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Research

Salix shrub encroachment along a 1000 m elevation gradient triggers a major ecosystem change in the European Alps

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Shrub encroachment, a globally recognized response to climate warming, usually involves late successional species in mountain environments, without alteration to climax communities. We show that a major ecosystem change is occurring in the European Alps across a 1000 m elevation gradient, with pioneer hygrophilous *Salix* shrubs, previously typical of riparian forests, wetlands and avalanche ravines, encroaching into the climax communities of subalpine and alpine belts shrublands and grasslands, as well as snowbeds, pioneer vegetation and barren grounds in the nival belt.

We analyzed *Salix* recruitment through dendrochronological methods, and assessed its relationships with climate and atmospheric CO_2 concentration. The dendrochronological data indicated that *Salix* encroachment commenced in the 1950s (based on the age of the oldest *Salix* individuals, recruited in 1957), and that it was correlated with increasing atmospheric CO_2 concentration, spring warming and snow cover decrease. Hygrophilous *Salix* shrubs are expanding their distribution both through range filling and upwards migration, likely achieving competitive replacement of species of subalpine and alpine climax communities. They benefit from climate warming and CO_2 fertilization and are not sensitive to spring frost damage and soil limitations, being observed across a gradient of soil conditions from loose glacial sediments in recently deglaciated areas (where soils had not had sufficient time to develop) to mature soils such as podzols (when colonizing late successional subalpine shrublands).

Salix encroachment may trigger ecosystem and landscape transformations, promoting the development of forests that replace pre-existing subalpine shrublands, and of open woodlands invading alpine grasslands and snowbeds, making the alpine environment similar to sub-Arctic and Arctic areas. This results in a new threat to the conservation of the plant species, communities and landscapes typical of the alpine biota, as mountain ranges such as the Alps provide limited opportunities for upward migration and range-shift.

Keywords: alpine ecosystems, CO_2 increase, elevation gradient, landscape alteration, pioneer hygrophilous *Salix* shrubs, shrub encroachment, spring warming

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Introduction

Recent climate warming has been recognized to be unprecedented in rate and magnitude (IPCC 2014). Shrub encroachment is one of the most widespread responses to climate warming globally (Elmendorf et al. 2012a, b), with feedbacks involving the surface energy budget, soil temperature and moisture, snow cover, surface albedo, biogeochemical cycles, active layer thickness and permafrost conditions (Chapin et al. 2005, Sturm et al. 2005, Lawrence and Swenson 2011, Loranty et al. 2011, Myers-Smith et al. 2011, DeMarco et al. 2014). Shrub encroachment has been observed in high latitude areas from Alaska, Greenland, Svalbard and Siberia (Sturm et al. 2001, Tape et al. 2006, 2012, Forbes et al. 2010, Elmendorf et al. 2012a, b, Frost and Epstein 2014, Jørgensen et al. 2015, Myers-Smith and Hik 2018, Salmon et al. 2019), as well as in high elevation areas including the Rocky Mountains (Formica et al. 2014), the Tibetan Plateau and Himalayas (Brandt et al. 2013, Klein et al. 2014, Lehnert et al. 2016), the European Scandes (Kullman 2002, Hallinger et al. 2010, Rundqvist et al. 2011, Myers-Smith et al. 2015) and the European Alps (Dullinger et al. 2003, Cannone et al. 2007, Stöckli et al. 2011, Carlson et al. 2017, Francon et al. 2020). In the European Alps shrub encroachment involves late successional species (e.g. species of the genera *Rhododendron*, *Vaccinium*, *Juniperus*, *Kalmia*, *Empetrum*) (Dullinger et al. 2003, Cannone et al. 2007, Stöckli et al. 2011, Cannone and Pignatti 2014, Francon et al. 2020, Malfasi and Cannone 2020). In Arctic and sub-Arctic regions encroachment mainly involves species of *Alnus*, *Salix* and *Betula* (Tape et al. 2006, 2012, Forbes et al. 2010, Myers-Smith et al. 2011, Jørgensen et al. 2013, 2015, Rinas et al. 2017, Myers-Smith and Hik 2018), which are pioneer deciduous tall shrubs generally found in close association with each other. These shrub species are able to colonize newly exposed substrates and mineral soils on floodplain terraces, valley slopes, interfluves and river channels (Rhoades et al. 2001), as well as being able to encroach into undisturbed Arctic and alpine tundra communities, giving way to tall shrubs and open woodland, with the former being the more common transition pathway (Terskaia et al. 2020).

In the European Scandes, in addition to encroachment by deciduous shrubs, large increases of the evergreen shrub *Empetrum hermaphroditum* have also been reported (Klanderud and Birks 2003, Wilson and Nilsson 2009). This suggests that communities with different floristic composition and ecology (e.g. snow-protected versus wind-exposed communities) are converging in composition (Maliniemi et al. 2018), with large differences in the feedbacks promoted by the encroachment of evergreen or deciduous shrubs (Hallinger et al. 2010, Vowles and Björk 2019).

