

Glacier shrinkage and slope processes create habitat at high elevation and microrefugia across treeline for alpine plants during warm stages

Rodolfo Gentili^a, Carlo Baroni^{b,c}, Cinzia Panigada^a, Micol Rossini^{a,*}, Giulia Tagliabue^a, Stefano Armiraglio^d, Sandra Citterio^a, Alberto Carton^e, Maria Cristina Salvatore^{b,c}

^a Dipartimento di Scienze dell'Ambiente e della Terra, University of Milano - Bicocca, Piazza della Scienza 1, 20126 Milan, Italy

^b Dipartimento di Scienze della Terra, University of Pisa, Via S. Maria 53, 56126 Pisa, Italy

^c Istituto di Geoscienze e Georisorse – Consiglio Nazionale delle Ricerche, Via G. Moruzzi 1, 56124 Pisa, Italy

^d Museo di Scienze Naturali di Brescia, Via Ozanam 4, 25128 Brescia, Italy

^e Dipartimento di Geoscienze, University of Padova, Via Gradenigo 6, 35123 Padova, Italy

ARTICLE INFO

Keywords:

Species' resilience
Periglacial refugia
Evolutionary geomorphology
Microclimate
Glacier retreat
Satellite remote sensing

ABSTRACT

The temperature rise at the global level and glacier shrinkage are deemed to induce new dynamics between biotic and abiotic factors, especially in mountain regions. In this work, we aimed to assess: (a) the area made available after glacier retreat since the Little Ice Age (LIA) for the colonization of alpine plants; (b) the ability of 14 alpine and nival species, typically growing on peaks and in deglaciated areas, to migrate and survive at lower elevations in microrefugia across the treeline ecotone. In the Adamello-Presanella Massif (Rhaetian Alps), we collected presence data on 14 alpine species within 3×3 or 5×5 m plots according to slope landforms and deposits. The analysis of the elevation range of the investigated species across the treeline was performed using Sentinel-2 satellite images to derive the actual position of the upper and lower treeline. The differences in the species elevation ranges across slope landforms, in relation to the treeline elevation and aspect, were detected with linear mixed models. Results showed that glaciers contracted sharply by more than 50% between the LIA and 2006, making large deglaciated areas available (more than 57 km²). All the studied species were found at low altitudes across the treeline ecotone, from about 500 to 1200 m below their typical habitat. Six species (*Cardamine resedifolia*, *Cerastium uniflorum*, *Leucanthemopsis alpina*, *Luzula alpinopilosa*, *Oxyria digyna*, *Saxifraga oppositifolia*) significantly exceeded the upper treeline in correspondence of alpine composite channels ($p < 0.001$ for all species). One species (*Adenostyles leucophylla*) exceeded the upper treeline in correspondence of composite slope deposits ($p < 0.05$). Two species (*Ranunculus glacialis* and *S. oppositifolia*) reached the lower treeline in composite channels and slope deposits ($p = 0.800$, and $p = 0.519$, respectively).

The retreat of the alpine glaciers, coupled with the intensification of paraglacial processes, may favor new habitat opportunities at high elevation and microrefugia at low altitudes for nival and alpine species. The widespread presence of microrefugia for alpine plants downslope during warm periods suggests a low incidence of biodiversity loss in the alpine regions due to climate change.

1. Introduction

The widely recognized temperature rise at the global scale has caused over the last two centuries a worldwide rapid recession of the glaciers (IPCC, 2014; Zemp et al., 2015). In the Alps, air temperature increase has been more than twice higher than the global average over the same period (Böhm et al., 2001; Gobiet et al., 2014), with a pronounced summer warming which has been particularly evident after 1970 (Casty et al., 2005). Therefore, numerous glaciers have retreated or have become extremely fragmented or extinct (Carturan et al., 2013;

Baroni and Salvatore, 2015; Salvatore et al., 2015). Following the current climatic trend, numerous small glaciers (i.e., with a surface smaller than 1 km²) located at lower elevation could completely melt within the next few decades (Carturan et al., 2016).

During glacial retreat periods, paraglacial processes are assumed to be the major drivers of landscape changes in alpine valleys due to the collapse of valley slopes after ice melting (Ballantyne, 2002; Baroni et al., 2014). The paraglacial land-system is very sensitive to climate change and can respond over time scales ranging from the instantaneous to the long-term response (million years; Mercier, 2008).

* Corresponding author.

E-mail address: micol.rossini@unimib.it (M. Rossini).

<https://doi.org/10.1016/j.catena.2020.104626>

Received 20 May 2019; Received in revised form 24 March 2020; Accepted 20 April 2020

Available online 30 April 2020

0341-8162/ © 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Paraglacial processes typically include slope processes such as rock/debris fall, debris flow, snow avalanches and gullying (Ballantyne, 2002). These processes are often associated to vegetation dynamics that are in turn influenced by terrain age, deposit stability and sediment properties (e.g., texture, moisture; Ballantyne, 2002; Eichel et al., 2016). Along alpine valleys, slope processes linked to the paraglacial dynamics play a key role in shaping the position of the local treeline ecotone, that is globally dependent on climatic variables (Baroni et al., 2007; Masseroli et al., 2016; Knight et al., 2018).

According to Jeník (1997), the altitudinal variation of the alpine treeline reflects the combination of two main processes along mountain slopes: the effects of the vertical climatic gradients and disturbing impacts of the anemo-orographical systems. Particularly, the rise in temperatures and glacier shrinkage are deemed to induce new dynamics between biotic and abiotic factors dependent on geomorphic processes acting in mountain and alpine ecosystems (Restrepo et al., 2009). Climate change is expected to affect the disturbance regimes (e.g., hydrologic regimes, mass movements) and therefore to impact the species, populations and communities growing along the mountain slopes (Turner, 2010; Gentili et al., 2013).

The fate of the alpine flora in European mountains during the past glacial periods has been widely discussed through scientific literature (Abbott, 2008; Birks and Willis, 2008; Birks, 2015). Accelerated temperature increase and glacier retreat are also expected to impact biodiversity at different spatial scales, from landscape and ecosystem to habitat and species levels (Miller and Lane, 2018). Alpine biodiversity is considered under threat due to the observed and expected shift of plants and animals towards higher elevations following more suitable environmental conditions (Pauli et al., 2012). Gottfried et al. (2012) provide evidence of a plant species turnover towards higher elevations across European mountains: cold adapted species are declining while warm adapted species are increasing. A too rapid or extreme temperature increase induced by climate change is believed to overtake the ability of alpine species to migrate or to adapt to such changes (Jump and Peñuelas, 2005). In the short term, such a fast species turnover has increased plant species richness of boreal-temperate mountains (+3.9 species during the period 2001–2008; Pauli et al., 2012).

Studies emphasize that air or ground temperature that species experience (i.e. microclimate) can greatly differ from air temperature due to vegetation type, local topography, aspect and soil characteristics (Ashcroft et al., 2012; Gentili et al., 2015a; Bátori et al., 2017). For instance, ground temperatures in mountain areas can differ up to 9 °C from the air temperature (De Frenne et al., 2013). Therefore, it is crucial to understand the ecological drivers of alpine ecosystems in order to predict future scenarios from the macro- to the micro- scales. Particularly, understanding how alpine flora will be able to adapt to warm interglacial periods avoiding extinction is a new exciting and narrowly treated topic across literature (Stewart et al., 2009; Gentili et al., 2015a). Previous studies suggest that species respond to climate change with different strategies: a) migration to new areas with suitable environmental conditions (Telwala et al., 2013); b) evolution through adaptation to the new environmental conditions (Sedlacek et al., 2016); c) reaction through adaptive phenotypic plasticity (Ghalambor et al., 2007). Conversely, recent studies highlight that alpine flora may be able to respond to increasing temperatures surviving in marginal or local warm stage refugium/microrefugium (Gentili et al., 2015a, 2015b).

During interglacial stages, microrefugia are those areas with favorable cold/fresh microclimates spread within larger areas or regions (i.e., macrorefugia) characterized by unfavorable warm climate (Rull, 2009). In these areas, populations of species can persist isolated from their core distributions (Stewart et al., 2009; Dobrowski, 2011) from short to long time scales (Kiedrzyński et al., 2017). Gentili et al. (2015a) characterized from an ecological perspective glacial, nival, periglacial and composite landforms and deposits that may function as potential microrefugia during warmer periods in alpine areas. Several authors

agree that during past interglacial warm periods, forest and cold-adapted species persisted through an upward migration to mountain refugia (sensu lato) or in other refugia in lowland areas (Bush, 2002; Bhagwat and Willis, 2008; Rull, 2009).

Until now, only few experimental works demonstrated the current locations of alpine microrefugia for cold/cool-adapted species at lower elevations, close to the timberline. For instance, Bátori et al. (2017) identified karst dolines as microrefugia for some boreal cold-adapted species in East-European mountains. Within these landforms, the thermal inversion often maintains cooler conditions in grassland and forest ecosystem contexts. Shimokawabe et al. (2015) found alpine shrub species occurring at “wind-hole sites” in lowland forested landscape, isolated from alpine zones. To the best of our knowledge, no studies treated the occurrence and microrefugia of high alpine and nival species across treeline so far.

In this work, we hypothesize that geomorphological processes deriving from paraglacial activity can increase habitat heterogeneity and climatic shelter along valley slopes. Across the treeline ecotone, microrefugia for alpine plants could increase as a consequence of such heterogeneity.

The treeline ecotone in alpine regions was derived for the first time from the newly available European Space Agency (ESA) Sentinel-2 (S2) images. S2 carries an innovative imaging spectrometer covering the visible, near infrared and shortwave infrared spectral regions with a spatial resolution of 10–60 m depending on the spectral band and a temporal resolution of five days (Drusch et al., 2012).

The specific goals of this work are: a) to assess the extent of ice-free area due to the glacial retreat since the Little Ice Age (LIA) as new habitat available for alpine species colonization; b) to quantify the ability of 14 plant species (*Adenostyles leucophylla*, *Cardamine resedifolia*, *Carex curvula*, *Cerastium uniflorum*, *Doronicum clusii*, *Festuca halleri*, *Leucanthemopsis alpina*, *Luzula alpinopilosa*, *Oxyria digyna*, *Poa laxa*, *Ranunculus glacialis*, *Saxifraga bryoides*, *S. oppositifolia* and *Veronica alpina*), generally living at glacial fronts and/or at mountain peaks, to migrate and survive at lower elevations in microrefugia across the treeline ecotone.

2. Methods

2.1. Study area

The study area is situated in the Adamello-Presanella mountain group (Italian Rhaetian Alps; 46°09' N, 10°29' E; Fig. 1). The bedrock primarily consists of tonalite, granodiorite and quartz diorite rocks and small basic plutons (Brack et al., 2008; Callegari and Brack, 2002).

The study sites are located along an altitudinal gradient ranging from the timberline to the summit areas, approximately from 1500 to 3200 m above sea level (a.s.l.) (Fig. 1). The summit areas of the Adamello-Presanella host the Adamello Glacier, the largest glacier of the Italian Alps (about 16 km² in 2007), as well as about 90 other minor glacial bodies (Salvatore et al., 2015). Several alpine valleys originate from the summit area of the massif in a radial pattern. The landscape shows a well-defined Alpine glacial morphology, characterized by deep glacial troughs with a succession of several basins and steps, steep glacial shoulders, truncated spurs, glacial cirques, sharp ridges (arêtes) and horns (Baroni et al., 2014; Carton and Baroni, 2017; Fig. 2). The most incisive morphogenesis is presently due to mass wasting, water runoff and cryonival processes (Baroni et al., 2004, 2007). At the toe of valleys slopes, debris production, mass movement, debris flow, running water and snow avalanches generate composite debris cones (Baroni et al., 2007; Seppi et al., 2019).

