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RESEARCH ARTICLE

Rapid vegetation responses over the last seven decades revealed by an alpine ice core and land-cover patterns

Daniela Festi · Nicola Alessi · Camilla Wellstein · Stefan Zerbe · Klaus Oeggl

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Abstract
Context Syntheses of vegetation responses over the last century are rare for the Alps, and limited in chronological and taxonomical resolution. We propose that pollen records from glaciers can be used to fill this gap.
Objectives Our aim is to evaluate the reliability of glacier pollen records as historical archives of biodiversity to obtain plant diversity data and landscape changes. In detail, we aim at reconstructing taxa and vegetation trends in central sector of the Italian Alps over the last century integrating pollen-inferred vegetation trends with drifts in spatially explicit land-cover.
Methods Our study area is the Lombardy region (Italy). We performed pollen analyses of Adamello glacier cores, and reconstructed trends of single taxa and main vegetation types since the 1950s. Pollen-inferred vegetation trends were calculated using pollen indicators obtained from a database of vegetation-plot observations. The reliability of these trends is evaluated by comparison with spatially explicit tendencies reconstructed with a time-series of land-cover maps.
Results Pollen records well represent the natural vegetation types as the temperate and the riverine forests, and the anthropic vegetation as crops and alien species. From the 1980s a thermophilisation took place, and warm-demanding native and alien species expanded. The contraction of cultivated land since the 1970s, and the decline of the riverine forest appear driven by socio-economic factors.
Conclusions We conclude that pollen-inferred vegetation trends from glaciers can be used to obtain large scale biodiversity information. This is relevant also for areas where biodiversity data are scarce but needed for landscape management planning.

Keywords Alps · Glacier · Land-use intensification · Pollen · Vegetation-plots database

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D. Festi (✉)
Palaeonotology and Collections, Geosphere Austria, Neuliggasse 38, Vienna 1030, Austria
e-mail: daniela.festi@geosphere.at

D. Festi · C. Wellstein · S. Zerbe (✉)
Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen-Bolzano, 37100 Bolzano, Italy
e-mail: stefan.zerbe@unibz.it

N. Alessi
Italian Institute for Environmental Protection and Research, Via Vitaliano Brancati 48, 00144 Roma, Italy

N. Alessi · K. Oeggl
Department of Botany, University of Innsbruck, Sternwartestraße 15, Innsbruck 6020, Austria

Introduction

Climate change is one of the most pressing issues on the global environmental agenda together with the underlying processes of adaptation and mitigation (IPCC 2021). The knowledge gained from reliable observations over wide spatiotemporal scales is crucial to develop mitigation measures, and to better interpret past records with similar climatic patterns (Fordham et al. 2020). Historical observations are therefore a unique possibility to gain an understanding on the speed and entity of vegetation responses to abrupt environmental variations (Steinbauer et al. 2018).

The European Alps are an interesting region to investigate ecosystem responses to climate, because temperature here is rising at twice the global rate, and the effects of the warming are reinforced by the accelerated rates of land-use change registered over the past decades (Schneeberger et al. 2007; IPCC 2014). In the Alps, minor perturbations in global processes can cascade down to originate major changes (Helbing 2013). In addition, the steep altitudinal gradient causes climate and vegetation to vary quickly over short horizontal distances (Scherrer and Körner 2011). This complex situation offers a stimulating background, and justifies the high interest of the research community for the Alps. Nevertheless, despite a vast literature, only rare synoptic attempts on vegetation responses over the last century for the Alps as a whole, or larger parts, can be found. These studies are based on land-cover maps (Falcucci et al. 2007; Garbarino et al. 2020), and while they are highly valuable, they are limited in their spatial and chronological resolution, as well as in their temporal coverage because of the scarcity of suitable past observations - e.g. aerial photographs or satellite images. Historical vegetation changes can also be traced by the resurvey of historical biodiversity data (e.g., Steinbauer 2018), but the temporal resolution is low due to the high labor cost for field surveys (Kapfer et al. 2017). As a result, large-scale syntheses with a detailed chronological and taxonomical resolution are still lacking for the Alps (Grabherr 2000).

In this framework, we present an approach based on ice core pollen records obtained from a temperate glacier. Glaciers are valuable pollen archives to infer past vegetation at annual or seasonal resolution; in fact, they present snow accumulation rates up to 1 m water equivalent per year (Pavlola et al. 2015; Gabrielli et al. 2016; Festi et al. 2021). To date, palynological studies on temperate alpine glaciers are rare, often restricted to superficial layers, or focus on providing a detailed timescale of the ice core (Vareschi 1934; Bortenschlager 1970; Festi et al. 2015, 2017, 2021). These studies are essential as they show that alpine ice cores contain abundant pollen, and pollen assemblages are coherent with the regional vegetation (Festi et al. 2015, 2017). Considering the high number of glaciers in the Alps (Paul et al. 2020), we argue that ice deposits could partially fill the gap of a large-scale synthesis providing precisely datable archives for the historical reconstruction of vegetation changes.

Studies on ice cores from other region of the world also show that pollen from the ice can provide useful information about past vegetation (Andreev et al. 1997; Bourgois 2000; Liu et al. 2007; Eichler 2011; Rese et al. 2013; Papina et al. 2013; Li et al. 2019). In general, what emerges is that defining the spatial dimension of the reconstructed vegetation is a challenging task, mainly because of the undefined extension of catchment area. We therefore present here an approach that integrates new palynological observations from an Alpine ice core with spatially-explicit regional archives of vegetation-plot data and land-cover maps over time. By doing this, we add to the high-resolution pollen record from the ice core, a precise spatial dimension. We use geo-localized vegetation plots to obtain pollen indicators for vegetation types that act as pollen sources in the catchment area. In past studies, pollen types have been assigned to main vegetation types using expert opinions aiming to describe vegetation changes and dynamics over time (Behre 1981; Lang 1994; Leuschner and Ellenberg 2017). Only recently, numerical, data-driven frameworks have been tested to obtain an objective classification of pollen types and characterizing vegetation communities or land-cover types providing a pseudo-biomization technique (Fyfe et al. 2010, 2015; Woodbridge et al. 2014). These approaches highlight the importance of considering robust pollen groups mirroring the heterogeneity of vegetation communities in a study area, and defined by a list of indicator species of plant communities (Chytrý et al. 2002).

In summary, our study aims at reconstructing past vegetation responses since 1950 by means of several historical archives that integrate the spatial and temporal dimension to biodiversity trends. It provides original insights on climate and human-driven vegetation dynamics on a broad spatial and ecological scale, i.e. from the taxonomical level, to vegetation types and spatially-explicit land-cover types, occurred over the last century. In detail, we aim to (i) evaluate vegetation changes that occurred in the last century derived from pollen deposits of an alpine ice core, and (ii) compare and integrate pollen-inferred vegetation trends with drifts in land-cover at different spatial scales.