The European Alps can be considered as a model system for studies of ecosystem responses to climate change. The region has experienced very strong atmospheric warming, especially in the period 1950–2000 (Auer et al. 2007, Cannone et al. 2007). This has triggered a wide range of ecosystem responses, including all four types described by Walther et al. (2002) to recent climate change. These include: a) changes in plant phenology (Theurillat and Guisan 2001, Rogora et al. 2018); b) changes in the range and distribution of species; c) of composition and interactions within communities, with upwards migration of alpine species towards mountain summits (Lenoir et al. 2008, Pauli et al. 2012, Steinbauer et al. 2018), changes in floristic composition, extinction debt and thermophilization of mountain floras (Cannone et al. 2007, Gottfried et al. 2012, Cannone and Pignatti 2014); and d) changes in the structure and dynamics of ecosystems, including shrub and tree encroachment (Cannone et al. 2007, Leonelli et al. 2016, Malfasi and Cannone 2020) and surface area changes (Cannone et al. 2007).

In Europe, *Salix* shrubs are typical of alluvial and riparian forests (e.g. *S. caprea*, *S. cinerea*, *S. foetida*, *S. hastata*), flood plains, streams, creeks (e.g. *S. caesia*, *S. purpurea*), wetlands (*S. aurita*) and of avalanche ravines (e.g. *S. breviserrata*, *S. foetida*, *S. helvetica*, *S. waldsteiniana*), occurring from the colline to the subalpine belts (Ozenda 1985, Ellenberg 1988, Delarze et al. 2015, Mucina et al. 2016). None of these hygrophilous pioneer *Salix* species belongs to the ecological series of the climax shrubs and dwarf-shrubs of the subalpine belt, the climax high-elevation primary grasslands of the alpine belt, or the chionophilous (i.e. adapted to extended snow persistence) dwarf *Salix* shrubs of the snowbeds of the alpine and nival belts (*S. herbacea*, *S. reticulata*, *S. retusa*, *S. serpyllifolia*) (Ozenda 1985, Ellenberg 1988, Delarze et al. 2015, Mucina et al. 2016).

Climate change triggers changes in ecosystem dynamics, including in both the spatial and temporal patterns of vegetation communities. In the European Alps, temporal patterns of vegetation change follow established successional patterns, with communities moving from earlier to more mature stages through increases in total vegetation cover, changes in floristic composition (with the replacement of pioneer by late successional species) and, in some cases, with changes in the community structure (e.g. from grasslands to shrublands) and in the dominant growth form (e.g. from graminoids to shrubs) (Cannone et al. 2007, 2009, Cannone and Pignatti 2014, Malfasi and Cannone 2020). Similar changes have been observed worldwide both at high elevation and at high latitudes (Elmendorf et al. 2012a, b).

To date, although climate change impacts have been documented to involve several levels of ecological hierarchy from species to communities but do not appear to have included alterations to successional pathways, in particular involving climax communities (i.e. mature communities, characterized by closed canopy, high ground cover, dominance of late successional species, high resilience to environmental change and resistance to the ingression of pioneer and/or early successional species). Here, we show that, since the 1950s, a major vegetation change has occurred in the European Alps across a 1000 m elevation gradient from the subalpine, to the alpine and nival belts. This has involved the encroachment of hygrophilous pioneer *Salix* shrubs, colonizing both climax communities of the subalpine and alpine belts (shrublands and grasslands), as well as snowbeds, pioneer vegetation and barren grounds in the nival belt. We hypothesize that: a) this major vegetation change is related to climate change (spring warming and snow cover decrease) and to the increase of atmospheric CO_2 concentration, and b) that the hygrophilous pioneer *Salix* species are encroaching both through range filling with recruitment from the subalpine belt, as well as by upwards migration from lower elevation belts.

Material and methods

Study area and field survey

In the Italian Central Alps we investigated four major valleys of upper Valtellina (Supporting information) along elevation transects encompassing the subalpine (2000–2400 m a.s.l.), alpine (2400–2800 m a.s.l.) and nival belts (> 2800 m a.s.l.). These included both climax shrub and dwarf-shrub vegetation of the subalpine belt, climax alpine grasslands of the alpine belt, and snowbeds, pioneer vegetation and barren ground in the alpine and nival belts (Fig. 1) (Ellenberg 1988).

Field surveys were carried out in 2017 and 2018 during the peak of the growing season (July and August) along transects covering an elevation range ≤ 1000 m (Supporting information). We performed a systematic survey of the hygrophilous *Salix* shrub species (Supporting information) recording and mapping all living and dead individuals. For each of the 1055 identified pioneer *Salix* shrub individuals the following variables were recorded (Pornon and Doche 1995, Myers-Smith et al. 2015, Malfasi and Cannone 2020): geographic position, plant height (cm), longest canopy diameter (canD1; cm), second canopy diameter (canD2; cm), stem basal diameter (SBD; mm), presence of flowers or seeds, and signs of frost damage and/or pathogens. To assess whether the *Salix* shrubs had habitats preferential for encroachment, we recorded the habitat type surrounding each individual within a circular plot with a diameter of 2 m with reference to the following categories: 1) shrublands, 2) grasslands, 3) barren ground or pioneer or snowbed vegetation, 4) hygrophilous communities (rivers, streams, springs, wetlands), 5) anthropogenically influenced habitat. In the subalpine belt we recorded the co-occurrence of late successional shrubs (e.g. *Rhododendron*, *Juniperus*, *Empetrum*, *Vaccinium*). In the alpine and nival belts where snowbed and pioneer vegetation occurred, we recorded the co-occurrence of the hygrophilous *Salix* shrubs with the chionophilous dwarf shrub *Salix* species (*S. herbacea*, *S. retusa*, *S. reticulata*, *S. alpina*, *S. serpyllifolia*). In 2019 and 2020 all transects were re-surveyed during the peak of the growing season to assess the short-term survival of the individuals identified.