Composite debris cones are dominant elements in the alpine landscape. Channels cross cones and are frequently connected to deep gullies cutting rocky walls behind the cones (Baroni et al., 2013). Channels on composite debris cones are polygenic landforms converging running water, collecting avalanches and producing debris flows. Active

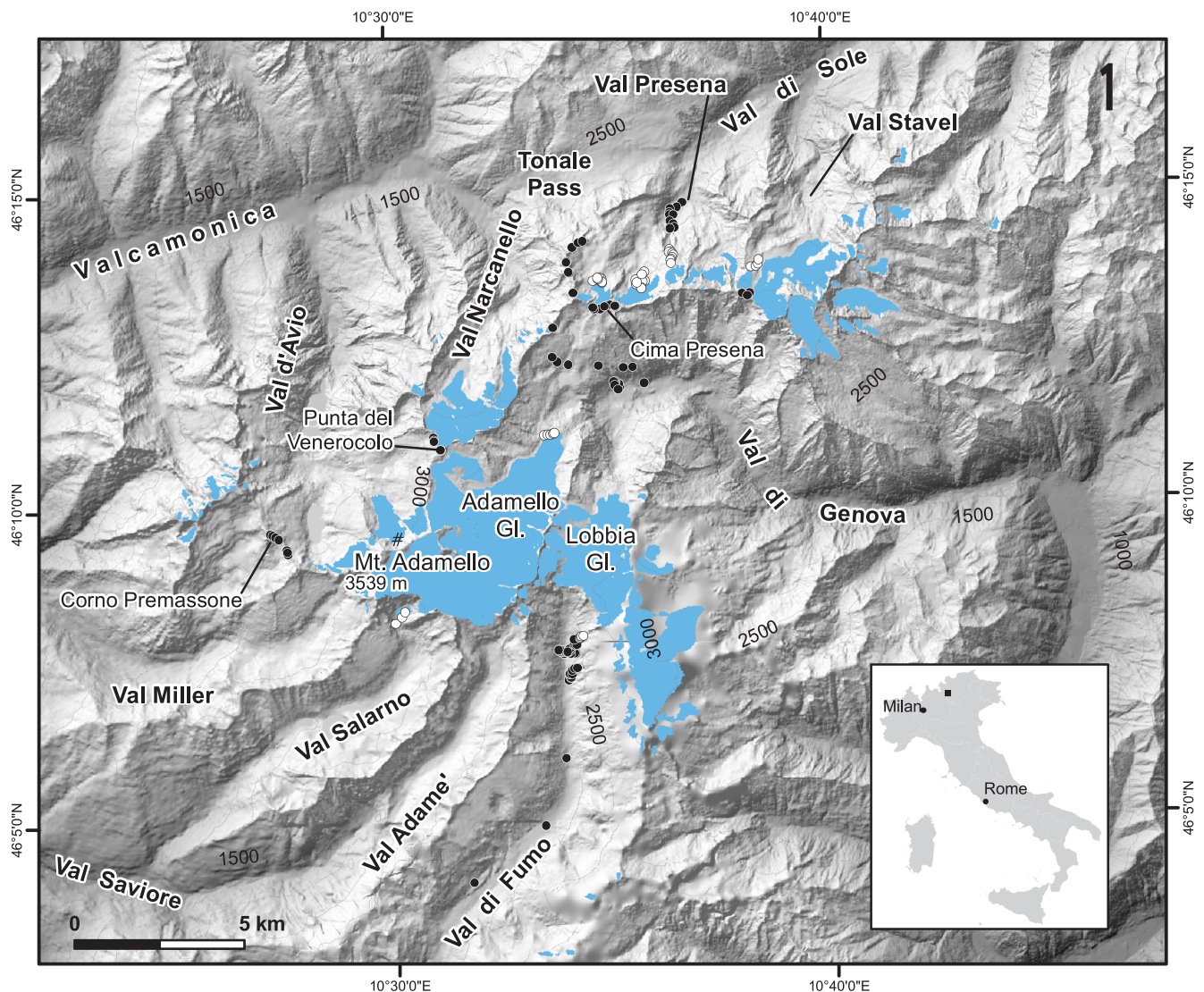


Fig. 1. Location map of the study area. White and black circles indicate plot sites on i) recent glacial deposits and ii) peak areas or active (or recently stabilized) landforms (avalanche deposits, channels, rock/debris fall deposits, debris flows deposits), respectively. Blue polygons indicate glaciers extension referred to 2006 (after Salvatore et al., 2015). Contour intervals are 500 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

geomorphological processes show different strengths and frequencies at different elevations. At lower elevations (approximately below 2100 m), stream deposits and alluvial fans prevail. Debris flows are mostly active at the foot of valley slopes. At mid elevations (over 2100 m), periglacial and paraglacial processes are more active, giving rise to nival landforms and deposits, such as avalanche tracks, avalanche debris deposits, avalanche cones and rock glaciers. Glacial processes and deposits (moraine ridges, glacial drifts and fluvioglacial deposits) increase at high elevation (over 2400 m) becoming almost exclusive above 2900 m. Soil patches cover the slopes depending on the activity of the geomorphological processes (Baroni et al., 2007).

The climate is inner-alpine and consists of cold winters and temperate summers. The mean annual air temperature, above treeline ranges from about -10°C to 13°C (meteorological data downloaded from: www.meteotrentino.it; Supplementary Material 1). Locally, channel beds, snow patches and other landforms act as microclimatic shelter favoring lower temperatures (until 3°C , see Supplementary Material 2) compared to surrounding areas. Precipitation increases with elevation and ranges from about 800 to 1500 mm year $^{-1}$ (Baroni et al., 2004).

In the study area, closed forests dominated by *Picea excelsa* are

replaced above ~ 1800 m by *Larix decidua* and *Picea excelsa* and open forests with localized presence of *Pinus cembra* (*Piceion excelsae*; Gentili et al., 2010). The vegetation close to the upper treeline primarily consists of heaths of ericaceous species (*Rhododendron ferrugineum*, *Vaccinium myrtillus*, *V. vitis-idaea*, and *V. uliginosum*; *Rhododendron ferruginei-Vaccinion*). Channels and avalanche tracks are characterised by *Alnus viridis* and *Salix* spp. shrublands (*Alnion viridis*). Above treeline, grassland vegetation is dominated by *Nardus stricta* grasslands (*Nardion strictae*) at the bottom valleys, and by *Festuca scabriculmis* ssp. *luedii* grasslands (*Festucion variaie*) and *Carex curvula* grasslands (*Caricion curvulae*) on slopes. The snowbed vegetation mostly consists of *Salix herbacea* dwarf shrubs and *Luzula alpinopilosa* discontinuous grasslands (*Salicion herbaceae*). *Rumex scutatus* (close to the treeline) and *Oxyria digyna* (*Androsacion alpinae*) communities characterize the pioneer vegetation (Gentili et al., 2010). Syntaxonomic nomenclature is based on Mucina et al. (2016).

2.2. Glacier retreat assessment

To assess recent glacier retreat we compared glacier outlines and extension between the LIA (that corresponds to the maximum Holocene



Fig. 2. Presanella and Passo di Stavel glaciers (on the right and on the left, respectively). The skyline is marked by sharp and narrow ridges and pyramid peaks. Trimlines are preserved on rocky outcrops above glaciers' accumulation areas and at the foot of the slopes along the valley marked by different colour of staining. In foreground, debris cone and moraines of the Little Ice Age. Present frontal margin of the Presanella Glacier retreated more than 1300 m since the Little Ice Age.

glacier extension in the Alpine region) and 2006 CE. The LIA glacier position in the Adamello–Presanella Group were derived from Zanoner et al. (2017) for the Trentino region and from Baroni et al. (2014) for Val Salarno and Val Adamè area. These data were integrated with our original research conducted in key sites, where glacier shrinkage was more significant. We reconstructed LIA glacial limits based on geomorphological and glacial geological field surveys, improved with interpretation of stereoscopic aerial photographs. LIA glacial bodies position was depicted considering glacial erosional trimlines and depositional landforms (moraines and glacial drifts) as well as key geomorphological features such as sharp ridge crests, steep flanks, superpositional moraine structures, absence of vegetation, and limited lichen cover (Baroni and Carton, 1996; Carturan et al., 2014; Zanoner et al., 2017). Furthermore, other important data source were historical maps compiled in the second half of the 19th and at the beginning of the 20th centuries depicting glacier boundaries almost contemporaneous to the Little Ice Age (Istituto Geografico Militare Italiano, IGMI, 1885a, 1885b, 1908, 1918; Payer, 1865) and in the first years of the 20th century (Deutschen und Österreichischen Alpenvereins, DÖAV, 1903).

Glacier extension in 2006 CE comes from glacier limits modified after Salvatore et al. (2015). Glacier outlines were inferred from the interpretation of digital RGB true-colour orthophotos with a radiometric resolution of 8 bit for channels and nominal geometric resolution of 50 cm × 50 cm provided by the Italian National Geoportal of the Ministry of Environment and Protection of Land and Sea (<http://www.pcn.minambiente.it/mattm/en/view-service-wms/>) through Web Map Service (WMS, last access 07/09/2019).

All glacial bodies outlines were manually digitized from maps and orthophotographs in GIS environment.

2.3. Extraction of the treeline ecotone from satellite images.

The treeline ecotone in the Adamello–Presanella mountain group was obtained integrating a supervised classification of multispectral S2 images and terrain parameters derived from a high spatial resolution digital elevation model (DEM).

A schematic workflow of the procedure showing input data, intermediate data and output data is presented in Fig. 3.

DEM data with 2 and 5 m spatial resolution were obtained from the cartographic portals of the Trentino (LIDAR rilievo 2006/2007/2008, Ufficio Sistemi Informativi – Servizio autorizzazioni e valutazioni ambientali, Provincia autonoma di Trento) and Lombardia (DTM 5x5 (WMS) – Modello digitale del terreno (ed. 2015), Servizi geografici, Regione Lombardia) regions, respectively. The DEM data were re-sampled to 10 m to match the S2 image pixel size and the watershed boundaries, elevation and aspects were derived using the ArcGIS software (Esri, Redlands, USA).

Four S2 images with cloud cover lower than 10% collected between June and September 2017 were used as input of the supervised classification. The S2 satellite carries a multi-spectral instrument measuring reflected radiance in 13 spectral bands spanning from the visible to the shortwave infrared spectral range (Table 1). The S2 images were calibrated and geometrically registered (LIB products) by the ESA S2 Mission Performance Centre and atmospherically corrected using the Sen2Cor processor.