Methods

Study area

The study area is the geographical region that includes the ice cores drilling sites and the main pollen sources, following the predominant wind direction at the coring site. The ice cores were retrieved from the Adamello glacier, in the central Italian Alpine region (Lombardy, Italy). The Adamello massive hosts the deepest and most extended glacier complex of Italy, including 92 glaciers with a cumulative area of 40.67 km² and a maximum depth of about 270 m (Smiraglia and Diolaiuti 2015; Picotti et al. 2017). The ice cores ADA15 and ADA16 analyzed in our study were extracted from the locality Pian di Neve, at 3200 m a.s.l. (Fig. 1) in February 2015 and April 2016, respectively. ADA15 is 5.5 m long while ADA16 reached a depth of 45.5 m. From a temporal perspective, the ADA15 ice core spans four years of accumulation (2014 to 2011), while ADA16 encompasses the years 1952 to 1993 (Festi et al. 2021). The cores were extracted next to each other. Due to its low altitude, the Adamello glacier is considered a temperate glacier, and as a matter of fact, the glacier is currently affected by conspicuous summer ablation.

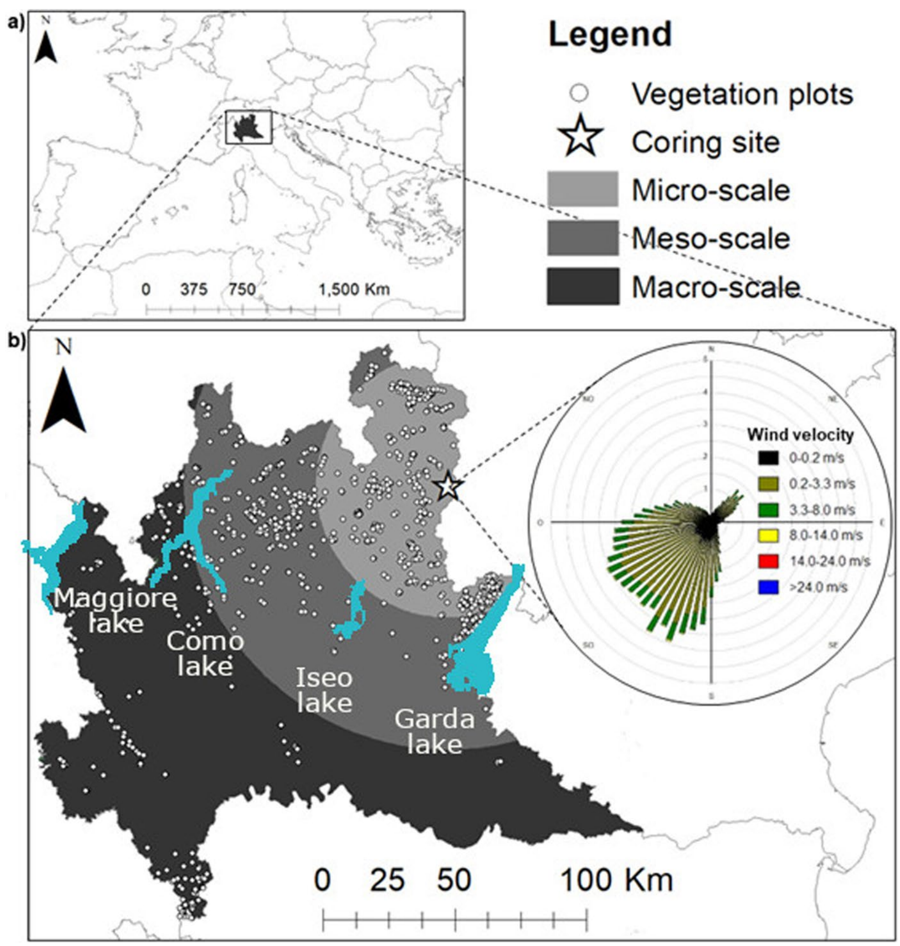

Fig. 1 Overview maps showing the study area, Lombardy. **a** Lombardy's location in Italy, and Europe; **b** subdivision of Lombardy according to the three spatial scales adopted; distribution of vegetation plots used to obtain pollen indicator types; major lakes in blue; location of the coring site (star) and main wind directions measured at the coring site

Fortunately, pollen grains have been proven to be resilient to percolation in alpine glaciers, ensuring a good preservation of the annual signal (Festi et al. 2021).

Following the main wind direction at the coring site, and data availability, the region Lombardy was identified as the main source of pollen on the glacier (Fig. 1b). We hence assume that the ice-core records mainly reflect the vegetation dynamics occurring in this region. Lombardy covers approximately 24,000 km^2, 41% of which is occupied by mountain relief, 12% by hills, and 47% by the Po river plain. The climate of the region is sub-continental-temperate, with a variety of micro- to meso-climates depending on the interplay between the orographic setting and the presence of great lakes. The high altitudes present a glacial climate, while an alpine climate characterizes the mountain areas, and a fresh temperate climate is found in the hills. The influence of lakes on the local climate is particularly marked around the great prealpine lakes (e.g. Lake Gada, Lake Como). This variety of climates and topography is reflected by a vegetation zonation defined by six vegetation types (Verde et al. 2010): (i) remnants of temperate oak forests are found in the Po plain, where species such as common oak (*Quercus robur* L.), common hornbeam (*Carpinus betulus* L.) and common ash (*Fraxinus excelsior* L.) occur; (ii) the Mediterranean evergreen forest characterized by evergreen oak (*Quercus ilex* L.), laurel (*Laurus nobilis* L.), mock privet (*Phyllirea latifolia* L.) grows around the large lakes (e.g. Lake Garda and others); (iii) a warm temperate forest dominated by deciduous oaks (*Q. pubescens* Willd., *Q. petraea* (Matt.) Liebl.) and pine (*Pinus sylvestris* L.) occurs at the pre-Alpine and Alpine foothills; (iv) the cool temperate broadleaved forest with beech (*Fagus sylvatica* L.) and fir (*Abies alba* Mill.) is recorded from the montane altitudes, and it is replaced in the subalpine zone by (v) the cool temperate coniferous forest with spruce (*Picea abies* (Mill) H. Karst.) and larch (*Larix decidua* Mill). The higher altitudes are characterized by (vi) an alpine vegetation where herb species dominate the landscape (e.g., *Poa alpina*, *Carex spp*., *Nardus stricta*). In addition to this remarkable mosaic of climates and vegetation, the Lombardy represents the highest anthropogenic pressure in Italy, with a population density of 423 inhabitants per km², and a highly developed industrial and agricultural sector (ISTAT, 2019).