Species determination was performed following Lauber and Wagner (1996). For each species, information on their ecological series, elevation belt, community type (Natura 2000, EUNIS, Italian and Swiss Vegetation Prodrome) and whether they are diagnostic and/or abundant were recorded (Ellenberg 1988, European Commission 1992, 2013, Davies et al. 2004, Biondi et al. 2014, Delarze et al. 2015) (Supporting information). Further analyses were carried out for the six more abundant species (*S. appendiculata*, *S. foetida*, *S. hastata*, *S. helvetica*, *S. purpurea*, *S. waldsteiniana*). To assess their upwards migration, we compared our data with the elevation ranges given in the literature (Lauber and Wagner 1996) for the European Alps. These data were integrated with data from GBIF (Global Biodiversity Information Facility, <https://gbif.org>), selecting the data source (e.g. Swiss national databank of vascular plants). Their ecology was compared with that of *Rhododendron ferrugineum* (as target species of the climax shrub communities) and of *Salix herbacea* (as target species of snowbeds) using their ecological indicator values (Lamprecht et al. 2018). For this purpose we used the Ellenberg indices modified for the Italian Flora (Pignatti 2005), for each species building an

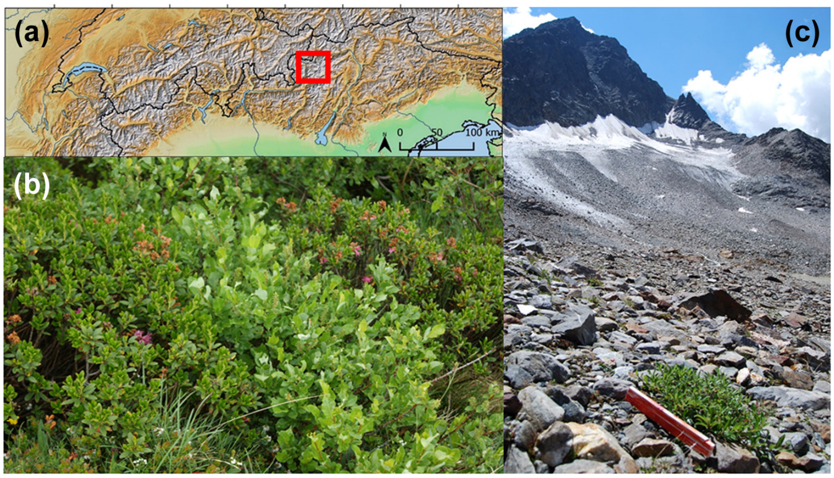

Figure 1. Study area location (a) in upper Valtellina (Italian Central Alps) (red square), (b) with an example of an hygrophilous *Salix* species (*S. foetida*) growing together with the climax subalpine shrub *Rhododendron ferrugineum* in the subalpine belt and (c) of one (*S. helvetica*) colonizing the Sforzellina glacier forefield in the nival belt.

ecogram showing their characteristic values of light (L, values ranging from 1 = full shadow to 12 = full light with high incoming radiation), temperature (T, values ranging from 1 = low temperatures indicating alpine and/or Arctic climates to 12 = high temperatures indicating submediterranean to hot desert climates), climate continentality (C, values ranging from 1 = oceanic to 9 = continental), soil moisture (M, values ranging from 1 = extremely dry to 12 = submerged), soil reaction (R, values ranging from 1 = soils with low pH to 9 = soils with high pH) and soil nutrients (N, values ranging from 1 = oligotrophic soil to 9 = eutrophic soils).

Dendrochronological and soil analyses

Following the protocol proposed by Myers-Smith et al. (2015), 117 of the 1055 censused individuals were sampled for age determination. Individuals with an SBD > 5 cm (n = 10) were cored, while individuals with SBD < 5 cm (n = 107) were harvested (Büntgen et al. 2015, Myers-Smith et al. 2015) obtaining, in total, 250 sections and 24 cores suitable for aging the 117 individuals. Ring number and width were measured along at least two radii using a measuring stage (Lintab 6) and the time series analysis program TSAPWin ver.4.64 (Rinntech, Heidelberg, Germany), with an accuracy of 0.01 mm. Cross-dating was always performed within all radii of the basal sections or cores using the cross-date index (CDI) values and visual inspection.

Because the occurrence of young individuals in the field could be under-estimated due to their small size we analysed the relationship between size and age of our sampled individuals, assessing that individuals with maximum canopy diameter ≤ 10 cm had a mean age of 7 ± 1.68 yrs (and plant height between 2 and 9 cm) (Supporting information). Based on these data, as the size of the very young individuals was small and these individuals could be difficult to detect in the field leading to their potential under-estimation, to avoid artefacts we excluded the most recent years and fixed the end of the study period at 2014 (Büntgen et al. 2015, Myers-Smith and Hik 2018). To finalize the duration of the study period for further analyses, we assessed its onset according to the recruitment date of the oldest individuals (in 1957). As no individuals were recruited before the 1950s, consistent with these data, we started our analyses in the 1950s and focused on the period 1950–2014.