Several vegetation indices (VI) were tested: the Normalized Difference Vegetation Index (NDVI, Rouse et al., 1974) related to vegetation green biomass, the Normalized Difference Infrared Index (NDII, Hardisky et al., 1983) related to changes in water content of plant canopies, the Normalized Difference Red-Edge (NDRE, Gitelson and Merzlyak, 1994) related to vegetation chlorophyll content and the GRVI (Green-Red Vegetation Index; Tucker, 1979) used as phenological indicator in previous studies (e.g., Motoshka et al., 2010). These indices were computed as reported in the following equations:

$$NDVI = \frac{R_{865} - R_{665}}{R_{865} + R_{665}}$$

$$NDII = \frac{R_{865} - R_{1610}}{R_{865} + R_{1610}}$$

$$NDRE = \frac{R_{740} - R_{705}}{R_{740} + R_{705}}$$

$$GRVI = \frac{R_{665} - R_{560}}{R_{665} + R_{560}}$$

where R is the reflectance at the specified wavelength (nm).

The shaded pixels, the glaciers and the areas below 1200 m (i.e., the typical upper limit of a continuous coniferous forest area in the study

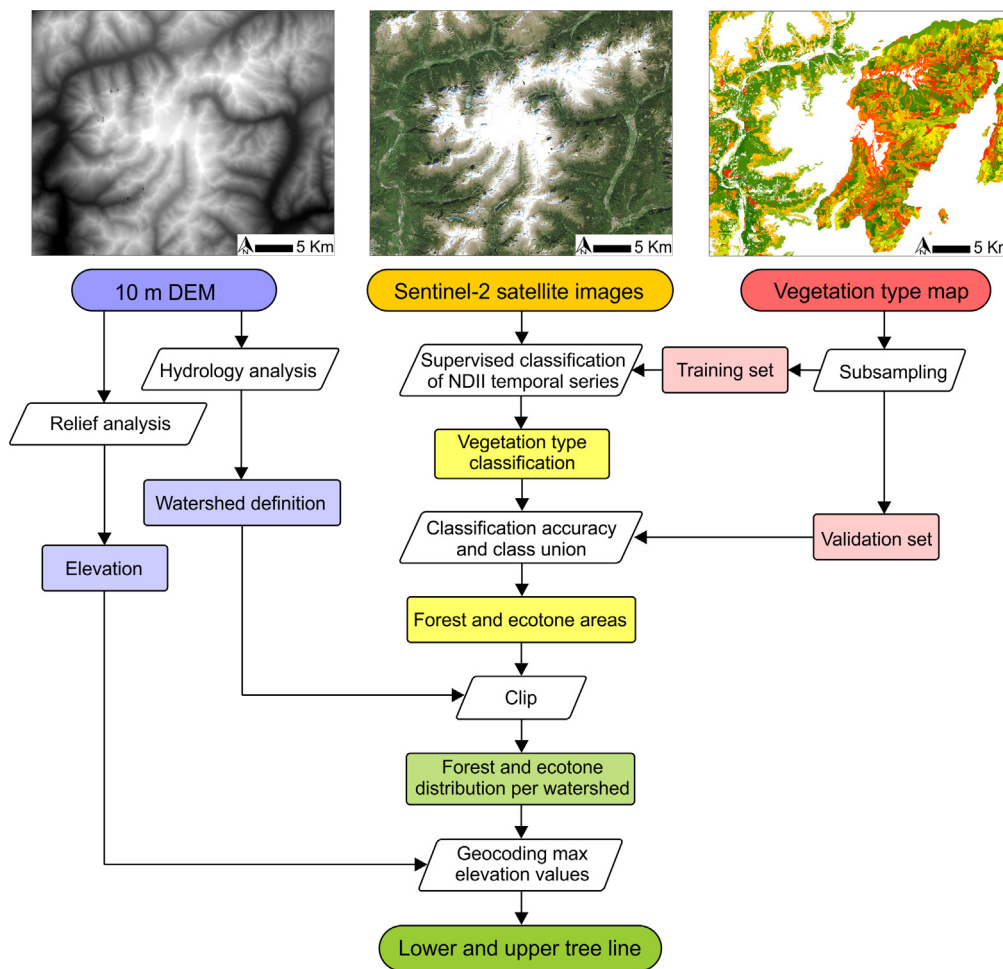


Fig. 3. Schematic workflow of the semi-automatic extraction of the upper and lower treelines from Sentinel-2 (S2) images. The box colours link the products obtained with the corresponding data source: “Elevation” and “Watershed definition” (blue) were derived from the Digital Elevation Model (DEM); “Vegetation type classification” and “Forest and ecotone areas” (yellow) were derived from S2 data; “Training set” and “Validation set” (red) were defined based on the Vegetation type map. The green boxes indicate the final products obtained. The parallelogram shapes mark the methodological steps.” (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Specification of the Sentinel-2 spectral bands.

Band number	Central wavelength (nm)	Bandwidth (nm)	Spatial resolution (m)
1	443	20	60
2	490	65	10
3	560	35	10
4	665	30	10
5	705	15	20
6	740	15	20
7	783	20	20
8	842	115	10
8a	865	20	20
9	945	20	60
10	1375	30	60
11	1610	90	20
12	2190	180	20

area; Caccianiga et al., 2008) were masked.

The training data set for S2 classification consisted of ten land cover classes identified and framed according to Janssen et al. (2016): 1) Temperate mountain *Picea* woodland, 2) Alpine *Larix-Pinus cembra* woodland, 3) *Picea* woodland/Beech woodland, 4) Beech woodland / *Abies* and *Picea* woodland, 5) *Abies* and *Picea* woodland, 6) Subalpine deciduous scrub (green alder and willow), 7) Subalpine *Pinus mugo* scrub, 8) Evergreen alpine and subalpine scrub, 9) Temperate acidophilous alpine grassland and 10) Acid siliceous inland cliffs / Temperate-montane acid siliceous screes. Based on these classes, a spectral endmember set composed of 20 homogeneous polygons of 25 pixels each per class (500 pixels per class in total) was defined to train the

algorithm to assign all the pixels of the image to the proper class automatically. The selection of the best performing VI to be used in the classification process was evaluated through a spectral separability analysis. Two spectral distance measures were calculated: the Jeffries-Matusita distance and the transformed divergence (Richards and Jia, 1986). The values obtained for each pair of classes were then averaged to compare the overall performance of the different VIs tested. The highest separability was obtained using the NDII time series as input according to both the distance metrics. Based on this evaluation, we selected the NDII as input of the maximum likelihood classification algorithm.

A majority filter with a kernel of 5×5 pixel was applied to improve the map patterns. The polygons of the ten classes were then merged in four main categories needed for the treeline ecotone definition (i.e., forest, ecotone, grassland, rock/debris). The accuracy was evaluated by comparing the classification result against the forest type maps of Lombardia (ERSAF, 2006) and Trentino regions (Odasso et al., 2018). The confusion matrix and k-statistics (Stehman, 1997) were calculated in correspondence of all the pixels (more than 3 millions) where both the forest type maps and the classification results were available.

The “forest” and “ecotone” classes were then converted into shapfiles after excluding the polygons with a smaller area than 0.8 ha to avoid the inclusion of small and fragmented stands which may hamper the definition of the treeline at the scale of this study. The upper and lower treelines were finally defined at the watershed level as the upper limits of the ecotone and forest polygons, respectively. The elevation and aspect values of each point constituting the upper and lower limits of the treeline ecotone were finally extracted from the DEM.

Table 2
Studied species and their main bio-ecological characteristics and downward migration ability across treelines. Abbreviation: AV = avalanche deposit; C = channel; COMP = composite stratum of slope deposit; D = rock/debris fall deposit; DF = debris flows deposit; GL = glacial deposit; Peak = peak area. Life form: G = geophytes; H = hemipterophytes; Ch = chamaephyte. Grime's CSR strategy: R = Ruderal species; S = Stress-tolerant species.

Abbreviation	Range	Successional status	Life form	Grime's CSR strategy	Frequency (%)	Crossing TL	Exceeding TL	Estimated downward migration (maximum range; m)
<i>Adenostyles leucophylla</i>	GL	Early-successional	H	R	13.0	C	COMP	485–469
<i>Carex curvula</i>	GL	Late-successional	H	S	3.5	C, COMP	–	292–280
<i>Cardamine resedifolia</i>	Peak	Ubiquitous	H	S	18.5	AV, D, DF	C	872–641
<i>Cerastium uniflorum</i>	Peak	Early-successional	Ch	R	16.9	AV, D, DF	C	977–825
<i>Doronicum clusii</i>	Peak	Ubiquitous	G	R	24.5	AV, C, D, DF	–	989–913
<i>Festuca halleri</i>	Peak	Late-successional	H	S	4.3	C, COMP	–	848–821
<i>Leucanthemopsis alpina</i>	Peak	Ubiquitous	H	R	28.8	AV, D, DF	C	1041–891
<i>Luzula alpinopilosa</i>	GL	Ubiquitous	H	R	24.7	AV, D, DF	C	467–354
<i>Oxyria digyna</i>	GL	Early-successional	H	R	18.5	AV, D, DF	C	559–436
<i>Poa laxa</i>	Peak	Early-successional	H	S	7.6	C, COMP	–	897–768
<i>Ranunculus glacialis</i>	Peak	Early-successional	H	R	8.0	C, COMP, COMP*	–	1070–977
<i>Saxifraga bryoides</i>	Peak	Mid-successional	Ch	S	15.0	C, COMP	–	911–878
<i>Saxifraga oppositifolia</i>	Peak	Mid-successional	Ch	S	7.2	C*, COMP	C	1206–908
<i>Veronica alpina</i>	GL	Late-successional	H	S	4.7	COMP, C	–	450–363

* Crossing lower treeline.

2.4. Alpine flora range

The survey was conducted in the main valleys of the study area (i.e., Adamè, Avio, Fumo, Genova, Miller, Nancanello, Presena, Salarno and Stavel valleys), between July and September from 2010 to 2016 (Fig. 1). The presence/absence of 14 alpine species selected from literature were assessed (see Supplementary Material 3 for the literature consulted). These species are typical of alpine and nival belts and very frequent in recent glacial deposits (GL) and peak areas (Peak) of the Central Alps (Table 2; see Festi and Prosser, 2008). The species typical of glacial deposits were: *Adenostyles leucophylla*, *Carex curvula*, *Luzula alpinopilosa*, *Oxyria digyna*, and *Veronica alpina*. The species typical of peak areas were: *Cardamine resedifolia*, *Cerastium uniflorum*, *Doronicum clusii*, *Festuca halleri*, *Leucanthemopsis alpina*, *Poa laxa*, *Ranunculus glacialis*, *Saxifraga bryoides*, and *Saxifraga oppositifolia*. Species were recorded within a total of 274 plots of 3 × 3 m or 5 × 5 m selected according to a stratified random sampling. In order to have more records of the elevational patterns of the selected species, 65 plots of 5 × 5 m were included from the previous study of Gentili et al. (2013). The 5 × 5 m plots were homogeneously distributed across the study area so we expect that the difference in plot sizes do not affect the presence/absence records of the studied species. Strata consisted of active landforms and deposits, in particular: avalanche deposits (AV; n = 26), alpine channels (C; n = 35), rock/debris fall deposits (D; n = 24) and debris flow deposits (DF; n = 49). As reference landforms, we selected three peaks and the surrounding crest areas above 2800 m in elevation (Peak; n = 32; a – Cima Venerocolo, 3323 m; b – Cima Presena 3069 m; Corno Premassone, 3070 m) and 5 glacial deposits (GL; n = 47; Val Presena, ~2750 m; Val Stavel, ~2650 m; Val di Fumo, ~2600 m; Val Salarno, ~2650 m; Val di Genova, ~2500 m) progressively deglaciated starting from the LIA maximum position. For species with low frequency of occurrence, AV, D and DF strata were grouped in a composite stratum of slope deposits (COMP; n = 61). Within each plot, the following information were recorded:

- elevation (m a.s.l.);
- presence of the 14 species;
- landform unit/deposit type: AV, C, D, DF, (or COMP), GL, Peak;
- prevalent aspect: 316°–360° and 0°–45° = N, 46°–135° = E, 136°–225° = S, 226°–315° = W.