Pollen analysis

Ice cores ADA16 and ADA15 were sampled at high resolution and using continuous sampling (without any gaps) in a −21 °C clean room at the Euro Cold Lab facility (University Milano Bicocca). ADA16 led to a set of 536 continuous samples (5 to 10 cm thick) and ADA15 to 55 continuous samples (10 cm thick). Pollen and microfossils were extracted according to Festi et al. (2017, 2019) and the complete content per sample was identified and quantified. Pollen and spores identification was performed according to standard identification keys (Faegri and Iversen 1989; Moore et al. 1991; Beug 2004;) and the pollen atlas by Reille (1992). To obtain a yearly time resolution in both of the cores, the 536 samples of ADA16 were merged into 31 macro-samples based on the ice-core timescales (Festi et al. 2021) and setting 400 terrestrial pollen grains as a minimum count per macro-sample. ADA15 samples have been merged into three macro-samples according to the peaks in pollen concentration reflecting a year of accumulation; Pollen counts of *Pinus, Betula, Alnus, Larix, Castanea*, and *Tilia* were corrected following correction factors (Lang 1994) in order to adjust for under- and over-representation of these pollen types in the record. The pollen diagram has been drawn with C2 Data Analysis vs. 1.4.2.

Trends in pollen-inferred vegetation types (PVT)

To allow the integration and comparison of pollen data with spatially explicit data, we grouped pollen types into pollen-inferred vegetation types (hereafter PVT). These categories correspond to the main land-cover types detectable by remote sensing. Pollen types recorded in the Adamello ice cores were grouped according to the current vegetation of the source area described by a regional dataset of field observations. The general workflow is graphically summarized in Fig. 2. The dataset described the close-to-nature vegetation types, while vegetation of anthropogenic origin and heavily disturbed sites (e.g., urban agglomerations, mining sites, gardens, agricultural crops) were not represented (Agrillo et al. 2017). In detail, the dataset was composed by 1014 vegetation plots recording co-occurrence patterns for 965 species standardized according to a national checklist (Conti et al. 2005), and their relative cover

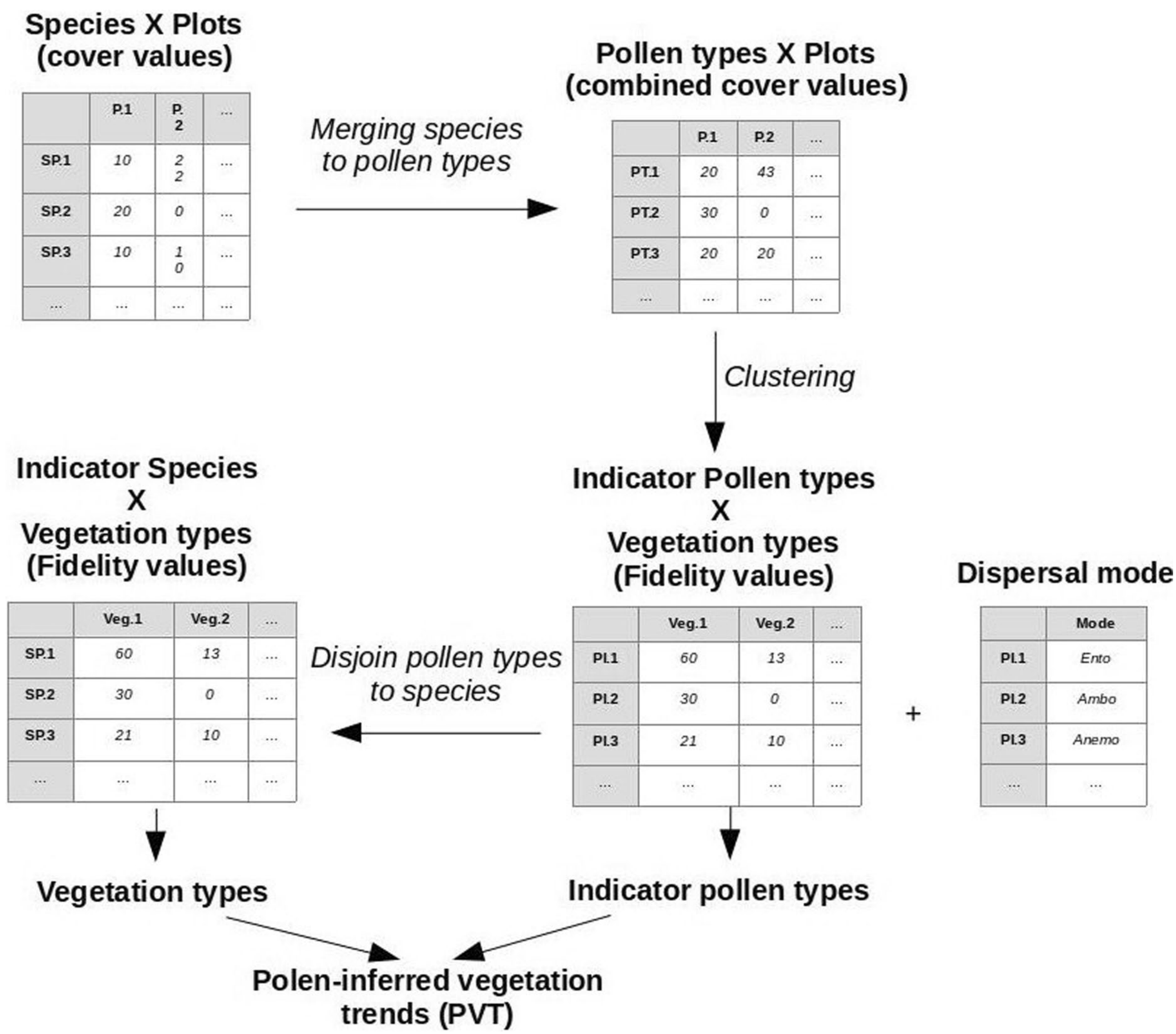

Fig. 2 Graphical summary of the workflow adopted to calculate pollen-inferred vegetation trends (PVT) by selecting pollen-indicator types for main vegetation types using a regional vegetation-plots dataset. *P* plot; *SP* species; *PT* pollen type; *Veg* Vegetation type

(Fig. 1b). Each pollen type found in the analysed ice cores was assigned to species occurring in the vegetation-plot dataset (Supplementary Material S1), thus providing a matrix that described the current vegetation in terms of pollen types. Accordingly, we found 91 pollen types out of 125 types with corresponding species occurring in the vegetation-plot dataset. The remaining 34 pollen types were checked for inclusion in anthropogenic vegetation types by expert opinions. Seven of them were categorized as indicators of anthropogenic vegetation (Table 1). On the other hand, 243 species were deleted from the dataset because they were not included in any of the pollen types observed in the ice core. The obtained matrix was clustered using a Modified TWINSPAN clustering (Roleček et al. 2009), which is a hierarchical divisive clustering technique that identifies species communities based on the main ordination axis provided by a Detrended Correspondence Analysis. This technique converts species into several pseudo-species based on cut levels of the cover values, which have been set at 5% and 25% for our analyses to emphasize the role of rare species in the species composition of clusters. The obtained matrix was then transformed to a distance matrix using the average Sørensen dissimilarity describing pairwise distances between