For each of the six more abundant species (*S. appendiculata*, *S. foetida*, *S. hastata*, *S. helvetica*, *S. purpurea*, *S. waldsteiniana*) we carried out linear regression between the measured age and the stem diameter, using this to reconstruct recruitment for the other individuals of the same species (Supporting information) (Myers-Smith et al. 2015). As the regression equations showed that the growth rates differed between species, we reconstructed the recruitment patterns only for the six more abundant species in order to avoid over- or under-estimating the recruitment dates of the other species. The recruitment dates were combined into five-year time intervals for further analyses (Büntgen et al. 2015, Malfasi and Cannone 2020).

To provide a general characterization of the range of soil conditions associated with the pioneer *Salix* shrub species, we analyzed three soil samples (collected at 1–4 cm depth excluding the overlying litter) from each habitat type (shrubland, grassland, snowbed, pioneer, barren ground) in the subalpine, alpine and nival belts. All chemical analyses were carried out on the 2-mm soil fraction following standard procedures (Cannone et al. 2012, 2021a, D'Alò et al. 2021). Specifically, soil pH was measured by adding 20 ml of distilled water to 10 g of air-dried soil, shaking the mixture vigorously and measuring the pH after several minutes. To quantify water content, soil samples were oven dried at 105°C for 24 h and the water content was calculated as the difference between the mass of the fresh and dried sample. Total C and total N contents were determined using an automatic elemental analyser (Carlo Erba), and % total organic matter was assessed by loss on ignition (LOI).

Climate and data analyses

We used climatic data recorded at the automatic weather station (AWS) Segl-Maria (Swiss National Basic Climatological Network), the closest station to our study sites providing a long climatic data series (1864–2018) including monthly air temperature, monthly total precipitation and total annual snow cover (Scherrer et al. 2013). Data from this AWS are representative of the climatic trends for the Swiss Alps (Klein et al. 2016, 2018) and specifically of the climatic trends of upper Valtellina, as confirmed by statistically significant linear regressions against data from the four main AWSs in operation across our study area, which individually have shorter data series (Supporting information).

Mean annual atmospheric CO_2 concentration (ppm) data were obtained from the historical CO_2 datasets (<www.co2.earth/historical-co2-datasets>) compiled by the Institute for Atmospheric and Climate Science (IAC) at Eidgenossische Technische Hochschule in Zurich, Switzerland.

The climate time series from the Segl-Maria AWS and of atmospheric CO_2, averaged over 5-year periods since 1950, were used to perform a product-moment correlation (Pearson correlation coefficient) to test correspondence between shrub recruitment, climate and environmental data (Büntgen et al. 2015, Malfasi and Cannone 2020), separating the subalpine and alpine belts from the nival belt. The correlation analysis referred to the 5-year during the recruitment period (Büntgen et al. 2015, Malfasi and Cannone 2020). These analyses were computed both at interspecific (e.g. focusing on the relationships between the six more abundant *Salix* species and the abiotic factors) and intraspecific levels (e.g. focusing on the relationship of each individual *Salix* species with the abiotic factors) using the software Statsoft©. The intraspecific analyses provide more information on the ecology of each of the six more abundant *Salix* species individually and on which factors may be more influential on their observed dynamics, while the interspecific analyses provided a more general integrated assessment of the patterns of ecosystem dynamics triggered by climate change.

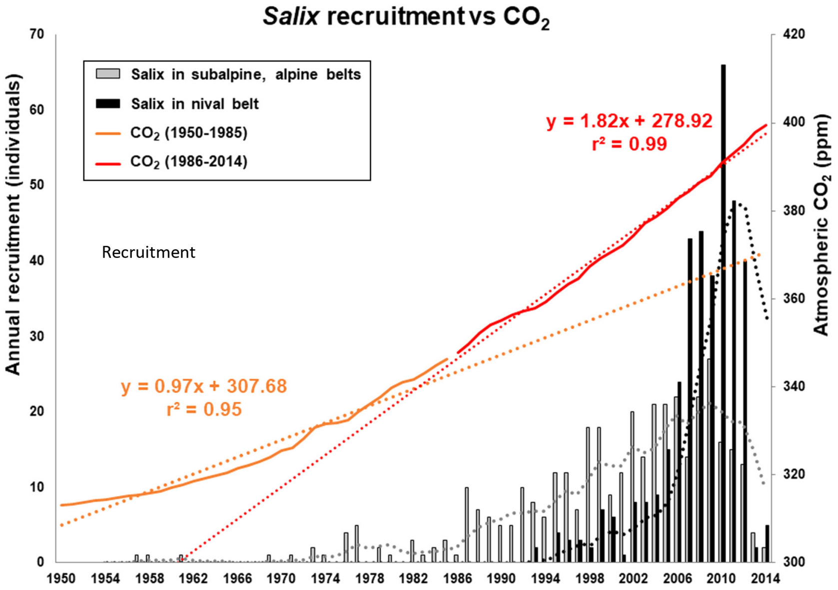

Figure 2. *Salix* annual recruitment at interspecific level separating the subalpine and alpine belts (grey bars) and the nival belt (black bars) in comparison with the increase of atmospheric CO_2 concentration (orange line = period 1950–1985; red line = period 1986–2014), showing a sharp increase since 1985 as shown by the regression equations. The orange and red dotted lines provide the linear trends with time of atmospheric CO_2 concentration; the grey and black dotted lines provide of the *Salix* recruitment over 5-year running average.