Taxonomic nomenclature used in this paper follows the Portal to the Flora of Italy (<http://dryades.units.it/floritaly/>).

2.5. Data analysis

Linear mixed models (LMM) were used to identify differences in the elevation (Elev) of the 14 alpine species recorded on the main alpine landforms: Peak, GL, AV, D, DF and COMP. Particularly, the difference with the elevation of the lower and upper treelines (TL_L and TL_U) was investigated. The effect of the main aspect (Aspect: N, S, E, W) of each plot was also considered. Landform (comprising the TL_L and TL_U categories) and Aspect were fitted as fixed factors, while the location in the nine investigated valleys (loc) was fitted as a random effect (see Supplementary Material 4). All statistical tests were performed using the R software (R Core Team, 2018) and the 'lme4' package (Bates et al., 2015). The post-hoc Tukey's HSD tests for multiple comparisons, and adjusted p-values, were performed using the 'multcomp' package (Hothorn et al., 2008).

With regards to the elevation range of the alpine species in relation to upper and lower treelines, we used the following terms:

- “species crossing the treelines”: when no significant differences occurred in the mean elevation range of the alpine species with respect to the mean elevation of the treelines;
- “species exceeding the treelines”: when the mean elevation range of

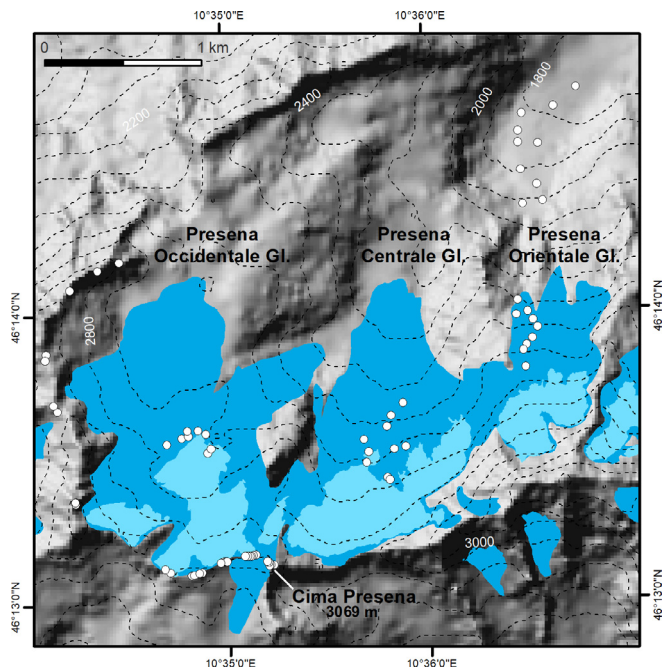


Fig. 4. Presena Glaciers’ outlines during the Little Ice Age (blue) and during 2006 (light blue, after Salvatore et al., 2015). White circles indicate samples sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the alpine species was significantly lower than the mean elevation of the treelines;

- “species not crossing (exceeding) the treelines”: when the mean elevation range of the alpine species was significantly higher than the mean elevation of the treelines.

3. Results

3.1. Glacier retreat assessment

During the LIA, the Adamello-Presanella Group hosted more than 100 glacial bodies. Our data show that between the maximum LIA extension and 2006 CE the Adamello-Presanella glaciers lost about 50% of the total area, which corresponds to more than 57 km² of newly ice-free area.

Under the ongoing withdrawal phase, it is worth noting that ice-free areas are gradually enlarging not only at the retreating frontal margin but also in the accumulation basins, being particular evident above the upper glacial limit. A relevant geomorphological consequence is that the upper trimline is progressively lowering in several sectors of the glaciers head (Fig. 4). Furthermore, rocky windows emerging from glaciers surface are progressively forming or enlarging thus providing

additional ice-free areas within glacial environment. Between 1850 and 2006, in the Adamello-Presanella group the newly released ice-free areas exceeded 7.8 km² above 3000 m a.s.l., assumed as conservative value of Equilibrium Line Altitude of these glaciers during 80 s and 90 s (Baroni and Carton, 1996). This significant lowering of glaciated surface is due to an accelerated negative mass balance of glaciers, which reflect an unprecedented glacial retreat also in the accumulation basin.

3.2. Treeline

The supervised classification of the multitemporal NDII series from S2 allowed to map the main vegetation belts over the Adamello-Presanella mountain group at 10 m spatial resolution. The categories (forest, ecotone, grassland and rock/debris) derived from the aggregation of the ten classes obtained with the supervised classification showed a satisfactory overall classification accuracy of 86% and k of 0.6, in line with literature (Immitzer et al., 2016; Radoux et al., 2016).

The average elevation of the lower and upper treelines in the investigated area ranged between 1812 and 2101 m and between 1908 and 2256 m, respectively (Table 3). On average, the lower treeline was found at the highest elevation on the western aspects and at the lowest elevation on the north exposed aspects. Whereas the higher treeline reached the highest elevation on the eastern aspects and the lowest elevation on the northern aspects.

3.3. Alpine flora range

All the 14 alpine species shifted from mountain peaks and recent glacial deposits to treelines in correspondence of the investigated landforms and deposits (Figs. 5 and 6). Regarding species that are typical of glacial deposits and peaks, the maximum extent of downward species migrations was registered in channel (C) for both recent glacial deposits (GL; 559 m for Oxy_dig) and mountain peaks (Peak; 1206 m for Sax_opp) species. Conversely, the minimum extent of downward migration was registered in COMP (292 m for Car_cur) for recent glacial deposit and in DF (872 m for Car_res) for mountain peak species.

All the species crossed the upper treeline (TL_U), i.e., no significant differences between the mean elevation of high alpine species and elevation of upper treeline (TL_U) at the different landforms and deposits (i.e., AV, C, D, DF and COMP; Table 2) were recorded (Figs. 5 and 6). Six species significantly exceeded the upper treeline in correspondence of channels (C): Car_res (z value = 6.18; p < 0.001), Cer_uni (z value = 3.67; p < 0.01), Leu_alp (z value = 4.96; p < 0.001), Lu_z_alp (z value = 3.13; p = 0.022), Oxy_dig (z value = 3.96; p < 0.01), Sax_opp (z value = 6.24; p < 0.001). One species exceeded the upper treeline (TL_U) in correspondence of composite slope deposits (COMP): Ade_leu (z value = 2.68; p = 0.044). Two species significantly crossed the lower treeline (TL_L; i.e., no significant differences between the mean elevation of high alpine species and elevation of lower treeline), one in channels (C) and one in composite slope deposits (COMP): Ran_gla (z value = - 1.19; p = 0.800), and Sax_opp (z value = 1.63;

Table 3
Average elevation (m) of the lower and upper treeline in the nine main valleys analysed in this study.

	Avio	Miller	Narcanello	Salarno	Adamè	Stavel	Fumo	Presena	Genova	Total area
Average elevation of the lower tree line (m)										
N	1861	1945	1956	1893	1812	1962	2060	1840	1900	1913
E	1841	1932	1988	1867	1820	1966	2068	1835	1909	1930
S	1843	1973	2101	1939	1837	2051	2073	1934	1906	1956
W	1872	1945	2005	1961	1848	2058	2094	1929	1883	1972
Average elevation of the upper tree line (m)										
N	2131	2020	2181	1936	2006	2235	2180	2175	2130	2131
E	2152	2090	2185	2008	2005	2239	2181	2164	2149	2161
S	2163	2049	2197	1957	2031	2256	2183	2215	2148	2135
W	2114	1908	2225	2032	2065	2230	2162	2129	2121	2133

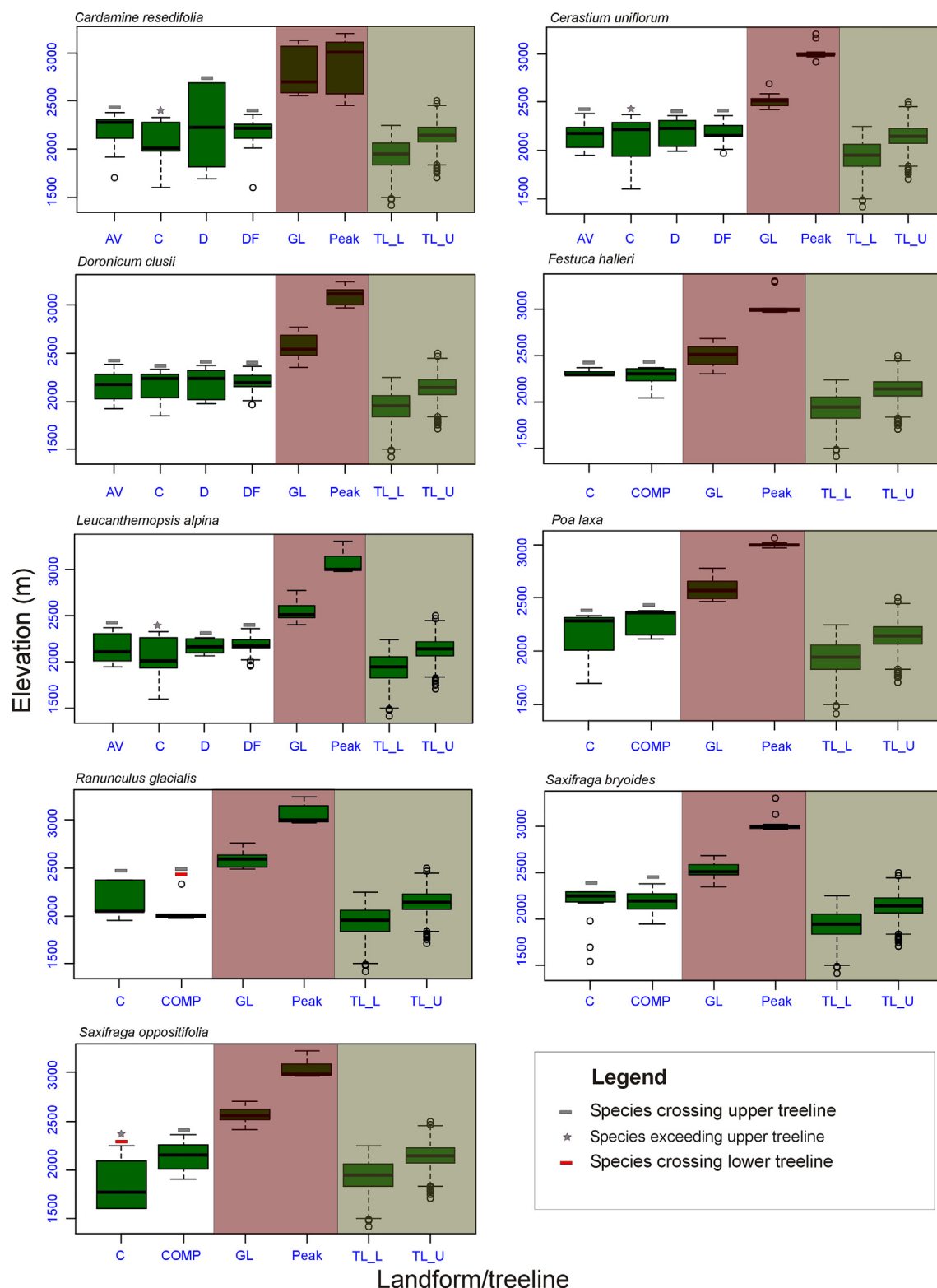


Fig. 5. Mean elevation of alpine species typical of peak areas at different landform slope deposits or landform units and compared with the mean elevation of treelines. Circles represent outliers. Brown background colour highlights the elevation range of the species in their typical alpine habitat. Green background colour highlights the elevation range of the upper and lower treelines. Legend: AV = Avalanche deposits; C = Channels; D = Rock/debris fall deposits; DF = Debris flows deposits; GL = Recent glacial deposits; Peak = Peak area; U_TL = Upper treeline; L_TL = Lower treeline. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