Table 1 List of pollen indicators used to obtain pollen-inferred trends for vegetation types and the description of the corresponding land-cover types, calculated respectively with warm and cool temperate forest as separated (a) as well as combined types (b), and the selection based on fidelity values calculated from a clustered vegetation-plots database and dispersal mode

Vegetation Types	Indicator Pollen Types	Land-cover Types
a) With warm and cool temperate forest separated		
Alpine vegetation	*Salix, Rumex acetosa T., Achillea T., Saxifraga oppositifolia T., Caryophyllaceae, Brassicaceae, Artemisia, Sedum, Trifolium T., Saxifraga granulata T., Senecio T.*	Grassland occurring above 2,000 m a.s.l.
Boreal forest	*Picea, Larix, Abies, Pinus cembra, Alnus viridis, Lycopodium annotinum, Polypodium*	Low and high density coniferous forest
Cool temperate forest	*Corylus avellana, Fraxinus excelsior, Tilia, Carpinus betulus, Castanea sativa, Ulmus, Fagus sylvatica*	Low and high density broadleaved forest
Warm temperate forest	*Fraxinus ornus, Ostrya T., Pinus, Quercus robur T., Quercus ilex, Juniperus, Taxus baccata*	Low and high density broadleaved forest
Riverine forest	*Alnus, Urtica, Filipendula, Cannabaceae*	Riverine and wetland vegetation
b) With temperate forest		
Alpine vegetation	*Salix, Rumex acetosa T., Achillea T., Saxifraga oppositifolia T., Caryophyllaceae, Brassicaceae, Artemisia, Sedum, Trifolium T., Saxifraga granulata T., Polygonum bistorta T, Senecio T., Ranunculaceae, Primulaceae*	Grassland occurring above 2000 m a.s.l.
Boreal forest	*Picea, Larix, Abies, Pinus cembra, Alnus viridis, Betula, Fagus sylvatica, Juniperus, Monolete/Trilete spores, Polypodium, Lycopodium annotinum*	Low and high density coniferous forest
Temperate forest	*Fraxinus ornus, Ostrya T., Quercus robur T., Corylus avellana, Hedera helix, Acer, Pinus, Castanea sativa, Tilia, Carpinus betulus, Fraxinus excelsior, Ulmus, Quercus ilex, Thalictrum*	Low and high density broadleaved forest
Riverine forest	*Alnus, Urtica, Filipendula, Cannabaceae*	Riverine and wetland vegetation
Cultivated crops	*Cerealia, Secale, Zea mays, Fagopyrum, Cannabis sativa, Olea europea*	Cultivated areas (arable lands, vineyards, rice fields, olive groves, etc.)
Anthropogenic vegetation	*Ambrosia, Carya, Cedrus, Eucalyptus, Nothofagus/Fuscospora, Platanus orientalis, Sequoia/Cryptomeria*	Urban area (urban parks, gardens and highly disturbed areas)

observations based on the pseudo-species presence/absence. Five clusters of plots were obtained with similar and interpretable composition in terms of pollen types, i.e. vegetation types. The clusters were interpreted by calculating the "phi" fidelity index of both pollen types and original species to groups (Supplementary material S2 and S3; Chytrý et al. 2002) using Juice software (Tichý 2002). The fidelity index measures the concentration of species occurrence in a cluster with respect to the other clusters. Accordingly, we named the vegetation types as follows: (i) alpine vegetation, (ii) boreal forest, (iii) cool-temperate forest, (iv) warm-temperate forest, and (v) riverine forest. Then, we selected as pollen indicators for the vegetation types, those types with a fidelity value higher than 20 for the target group and lower than 20 for the rest of the groups. Indicator pollen types were then assigned to a dispersal mode (i.e., anemophilous, entomophilous or ambophilous; Supplementary Material S4) in order to exclude types having little chances to reach the coring site from distant vegetation zones (e.g., *Ligustrum* pollen type with entomophilous dispersal mode and occurring in the warm-temperate forest of the foothill). Therefore, pollen indicator types with entomophilous dispersal mode were selected only if occurring in a vegetation type close to the coring site, i.e. the alpine vegetation. We thus obtained a list of classified pollen types into respective vegetation types, which summarized the different plant communities possibly acting as pollen sources for the analysed ice core (Table 1a). Eventually, PVT were obtained by summing pollen abundances of indicator types for each vegetation type.

Trends in spatially explicit land-cover types (SLT)

Trends in the area occupied by spatially-explicit land-cover types (hereafter SLT) were obtained for the Lombardy region from the project DUSAF (Geoportale di Lombardia). A chronosequence of land-cover types based on maps was built using five time-windows, i.e. 1954, 1999, 2007, 2012, and 2015. For a consistent comparison between SLT and PVT, compatible land-cover types were selected after several improvements of type definitions. In detail, a validation of the selection was obtained by comparing elevations of the spatially-explicit land-cover types and clustered vegetation plots. Accordingly, maps for the Alpine vegetation were reduced to areas above 2000 m a.s.l. since they covered a broader elevation range than the clustered vegetation plots. Land-cover maps for the boreal and temperate forests were obtained merging the maps for low and high-density coniferous and broad-leaved forest, respectively. Moreover, the broad-leaved forest occurring in the land-cover maps corresponded both, in the definition and in the occupied elevation range of the combination of warm and cool temperate forests defined by clustering the vegetation-plot dataset. Thus, to ensure a robust comparison, we merged the two vegetation types into the temperate forest type and recalculated the list of pollen indicator types for all the types (Table 1b, Supplementary Material 5). The two original maps of the riverine forest and wetland vegetation were merged to fit the altitudinal range displayed by plots belonging to the riverine forest. The elevational comparison for adjusted land-cover types and vegetation plots is shown in Supplementary Material 6. Classes for urban areas and cultivated crops were compared respectively with pollen types of cultivated and alien plants occurring within the list of previously excluded pollen types, i.e. those not occurring in the vegetation-plot dataset (Table 1b). The land-cover type characterized by pollen from alien species is assumed to be comparable to the urban areas since such species occur mainly in relation to highly disturbed areas or as ornamental species in gardens. To better understand the geographical scale to which the ice core works as past vegetation archive, we divided the spatially-explicit products in three scales, i.e. (i) the micro-scale, which represents the overlapping area between the Lombardy region and a circular area centred at the coring site with a radius of 50 km; (ii) the meso-scale, as the overlapping area between Lombardy region and a circular area centred at the coring site with a radius of 100 km; (iii) the macro-scale, which represents the whole Lombardy region, i.e. a maximum radius of about 190 km. The area occupied by each land-cover type in each time-window was calculated in square kilometres. For each of the four-time intervals delimited (1954–99, 1999–2007, 2007–12, and 2012–15), we calculated the growth rate as the relative difference between the latest and the earliest maps of the obtained SLT. Furthermore, we calculated the mean velocity of change of SLT dividing the growth rate by the number of years covered by each time interval. This approach enabled a comparison of SLT changes across the different spatial scales analysed. All the analyses were conducted using ArcGIS (v. 10.7.1, Redlands, CA, USA) and the R statistical programming language (v. 3.6.0, http://www.R-project.org).