Results

Temporal trends of *Salix* recruitment

Based on the data obtained, the encroachment of hygrophilous *Salix* shrubs commenced in 1957, the oldest recruitment date across all species and individuals, meaning that before 1950s the encroachment of hygrophilous pioneer *Salix* shrubs did not occur. At inter-specific level (considering all six more abundant *Salix* species), *Salix* recruitment in the subalpine and alpine belts followed a unimodal trend which commenced in 1957, remained low and not constant with time until 1986, and then exhibited a sharp increase with a peak in 2009 (Fig. 2). A similar but delayed trend characterized the nival belt, commencing in 1993, and culminating in a peak in 2010 (Fig. 2). Similar trends characterized the recruitment of each of the six more abundant species considered individually (Supporting information). The period of more intensive recruitment in the interspecific analysis was correlated with a sharp increase of atmospheric CO_2 concentration after 1986, doubling in the period 1986–2014 with respect to 1950–1985 (Fig. 2). The younger age of the populations of the nival belt (6–11 yrs) relative to the subalpine and alpine belts (10–21 yrs) indicated that the encroachment took place from lower to higher elevations (Supporting information). The proportions of individuals producing flowers and seeds ranged between ca 10% (*S. waldsteiniana* = 9.8%, *S. helvetica* = 10.3%, *S. appendiculata* = 11.5%, *S. purpurea* = 12%) to more than 20% (*S. foetida* = 23.1%, *S. hastata* = 28.6%). Interannual survival exceeded 97%, with sporadic evidence of frost damage (< 2 % of 1055 individuals).

Table 1. Mean values of soil pH, % total organic matter assessed through loss on ignition (LOI), % C, % N and water content (%) in the different habitat types and elevation belts where the hygrophilous pioneer *Salix* shrub encroachment occurred. n = number of samples.

Elevation belt	Habitat type	n	Ph	LOI	C %	N %	H_2O %
Subalpine	Shrublands	3	4.7	45.6	23	1.3	60.9
Alpine	Grasslands	3	3.6	29	14.8	0.97	46.6
Alpine	Snowbeds	3	3.5	27.5	12.5	0.89	39.9
Alpine	Pioneer	3	5	1.8	0.3	0.19	5.9
Alpine and nival	Barren grounds	3	6.7	1.5	0.2	0.1	85

Patterns of *Salix* encroachment

Encroaching *Salix* hygrophilous pioneer shrubs included 17 species typical of alluvial and riparian forest (e.g. *S. caprea*, *S. cinerea*, *S. foetida*, *S. hastata*), flood plains, streams, creeks (e.g. *S. caesia*, *S. purpurea*), avalanche ravines (e.g. *S. breviserrata*, *S. foetida*, *S. helvetica*, *S. waldsteiniana*) and wetlands (*S. aurita*), leading to massive colonization of this vegetation across the subalpine to the nival belts (Supporting information). In the subalpine and alpine belts these hygrophilous *Salix* shrubs were not limited to their original habitats (streams, rivers and peaty soils) or to disturbed (scree slopes, avalanche ravines) or anthropogenically impacted areas, and rather they colonized the climax communities of the subalpine heaths and alpine grasslands (Supporting information). In the subalpine and alpine belts the *Salix* encroachment into climax communities occurred with all types of soil conditions, from podzols to alpine brown soils to barren soils, with

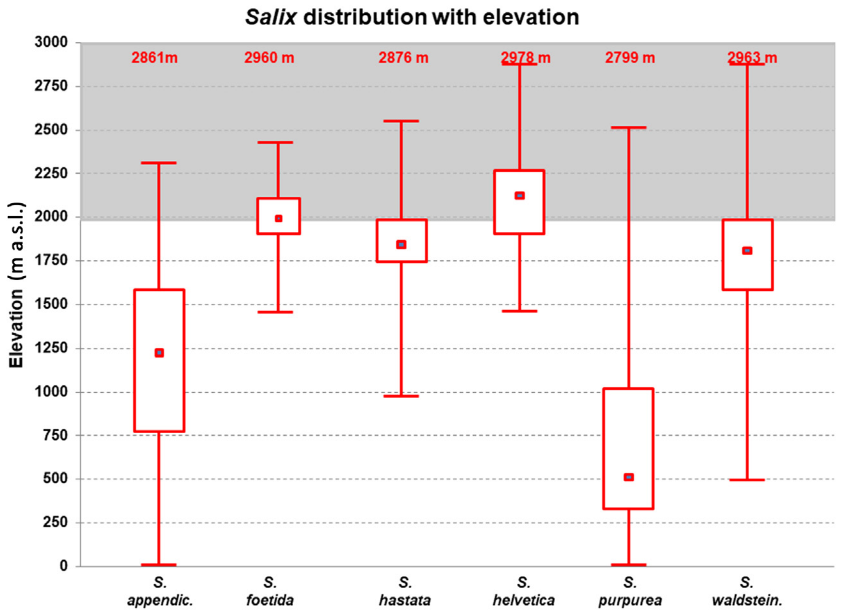

Figure 3. Distribution patterns with elevation of the six more abundant hygrophilous *Salix* showing their elevation range (minimum and maximum), quartiles (25% and 75%) and median derived from the available literature integrated with data available in GBIF (Global Biodiversity Information Facility) network (<https://gbif.org>) from selected datasets. The grey background shows the elevation gradient investigated with the red font the highest elevation recorded in this study.

their growth occurring across a wide gradient of soil conditions including pH, water content, organic matter, and C and N contents (Table 1). In the alpine and nival belts they encroached into snowbeds (growing with the chionophilous species *S. herbacea*, *S. reticulata*, *S. retusa*, *S. serpyllifolia*), and also into pioneer communities and previously barren ground, being found even on terrains deglaciated in the last year, growing on bare surfaces on glacial sediments (Table 1).