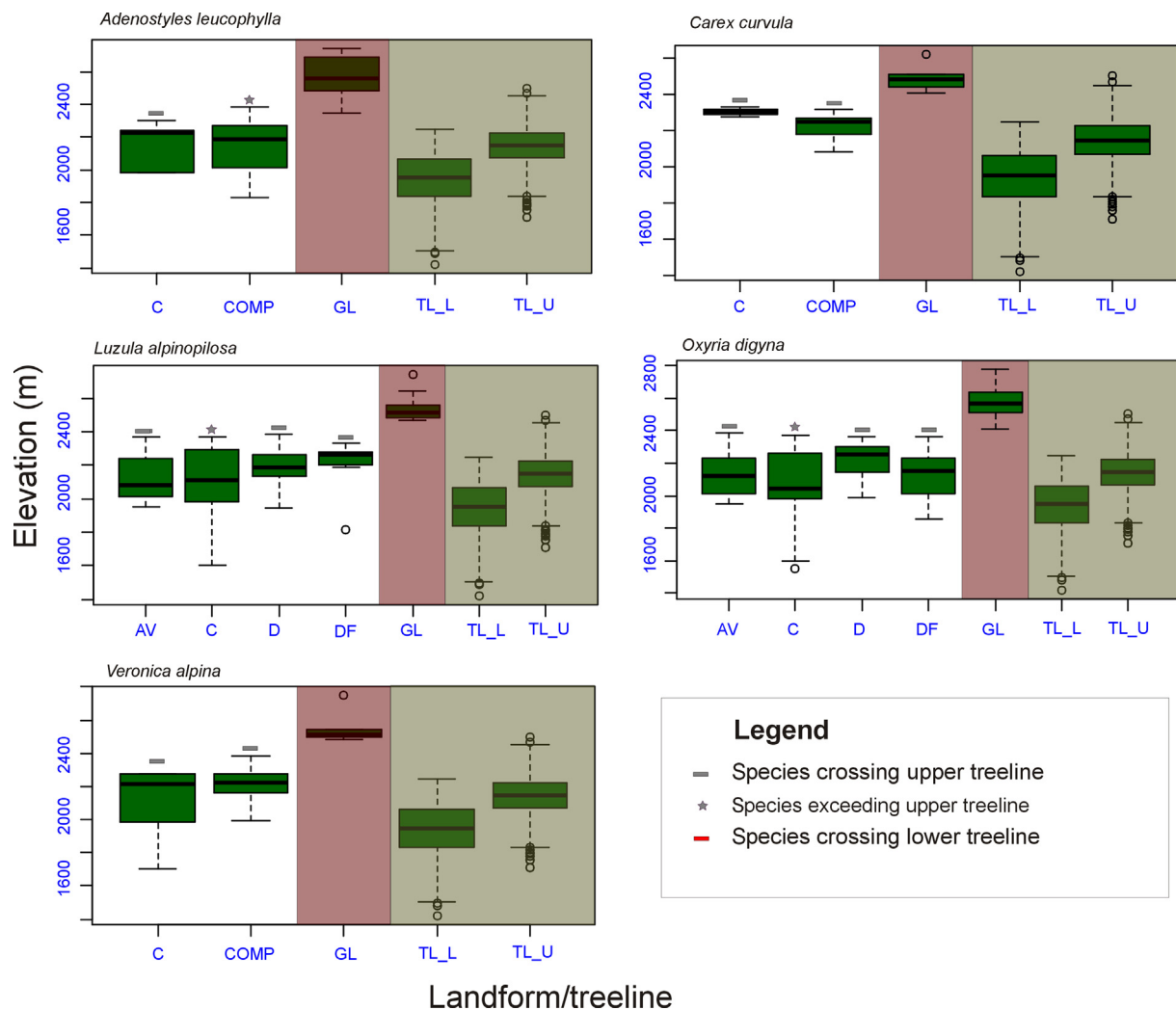


Fig. 6. Mean elevation of alpine species typical of recent glacial deposits on different landform slope deposits or landform units and compared with the mean elevation of treelines. Circles represent outliers. Brown background colour highlights the elevation range of the species in their typical alpine habitat. Green background colour highlights the elevation range of the upper and lower treelines. Legend: AV = Avalanche deposits; C = Channels; D = Rock/debris fall deposits; DF = Debris flows deposits; GL = Recent glacial deposits; Peak = Peak area; U.TL = Upper treeline; L.TL = Lower treeline. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$p = 0.519$).

Considering the Aspect factor, N vs S aspects were significantly different for all the species. W vs N were significantly different for 9 species, N vs E for 4 species and S vs E for 2 species. W vs E and W vs S aspects were never significantly different (Supplementary Material 4).

4. Discussion

Our work demonstrates that the link between glacier retreat and slope processes (paraglacial activity) creates new colonization areas for alpine plants at high elevation as well as widespread microrefugia at low elevation across treelines during the current warm period.

Over the past two centuries, glacier reduction made available 57 km² of terrain in the study area that has been partially colonized by alpine species. Contemporarily, the increased influence of paraglacial processes and geomorphic disturbance along slopes facilitated the migration and the colonization of all the studied alpine or nival species in free spaces across treelines. Our results registered species' downward migration exceeding 1000 m with respect to the usual habitat of the same species (peak areas or glacier deposits). Therefore, alpine plant migration and colonization is likely controlled by climatic stress and substrate disturbance by cryoturbation at high elevation. At lower

elevations, the controlling factors are biotic interactions and substrate instability (Matthews et al., 2018). Another important factor playing a key role in the position of the treeline ecotone and in plant migration along elevation is slope aspects. As expected, we found the main significant differences between N and S slopes. In S aspects, both treeline ecotone and alpine species had the highest mean elevations. Similarly, W aspects exhibited higher elevational range than E aspects for the studied species. Similarly to our findings, previous works demonstrated that across different aspects, exposure to direct sunlight, soil temperature, soil composition and soil water content greatly vary, determining different plant communities (Dearborn and Danby, 2017; Qin et al., 2019).

The ongoing plant migration at high elevation and the increase in species diversity on mountain summits due to climate change is widely recognized across literature (e.g. Steinbauer et al., 2018). However, our results support the evidence that plants species could be less susceptible to decline in mountain regions than predicted by several ecological models (Dullinger et al., 2012; Carlson et al., 2013; Wershow and DeChaine, 2018). Many examples come from marginal chains, generally deglaciated and with lower elevation than Alps: Apennines, Dinaric Alps, Central Massif, Corsica, and Balcan Mountains in Europe. During the current warm period, such mountains provide shelter for boreo-

alpine plants and vegetation associated to specific landforms like scree slopes, nivation niches, and moraine ridges (Ferrari and Rossi, 1995; Redzic, 2011; Gentili et al., 2015b). For instance, Tomaselli and Agostini (1990) recorded arctic-alpine species (*Empetrum hermaphroditum*, *Juncus trifidus* and *Luzula alpinopilosa*) surviving on inactive and/or relict rock glaciers in the Apennines at the boundary with the treeline.

4.1. Glacier retreat makes available new colonization areas

During the LIA, the Adamello-Presanella Group hosted more than 100 glacial bodies. Our data showed that between the maximum LIA extension and 2006 CE, the Adamello-Presanella glaciers have lost about 50% of the total area (more than 57 km²). Our results are in agreement with glacier retreat registered in the European Alps, where 35% of areal extension was lost between 1850 and 1970 s, followed by additional 22% at the end of the 21st century (Paul et al., 2004; Zemp et al., 2007). The maximum frontal withdrawal exceeds 2000 m as registered by Lobbia and Adamello (Mandrone) glaciers, which showed further acceleration in recent years (Baroni et al., 2016, 2017, 2018, 2019; WGMS, 2018).

Likewise, the mass balance records, which are frequently linked to signals of climate change, emphasized the volume reduction over the last century (Oerlemans, 2005).

The knowledge of the extent of glacier retreat may be extremely important in the future prediction of alpine plant migration and range loss as well as in the assessment of their extinction risk. The new colonization areas and habitats made available by glacier contraction might mitigate range loss of alpine species due to climate change (Carlson et al., 2014). The higher habitat availability following glacier contraction offsets the decrease of available areas for species establishment with altitude. Mountain topography (i.e., geometric constraints) reduce the range size of plants, limiting their possibility to migrate upward.

4.2. Plant species crossing treeline

The results of this study, by recording the elevation patterns of 14 alpine and nival plants, demonstrate their downward migration respect to the treelines following the active geomorphological processes acting along alpine slopes. Landforms and deposits at low elevation across treelines create both climatic shelter (for instance within channels or snow avalanche tracks) and continuous mechanical disturbance thus habitat heterogeneity. These factors can promote microhabitat (i.e. microrefugia) at low elevation where high alpine species can persist more than one thousand meters below their common distribution range (see Gentili et al., 2015a).

With respect to the trend of species and habitat shifts towards mountain summits (Dullinger et al., 2012; Steinbauer et al., 2018), this appears to be a kind of “counter-migration” that could enhance the resilience of alpine species. According to Ellenberg (1988), the presence of alpine species at lower elevation than their typical range (at mountain peak or at the glacier fronts) is a signal that they are not confined to higher elevations due to physiological limits; they are not enough competitive at lower elevations due to the presence of more competitive species. For this reason, active geomorphologic processes, creating continuous disturbance to the resident communities, open new roads for cold species colonization at low elevations. In this direction, Tampucci et al. (2016) highlighted that debris-covered glaciers are able to persist below the treeline supporting plant life. Given that geomorphological processes in alpine valleys act from short to long term along the slopes, the same will apply to the available habitats suitable for the species establishment.

Kulonen et al. (2018) recently performed a study on 11 alpine summits, founding that the long-term frequency of high alpine plants is strictly linked to their microhabitat preferences (i.e., scree, rocky slopes

or patches of organic soil, on warmer or colder aspects). In our study, we found that microhabitats suitable for alpine plant establishment can be also found at the treeline ecotone. Indeed, at the treeline, geomorphological disturbance favors the formation of microhabitat with peculiar microclimates facilitating the persistence of high alpine and nival species (Giaccone et al., 2019). Microhabitat and diversification is established by different abiotic characters linked to different landforms and deposits: a) presence of rocky outcrop; b) textural characteristics; c) presence of soil patches; d) frequency and type of disturbance of geomorphological processes (e.g., running water, avalanche, debris flow, rock debris fall, debris movement); e) snow cover duration (e.g., ground temperature); f) aspect, and g) microtopography (Baroni et al., 2007; Keller et al., 2005; Rossi et al., 2014; Pisabarro et al., 2017). All these characteristic factors of microhabitats, singularly or in combination, may create a plethora of climate and disturbance microrefugia for plants isolated from the matrix (Serra-Diaz et al., 2015).