Results

Pollen analyses

The proportion of trees, shrubs and herbs varies with time showing an increase in arboreal pollen from 20 to 60% indicating an expansion of woodland cover from 1952 to 2014 (Fig. 3). While *Picea* (spruce) presents a high inter-annual variability, a clear increase in *Castanea sativa* (sweet chestnut), *Ostrya*-type pollen (hop-hornbeam), and *Fraxinus ornus* (manna ash) is evident. The onset of *Quercus ilex* (evergreen oak) pollen type occurrence is in the 1980s. On the contrary, a decline in *Alnus glutinosa*-type (alder) and *Fraxinus excelsior* (common ash) starts with the 1970s.

Shrubs are particularly abundant in the 1950s, mainly due to the high occurrence of *Alnus viridis* (green alder), which then experiences a continuous decline. On the contrary, *Corylus avellana* (hazel) starts increasing with the beginning of the 1970s. Pollen of herbs shows a general drop, also reflected in the most important taxa i.e. Poaceae (true grasses), *Artemisia*-type (mugwort), Asteraceae (aster family), Brassicaceae (crucifers), Chenopodiaceae (chenopods), Ranunculacaeae (buttercup family), *Plantago* types (plantains) and *Saxifraga* types (saxifrages). Among herbs, the neophyte *Ambrosia* (rugweed)

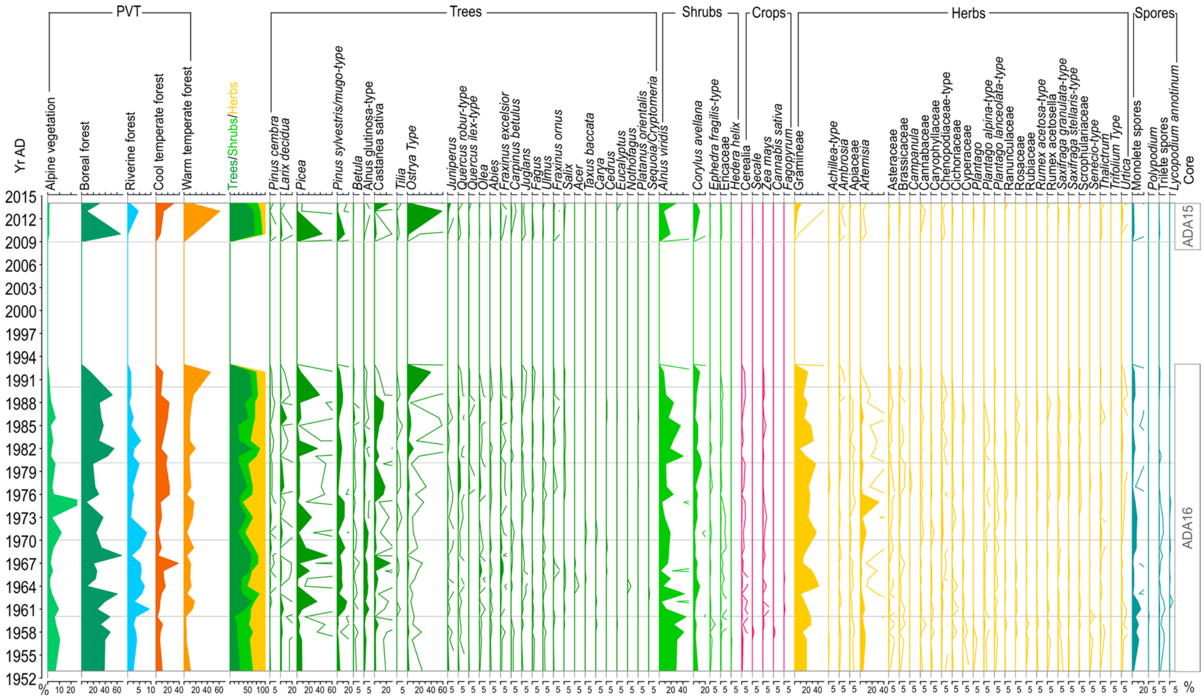

Fig. 3 Pollen diagram showing percentage values of pollen vegetation trends (PVT), life forms (trees, shrubs, herbs) as well as pollen (higher plants) and spore (ferns) types. Lines denote exaggeration values (x10)

displays a clear increase starting from the end of the 1980s.

Pollen-inferred and spatially-explicit trends

PVTs and SLTs for the period 1950s to 2015 clearly emerge (Figs. 3 and 4). Growth rates and velocity calculated for each time-window of the SLTs are shown in Supplementary Material 7 and Fig. 4. The Alpine vegetation PVT is composed of herbs and hence reflects mainly the alpine mats. This vegetation shows a decrease from 1963 to 2014, with a pronounced reduction from 1988 to 2014. In contrast, the Alpine vegetation shows a rapid increase in the SLT of the occupied area between 1999 and 2007 with an increase of about 14% at every spatial scale. The high year-to-year variability due to *Picea* variations makes it difficult to extrapolate a clear trend for boreal forest PVT over the complete time period (Fig. 3). The corresponding SLT shows an expansion of 12% between 1954 and 1999. The PVT for the cool temperate forest shows a moderate positive trend driven by *Corylus* and *Castanea*. Quite prominent is the expansion of the warm temperate forest PVT, reflecting the increase of *Ostrya* and the onset of *Quercus ilex* since the end of the 1980s. The temperate forest SLT shows a 31% increase, which mainly takes place between 1951 and 1999. The riverine forest PVT shows a clear negative trend with an abrupt decrease in the mid of the 1970s ascribed to an *Alnus glutinosa* decline. The corresponding SLT presents an area increase at the micro- and meso-scales of respectively 16 and 45%, while at macro scale during the last seven decades the occupied area experiences a 10% decrease. The cultivated crops PVT, mainly reflecting cereal pollen, declines from the 1940s to the year 2014. This decline is sustained by the SLT trends, and it is especially evident at meso-scale between 1954 and 1999, when the cultivated crops SLT loses 81% of its area. The anthropic vegetation PVT undoubtedly increases since the late 1980s, along with the massive increase in urban areas at all the geographical scales represented by the relative SLT between 1954 and 1999. This SLT presents conspicuous growing rates up to 387%.