The elevation of occurrence recorded for the six more abundant hygrophilous *Salix* shrubs exceeded their previous 75% percentile and, in most cases, their recorded known maximum elevation (Fig. 3). With the exception of *S. purpurea* (which requires higher temperature and soil moisture), these species showed a range of slightly different ecological requirements both with respect to the late successional *Rhododendron ferrugineum* and the snowbed species *S.*

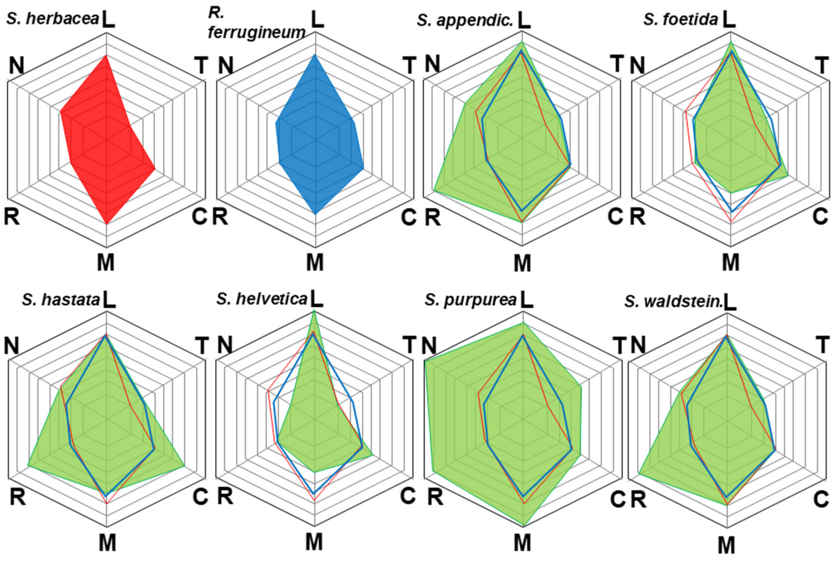

Figure 4. Ecograms showing the main ecological requirements of *Rhododendron ferrugineum* (as target species representative of the climax subalpine heaths) and *Salix herbacea* (as target species representative of the high elevation snowbeds) and of the six hygrophilous *Salix* species. L=light; T=temperature; C=continentality; M=soil moisture; R=soil reaction (pH); N=soil nutrients. Values of each index decrease from 9 on the outer boundary to 2 in the inner part of each diagram.

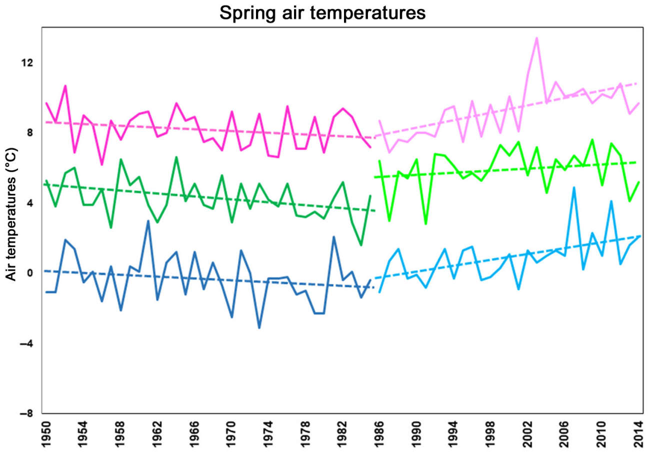

Figure 5. Comparison of the trends of spring air temperatures (°C) in the period 1950–1985 versus 1986–2014, showing statistically significant correlations with the recruitment of the hygrophilous *Salix* species. April = dark blue and pale blue line; May: dark green and pale green line; June: dark pink and pale pink line). β = Pearson's correlation coefficient. Statistically significant correlations $p < 0.05$.

herbacea (Fig. 4). They were able to adapt well to locations typically exposed to both full sun and frequent clouds (L = 9), cold environments (T = 2), continental climate (C = 7), dry to moist soils (M = 3–5) and extremely infertile/oligotrophic locations (N = 1 or 2).

Relationships between *Salix* recruitment and climate

In the overall study period (1950–2014) the mean annual air temperature (MAAT) exhibited a statistically significant increase of +0.024°C yr^{-1} ($p < 0.001$; $R^2 = 0.43$), resulting in a warming ≥ 1.5°C since 1950. The rate of change accelerated in the period 1986–2014 in comparison with 1950–1985, with pronounced spring warming (Fig. 5), which was statistically significant in April (+0.0824°C yr^{-1}; +1.2°C overall) and June (+0.1055°C yr^{-1}; +1.1°C overall) (Fig. 5, Table 2). In June, there was an increase of mean precipitation (+12%, from 102 to 116 mm), and decrease in mean snow cover depth (−20.8%, from 336 to 278 cm) corresponding with the large and persistent *Salix* encroachment since the late 1980s (Supporting information).