Despite numerous slope processes functioning as corridors favor the downward migration of alpine species, channels seem to have more energy to push species down valley (Butler, 2001). Indeed, in alpine and mountain environments most of the channels are polygenic as several seasonal processes are active within them: running water, avalanche track, debris flow, and debris/rock fall. Different micro-landforms and deposits (e.g., channel bed, banks, and levee) provide a multitude of micro-habitats for alpine species within small distances (Gentili et al., 2010).

Over the last centuries, the treeline shift toward higher elevation has been linked to vegetation dynamics, climatic trend and land use change (Leonelli et al., 2009; Bodin et al., 2013; Millar et al., 2018). However, the paraglacial processes are predicted to become dominant in glaciated mountains worldwide because of glacier retreat caused by global warming (Knight and Harrison, 2014). Therefore, geomorphological processes associated to slope instability and mass movement will modify their magnitude and frequency at multiple scales (Stoffel and Huggel, 2012; Einhorn et al., 2015). In this scenario, geomorphological processes will have an increasing importance in controlling future treeline dynamics (disturbance and succession; Serra-Diaz et al., 2015; Masseroli et al., 2016). They also will play a key role in controlling microrefugia location, thus colonization patterns of nival and alpine species across treelines.

4.3. Warm stage microrefugia for nival and alpine plants

In recent studies, microrefugia hypothesis has been invoked to explain the persistence of some mountain species during Quaternary climate oscillations, particularly during cold periods (Mee and Moore, 2014; Patsiou et al., 2014). Following this hypothesis, our study emphasizes the presence of new habitat and widespread microrefugia in alpine areas during warm stages, at the top of the mountains and the treeline ecotone. Glacier shrinkage furnished about 50% of previously glaciated area, of which more than 25% located above 3000 m a.s.l., being available as newly formed rocky surface for plant colonization. Furthermore, mass movement acting along slopes produced new habitat opportunities also at lower elevation. Widespread microrefugia would partially explain the ascertained tendency for certain species that shifted their mid-range downward over the last decades (Grytnes et al., 2014).

5. Conclusions

For the first time, this study ascertains the widespread presence of microrefugia for typical alpine species across the treeline ecotone favored by deglaciation and the subsequent increased influence of geomorphological processes along slopes. Slope landforms provide widespread microrefugia in the current warm period and may provide in the future suitable microhabitat and climatic shelter to alpine species, favoring their survival. Therefore, our study suggests low incidence of

biodiversity loss in the alpine mountains, in the short and medium term, because of climate change. Future studies should consider the geomorphological processes acting along slopes in predictive models to avoid misjudging of ecosystems changes and overestimating the extinction risk of alpine species. In addition, genetic and evolutionary role of alpine species living at the treeline ecotone will have to be deepened and clarified.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

This study was funded by Milano-Bicocca University and Pisa University and by project of strategic interest NEXTDATA (PNR National Research Programme 2011-2013; project coordinator A. Provenzale CNR-IGG, WP 1.6, leader C. Baroni UNIPI and CNR-IGG). The authors gratefully acknowledge Martina Anelli for the technical support during satellite image processing.

Author contribution

The study was conducted with contributions from all authors that authored or reviewed drafts of the paper and approved the final version. RG, SA and CB conceived the work. RG designed and performed the plant sampling, analysed the data and coordinated the manuscript writing. MCS, CB and AC reconstructed glaciers outlines and shrinkage, and defined geomorphological context. MR and CP designed the conceptual workflow of treeline extraction from satellite data and defined the satellite data processing steps. MR, CP and GT performed the satellite data analysis and contributed to the interpretation of the results.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2020.104626>.

References

- Abbott, R.J., 2008. History, evolution and future of arctic and alpine flora: overview. *Plant Ecol. Div.* 1, 129–133. <https://doi.org/10.1080/17550870802460976>.
- Ashcroft, M.B., Gollan, J.R., Warton, D.I., Ramp, D., 2012. A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Glob. Change Biol.* 18, 1866–1879. <https://doi.org/10.1111/j.1365-2486.2012.02661.x>.
- Ballantyne, C.K., 2002. Paraglacial geomorphology. *Quat. Sci. Rev.* 21, 1935–2017. [https://doi.org/10.1016/S0277-3791\(02\)00005-7](https://doi.org/10.1016/S0277-3791(02)00005-7).
- Baroni, C., Armiraglio, S., Gentili, R., Carton, A., 2007. Landform-vegetation units for investigating the dynamics and geomorphologic evolution of alpine composite debris cones (Valle dell'Avio, Adamello Group, Italy). *Geomorphology* 84, 59–79. <https://doi.org/10.1016/j.geomorph.2006.07.002>.
- Baroni, C., Carton, A., 1996. Carta geomorfologia dell'alta Val di Genova (Gruppo dell'Adamello, Alpi Centrali) alla scala di 1:15.000 con note illustrative. *Geogr. Fis. Din. Quat.* 19, 3–17.
- Baroni, C., Carton, A., Seppi, R., 2004. Distribution and behaviour of rock glaciers in the Adamello-Presanella Massif (Italian Alps). *Permafrost Periglac.* 15, 243–259. <https://doi.org/10.1002/ppp.497>.
- Baroni, C., Gentili, R., Armiraglio, S., 2013. Vegetation analysis on composite debris cones. *Adv. Global Change Res.* 47, 187–201. https://doi.org/10.1007/978-94-007-4336-6_12.
- Baroni, C., Martino, S., Salvatore, M.C., Scarascia Mugnozza, G., Schilirò, L., 2014. Thermomechanical stress-strain numerical modelling of deglaciation since the Last Glacial Maximum in the Adamello Group (Rhaetian Alps, Italy). *Geomorphology* 226, 278–299. <https://doi.org/10.1016/j.geomorph.2014.08.013>.
- Baroni, C., Salvatore, M.C., 2015. The future of the glaciers from the past to the next 100 years. In: *Proceedings of the International Symposium, Torino (Italy)* 18–21 September, 2014. *Geogr. Fis. Din. Quat.* 38, 97–104. <https://doi.org/10.4461/GFDQ.2015.38.09>.
- Baroni, C., Bondesan, A., Mortara, G., 2016. Report of the Glaciological Survey 2015. *Relazioni della Campagna Glaciologica* 2015. *Geogr. Fis. Din. Quat.* 39, 215–295. <https://doi.org/10.4461/GFDQ.2016.39.20>.
- Baroni, C., Bondesan, A., Carturan, L., Chiarle, M., 2019. Annual glaciological survey of Italian glaciers (2018). *Geogr. Fis. Din. Quat.* 42, 113–202. <https://doi.org/10.4461/GFDQ.2019.42.9>.
- Baroni, C., Bondesan, A., Chiarle, M., 2017. Report of the Glaciological Survey 2016. *Relazioni della Campagna Glaciologica* 2016. *Geogr. Fis. Din. Quat.* 40, 233–320. <https://doi.org/10.4461/GFDQ.2017.40.14>.
- Baroni, C., Bondesan, A., Carturan, L., Chiarle, M., 2018. Report of the Glaciological Survey 2017. *Relazioni della Campagna Glaciologica* 2017. xxx-xxx. *Geogr. Fis. Din. Quat.* 41, 115–193. <https://doi.org/10.4461/GFDQ.2018.41.17>.
- Carton, A., Baroni, C., 2017. The Adamello-Presanella and Brenta Massifs, Central Alps: Contrasting High-Mountain Landscapes and Landforms. In: Soldati, M., Marchetti, M. (Eds.), *Landscapes and Landforms of Italy, World Geomorphological Landscapes*, pp. 101–112. https://doi.org/10.1007/978-3-319-26194-2_8.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bátóri, Z., Vojtkó, A., Farkas, T., Szabó, A., Havadtó, K., Vojtkó, A.E., Tölgyesi, C., Cseh, V., Erdős, L., Maák, I.E., Keppel, G., 2017. Large- and small-scale environmental factors drive distributions of cool-adapted plants in karstic microrefugia. *Ann. Bot.* 119, 301–309. <https://doi.org/10.1093/aob/mcw233>.
- Bhagwat, S.A., Willis, K.J., 2008. Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *J. Biogeogr.* 35, 464–482. <https://doi.org/10.1111/j.1365-2699.2007.01861.x>.
- Birks, H.J.B., 2015. Some reflections on the refugium concept and its terminology in historical biogeography, contemporary ecology and global-change biology. *Biodiversity* 16, 196–202. <https://doi.org/10.1080/14888386.2015.1117022>.
- Birks, H.J.B., Willis, K.J., 2008. Alpines, trees, and refugia in Europe. *Plant Ecol. Div.* 1, 147–160. <https://doi.org/10.1080/17550870802349146>.
- Bodin, J., Badeau, V., Bruno, E., Cluzeau, C., Moisselin, J.-M., Walther, G.-R., Dupouey, J.-L., 2013. Shifts of forest species along an elevational gradient in Southeast France: climate change or stand maturation? *J. Veg. Sci.* 24 (2), 269–283. <https://doi.org/10.1111/j.1654-1103.2012.01456.x>.
- Böhm, R., Auer, I., Brunetti, M., Maugeri, M., Nanni, T., Schöner, W., 2001. Regional temperature variability in the European Alps: 1760–1998 from homogenized instrumental time series. *Int. J. Climatol.* 21, 1779–1801. <https://doi.org/10.1002/joc.689>.
- Brack, P., Dal Piaz, G.V., Baroni, C., Carton, A., Nardin, M., Pellegrini, G.B., Pennacchioni, G., 2008. Note Illustrative Della Carta Geologica d'Italia Alla Scala 1:50,000. Foglio 058M. Adamello. APAT — Dipartimento Difesa del Suolo, Servizio Geologico d'Italia, Provincia Autonoma di Trento, Servizio Geologico, Progetto CARG, Trento, Italy.
- Bush, M.B., 2002. Distributional change and conservation on the Andean flank: a palaeoecological perspective. *Global Ecol. Biogeogr.* 11, 463–473. <https://doi.org/10.1046/j.1466-822X.2002.00305.x>.
- Butler, R.D., 2001. Geomorphic process-disturbance corridors: a variation on a principle of landscape ecology. *Prog. Phys. Geog.* 25, 237–248. <https://doi.org/10.1177/030913330102500204>.
- Caccianiga, M., Andreis, C., Armiraglio, S., Leonelli, G., Pelfini, M., Sala, D., 2008. Climate continentality and treeline species distribution in the Alps. *Plant Biosyst.* 142, 66–78. <https://doi.org/10.1080/11263500701872416>.
- Callegari, E., Brack, P., 2002. Geological map of the Tertiary Adamello batholith (Northern Italy). *Explanatory notes and legend. Mem. Sci. Geol.* 54, 19–49.
- Carlson, B.Z., Randin, C.F., Boulangeat, I., Lavergne, S., Thuiller, W., Choler, P., 2013. Working toward integrated models of alpine plant distribution. *Alp. Bot.* 123, 41–53. <https://doi.org/10.1007/s00035-013-0117-4>.
- Carlson, B.C., Damien, G., Rabatel, A., Randin, C., Renaud, J., Delestrade, A., Zimmermann, N., Choler, P., Thuiller, W., 2014. Accounting for tree line shift, glacier retreat and primary succession in mountain plant distribution models. *Divers. Distrib.* 20, 1379–1391. <https://doi.org/10.1111/ddi.12238>.
- Carturan, L., Baroni, C., Becker, M., Bellin, A., Cainelli, O., Carton, A., Casarotto, C., Dalla Fontana, G., Godio, A., Martinelli, T., Salvatore, M.C., Seppi, R., 2013. Decay of a long-term monitored glacier: Careser Glacier (Ortles-Cevedale, European Alps). *The Cryosphere* 7, 1819–1838. <https://doi.org/10.5194/tc-7-1819-2013>.
- Carturan, L., Baroni, C., Brunetti, M., Carton, A., Dalla Fontana, G., Salvatore, M.C., Zanoner, T., Zuecco, G., 2016. Analysis of the mass balance time series of glaciers in the Italian Alps. *The Cryosphere* 10, 695–712. <https://doi.org/10.5194/tc-10-695-2016>.
- Carturan, L., Baroni, C., Carton, A., Cazorzi, F., Dalla Fontana, G., Delperio, C., Salvatore, M.C., Seppi, R., Zanoner, T., 2014. Reconstructing fluctuations of La Mare Glacier (Eastern Italian Alps) in the Late Holocene: new evidences for a Little Ice Age maximum around 1600 AD. *Geogr. Ann.* A 96, 287–306. <https://doi.org/10.1111/geoa.12048>.
- Casty, C., Wanner, H., Luterbacher, J.L., Esper, J., Böhm, R., 2005. Temperature and Precipitation variability in the European Alps since 1500. *Int. J. Climatol.* 25, 1855–1880. <https://doi.org/10.1002/joc.1216>.
- Dearborn, K.D., Danby, R.K., 2017. Aspect and slope influence plant community composition more than elevation across forest-tundra ecotones in subarctic Canada. *J. Veg. Sci.* 28, 595–604. <https://doi.org/10.1111/jvs.12521>.
- De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, et al., 2013. Microclimate moderates plant responses to macroclimate warming. *Proc. Natl. Acad. Sci. USA* 110, 18561–18565. <https://doi.org/10.1073/pnas.1311190110>.
- Deutschen und Österreichischen Alpenvereins, DÖAV, 1903. Karte der Adamello und Presanella Gruppe. Scale 1:50.000. *Zeitschrift der DÖAV*.
- Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Glob. Change Biol.* 17, 1022–1035. <https://doi.org/10.1111/j.1365-2486.2010.02263.x>.

- Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., Hoersch, B., Isola, C., Laberinti, P., Martimort, P., Meygret, A., Spoto, F., Sy, O., Marchese, F., Bargellini, P., 2012. Sentinel-2: ESA's Optical High-Resolution Mission for GMES Operational Services. *Remote Sens. Environ.* 120, 25–36. <https://doi.org/10.1016/j.rse.2011.11.026>.
- Dullinger, S., Gattlinger, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, et al., 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat. Clim. Change* 2, 619–622. <https://doi.org/10.1038/nclimate1514>.
- Eichel, J., Corenblit, D., Dikau, R., 2016. Conditions for feedbacks between geomorphic and vegetation dynamics on lateral moraine slopes: a biogeomorphic feedback window. *Earth Surf. Proc. Land.* 41, 406–419. <https://doi.org/10.1002/esp.3859>.
- Einhorn, B., Eckert, N., Chaix, C., Ravel, L., Deline, P., Gardent, M., Boudières, V., Richard, D., Vengeon, J.M., Giraud, G., Schoeneich, P., 2015. Climate change and natural hazards in the Alps. *J. Alp. Res.* 103, 2–31. <https://doi.org/10.4000/rga.2878>.
- Ellenberg, H., 1988. *Vegetation Ecology of Central Europe*, fourth ed. Cambridge University Press, Cambridge.
- ERSAF, 2006. Progetto Carta dei tipi forestali. Relazione Finale. Ente Regionale per i Servizi all'Agricoltura e alle Foreste, Regione Lombardia, settore Agricoltura. Shapefile updated at 2018, available at: <http://www.geoportale.regione.lombardia.it/>.
- Ferrari, C., Rossi, G., 1995. Relationships between plant-communities and late snow melting on Mount Prado (Northern Apennines, Italy). *Vegetatio* 120, 49–58.
- Festi, F., Prosser, F., 2008. *Flora del Parco naturale Adamello Brenta*. Edizioni Osiride, Rovereto, Italy.
- Gentili, R., Armiraglio, S., Rossi, G., Sgorbati, S., Baroni, C., 2010. Floristic patterns, ecological gradients and biodiversity in the composite channels (Central Alps, Italy). *Flora* 205, 388–398. <https://doi.org/10.1016/j.flora.2009.12.013>.
- Gentili, R., Armiraglio, S., Sgorbati, S., Baroni, C., 2013. Geomorphological disturbance affects ecological driving forces and plant turnover along an altitudinal stress gradient on alpine slopes. *Plant Ecol.* 214, 571–586. <https://doi.org/10.1007/s11258-013-0190-1>.
- Gentili, R., Bacchetta, G., Fenu, G., Cogoni, D., Abeli, T., Rossi, G., Salvatore, M.C., Baroni, C., Citterio, S., 2015a. From cold to warm-stage refugia for boreo-alpine plants in southern European and Mediterranean mountains: the last chance to survive or an opportunity for speciation? *Biodiversity* 16, 247–261. <https://doi.org/10.1080/1488386.2015.1116407>.
- Gentili, R., Baroni, C., Caccianiga, M., Armiraglio, G., Ghiani, A., Citterio, S., 2015b. Potential warm-stage microrefugia for alpine plants: feedback between geomorphological and biological processes. *Ecol. Complex.* 21, 87–99. <https://doi.org/10.1016/j.ecocom.2014.11.006>.
- Ghalambor, C.K., McKay, J.K., Carroll, S.P., Reznick, D.N., 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation adaptation in new environments. *Funct. Ecol.* 21, 394–407. <https://doi.org/10.1111/j.1365-2435.2007.01283.x>.
- Giaccone, E., Luoto, M., Vittoz, P., Guisan, A., Mariéthoz, G., Lambiel, C., 2019. Influence of microclimate and geomorphological factors on alpine vegetation in the Western Swiss Alps. *Earth Surf. Process. Landforms* 44, 3093–3107. <https://doi.org/10.1002/esp.4715>.
- Gitelson, E., Merzlyak, M.N., 1994. Quantitative estimation of chlorophyll-a using reflectance spectra: experiments with autumn chestnut and maple leaves. *J. Photochem. Photobiol. B* 22, 247–252. [https://doi.org/10.1016/1011-1344\(93\)06963-4](https://doi.org/10.1016/1011-1344(93)06963-4).
- Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., Stoffel, M., 2014. 21st century climate change in the European Alps—A review. *Sci. Total Environ.* 493, 1138–1151. <https://doi.org/10.1016/j.scitotenv.2013.07.050>.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barancok, P., Benito Alonso, J.L., et al., 2012. Continent-wide response of mountain vegetation to climate change. *Nat. Clim. Change* 2, 111–115. <https://doi.org/10.1038/nclimate1329>.
- Grytness, J.-A., Kapfer, J., Jurasinski, G., Birks, H.H., Henriksen, H., Klanderud, K., Odland, A., Ohlson, M., Wipf, S., Birks, H.J.B., 2014. Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecol. Biogeogr.* 23, 876–884. <https://doi.org/10.1111/geb.12170>.
- Hardisky, M., Klemas, V., Smart, R., 1983. The influence of soil salinity, growth form, and leaf moisture on the spectral radiance of *Spartina alterniflora* canopies. *Photogramm. Eng. Rem. S.* 49, 77–83.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biometrical J.* 50, 346–363. <https://doi.org/10.1002/bimj.200810425>.
- IGMI, 1885. *Tavoletta Temù - 20 IV SO (1:25,000)*. Istituto Geografico Militare Italiano.
- IGMI, 1885. *Tavoletta Monte Adamello - 20 III NO (1:25,000)*. Istituto Geografico Militare Italiano.
- IGMI, 1908. *Tavoletta Passo del Monticello - 20 IV SE (1:25,000)*. Istituto Geografico Militare Italiano.
- IGMI, 1918. *Tavoletta Monte Caré Alto - 20 III NE (1:25,000)*. Istituto Geografico Militare Italiano.
- Immitzer, M., Vuolo, F., Atzberger, C., 2016. First experience with sentinel-2 data for crop and tree species classifications in central Europe. *Remote Sens.* 8, 166. <https://doi.org/10.3390/rs8030166>.
- IPCC, 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Core Writing Team, Pachauri R.K. and Meyer L.A. (eds), IPCC, Geneva, Switzerland, 151 pp., <http://www.ipcc.ch/report/ar5/syr/>.
- Janssen, J.A.M., Rodwell, J.S., García Criado, M. et al., 2016. European Red List of Habitats. Part 2. Terrestrial and freshwater habitats. European Union, 44 p. <http://forum.eionet.europa.eu/european-red-list-habitats/library>.
- Jenfk, J., 1997. Anemo-orographic systems in the Hercynian Mts. and their effects on biodiversity. *Acta Universitatis Wratislaviensis*, no 1950, C. Meteorol. i Klimatol. 4, 9–21.
- Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.* 8, 1010–1020. <https://doi.org/10.1111/j.1461-0248.2005.00796.x>.
- Keller, F., Goyette, S., Beniston, M., 2005. Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in alpine terrain. *Clim. Change* 72, 299–319. <https://doi.org/10.1007/s10584-005-5360-2>.
- Kiedrzyński, M., Zielińska, K.M., Kiedrzyńska, E., Rewicz, A., 2017. Refugial debate: on small sites according to their function and capacity. *Evol. Ecol.* 31, 815–827. <https://doi.org/10.1007/s10682-017-9913-4>.
- Knight, J., Grab, S.W., Carbutt, C., 2018. Influence of mountain geomorphology on alpine ecosystems in the Drakensberg Alpine Centre. *Southern Africa. Geogr. Ann. A* 100, 140–162. <https://doi.org/10.1080/04353676.2017.1418628>.
- Knight, J., Harrison, S., 2014. Mountain glacial and paraglacial environments under global climate change: lessons from the past, future directions and policy implications. *Geogr. Ann. A* 96, 245–264. <https://doi.org/10.1111/geoa.12051>.
- Kulonen, A., Imboden, R.A., Rixen, C., Maier, S.B., Wipf, S., 2018. Enough space in a warmer world? Microhabitat diversity and small-scale distribution of alpine plants on mountain summits. *Divers. Distrib.* 24, 252–261. <https://doi.org/10.1111/ddi.12673>.
- Leonelli, G., Pelfini, M., Morra Di Cella, U., 2009. Detecting climatic treelines in Italian Alps: the influence of geomorphological factors and human impacts. *Phys. Geogr.* 30, 338–352. <https://doi.org/10.2747/0272-3646.30.4.338>.
- Masseroli, A., Leonelli, G., Bolati, I., Trombino, L., Pelfini, M., 2016. The influence of geomorphological processes on the treeline position in Upper Valtellina (Central Italian Alps). *Geogr. Fis. Din. Quat.* 39, 171–182. <https://doi.org/10.4461/GFDQ.2016.39.16>.
- Matthews, J.A., Hill, J.L., Winkler, S., Owen, G., Vater, A.E., 2018. Autosuccession in alpine vegetation: Testing the concept on an altitudinal bioclimatic gradient, Jotunheimen, southern Norway. *Catena* 170, 169–182. <https://doi.org/10.1016/j.catena.2018.06.012>.
- Mee, J.A., Moore, J.-S., 2014. The ecological and evolutionary implications of micro-refugia. *J. Biogeogr.* 41, 837–841. <https://doi.org/10.1111/jbi.12254>.
- Mercier, D., 2008. Paraglacial and paraperiglacial landsystems: concepts, temporal scales and spatial distribution. *Géomorphologie* 14, 223–233. <https://doi.org/10.4000/geomorphologie.7396>.
- Miller, C.I., Charlet, D.A., Delany, D.L., King, J.C., Westfall, R.D., 2018. Shifts of demography and growth in limber pine forests of the Great Basin, USA, across 4000 yr of climate variability. *Quat. Res.* <https://doi.org/10.1017/qua.2018.120>.
- Miller, H.R., Lane, S.N., 2018. Biogeomorphic feedbacks and the ecosystem engineering of recently deglaciated terrain. *Progr. Phys. Geogr.* <https://doi.org/10.1177/0309133318816536>.
- Motahka, T., Nasahara, K.N., Oguma, H., Tsuchida, S., 2010. Applicability of Green-Red Vegetation Index for Remote Sensing of Vegetation Phenology. *Remote Sens.* 2, 2369–2387. <https://doi.org/10.3390/rs2102369>.
- Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., et al., 2016. Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Appl. Veg. Sci.* 19 (Suppl. 1), 3–264. <https://doi.org/10.1111/avsc.12257>.
- Odasso, M., Miori, M., Gandolfo, C., 2018. I tipi forestali del Trentino: descrizione e aspetti dinamici. Provincia autonoma di Trento. Servizio foreste e fauna, Trento, Italy.
- Oerlemans, J., 2005. Extracting a climate signal from 169 glacier records. *Science* 308, 675–677. <https://doi.org/10.1126/science.1107046>.
- Patsiou, T.S., Conti, E., Zimmermann, N.E., Theodoridis, S., Randin, C.F., 2014. Topo-climatic microrefugia explain the persistence of a rare endemic plant in the Alps during the last 21 millennia. *Glob. Chang. Biol.* 20, 2286–2300. <https://doi.org/10.1111/gcb.12515>.
- Paul, F., Käb, A., Maisch, M., Kellenberger, T., Haeberli, W., 2004. Rapid disintegration of Alpine glaciers observed with satellite data. *Geophys. Res. Lett.* 31, L21402. <https://doi.org/10.1029/2004GL020816>.
- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Benito Alonso, J.L., et al., 2012. Recent Plant Diversity Changes on Europe's Mountain Summits. *Science* 336, 353–355. <https://doi.org/10.1126/science.1219033>.
- Payer, J., 1865. *Die Adamello-Presanella-Alpen nach den Forschungen und Aufnahmen. Mit einer Original-Karte, einer Ansicht in Farbendruck und 6 chemotypierten Profilen u.s.w.* Perthes, Gotha.
- Pisabarro, A., Pellitero, R., Serrano, E., Gómez-Lende, M., González-Trueba, J.J., 2017. Ground temperatures, landforms and processes in an Atlantic mountain. *Cantabrian Mountains (Northern Spain)*. *Catena* 149, 623–636. <https://doi.org/10.1016/j.catena.2016.07.051>.
- Qin, Y., Adamowski, J.F., Deo, R.C., Hu, Z., Cao, J., Zhu, M., Feng, Q., 2019. Controlling factors of plant community composition with respect to the slope aspect gradient in the Qilian Mountains. *Ecosphere* 10 (9), e02851. <https://doi.org/10.1002/ecs2.2851>.
- R Core Team, 2018. *R: A Language and Environment for Statistical Computing*. R Foundation for statistical computing, Vienna.
- Radoux, J., Chomé, G., Jacques, D.C., Waldner, F., Bellemans, N., Matton, N., Lamarche, C., D'Andrimont, R., Defourny, P., 2016. Sentinel-2's potential for sub-pixel landscape feature detection. *Remote Sens.* 8 (6), 488. <https://doi.org/10.3390/rs8060488>.
- Redzic, S., 2011. Phytogeographic and syntaxonomic diversity of high mountain vegetation in Dinaric Alps (Western Balkan, SE Europe). *J. Mt. Sci.* 8, 767–786. <https://doi.org/10.1007/s11629-011-2047-1>.
- Restrepo, C., Walker, L.R., Shiels, A.B., Bussmann, R., Claessens, L., Fisch, S., Lozano, P., Negi, G., Paoletti, L., Poveda, G., Ramos-Scharron, C., Richter, M., Velazquez, E., 2009. Landsliding and Its Multiscale Influence on Mountainscapes. *Bioscience* 59, 685–698. <https://doi.org/10.1525/bio.2009.59.8.10>.