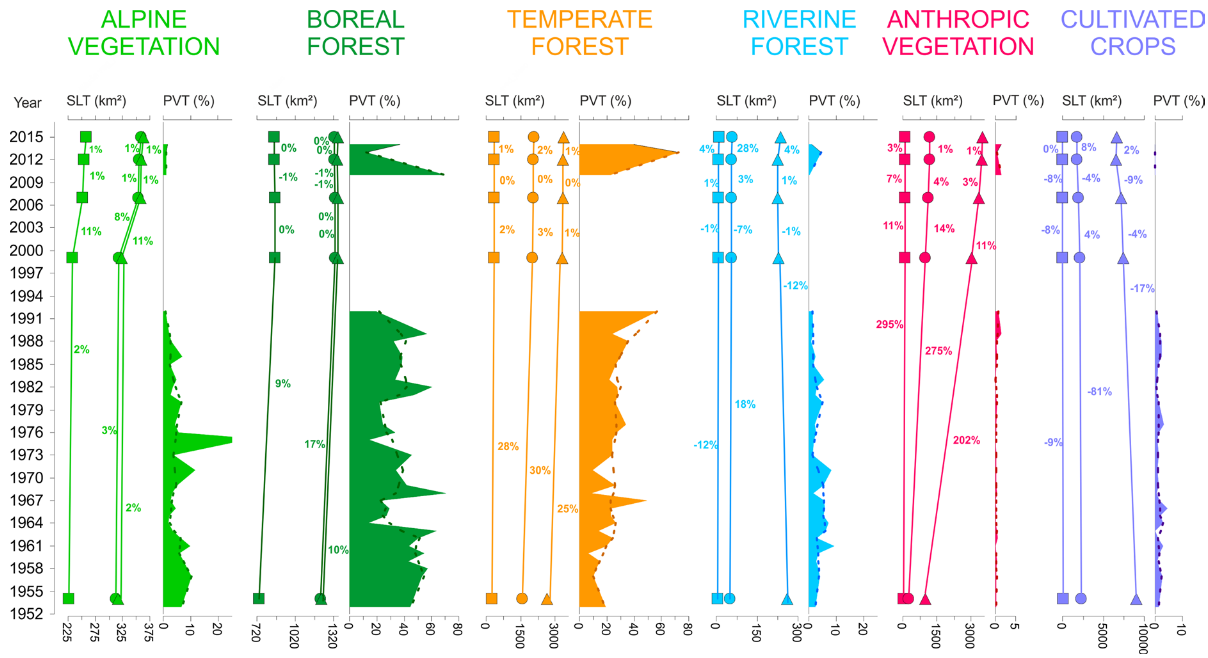

Fig. 4 Trends in spatially-explicit land-cover types (SLTs) and in pollen-inferred vegetation types (PVTs, expressed in pollen percentage values). In SLT graphs: Triangle-macro-scale; circle- meso-scale, square- micro-scale; values indicate SLTs growth rates (details in Supplementary Material 7). In PVT graphs: dashed lines indicate PVT smoothed values

Discussion

The Adamello ice-core pollen record is an exceptional case of seven decades-long vegetation time series with a yearly time resolution (with a gap between 1994 and 2009) and covering a large spatial scale. Our integrated study, combining pollen- and spatially-inferred estimates of landscape changes, reveals a gradual but profound transformation for the central Alps that likely took place as consequence of land-use changes and global warming. Over the last seven decades, we report clear trends in taxa, vegetation and land-cover types occurrences and abundances, mostly on a yearly timescale. In the pollen records, a general decline of the riverine forest and related taxa is recorded, along with a drastic contraction of the area devoted to crop production, and an enlargement of the urban areas. Moreover, a thermophilisation of temperate forests took place, with an expansion of warm-demanding species observed in both the native (e.g. *Quercus ilex*) and alien species pools (e.g. *Ambrosia artemisifolia*). From a temporal perspective, vegetation changes that started during the 1970s can be explained mainly by land-use and socio-economic changes, whereas changes that occurred during the 1980s may be amplified by the interplay of land-use and climate change.

The comparison with regional land-cover maps revealed a good similarity between pollen-inferred and spatially-explicit vegetation trends. Generally, the coherency of results suggests a robust and reliable reconstruction of vegetation patterns. Our approach showed consistent results particularly for vegetation types characterized by wind dispersed pollen operating on the meso- (100 km) and macro-scale (200 km), indicating that the glacier pollen record is primarily representative of these, or possibly even larger spatial scales. The pollen record appears to be less representative of the high-altitude grassland vegetation trends, despite being the closest to the deposition site. This is likely because high-altitude plant species are characterized by isolated distribution on mountain peaks, limitations in the length of the flowering season, and low pollen production and dispersion (Erschbamer et al. 2008 and 2016). This limits a straight-forward interpretation of the pollen-inferred alpine vegetation in the immediate surrounding of the glacier. On the other hand, the low concentration of alpine pollen types could reflect the decline of high alpine-nival ecotone (Pauli et al. 2003; Raffl et al. 2006; Matteodo et al. 2013; Lamprecht et al. 2018; Steinbauer et al. 2020). In the same geographical area of the present study, Alessi et al. (2021) used a three decades-long time-series of LANDSAT images (~30 m of resolution) and suggested a cover increase of subalpine grasslands to the detriment of the high alpine-nival ecotone. Thus, the increase of alpine grassland cover observed in the present study using land-cover maps might correspond to a surface trade-off among grassland types as observed using historical satellite observations (Alessi et al. 2021). In this context, remotely sensed approaches can improve detectability of vegetation changes over time within a temporal limitation of the last four decades. In general, the combination of the different historical archives of vegetation-plot data provides a detailed description of the landscape transformations, occurred at the regional scale in an era of global change. The consistency of results for landscape and vegetation changes benefited from both, the fine temporal resolution provided by the ice core stratigraphy and the well-defined spatial resolution and dimension offered by the land-cover time series.

Consequences of land abandonment and global warming

The main vegetation response emerging from our analyses is the expansion of tree and shrub species during the 1960s and 1970s related to a post-World War II land-abandonment phase (Tasser et al. 2007; Romano et al. 2017). In line with respective studies, the temperate forest shows a more pronounced expansion with respect to other forest types (Tasser et al. 2007). The boreal forest shows a clear expansion according to the spatially-explicit land cover, while it is more difficult to detect a clear trend according to the pollen-inferred vegetation types due to the high variability of the values deriving from *Picea*'s (spruce) fluctuations (Fig. 3). Periodically high values in spruce represent masting events, i.e. the intermittent and large-scale synchronized production of large pollen amounts by one species, which are known to occur in *Picea* (Kelly 1994; Lamontagne and Bouting 2007; Geburek et al. 2012). With this respect, since glaciers provide annual pollen records, they are therefore suitable archives to investigate questions related not only to climate, but also to trees masting and their environmental drivers. New insights in this topic are needed to predict tree reproductive strategies and their responses to a changing environment (Ascoli et al. 2017).