Correlation between the *Salix* recruitment and the measured climatic variables and atmospheric CO_2 concentrations was assessed using product-moment correlation (Table 3). These analyses were performed separately for the subalpine, alpine and for the nival belts (Table 3), as the recruitment patterns differed with time in the former (subalpine and alpine) and the latter (nival belt) (Fig. 2, Supporting information). Within each elevation belt, the analyses were performed at both interspecific level (providing the general picture of the climatic and environmental conditions associated to *Salix* encroachment) and on each of the six most abundant individual species (allowing to highlight eventual differences in their ecological requirements). At inter-specific level and across all three elevation belts *Salix* recruitment was correlated with increasing atmospheric CO_2 concentration, spring monthly (April, May, June) air temperature, and precipitation in November while, only in the subalpine and alpine belts, with decreasing snow cover depth (Table 3).

Discussion

Our data show that shrub encroachment in the European Alps has been occurring through a previously undescribed successional pathway involving pioneer hygrophilous *Salix* shrubs that are able to colonize both climax and pioneer vegetation across different elevation belts up to 3000 m a.s.l. This pathway is similar to processes reported in sub-Arctic and Arctic regions (Tape et al. 2006, 2012, Forbes et al. 2010, Myers-Smith et al. 2011, Jørgensen et al. 2013, 2015, Rinas et al. 2017, Myers-Smith and Hik 2018, Terskaia et al. 2020), but has not been reported previously in the Alps, where shrub encroachment has previously been reported involving late successional species typical of climax subalpine shrub vegetation (Dullinger et al. 2003, Cannone et al. 2007, Stöckli et al. 2011, Cannone and Pignatti 2014, Francon et al. 2020, Malfasi and Cannone 2020). The successful encroachment of these *Salix* shrubs initiated more recently (late 1950s) than did that of late successional species (e.g. *R. ferrugineum*), which initiated as early as 1867 in the Italian central Alps, at the end of the Little Ice Age in response to regional air warming (Malfasi and Cannone 2020). Major ecosystem changes involving the climax vegetation of the subalpine and alpine belts, which are generally considered able to withstand competition from pioneer species, have not previously been reported. We hypothesize that these hygrophilous *Salix* species are capable of achieving competitive replacement through species-specific mechanisms, which involve range filling through recruitment both from neighboring habitats in the subalpine belt (e.g. *S. helvetica*, *S. foetida*, *S. waldsteiniana* from avalanche ravines), as well as through upwards migration from lower elevation belts (e.g. *S. purpurea*, *S. cinerea*, *S. caprea* from riparian and alluvial forest habitats) (Supporting information). The encroachment of these *Salix* shrubs, most representing community types considered as pre-forest and

Table 2. Mean spring air temperatures (°C) (April, May, June) showing the warming trend comparing the period 1950–1985 versus 1986–2014 as obtained by linear regression. β = regression coefficient. Statistically significant values $p < 0.05$.

	1950–1985				1986–2014			
	Mean	β	p	r^2	Mean	β	p	r^2
April	−0.3	−0.0262	0.16	0.04	+0.9	0.0824	< 0.001	0.276
May	+4.2	−0.0404	0.025	0.1391	+5.9	0.0285	0.29	0.0403
June	+8.2	−0.0246	0.24	0.0562	+9.3	0.1055	0.003	0.3907

Table 3. Pearson's correlation coefficients between the recruitment of the most abundant hygrophilous *Salix* shrub species, atmospheric CO_2 concentration and climatic data [air temperature (T), precipitation (P), snow cover height] computed in 5-year periods over the whole study period (1950–2014) and separating subalpine and alpine belts (left side of the table) from nival belts (right side of the table). Only statistically significant correlations are shown ($p < 0.05$; in bold correlations $p < 0.001$).

	Subalpine and alpine belts							Nival belt			
	S. appendiculata	*S. foetida*	*S. hastata*	*S. helvetica*	*S. purpurea*	*S. waldsteiniana*	All species	*S. foetida*	*S. helvetica*	*S. waldsteiniana*	All species
CO_2		0.89	0.83	**0.92**		**0.92**	**0.96**	0.85	0.88		0.88
T_April		0.88		0.87			0.88				
T_May		0.91		0.9			0.91				
T_June	**0.96**				**0.93**	0.89		0.9	0.91		0.88
P_November	**0.97**		0.84		0.87	**0.95**	0.83	**0.97**	**0.97**		**0.95**
Snow Height		−0.86		−0.88			−0.83				

forest vegetation, or mantle communities dynamically related to deciduous forests (Ellenberg 1988, Davies et al. 2004, Biondi et al. 2014, Delarze et al. 2015), further allows us to hypothesize that this process will likely lead to the development of open woodlands, similarly to reports from the Arctic (Terskaia et al. 2020), as well as to forest in approaching decades. The available palynological analogs do not indicate that the successional pathways identified in this study have occurred previously in this study area during the Holocene (Tinner and Theurillat 2003, Carnelli et al. 2004).

The recruitment peak of these vigorous and rapid reproducing *Salix* shrubs (Fig. 2), which also have high dispersal capacity and are capable of clonal growth (Formica et al. 2014), coincided with the highest rate of species richness increase recorded on European mountain summits (2007–2016) in response to accelerated climate warming (Steinbauer et al. 2018). Our data indicate that this recruitment surge was correlated with climatic warming trends in spring (Table 3, Fig. 5) and with increase in atmospheric CO_2 concentration (Table 3, Fig. 2). The positive relationship between *Salix* recruitment and air warming as seen in the Alps also mirrors observations in the Arctic, where both long term monitoring of natural habitats and field warming experiments have identified enhanced *Salix* growth (Post and Pedersen 2008, Forbes et al. 2010, Macias-Fauria et al. 2012, Tape et al. 2012, Dial et al. 2016, Rinas et al. 2017).

Spring warming, decreased snow cover depth, advance in timing of spring snowmelt and growing season extension have occurred widely across the European Alps irrespective of elevation or location (Klein et al. 2016). Various studies have demonstrated that spring warming, earlier snowmelt and increased atmospheric CO_2 concentrations have led to decreased performance of late successional (e.g. *Vaccinium* spp., *Empetrum* spp.) and snowbed shrubs (e.g. *S. herbacea*) through damage to their apical buds, leaves, flowers and fruit due to exposure to spring frost (Wipf et al. 2009, Bokhorst et al. 2010, Wipf and Rixen 2010, Rixen et al. 2012, Gerdol et al. 2013, Wheeler et al. 2014). The sensitivity of *R. ferrugineum* to frost events in spring (Wheeler et al. 2014) is greatest at lower elevations, where snow cover is typically thinner and melts earlier (Francon et al. 2020). In contrast, our data indicate that < 2% of the *Salix* shrubs examined exhibited frost damage, possibly through being less exposed to the risk of spring frost damage as these species produce leaves only after flowering, during the peak of the growing season.

The recent success of these *Salix* shrubs in the Alps could be related to the increasing atmospheric CO_2 concentration. The combination of artificial warming and CO_2 enrichment exerted positive effects on different *Salix* species, resulting in increased leaf and stem biomass and suggesting that they could benefit from climate change (Paajanen et al. 2011, Nissinen et al. 2016). In contrast, several years of free air CO_2 enrichment and soil warming of treeline species and their associated shrub vegetation (e.g. *Vaccinium* spp., *Empetrum*) indicated that soil warming was more effective than CO_2 enrichment in enhancing plant growth, with the exception of *Vaccinium myrtillus* (Dawes et al. 2013, 2015). Furthermore, a lack of beneficial effects of CO_2 enrichment (both alone and in combination with nutrient addition) has also been documented for several alpine glacier forefield species of forbs and graminoids (Inauen et al. 2012).

In addition, our data show that these hygrophilous *Salix* shrubs are not linked to soil occurrence or type (Table 1), differently to what happens to warming-driven upwards migration of vegetation, in particular of shrubs and trees, that can be constrained by a low rate of soil development or a lack of soils (Henne et al. 2011, Hagendorn et al. 2019). The lack of soil limitation for *Salix* shrubs (especially relevant to encroachment into pioneer vegetation and barren ground habitats in the alpine and nival belts) may be underlain by their symbiosis with ectomycorrhizal fungi, which enhance plant nutrient and water uptake (Arraiano-Castilho et al. 2020). The large gradient of soil water content over which encroachment occurred is notable and could also explain why precipitation was not identified as a key factor (Table 3, Fig. 4).

The current rapid rate of *Salix* shrub encroachment could be accelerated further under future scenarios of climate change in higher elevation areas where permafrost occurs, as a result of increasing surface instability triggered by permafrost degradation (Ponti et al. 2021). This will create disturbed surfaces where *Salix* shrubs (such as *S. helvetica*, Gärtner-Roer et al. 2013) may further encroach due to their tolerance of physical damage from surface disturbance and ability to resprout and spread through clonal growth, again as already reported in the Arctic in response to climate-driven permafrost degradation (Huebner et al. 2019, Jin et al. 2021).

This study demonstrates that high alpine vegetation is currently experiencing a major change linked with climate warming and increased atmospheric CO_2 concentration, both of which have positive effects on *Salix* shrub growth. The encroachment of pioneer *Salix* shrubs, now documented in climax and pioneer communities as well as barren grounds across a 1000 m elevation gradient, may be an indication of their competitive ability with respect to climax species of subalpine shrublands and alpine grasslands.

This new successional pathway, not previously reported in the European Alps, may induce landscape transformations through the replacement of subalpine shrublands (with the decline of species such as *Rhododendron* spp., *Vaccinium* spp.) with forests, and of alpine grasslands and snowbeds (with the decline of species such as *Carex curvula* and *Salix herbacea*) with open woodlands. Such changes would result in these alpine environments becoming more similar to sub-Arctic and Arctic regions, bringing a new threat to the conservation of high alpine ecosystems, as mountains provide limited opportunities for upwards migration and range-shifts of species.

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Nicoletta Cannone: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead). **Mauro Guglielmin**: Formal analysis (equal); Investigation (equal); Methodology (equal). **Chiara Casiraghi**: Data curation (equal); Formal analysis (equal); Investigation (equal). **Francesco Malfasi**: Data curation (equal); Formal analysis (equal); Investigation (equal).

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Data availability statement

The datasets generated during and/or analysed during the current study are available from Figshare: <https://doi.org/10.6084/m9.figshare.14932902> (Cannone et al. 2021b).

Supporting information

Any supporting information associated with this article is available from the online version.

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