- Richards, J.A., Jia, X., 1986. Remote sensing digital image analysis, fourth ed. Springer-Verlag, Berlin Heidelberg New York.
- Rouse, J., Haas, J., Deering, D., 1974. Monitoring vegetation systems in the Great Plains with ERTS. Third Earth Resources Technology Satellite-1 Symposium - Volume I: Technical Presentations. Washington D.C. NASA, 309–317.
- Rossi, G., Ferrarini, A., Dowgiallo, G., Carton, A., Gentili, R., Tomaselli, M., 2014. Detecting complex relations among vegetation, soil and geomorphology. An in-depth method applied to a case study in the Apennines (Italy). *Ecol. Complex.* 17, 87–98. <https://doi.org/10.1016/j.ecocom.2013.11.002>.
- Rull, V., 2009. Microrefugia. *J. Biogeogr.* 36, 481–484. <https://doi.org/10.1111/j.1365-2699.2008.02023.x>.
- Sedlacek, J., Cortés, A.J., Wheeler, J., Bossdorf, O., Hoch, G., Klápště, J., Lexer, C., Rixen, C., Wipf, S., Karrenberg, S., van Kleunen, M., 2016. Evolutionary potential in the Alpine: trait heritabilities and performance variation of the dwarf willow *Salix herbacea* from different elevations and microhabitats. *Ecol. Evol.* 6, 3940–3952. <https://doi.org/10.1002/ece3.2171>.
- Salvatore, M.C., Zanoner, T., Baroni, C., Carton, A., Banchieri, F.A., Viani, C., Giardino, M., Perotti, L., 2015. The state of Italian glaciers: a snapshot of the 2006–2007 hydrological period. *Geogr. Fis. Din. Quat.* 38, 175–198. <https://doi.org/10.4461/GFDQ.2015.38.16>.
- Seppi, R., Carturan, L., Carton, A., Zanoner, T., Zumiani, M., Cazorzi, F., Bertone, A., Baroni, C., Salvatore, M.C., 2019. Decoupled kinematics of two neighbouring permafrost creeping landforms in the Eastern Italian Alps. *Earth Surf. Processes Landforms*. <https://onlinelibrary.wiley.com/doi/epdf/10.1002/esp.4698>.
- Serra-Diaz, J.M., Scheller, R.M., Syphard, A.D., Franklin, J., 2015. Disturbance and climate microrefugia mediate tree range shifts during climate change. *Landscape Ecol.* 30, 1039–1053. <https://doi.org/10.1007/s10980-015-0173-9>.
- Shimokawabe, A., Yamaura, Y., Akasaka, T., Sato, T., Shida, Y., Yamanaka, S., Nakamura, F., 2015. The Distribution of Cool Spots as Microrefugia in a Mountainous Area. *PloS one* 10, e0135732. <https://doi.org/10.1371/journal.pone.0135732>.
- Stehman, S.V., 1997. Selecting and interpreting measures of thematic classification accuracy. *Remote Sens. Environ.* 62, 77–89. [https://doi.org/10.1016/S0034-4257\(97\)00083-7](https://doi.org/10.1016/S0034-4257(97)00083-7).
- Steinbauer, M.J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., et al., 2018. Accelerated increase in plant species richness on mountain summits linked to warming. *Nature* 556, 231–234. <https://doi.org/10.1038/s41586-018-0005-6>.
- Stewart, J.R., Lister, A.M., Barnes, I., Dalen, L., 2009. Refugia revisited: individualistic responses of species in space and time. *Proc. Roy. Soc. B-Biol. Sci.* 277, 661–671. <https://doi.org/10.1098/rspb.2009.1272>.
- Stoffel, M., Huggel, C., 2012. Effects of climate change on mass movements in mountain environments. *Prog. Phys. Geog.* 36, 421–439. <https://doi.org/10.1177/0309133312441010>.
- Tampucci, D., Citterio, C., Gobbi, M., Caccianiga, M., 2016. Vegetation outlines of a debris-covered glacier descending below the treeline. *Plant Sociol.* 53, 45–54. <https://doi.org/10.7338/pls2016531/03>.
- Telwala, Y., Brook, B.W., Manish, K., Pandit, M.K., 2013. Climate-Induced Elevational Range Shifts and Increase in Plant Species Richness in a Himalayan Biodiversity Epicentre. *PLoS ONE* 8 (2), e57103. <https://doi.org/10.1371/journal.pone.0057103>.
- Tomaselli, M., Agostini, N., 1990. Vegetation patterns and dynamics and on rock glacier in the Northern Apennines. *Pirineos* 136, 33–46.
- Tucker, C.J., 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sens. Environ.* 8, 127–150. [https://doi.org/10.1016/0034-4257\(79\)90013-0](https://doi.org/10.1016/0034-4257(79)90013-0).
- Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849. <https://doi.org/10.1890/10-0097.1>.
- Wershow, S.T., DeChaine, E.G., 2018. Retreat to refugia: Severe habitat contraction projected for endemic alpine plants of the Olympic Peninsula. *Am. J. Bot.* 105, 760–778. <https://doi.org/10.1002/ajb2.1042>.
- WGMS, 2018. Fluctuations of Glaciers Database. World Glacier Monitoring Service, Zurich, Switzerland. <https://doi.org/10.5904/wgms-fog-2018-11>. Online access: <http://dx.doi.org/10.5904/wgms-fog-2018-11>.
- Zanoner, T., Carton, A., Seppi, R., Carturan, L., Baroni, C., Salvatore, M.C., Zumiani, M., 2017. Little Ice Age mapping as a tool for identifying hazard in the paraglacial environment: The case study of Trentino (Eastern Italian Alps). *Geomorphology* 295, 551–562. <https://doi.org/10.1016/j.geomorph.2017.08.014>.
- Zemp, M., Hoelzle, M., Haeberli, W., 2007. Distributed modelling of the regional climatic equilibrium line altitude of glaciers in the European Alps. *Global Planet. Change* 56, 83–100. <https://doi.org/10.1016/j.gloplacha.2006.07.002>.
- Zemp, M., Frey, H., Gärtner-Roer, I., Nussbaumer, S.U., Hoelzle, M., Paul, F., et al., 2015. Historically unprecedented global glacier decline in the early 21st century. *J. Glaciol.* 61, 745–762. <https://doi.org/10.3189/2015JoG15J017>.