Our results show that the expansion of the temperate forest is observed consistently throughout the study period in both PVT and SLT, displaying a gain in area of 26 to 36% across the three spatial scales. This uniformity indicates that our pollen record from the glacier is adequate to reconstruct quantitative changes of this vegetation type. The palynological signal contained in the ice, mirrors the extension of the temperate forest area starting at the end of the 1970s at the expense of the boreal and riverine forest. A part of this process is probably due to an enhanced pollen production due to temperature increase (Bogawski et al. 2014). This is exemplified in the pollen record by the appearance of the *Quercus ilex* pollen grains in the ice record, starting from the 1980s. *Quercus ilex* was certainly part of the vegetation in the study area at least in the meso- and macro-scale areas before the 1980s (Marchesoni 1958; Lona et al. 1965), however the pollen production might have been too low to enable a constant arrival on the glacier. Considering that modern pollen monitoring studies link higher pollen production to increasing temperature (Bogawski et al. 2014) it seems plausible that the sudden and persistent occurrence of the evergreen oak in the ice record is due to an increased pollen production of this taxon due to climate warming (Gobiet et al. 2014; IPCC et al. 2014). Furthermore, the climatic driver might also overlap with the abandonment of land management practices leading to a densification of the forest stands. As a matter of fact, on a species level the two expansion phases of the temperate forest are related to two distinct events: first, an increase in the cool temperate forest related to higher *Corylus avellana* pollen occurred at the end of the 1970s, and secondly, an expansion of the warm temperate forest mainly driven by an increase in *Ostrya* taking place in the years 1990–2014.

In contrast to the general trend of expansion of forest and scrubland, a decline in *Alnus viridis* is partially recorded by our ice core pollen record starting from the year 1988, and it is most likely of semi-natural origin. Studies indicate that since the 1990s a disease that causes a progressive necrosis and dissection of the tree has been spreading in the Alps, where green alder populations have been undergoing a severe decline. The primary cause has not yet been identified, but Pisetta el al. (2012) show convincing evidence that the occurrence of the disease is closely linked to a reduction in the duration of the winter snow cover. In fact, green alder requires specific climate conditions, with optimal winter temperatures between −10 °C and −1 °C, and constant and abundant winter snow cover. In this case, the cause of the decline is therefore linked to the increase in temperature caused by the anthropogenic climate warming. Since the green alder requires a moist soil during the growing season (Mauri and Cadullo, 2016), a decrease in snow cover can have negative effects.

Consequences of river management

The trend of forest expansion is coupled with the riverine forest decline, triggered by the heavy management of rivers that lead to severe alternation of river morphology and riparian ecosystems by lowering the water table and draining the soil (Robbins 2007; Comiti 2012; Belletti et al. 2020). Both PVT and SLT of riverine and wetland vegetation show a spatial reduction from 1944 to 2012 with a final recovery from 2012 to 2015, which for the SLTs is stronger at finer geographical scales. The consistency of the two trends is an indication of the reliability of the pollen reconstruction obtained from the ice core. In detail, pollen data point to the fact that the reduction mainly reflects the decline of *Alnus glutinosa* and *A. incana* (included in the *Alnus glutinosa*-pollen type), starting with the beginning of the 1970s. This decrease is most likely caused by human intervention in connection with a substantial stabilization of steep channels carried out in the Alps from the 1950s and peaking in the 1970s (Benini 1990). This left rivers literally “broken” by artificial barriers, and even today our study region presents one of the highest river fragmentation values in Europe, with more than one barrier per kilometer (Belletti et al. 2020).

In the 1950s and 1960s the Alps also became an essential source of electric power, and the construction of hydropower dams peaked. In this phase, around the Adamello glacier several artificial lakes were built by flooding vast areas, and causing a loss of land for the subalpine vegetation. To date, there are at least 550 hydropower stations spread on the Alpine territory (http://webgis.alpconv.org/). This phenomenon left a clear sign in the pollen record represented in the sharp decrease of *Alnus viridis* in the 1960s. This shrub thrives on rather impervious and moisty slopes especially on silicate rocks, as those of the Adamello massif (Callegari and Brack 2002), in the subalpine and lower alpine belt forming extended stands, which are a prominent feature of the landscape. Above 1300–1500 m a.s.l., green alder is the main shrub growing on mountain riversides that are not often flooded (Ellenberg 1988). Due to the heavy modifications of riverbed and adjacent areas, already the ‘90s less than 10% of the river in the Alps could be considered natural (CIPRA, 1992). Our data therefore suggest that exploitation of the water resources for energy production and heavy river management left a major scar in the vegetation record causing the decline of the riverine forest and wetland ecosystems.

Consequences of urbanization

PVT and SLT for cultivated crops display a common negative trend clearly indicating the contraction of the areas dedicated to cereal agriculture and olive plantation. This trend is a reflection of post-World War II transformation process of rural land into urbanized areas (here intended as build-up land and land used for ancillary settlement functions such as gardens, sport facilities, roads). The result is a steep and widespread enlargement of urbanized spaces on all spatial scales, i.e. from a minimum increase of 250% as in the macroscale to a maximum of 390% in the microscale. This conversion from cropland to urban ground happened at the impressive rate of 33 ha/day in the Po plain, where the lack of consistent planning generated a sort of endless suburb region with a great loss of fertile land and ecosystem in the lowlands, also leading to habitat fragmentation (Romano et al. 2017). This uncontrolled urbanization progression followed the massive demographic increase in Lombardy (40% between 1950 and 2000) driven by the fact that the Po plain quickly became a center for industry and business.

In the pollen diagram the loss of fertile land and decrease in primary production is clearly visible especially in the *Zea mays* and other cereals pollen, as well as in the *Olea europea* decline of percentage values starting with the 1990s. Our data are consistent with historical sources that report a loss in agricultural land use starting from the 1950 (Agnoletti and Santoro 2012). Pollen of *Cannabis sativa*, which was present only as a single finding around 1958, reflected the cultivation of this species in the study area. A further indication of widespread urbanization is the increased occurrence of alien species. The presence of aliens is mainly related to urban areas, as in gardens, and can hence be considered indicative of urbanization rate that emerges from maps. While pollen of trees like *Platanus orientalis, Carya, Eucalyptus* are occasional, the positive trend of the anthropic vegetation PVT starting from the 1980s mainly reflects the spread of *Ambrosia* (rugweed). *Ambrosia artemisifolia* is an annual plant native to the prairies of North America that has become a great concern in Italy and Europe due to its invasiveness and high allergenic pollen (D'Amato et al. 2007; Gentili et al. 2017). The first reported specimen in Italy was described in 1902 in the north-west region of Piedmont (Vignolo-Lutati 1934), and first occurrences of invasion were recorded in Piedmont and Lombardy. To date, these regions present the highest airborne concentration of ragweed pollen (Makra et al. 2011). *Ambrosia* grows particularly in anthropic habitats and it is widely distributed in disturbed areas like wastelands, roadsides, as it tolerates different soil and climate conditions (Smith at al 2013). Being an annual plant, the quantity of pollen it produces and that can be deposited on the glacier, is directly proportional to the number of individuals. Therefore, the increase in pollen percentage of *Ambrosia artemisifolia* in the ice record since the 1950s clearly indicates that this species was already quite widespread in Lombardy at that time, supporting previous studies (Celesti-Grapow et al. 2009). Most importantly, our palynological data indicate a faster spreading since the end of the 1980s that could be connected to the increased availability of disturbed areas due to rapid urbanization (200 to 300% of increase according to the spatially explicit land cover analyses), but also to more favorable climatic conditions brought about by the climate warming (Cunze et al. 2005).

Conclusion

Our study shows that ice cores from temperate glaciers are suitable archives to reconstruct vegetation changes over the last century with a yearly time resolution and reasonable taxonomical precision. In comparison to the spatially explicit reconstruction, the pollen record is particularly reliable for the temperate and the riverine forest, cultivated crops and anthropic vegetation. In general, the main variations recorded are linked to urbanization, land abandonment, river management, and are possibly amplified by the ongoing climate warming. While pollen analyses do not reach the taxonomical accuracy of vegetation surveys, they have the advantage that they are not limited by the availability of historical data, and by their time resolution. Similarly, vegetation trends can be deduced using remote sensed data, however, these instruments are limited in temporal coverage and resolution, and enable to recognize only main vegetation types. Merging different methods clearly allowed a better understanding of the vegetation and landscape changes in the Adamello region.

Our study shows that reconstructing vegetation trends over the last century on the base of pollen records from glacier ice is a valid option to obtain vegetational information on a large scale in areas for which aereophotos and historical biodiversity data are scarce or limited in time and space, preventing a comprehensive overview. In this perspective, our approach is applicable in other glaciated mountain regions, for which biodiversity data are scarce, e.g. Central Asia (Nowak et al. 2020; Kandel et al. 2016), and the Andes in South America (Comer et al. 2022; Payne et al. 2017). The advantage of using a glacier archive is that if the climatic record is still preserved in the ice, causal relationship between biodiverstiy and climate can be assessed for these remote areas. Clearly, the presence of a glacier unaffected by heavy percolation remains a prerequisite, and therefore action must be taken before the integrity of these precious archives is compromised.

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Author contributions DF and NA made formal analyses, developed methodology, prepared figures, tables and wrote the manuscript. KO, SZ, DF and CW obtained funding, partecipated to the conceptualization and reviewed the manuscript.

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Declarations

Competing interest The authors declare no competing interests.

References

Agnoletti M, Santoro A (2012) The Lombard forest landscape. A historical summary. ERSAF, Regione Lombardia

Agrillo E, Alessi N, Massimi M, Spada F, De Sanctis M, Francesconi F, Cambria VE, Attore F (2017) Nationwide vegetation plot database - Sapienza University of Rome: state of the art, basic figures and future perspectives. Phytocoenologia 7:221–229

Alessi N, Wellstein C, Rocchini D, Midolo G, Oeggl K, Zerbe S (2021) Surface tradeoffs and Elevational shifts at the Largest Italian Glacier: a thirty-years Time Series of remotely-sensed images. Remote Sens 13(1):134

Andreev AA, Nikolaev VI, Yu D (1997) Pollen and isotope investigations of an ice core from Vavilov Ice Cap, October Revolution Island, Severnaya Zemlya Archipelago. Géogr Phys Quat 51(March):379–389

Ascoli D, Maringer J, Hacket-Pain A et al (2017) Two centuries of masting data for european beech and Norway spruce across the european continent. Ecology 98:1473–1473

Behre KE (1981) The interpretation of anthropogenic indicators in pollen diagrams. Pollen Spores 23:225–245

Belletti B, de Leaniz GC, Jones J, Bizzi S, Börger L, Segura G, Castelletti A, van de Bund W, Aarestrup K, Barry J, Belka K, Berkhuysen A, Birnie-Gauvin K, Bussettini M, Carolli M, Consuegra S, Dopico E, Feierfeil T, Fernández S et al (2020) More than one million barriers fragment Europe's rivers. Nature 588(7838):436–441

Benini G (1990) Sistemazioni idraulico-forestali, 283 edn. Torino, UTET

Beug HJ (2004) Leitfaden der Pollenbestimmung für mitteleuropa und angrenzende Gebiete. Verlag Dr. Friedrich Pfeil, München

Bogawski P, Grewling Ł, Nowak M, Smith M, Jackowiak B (2014) Trends in atmospheric concentrations of weed pollen in the context of recent climate warming in Poznań (Western Poland). Int J Biometeorol 58:1759–1768

Bortenschlager S (1970) Neue Pollenanalytische Untersuchungen von Gletschereis und Gletschernahen Mooren in den Ostalpen. Z Gletsch kd Glazialgeol 6:107–118

Bourgeois JC (2000) Seasonal and interannual pollen variability in snow layers of arctic ice caps. Rev Palaeobot Palynol 108(1–2):17–36

Callegari E, Brack P (2002) Geological map of the Tertiary Adamello batholith (Northern Italy). Explanatory notes and legend. Mem Sci Geol 54(2002):19–49

Celesti-Grapow L, Pretto F, Brundu G, Carli E, Blasi C (eds) (2009) Plant invasion in Italy, an overview. A thematic contribution to the national biodiversity strategy. Ministry for the Environment, Land and Sea Protection, Nature Protection Directorate, Palombi & Partner. Roma

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. J Veg Sci 13(1):79–90

Comer PJ, Valdez J, Pereira HM et al (2022) Conserving ecosystem diversity in the Tropical Andes. Remote Sens 14:2847

Comiti F (2012) How natural are Alpine mountain rivers? Evidence from the italian Alps. Earth Surf Process Landf 37(7):693–707

CIPRA Internationale Alpenschutzkommission Internet (1992) Gli ultimi fiumi naturali delle Alpi. CIPRA piccola serie di documentazioni 11/92:72

Conti F, Bonacquisti S, Scassellati E (2005) An annotated checklist of the Italian vascular flora. Palombi

Cunze S, Leiblein MC, Tackenberg O (2013) Range expansion of *Ambrosia artemisiifolia* in Europe is promoted by climate change. ISRN Ecol. https://doi.org/10.1155/2013/610126

D'Amato G, Cecchi L, Bonini S, Nunes C, Annesi-Maesano I, Behrendt H, Liccardi G, Popov T, van Cauwenberge P (2007) Allergenic pollen and pollen allergy in Europe. Allergy 62(9):976–990

Eichler A, Tinner W, Brütsch S, Olivier S, Papina T, Schwikowski M (2011) An ice-core based history of siberian forest fires since AD 1250. Quat Sci Rev 30(9–10):1027–1034

Ellenberg H (1988) Vegetation ecology of Central Europe, 4th edn. Cambridge University Press, Cambridge

Erschbamer B, Caccianiga MS (2016) Glacier Forelands: lessons of plant population and community development. Prog Bot 78:259–284

Erschbamer B, Niederfriniger Schlag R, Winkler E (2008) Colonization processes on a central alpine glacier foreland. J Veg Sci 19:855–862

Faegri, Iversen (1989) Textbook of pollen analysis. John Wiley, Chichester

Falcucci A, Maiorano L, Boitani L (2007) Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. Lands Ecol 22(4):617–631

Festi D, Kofler W, