm5	1b	SF	SFm	M	89	5	120			
OTCeb-M	2a	OTC	OTC	M	28	7	260	x		
OTCeb-Mc	2a	OTC	OTCc	M	28	7	280	x		
OTCeb-MP	2a	OTC	OTC	MP	28	5	260	x		
OTCeb-MPc	2a	OTC	OTCc	MP	28	5	270	x		
PSeb-M	2a	PS	PS	M	30	7	265			
PSeb-Mv1	2a	PS	PSv1	M	30	7	265			
PSeb-Mv2	2a	PS	PSv2	M	30	6	265			
PSeb-Mc	2a	PS	PSc	M	30	7	265			
PSeb-MP	2a	PS	PS	MP	30	3	250			
PSeb-MPv1	2a	PS	PSv1	MP	30	4	250			
PSeb-MPv2	2a	PS	PSv2	MP	30	4	250			
PSeb-MPc	2a	PS	PSc	MP	30	4	250			
OTCeb-M2	2a	OTC	OTC	M	22	7	220			
OTCeb-M2c	2a	OTC	OTCc	M	22	8	220			
OTCeb-M2P	2a	OTC	OTC	MP	22	7	220			
OTCeb-M2Pc	2a	OTC	OTCc	MP	22	7	220			
OTCea-M	2b	OTC	OTC	M	105	10	230	x		
OTCea-Mc	2b	OTC	OTCc	M	105	10	230	x		
OTCea-MP	2b	OTC	OTC	MP	105	10	255	x		
OTCea-MPc	2b	OTC	OTCc	MP	105	10	255	x		
OTCea-L	2b	OTC	OTC	L	105	5	300			
OTCea-Lc	2b	OTC	OTCc	L	105	9	250			
OTCea-LP	2b	OTC	OTC	LP	105	10	260			
OTCea-LPc	2b	OTC	OTCc	LP	105	12	260			
PSea-M	2b	PS	PS	M	108	12	235	x	x	
PSea-Mv1	2b	PS	PSv1	M	108	12	235	x	x	
PSea-Mv2	2b	PS	PSv2	M	108	12	235	x	x	x
PSea-Mc	2b	PS	PSc	M	108	12	235	x	x	
PSea-MP	2b	PS	PS	MP	108	6	260			
PSea-MPv1	2b	PS	PSv1	MP	108	6	260			
PSea-MPv2	2b	PS	PSv2	MP	108	6	260			
PSea-MPc	2b	PS	PSc	MP	108	6	260			

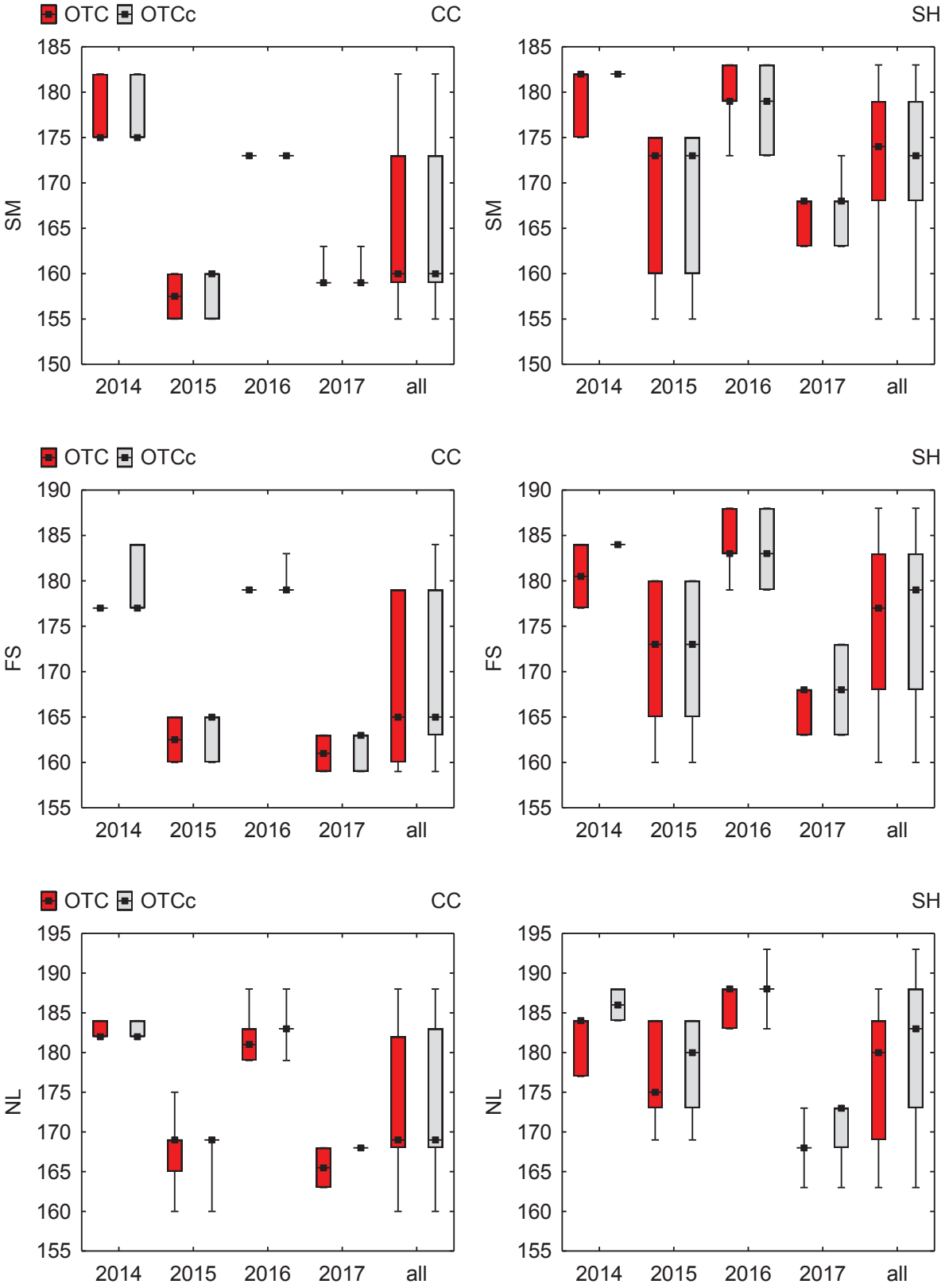

Fig. S1 - Descriptive statistics of snowmelt (SM), first shoot (FS) and new leaves (NL) in warming (OTC) and control (OTCc) plots for the whole study period (2014-2017) for ***A. pentaphyllea*** at intra-annual level for both the plant communities (CC = alpine grassland; SH = snowbed). Black squares = medians, boxes = 25%-75%, whiskers = min-max.

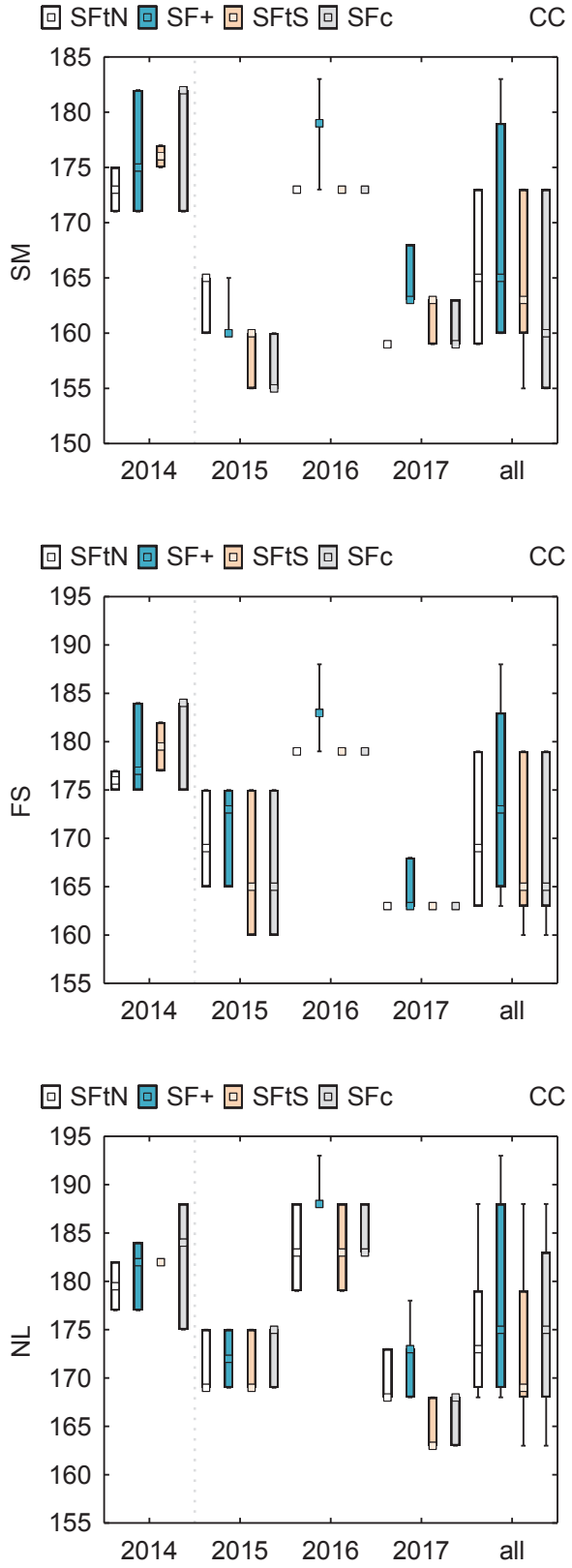

Fig. S2 - Descriptive statistics of snowmelt (SM), first shoot (FS) and new leaves (NL) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***A. pentaphyllea***, at intra-annual level. Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

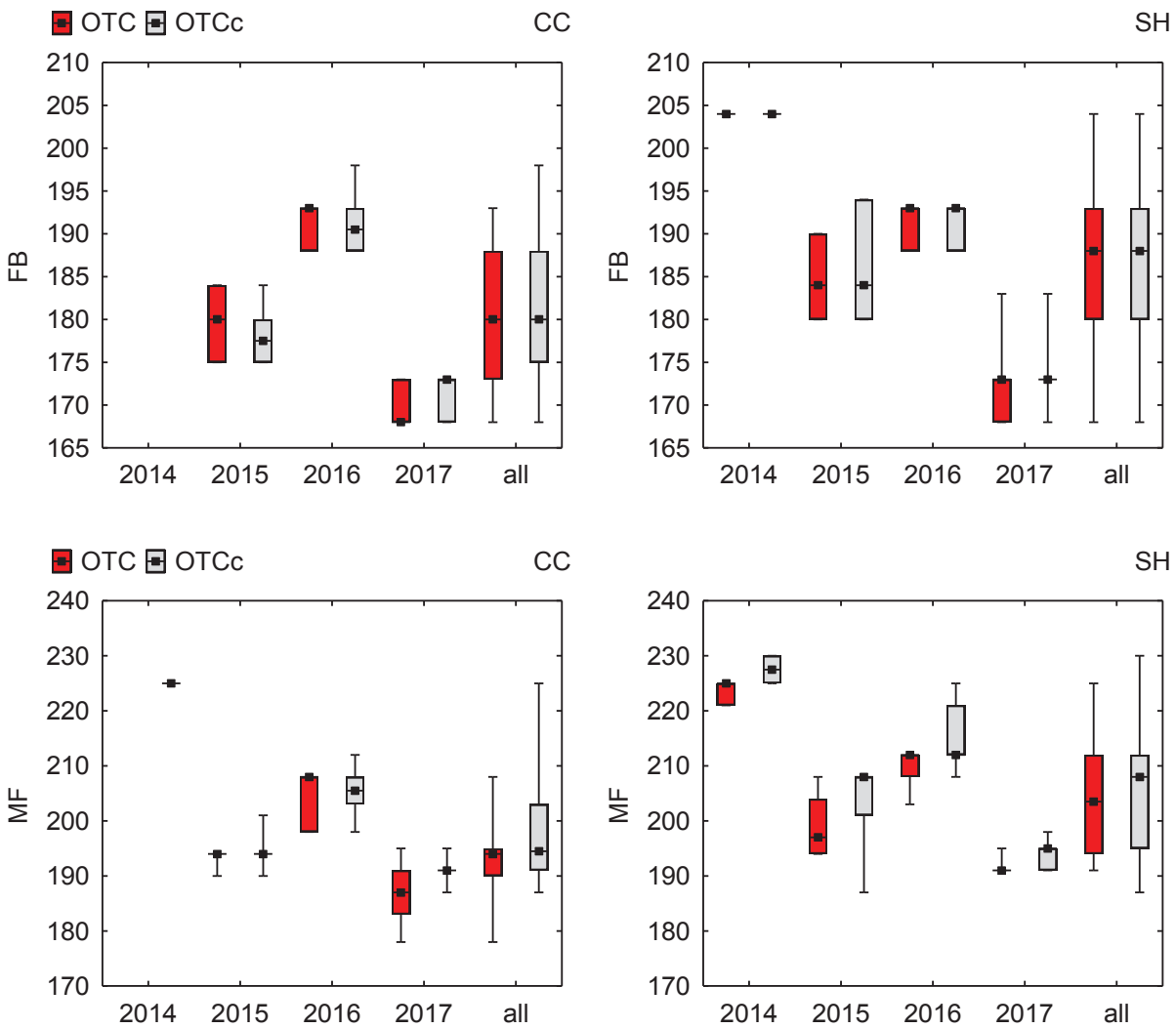

Fig. S3 - Descriptive statistics of flower bud (FB) and peak of flowering (MF) computed in warming (OTC) and control (OTCc) plots of ***A. pentaphyllea*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max. Note the different scales in y-axis values.

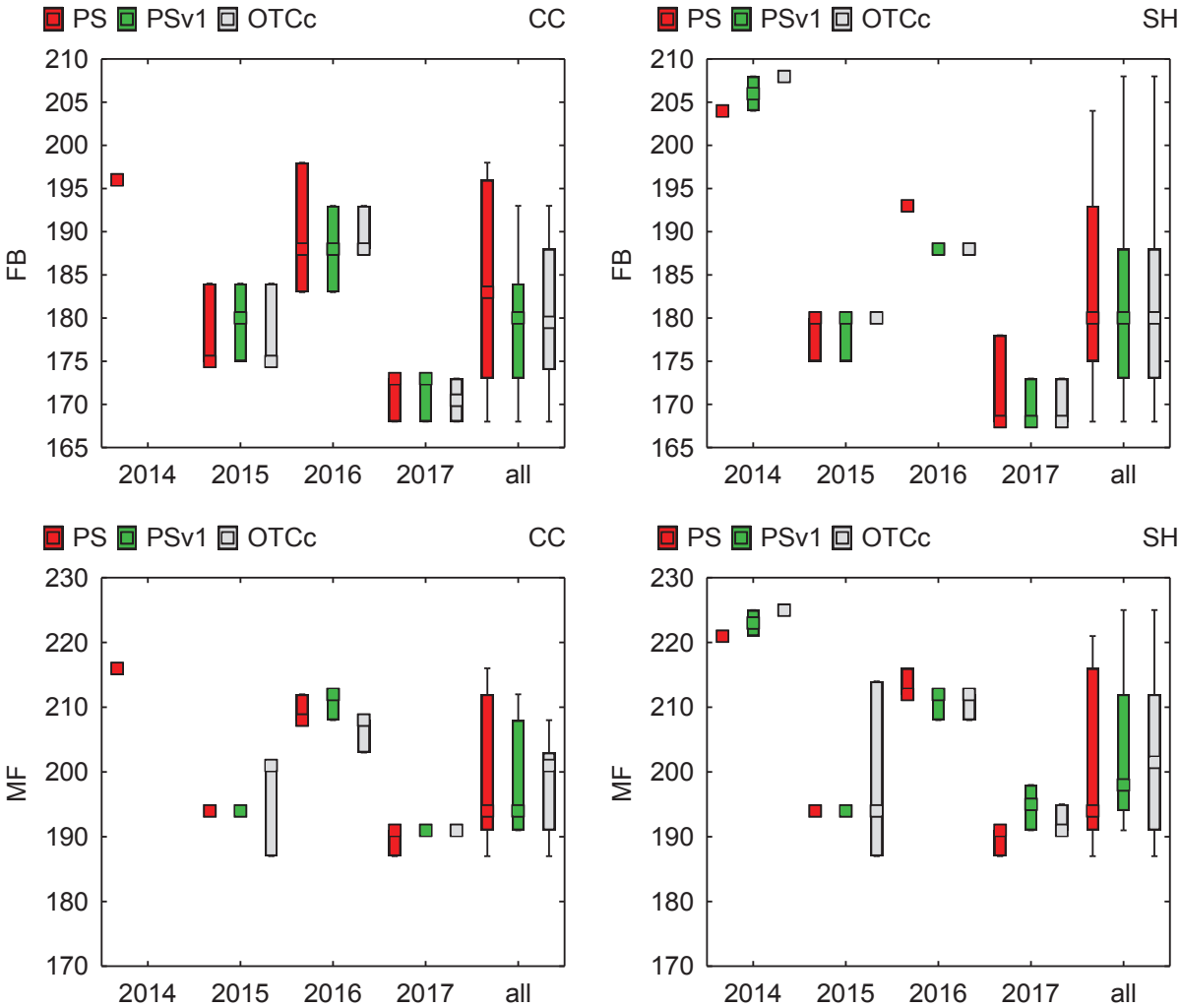

Fig. S4 - Descriptive statistics of flower bud (FB) and peak of flowering (MF) in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***A. pentaphyllea*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured square = medians, boxes = 25%-75%, whiskers = min-max. Note the different scales in y-axis values.

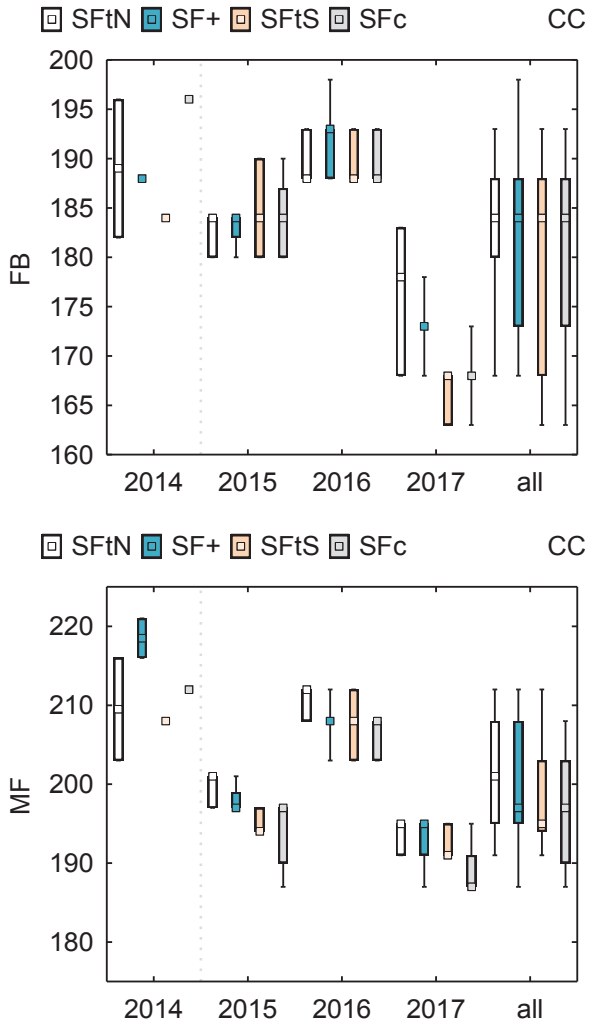

Fig. S5 - Descriptive statistics of flower bud (FB) and peak of flowering (MF) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***A. pentaphyllea***, at intra-annual level. Coloured squares = medians, boxes = 25%-75%, whiskers = min-max. Note the different scales in y-axis values.

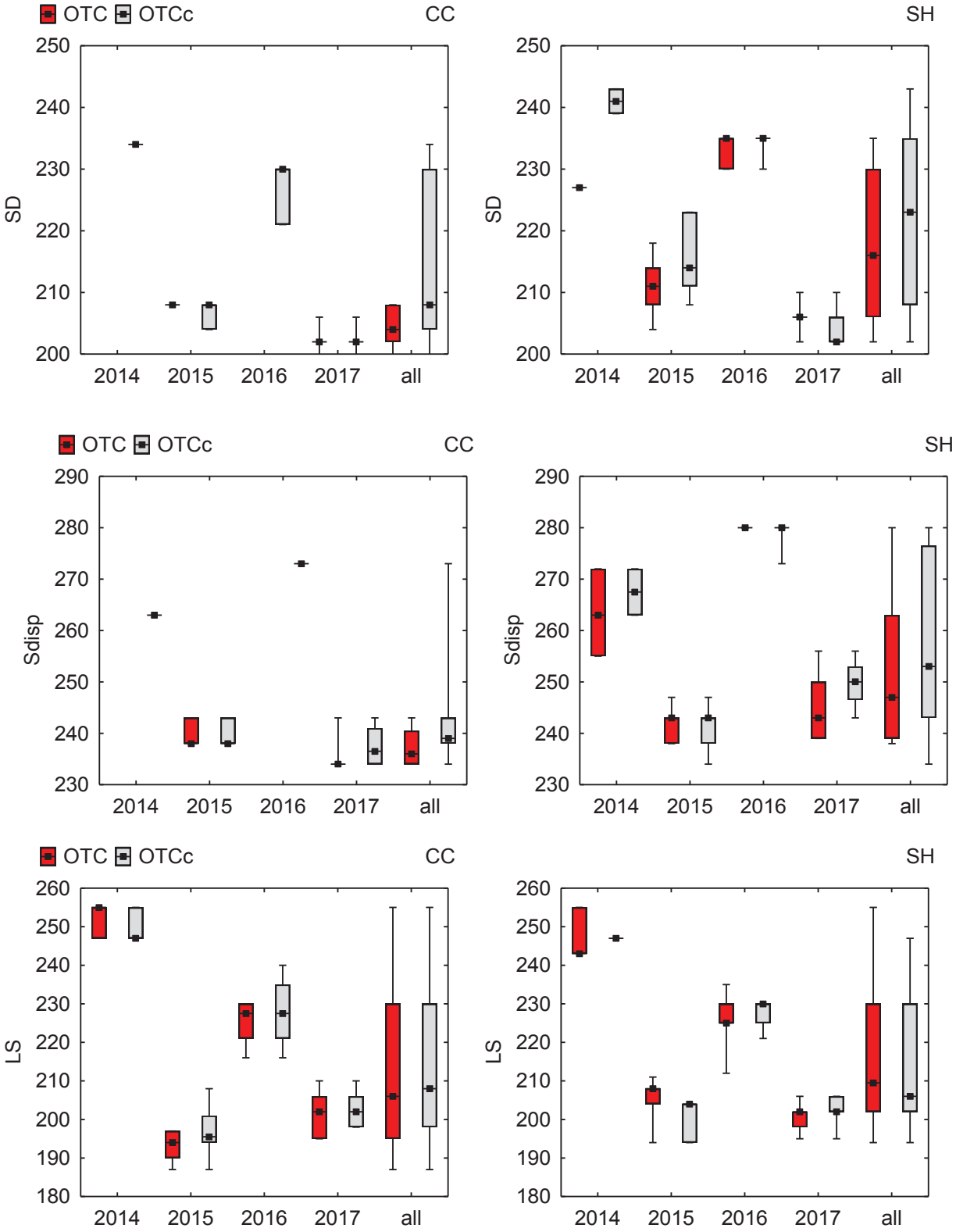

Fig. S6 - Descriptive statistics of seed development (SD), seed dispersal (Sdisp) and leaf senescence (LS) computed in warming (OTC) and control (OTCc) plots of ***A. pentaphyllea*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max. Note the different scales in y-axis values

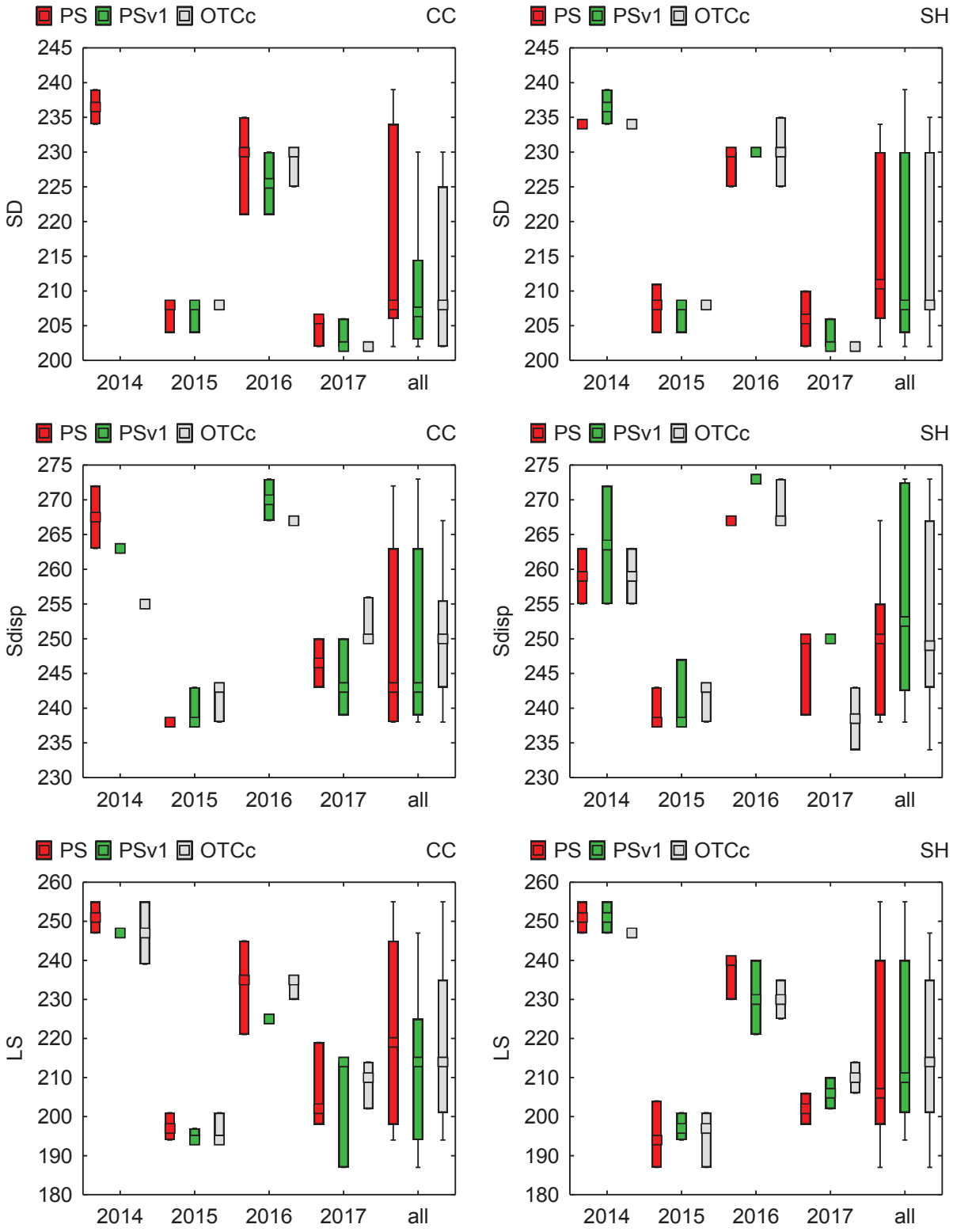

Fig. S7 - Descriptive statistics of seed development (SD), seed dispersal (Sdisp) and leaf senescence (LS) in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***A. pentaphyllea*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

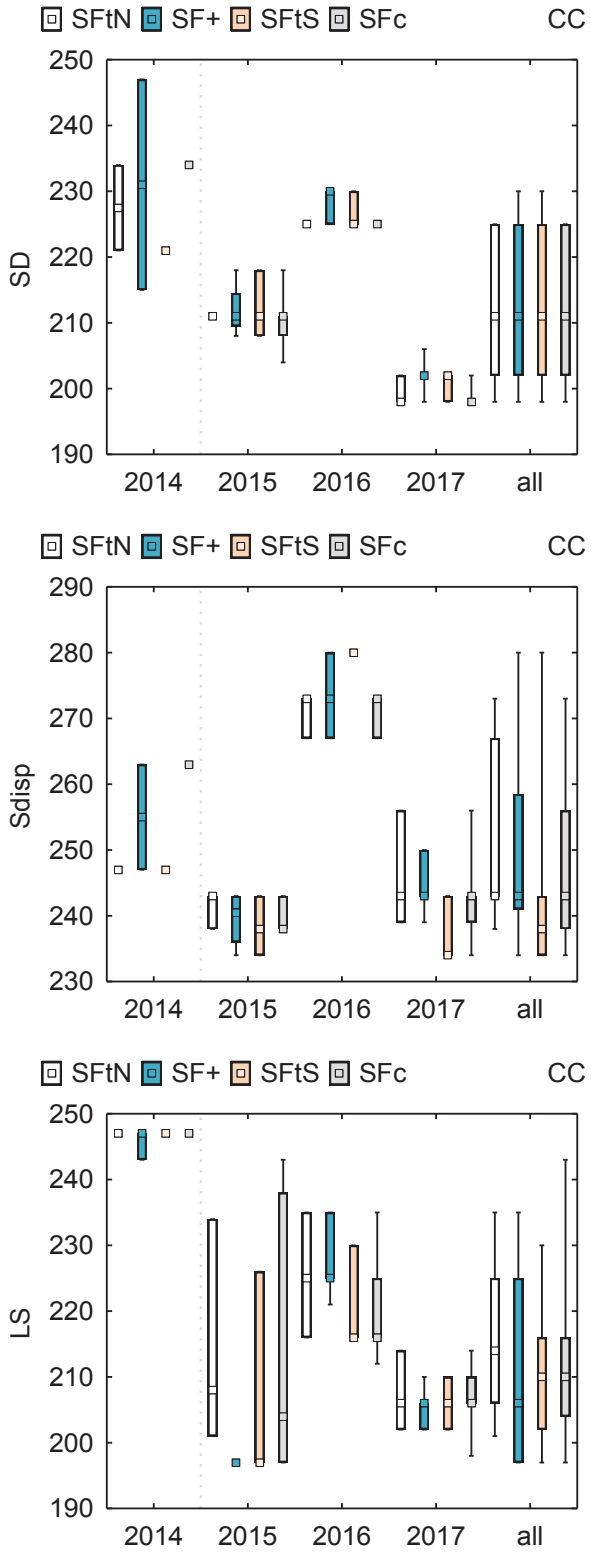

Fig. S8 - Descriptive statistics of seed development (SD), seed dispersal (Sdisp) and leaf senescence (LS) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***A. pentaphyllea*** at intra-annual level. Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

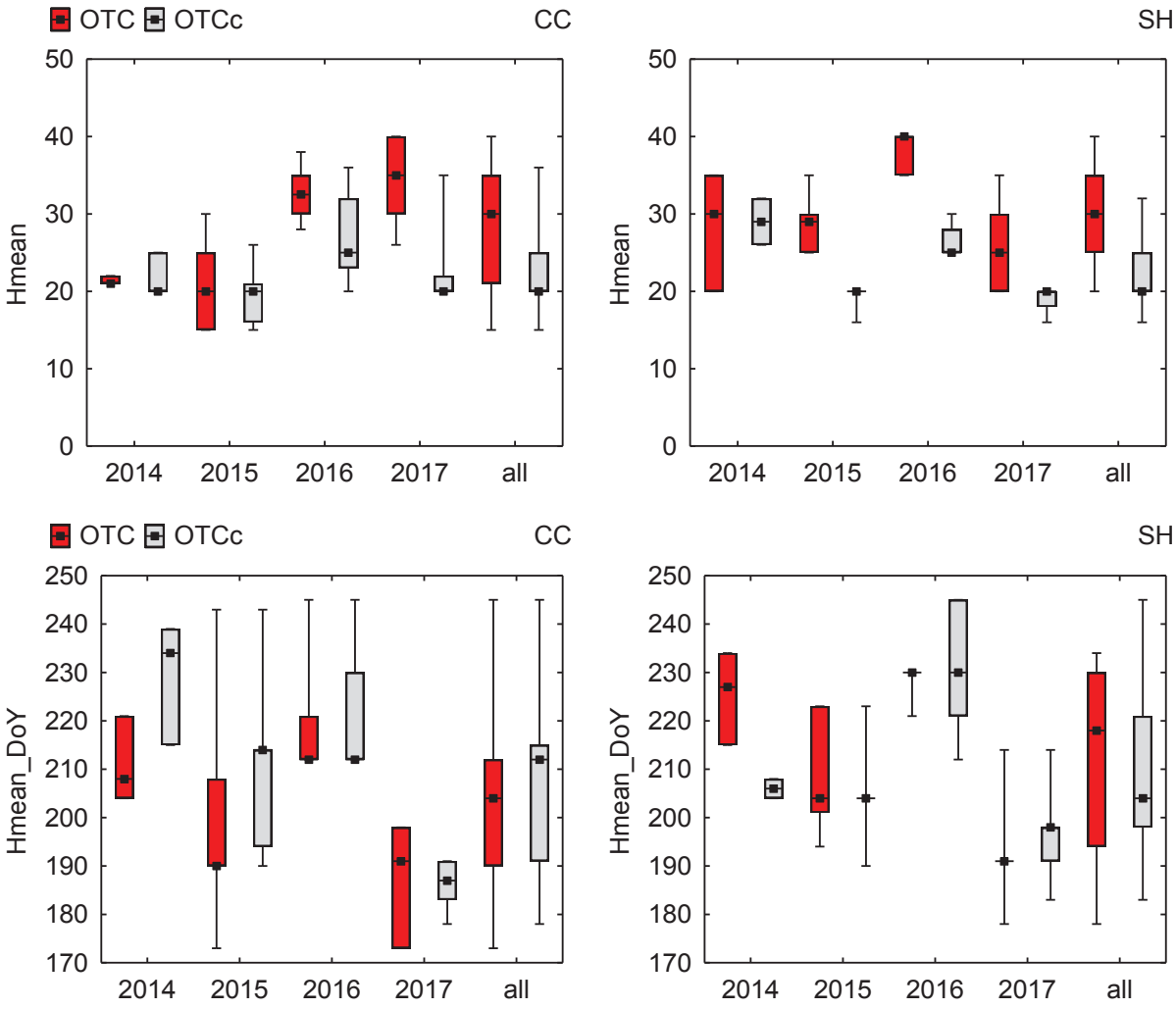

Fig. S9 - Descriptive statistics of the mean height (Hmean) and of the day of achievement of the maximal mean height (Hmean_DoY) computed in warming (OTC) and control (OTCc) plots of ***A. pentaphyllea*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max.

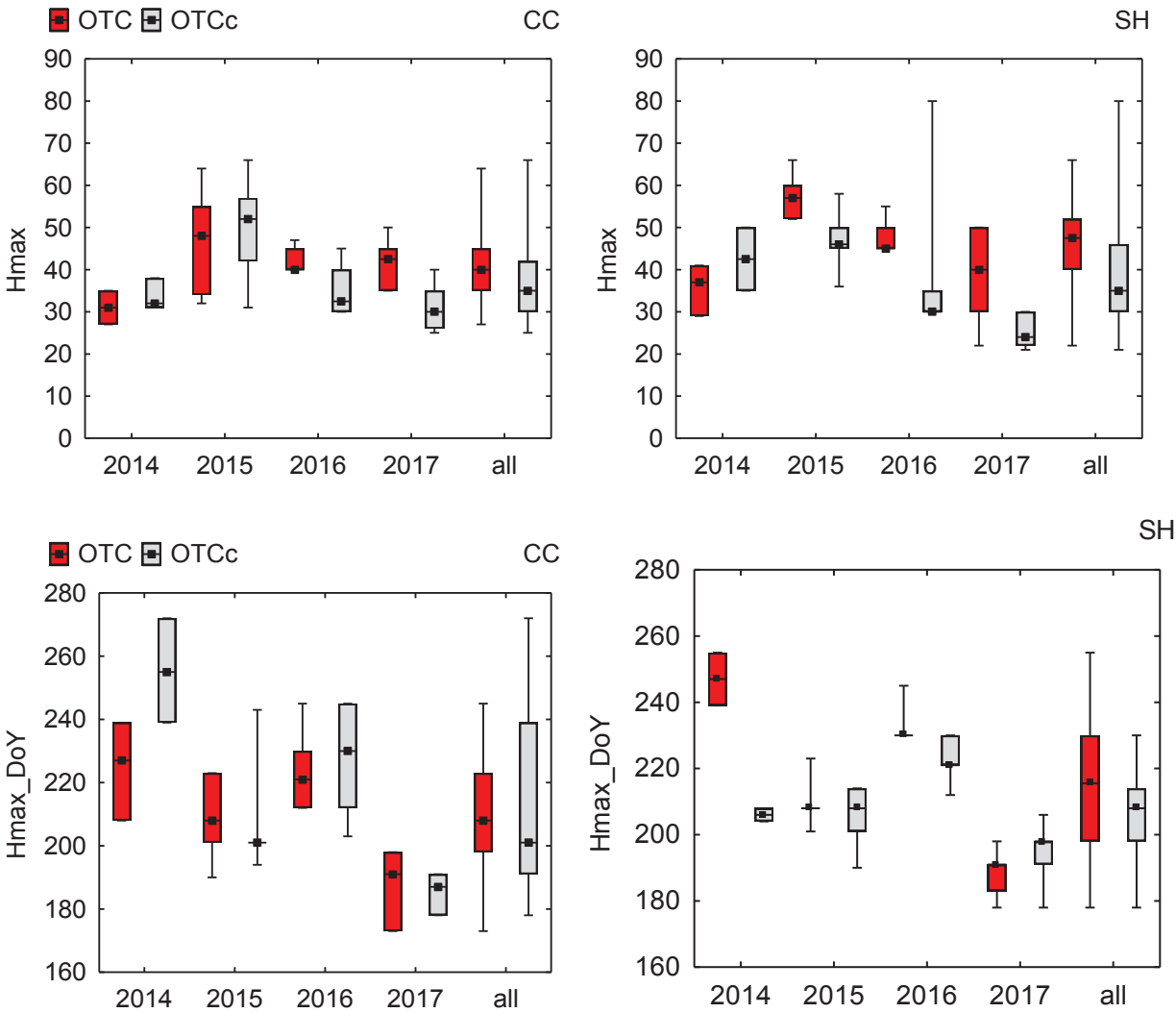

Fig. S10 - Descriptive statistics of the maximum height (Hmax) and of the day of achievement of the maximum height (Hmax_DoY) computed in warming (OTC) and control (OTCc) plots of ***A. pentaphyllea*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max.

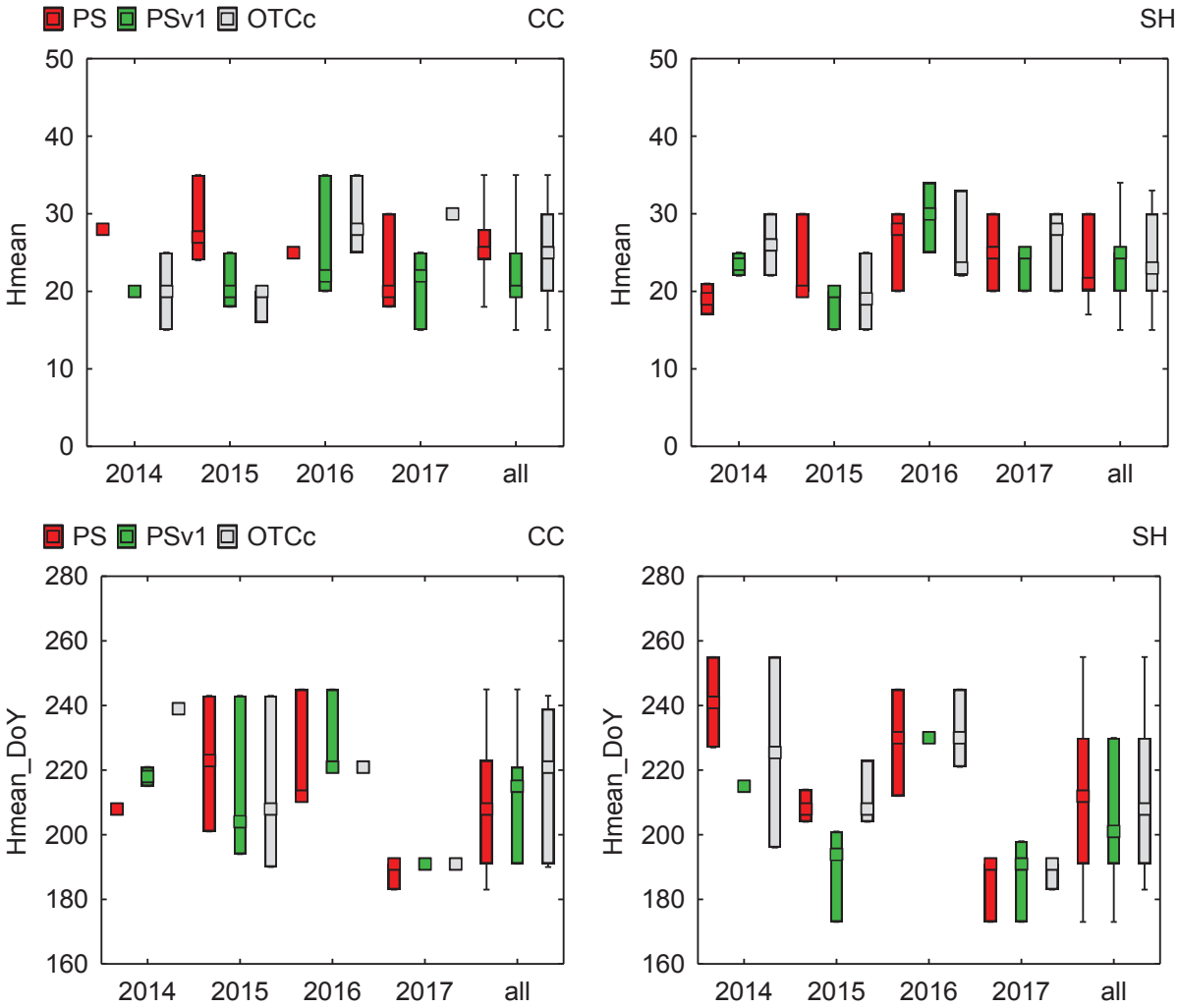

Fig. S11 - Descriptive statistics of mean height (Hmean) and of the day of achievement of the maximal mean height (Hmean_DoY) in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***A. pentaphyllea*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

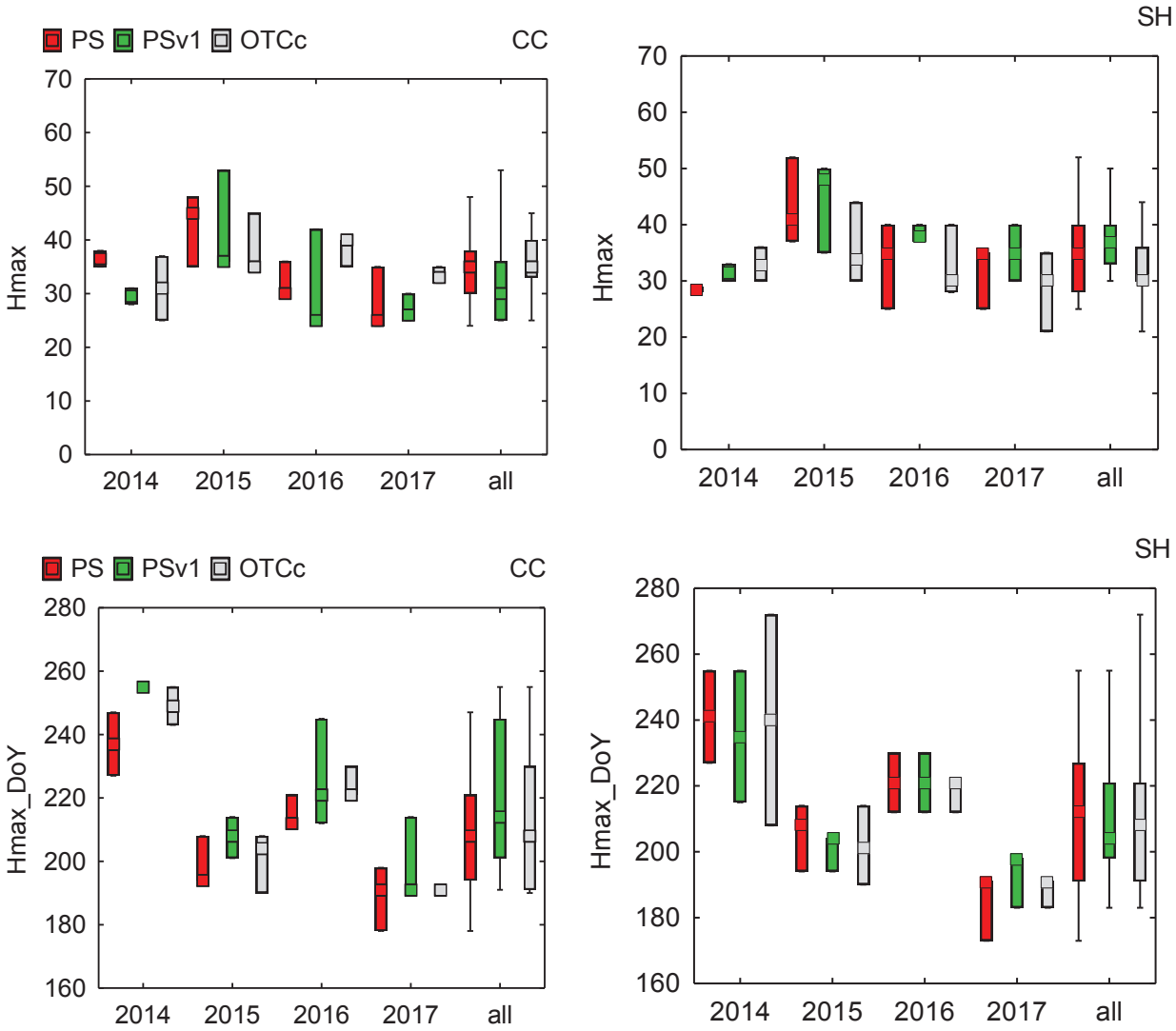

Fig. S12 - Descriptive statistics of maximal height (Hmax) and of the day of achievement of the maximum height (Hmax_DoY) in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***A. pentaphyllea*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

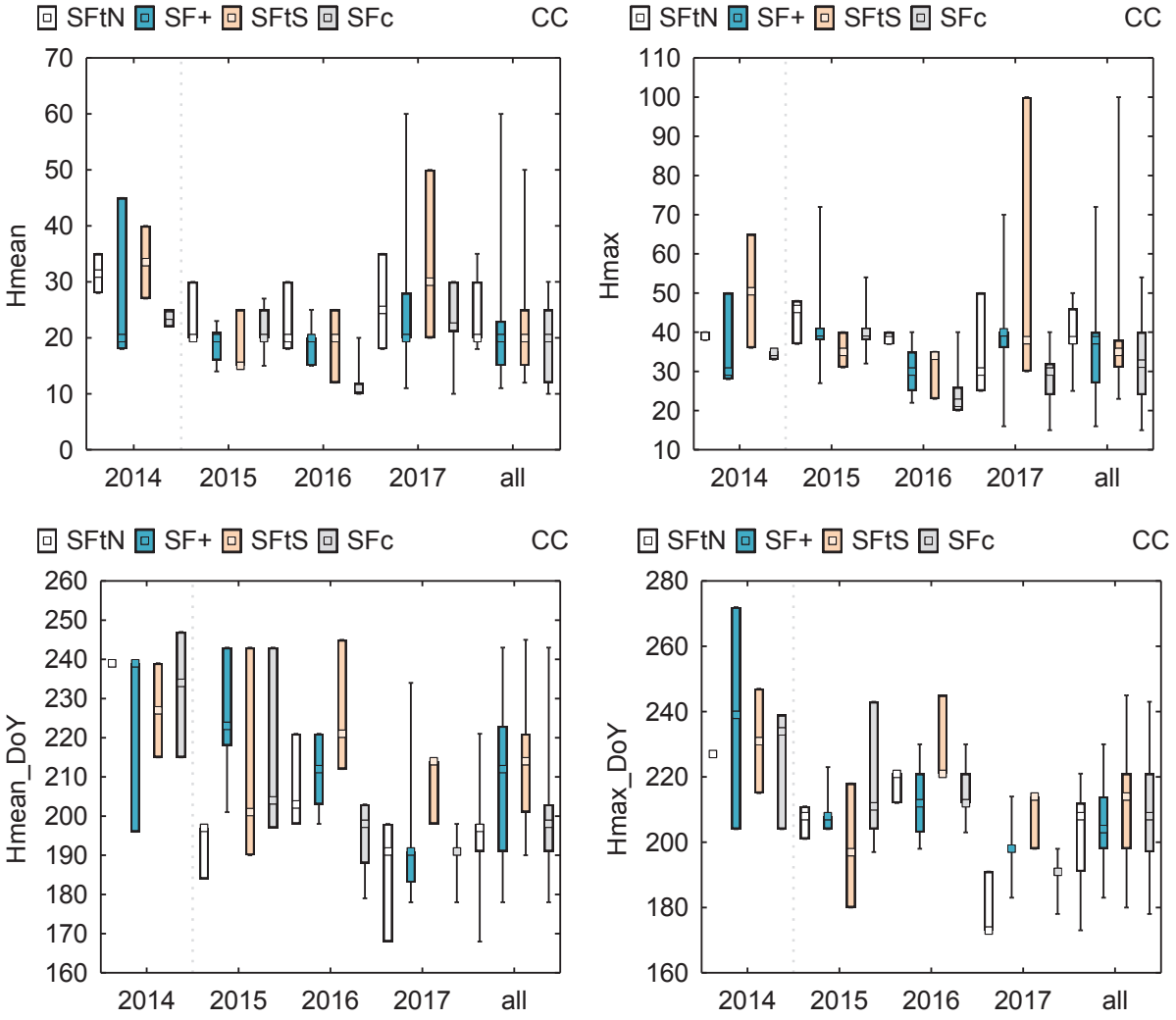

Fig. S13 - Descriptive statistics of mean height (Hmean), maximum height (Hmax) and day of achievement of the maximal mean height (Hmean_DoY) and maximum height (Hmax_DoY) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***A. pentaphyllea***, at intra-annual level. Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

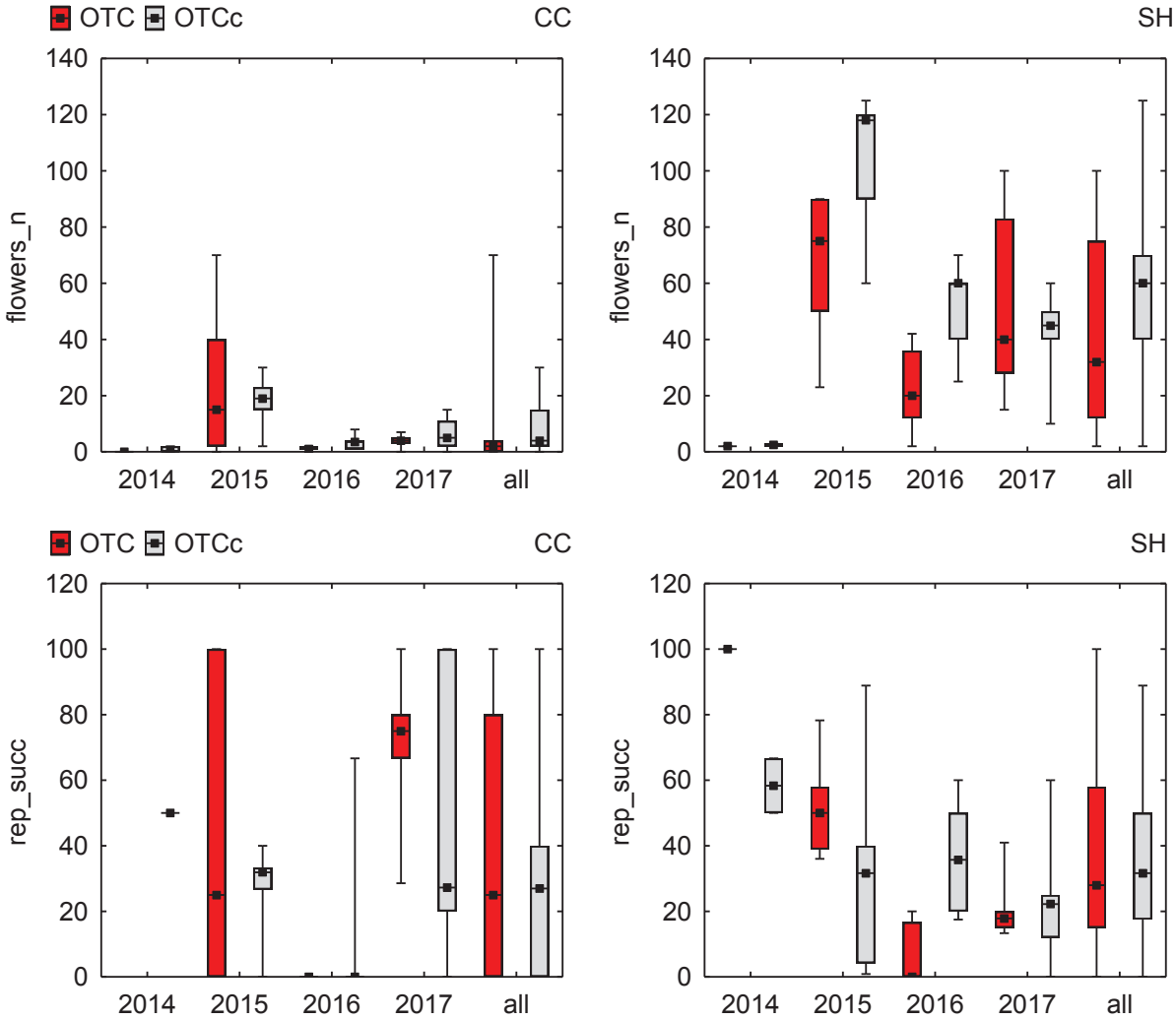

Fig. S14 - Descriptive statistics of the number of reproductive individuals (flowers_n) and of the reproductive success (rep_succ) computed in warming (OTC) and control (OTCc) plots of ***A.pentaphyllea*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max.

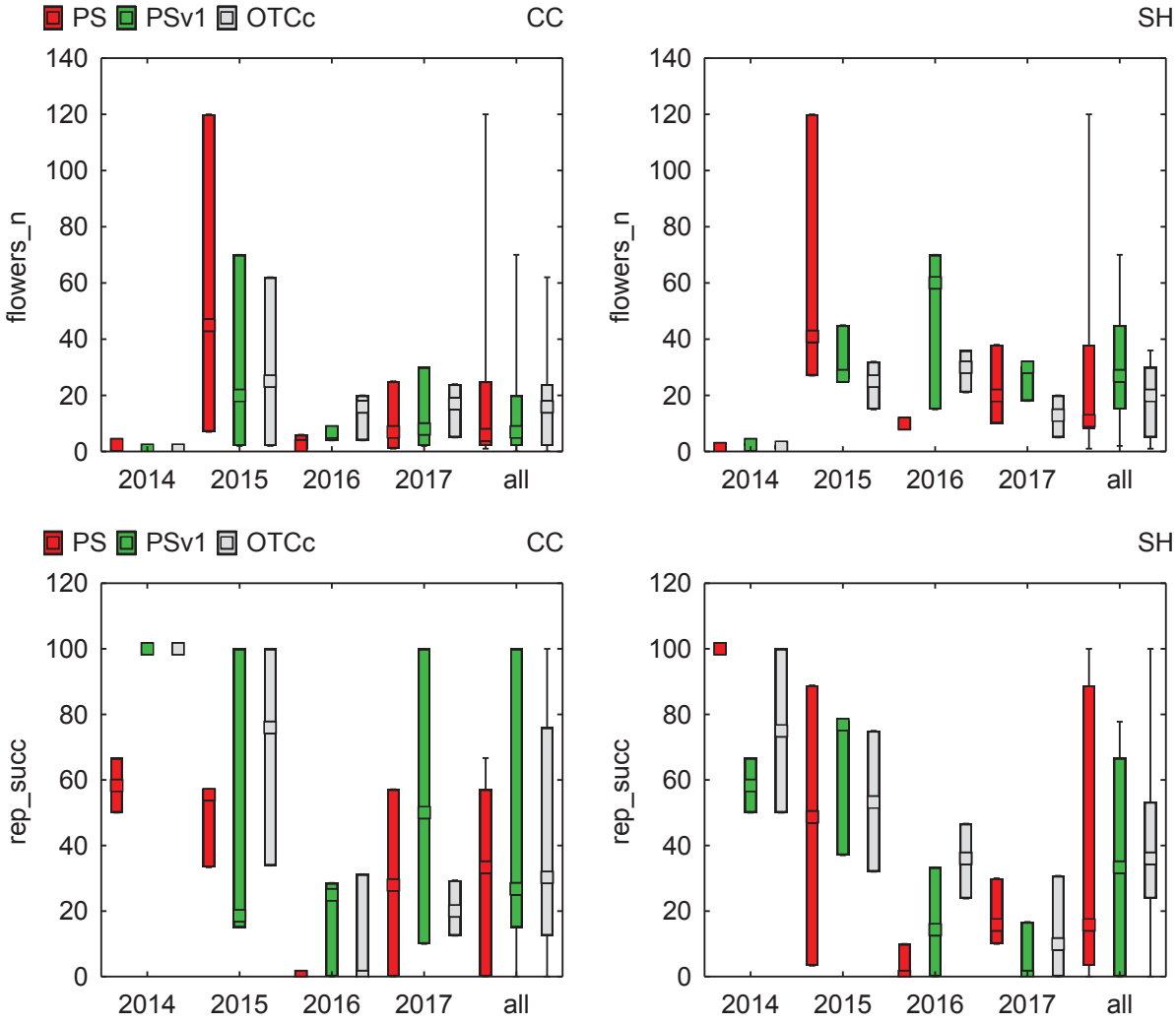

Fig. S15 - Descriptive statistics of the number of reproductive individuals (flowers_n) and of the reproductive success (rep_succ) computed in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***A. pentaphyllea*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

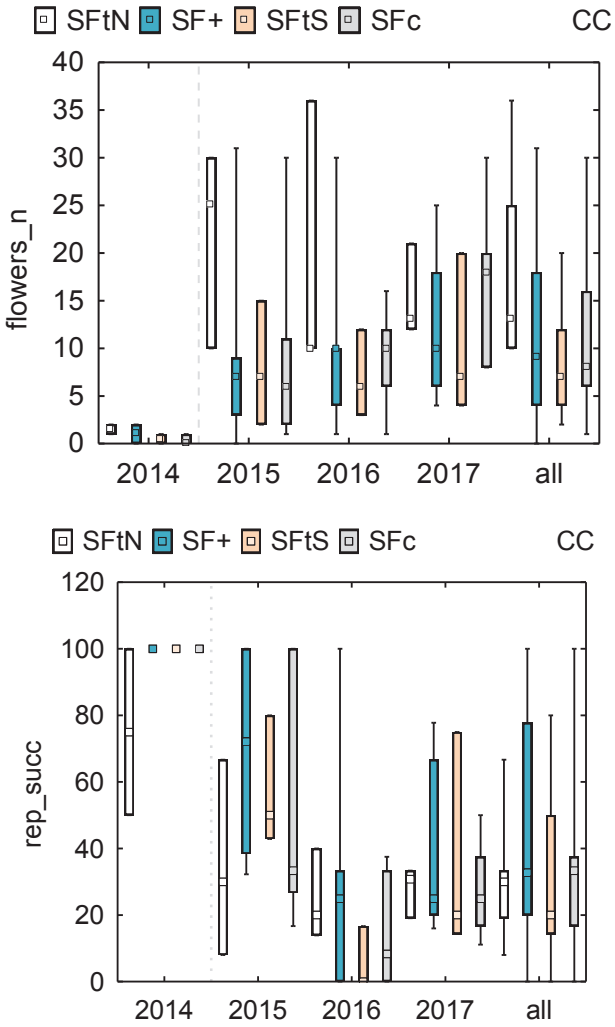

Fig. S16 - Descriptive statistics of the number of reproductive individuals (flowers_n) and of the reproductive success (rep_succ) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***A. pentaphyllea***, at intra-annual level. Coloured square = medians, boxes = 25%-75%, whiskers = min-max.

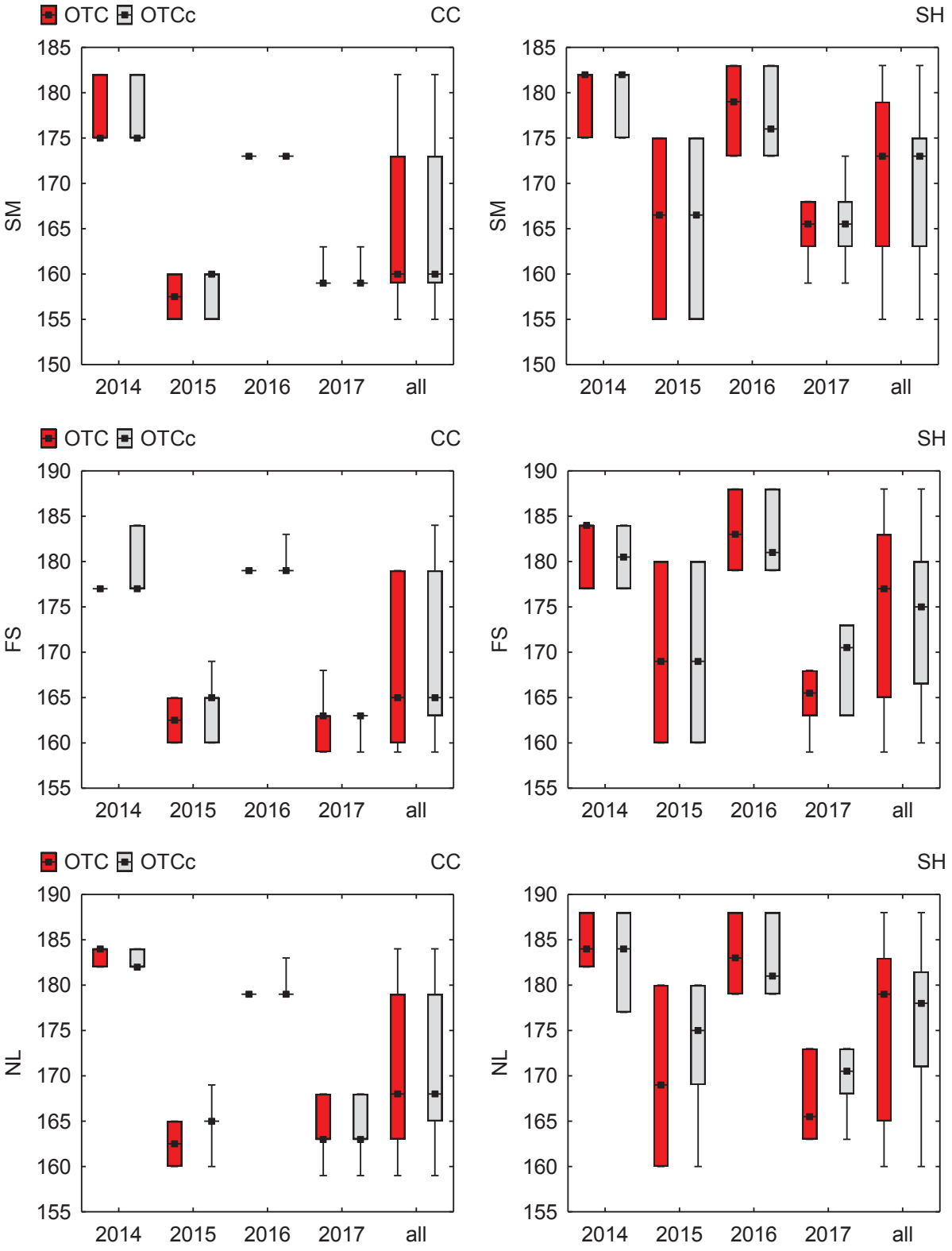

Fig. S17 - Descriptive statistics of snowmelt (SM), first shoot (FS) and new leaves (NL) in warming (OTC) and control (OTCc) plots for the whole study period (2014-2017) for ***G.supinum*** at intra-annual level for both the plant communities (CC = alpine grassland; SH = snowbed). Black squares = medians, boxes = 25%-75%, whiskers = min-max.

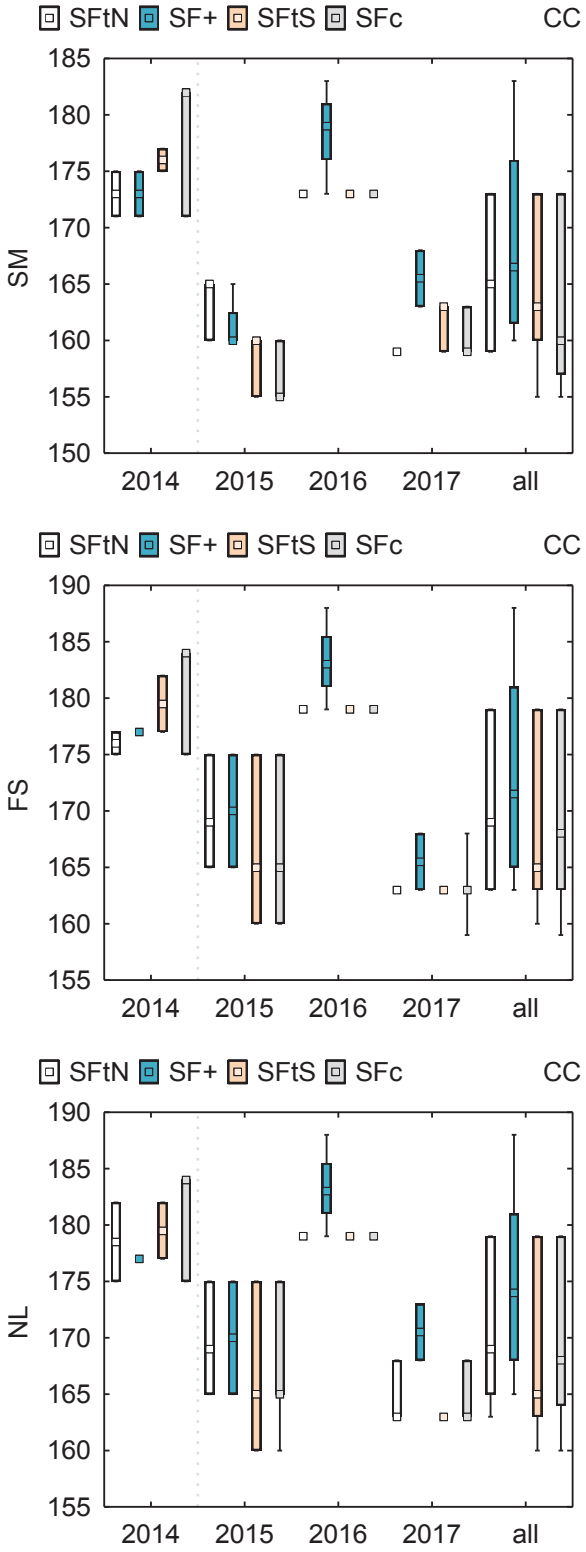

Fig. S18 - Descriptive statistics of snowmelt (SM), first shoot (FS) and new leaves (NL) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***G.supinum***, at intra-annual level. Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

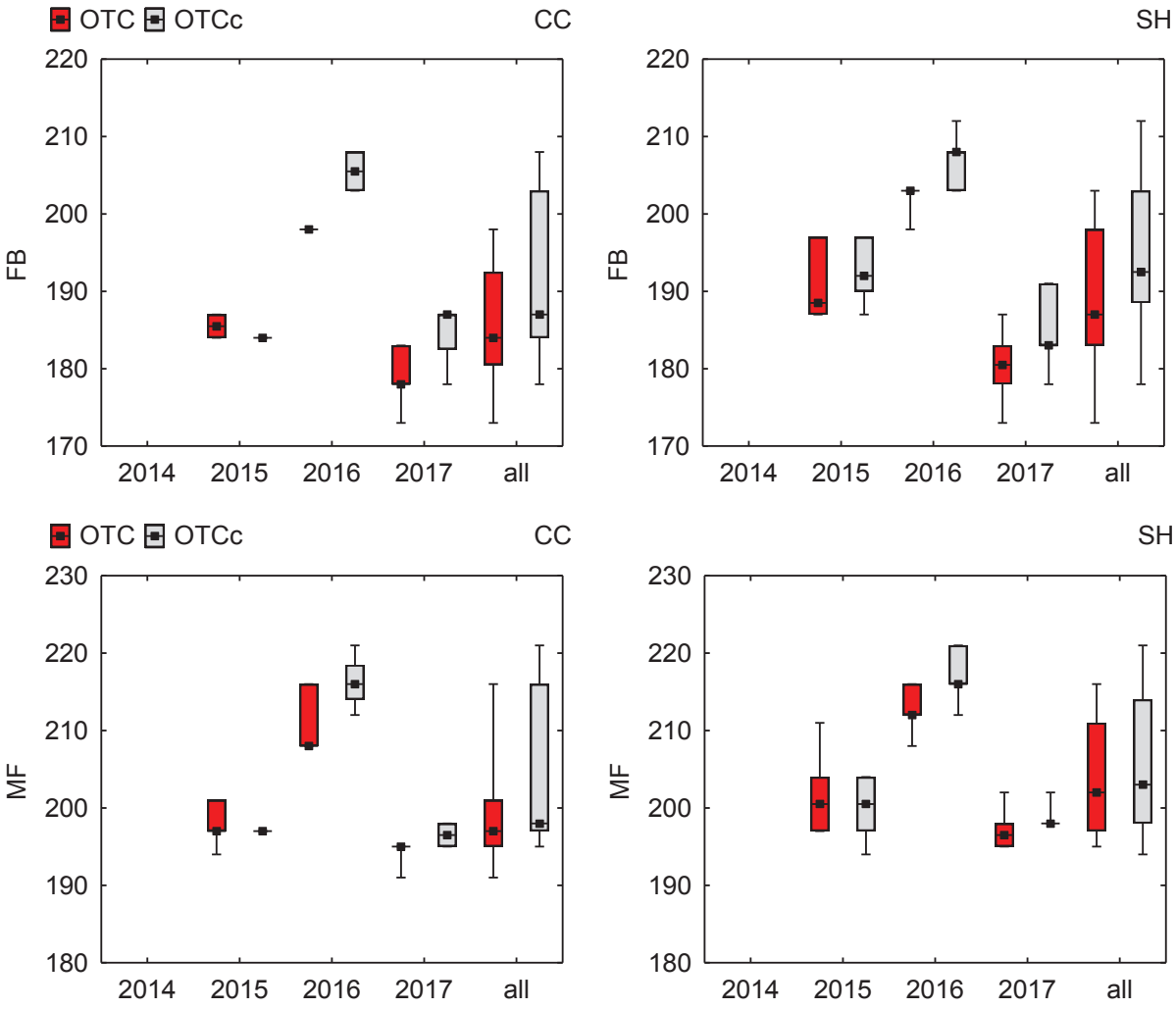

Fig. S19 - Descriptive statistics of flower bud (FB) and peak of flowering (MF) computed in warming (OTC) and control (OTCc) plots of ***G. supinum*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max. Note the different scales in y-axis values.

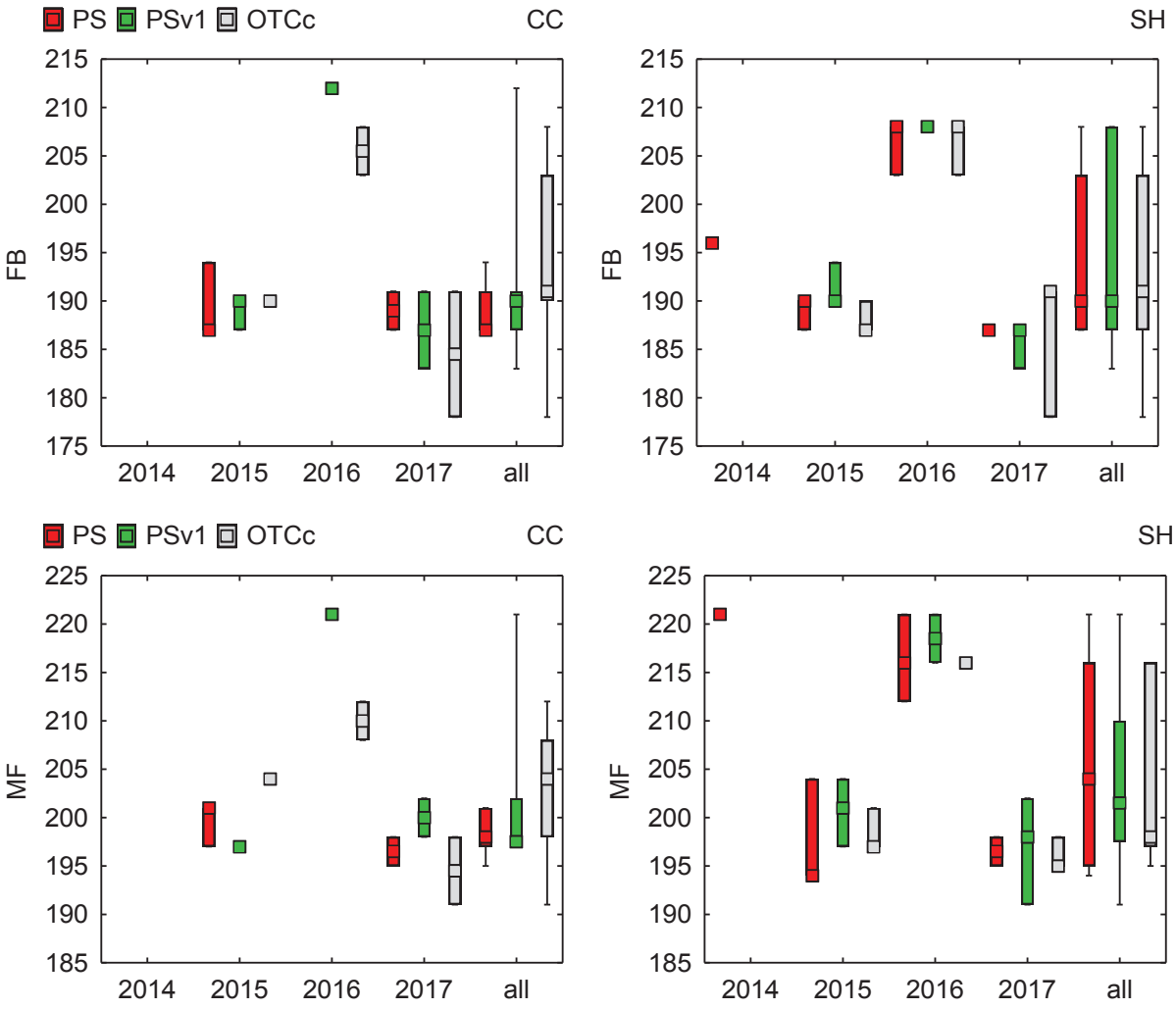

Fig. S20 - Descriptive statistics of flower bud (FB) and peak of flowering (MF) in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***G. supinum*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured square = medians, boxes = 25%-75%, whiskers = min-max. Note the different scales in y-axis values.

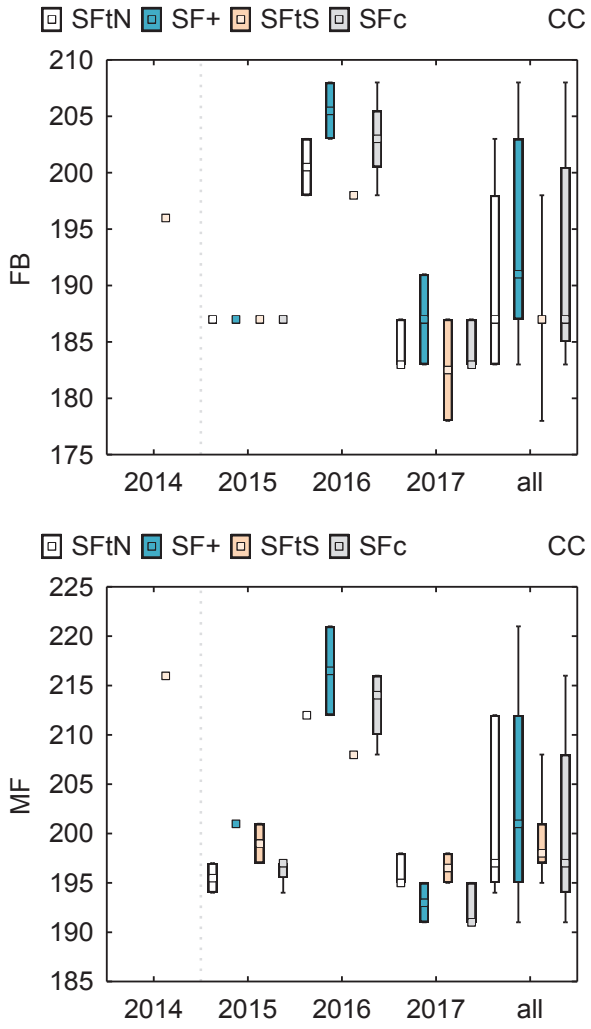

Fig. S21 - Descriptive statistics of flower bud (FB) and peak of flowering (MF) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***G. supinum***, at intra-annual level. Coloured squares = medians, boxes = 25%-75%, whiskers = min-max. Note the different scales in y-axis values.

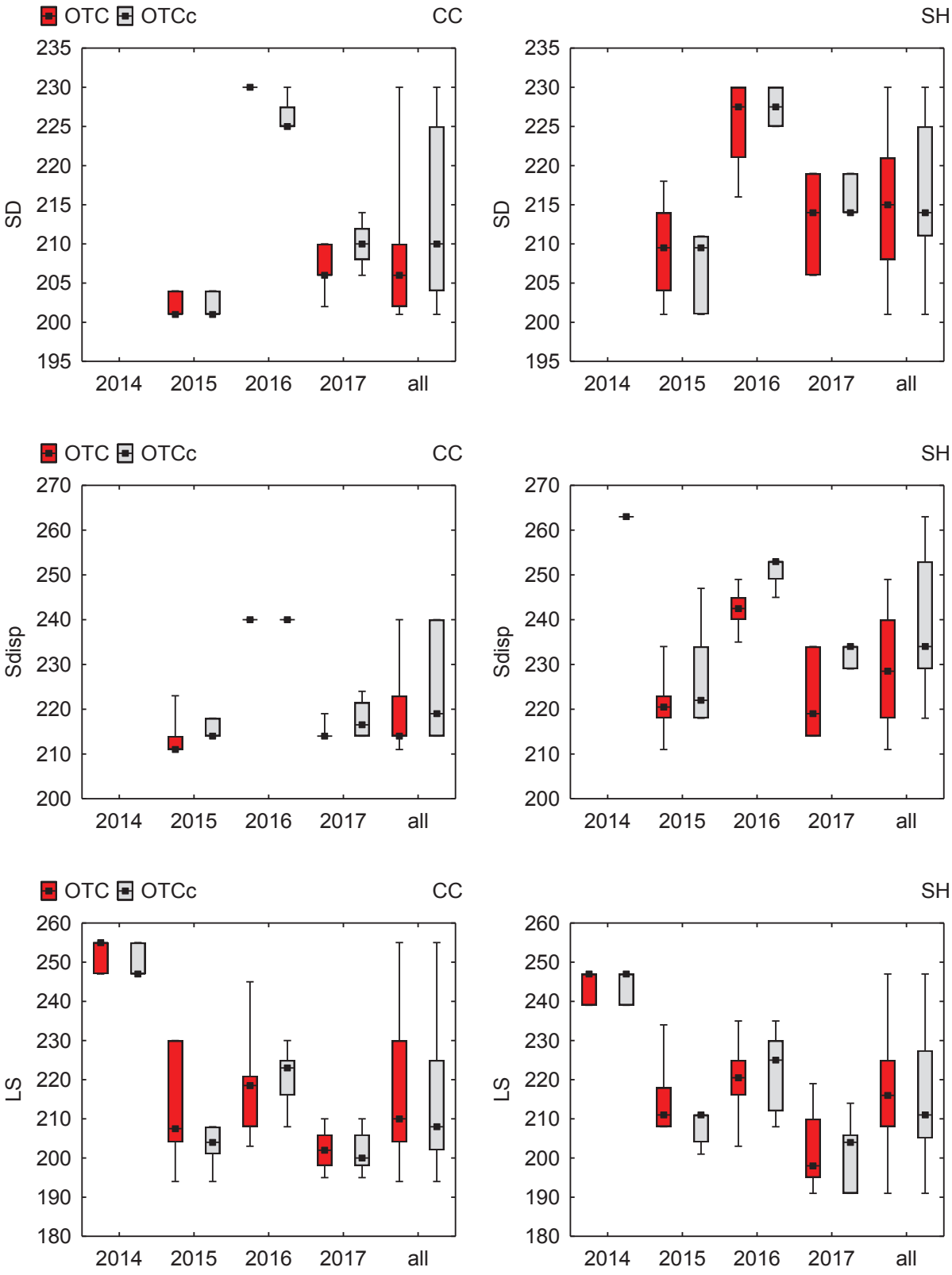

Fig. S22 - Descriptive statistics of seed development (SD), seed dispersal (Sdisp) and leaf senescence (LS) computed in warming (OTC) and control (OTCc) plots of ***G. supinum*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max. Note the different scales in y-axis values.

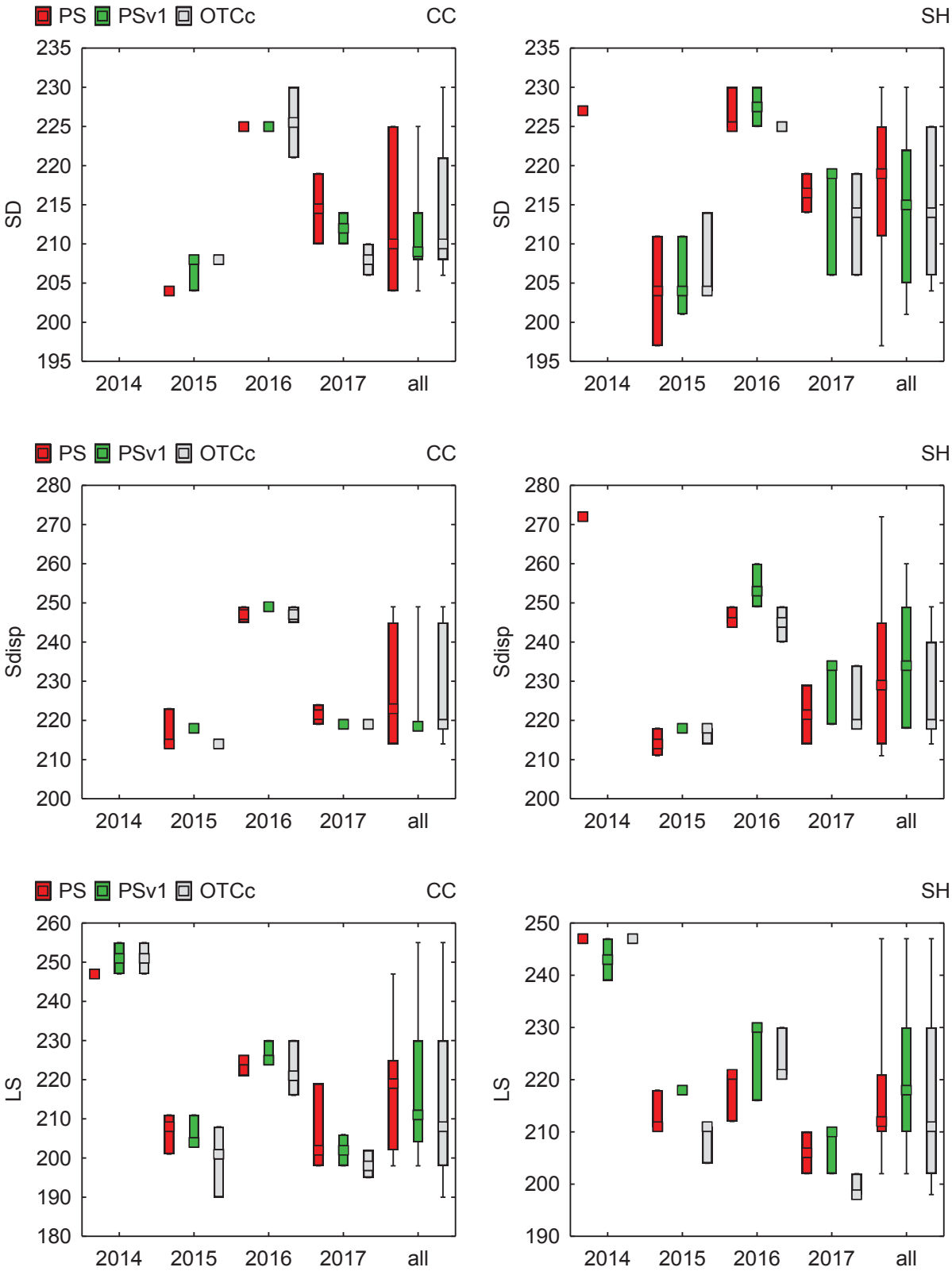

Fig. S23 - Descriptive statistics of seed development (SD), seed dispersal (Sdisp) and leaf senescence (LS) in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***G. supinum*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

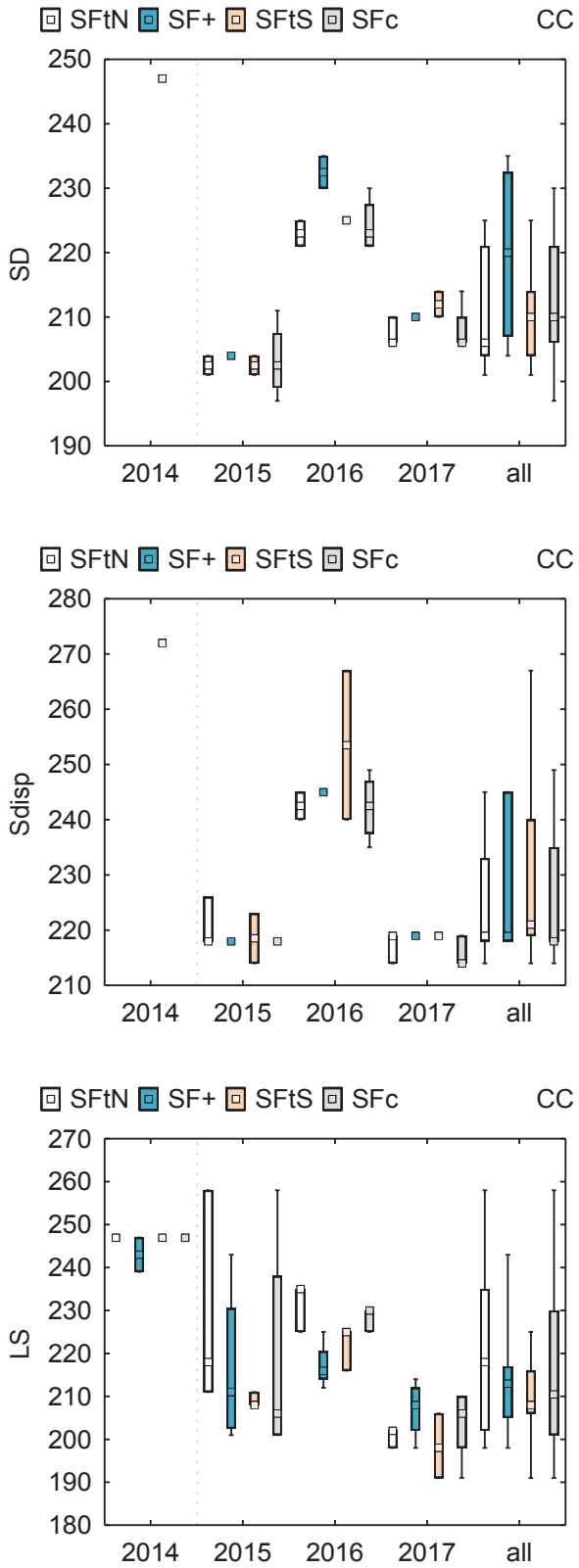

Fig. S24 - Descriptive statistics of seed development (SD), seed dispersal (Sdisp) and leaf senescence (LS) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***G. supinum*** at intra-annual level. Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

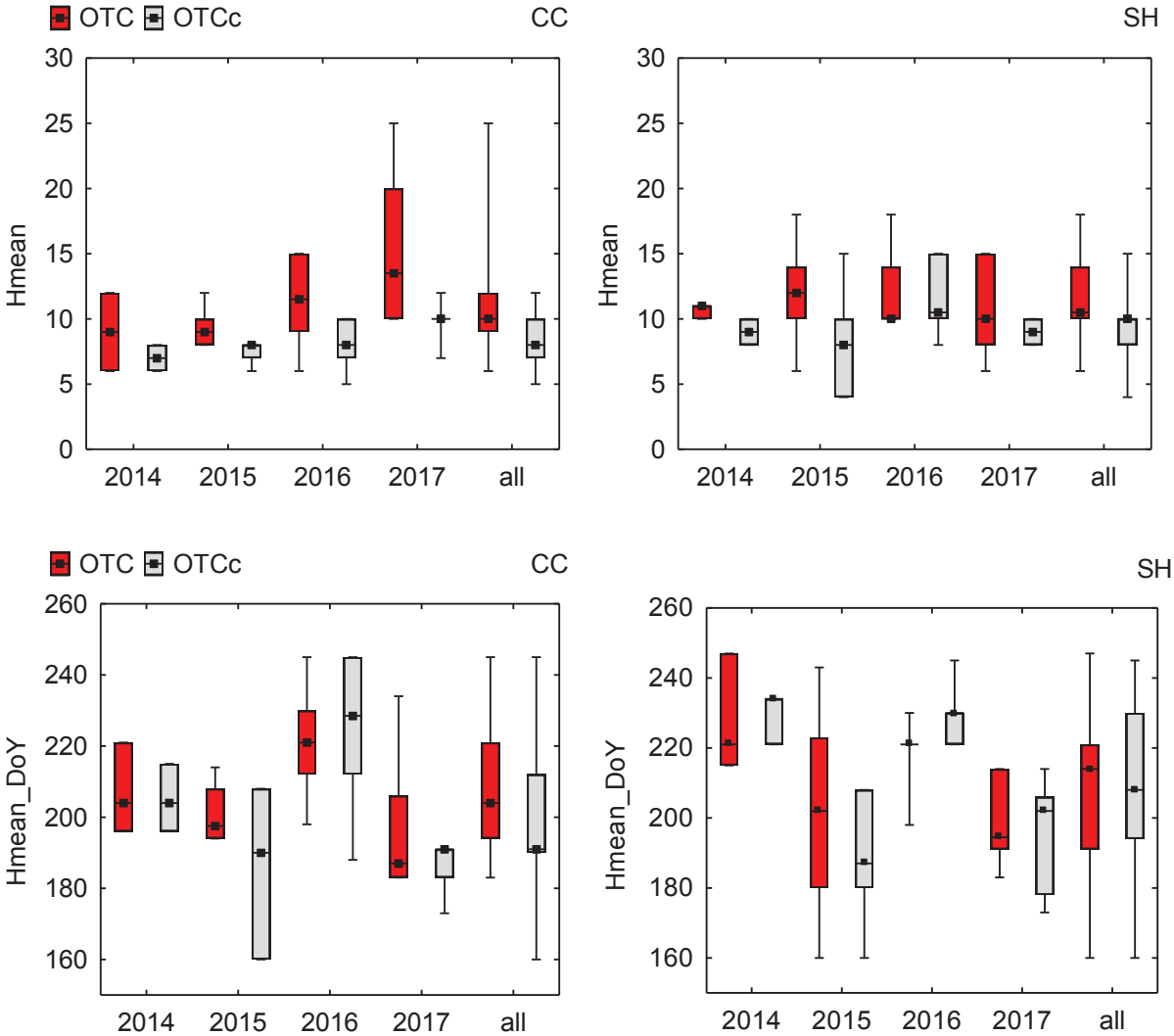

Fig. S25 - Descriptive statistics of the mean height (Hmean) and of the day of achievement of the maximal mean height (Hmean_DoY) computed in warming (OTC) and control (OTCc) plots of ***G. supinum*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max.

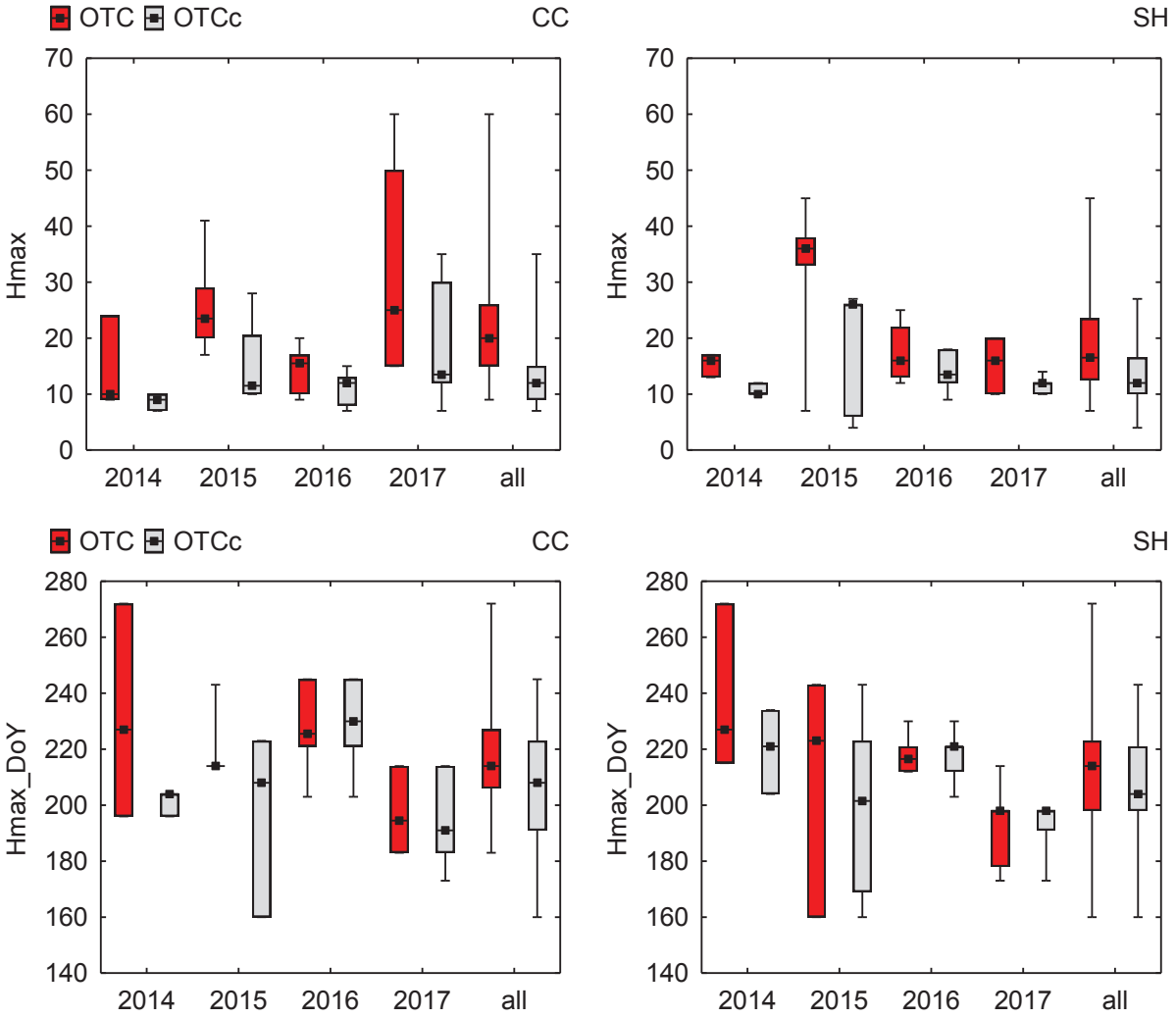

Fig. S26 - Descriptive statistics of the maximum height (Hmax) and of the day of achievement of the maximum height (Hmax_DoY) computed in warming (OTC) and control (OTCc) plots of ***G. supinum*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max.

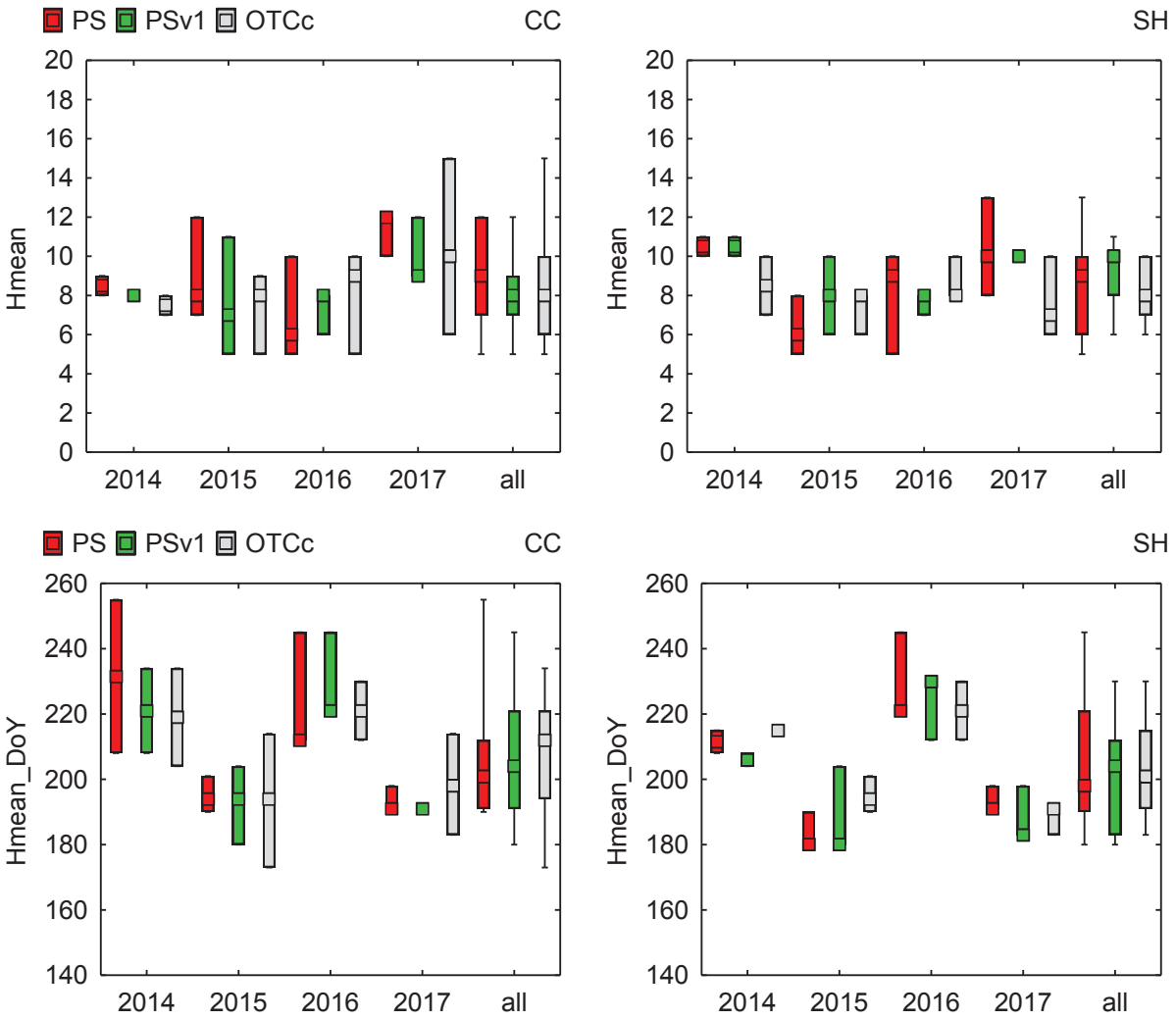

Fig. S27 - Descriptive statistics of mean height (Hmean) and of the day of achievement of the maximal mean height (Hmean_DoY) in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***G. supinum*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

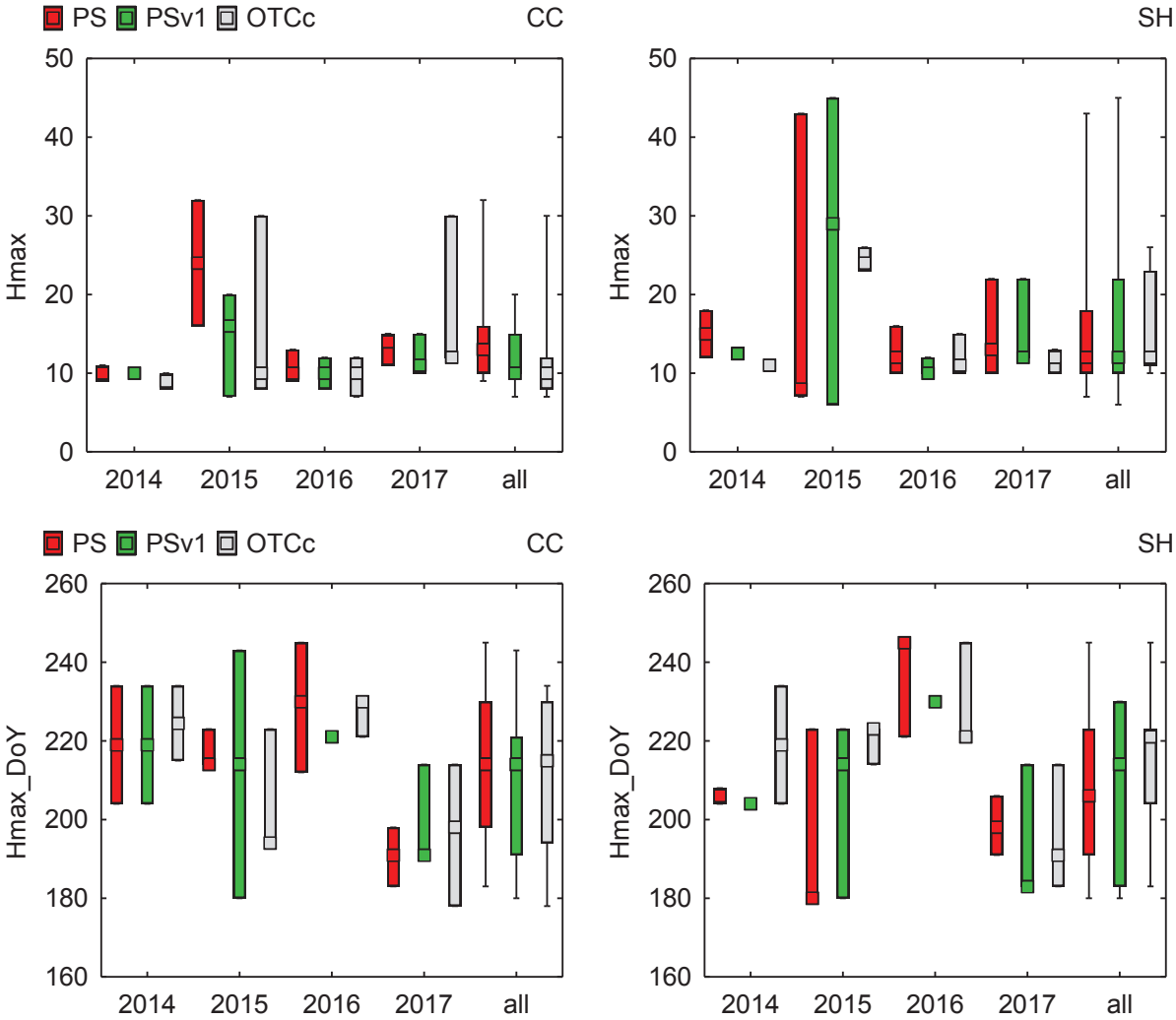

Fig. S28 - Descriptive statistics of maximal height (Hmax) and of the day of achievement of the maximum height (Hmax_DoY) in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***G. supinum*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

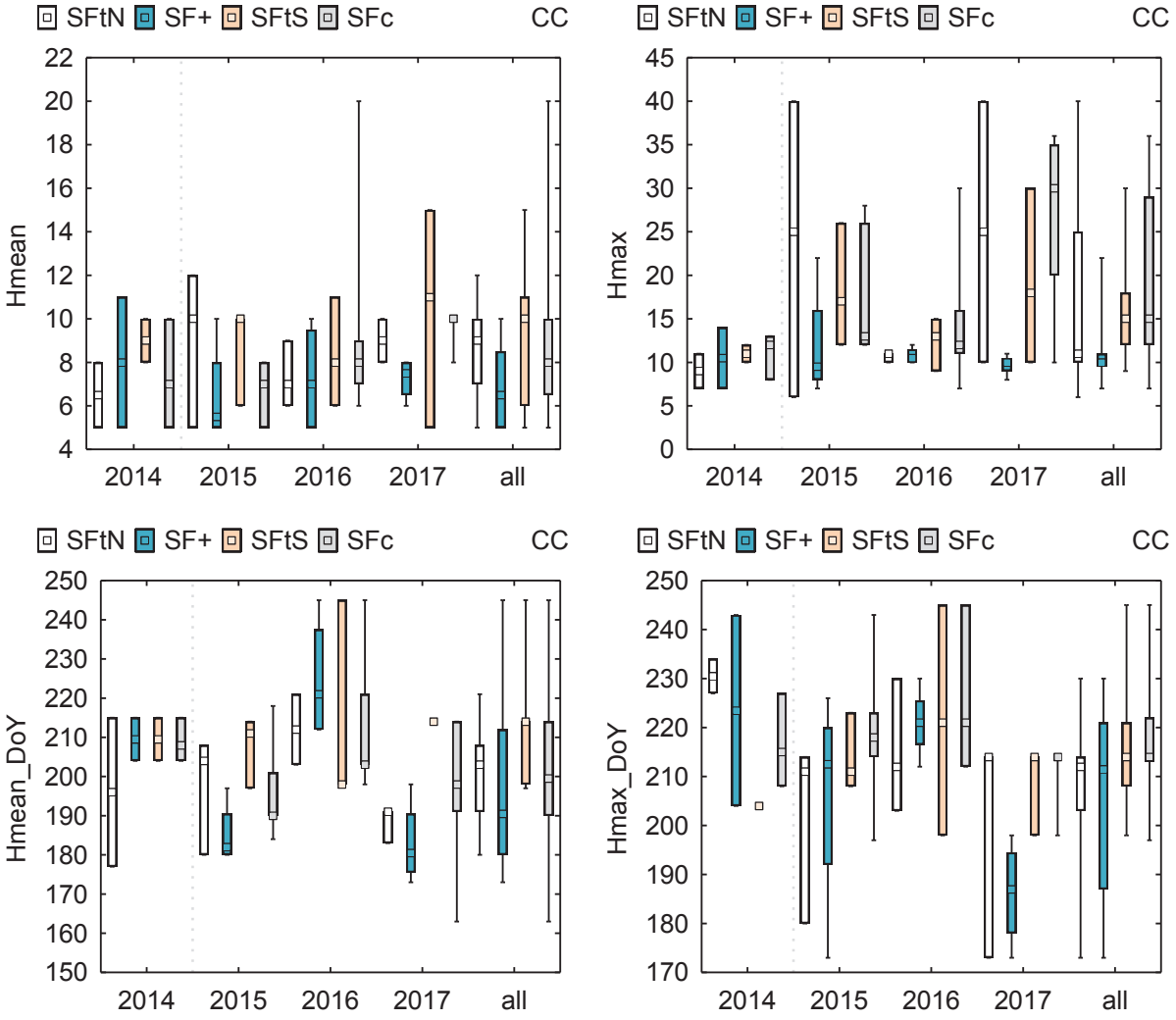

Fig. S29 - Descriptive statistics of mean height (Hmean), maximum height (Hmax) and day of achievement of the maximal mean height (Hmean_DoY) and maximum height (Hmax_DoY) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***G. supinum***, at intra-annual level. Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

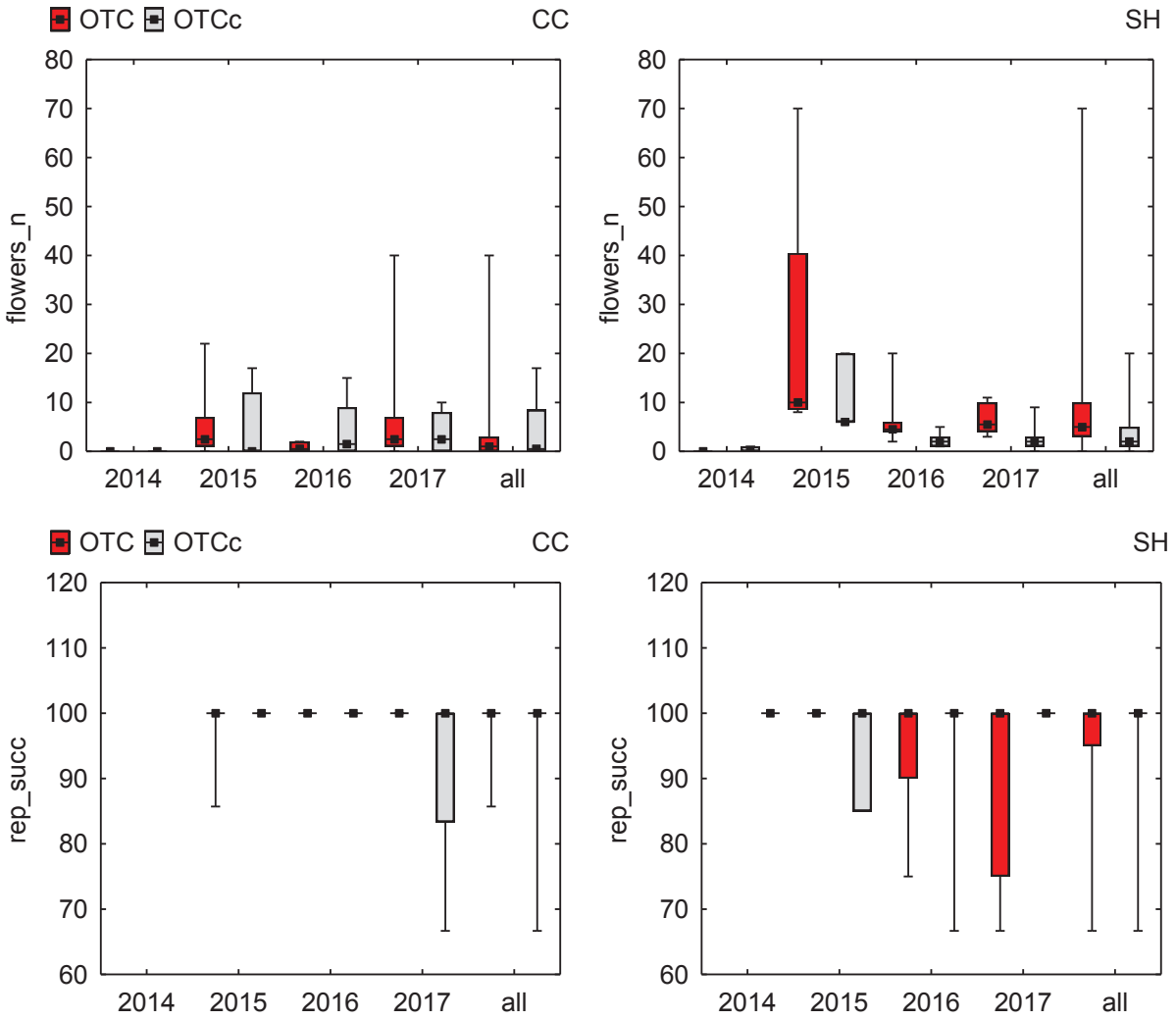

Fig. S30 - Descriptive statistics of the number of reproductive individuals (flowers_n) and of the reproductive success (rep_succ) computed in warming (OTC) and control (OTCc) plots of ***G. supinum*** at inter-annual level, for both the plant communities (CC= alpine grasslands; SH=snowbeds). Black squares = medians, boxes = 25%-75%, whiskers = min-max.

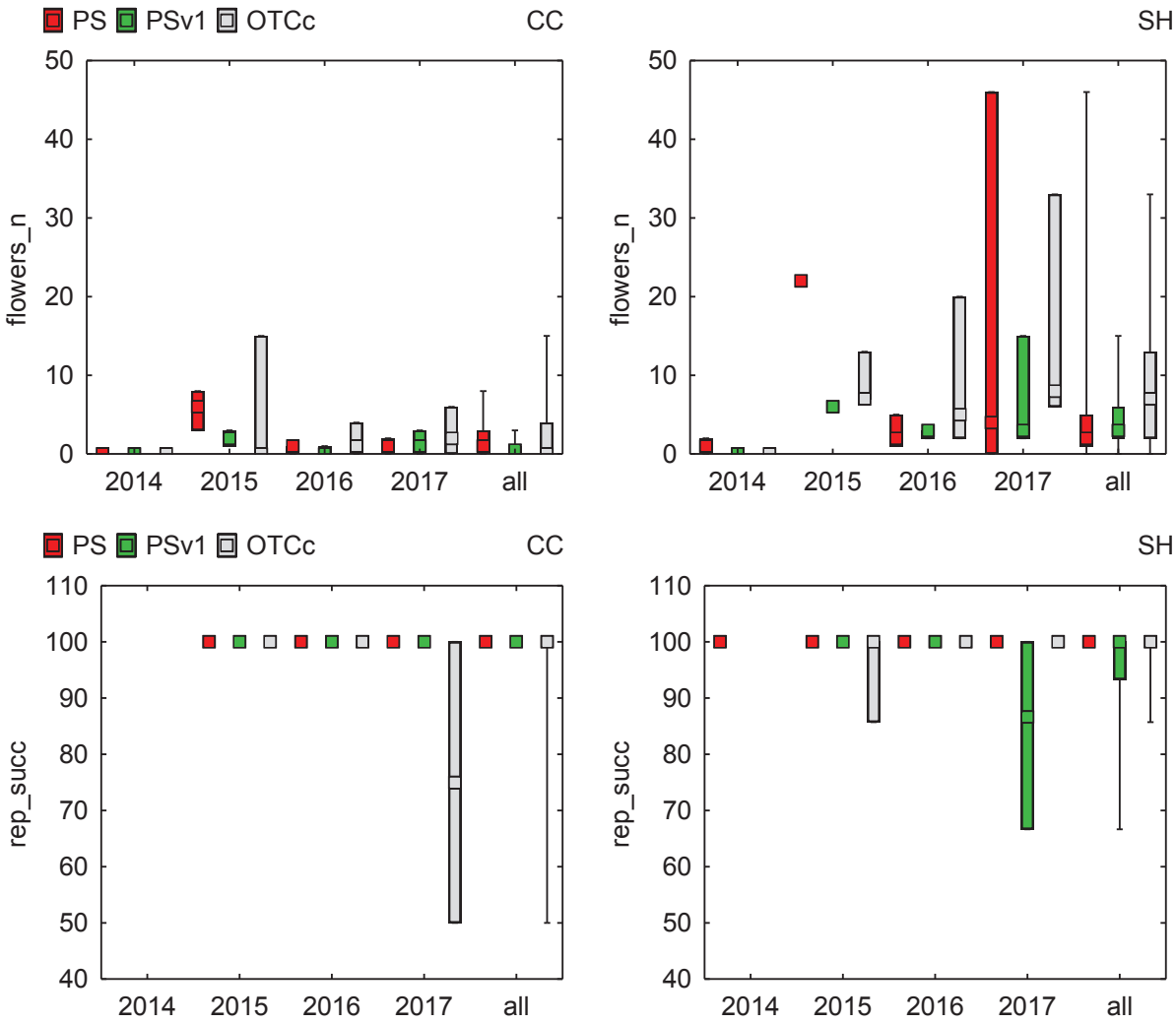

Fig. S31 - Descriptive statistics of the number of reproductive individuals (flowers_n) and of the reproductive success (rep_succ) computed in dry+warm (PS), moist (PSv1) and control (OTCc) plots for the whole study period (2014-2017) for ***G. supinum*** at intra-annual and intra-plant communities levels (CC = alpine grassland; SH = snowbed). Coloured squares = medians, boxes = 25%-75%, whiskers = min-max.

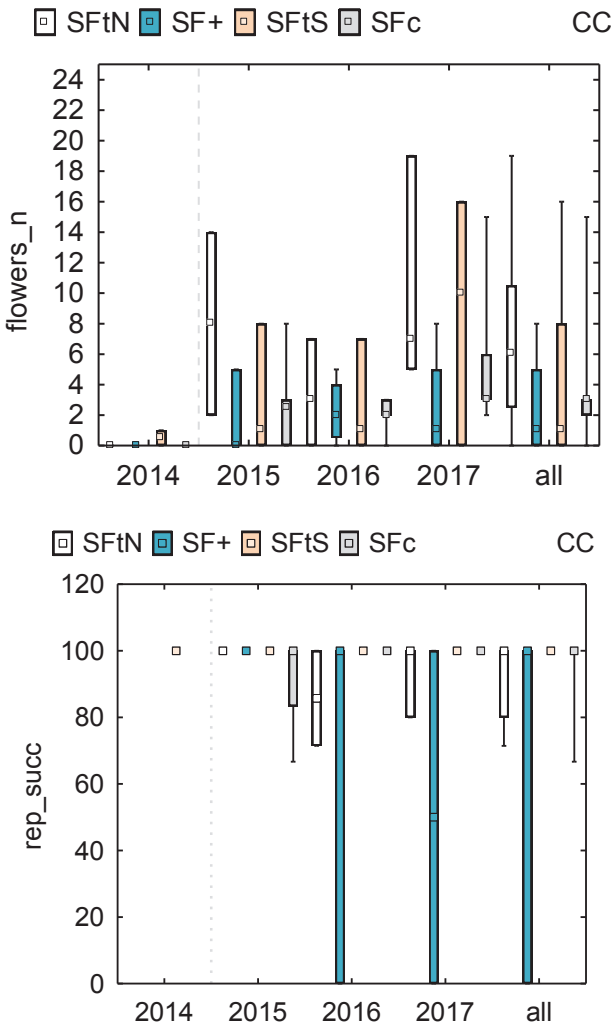

Fig. S32 - Descriptive statistics of the number of reproductive individuals (flowers_n) and of the reproductive success (rep_succ) computed in plots with artificially delayed snow melt (SF+), in plots with naturally delayed snow melt induced by terrain morphology on the north side (SFtN) and south side (SFtS) of the fence and in control plots (SFc) for ***A. pentaphyllea***, at intra-annual level. Coloured square = medians, boxes = 25%-75%, whiskers = min-max.

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VIII. REFERENCES

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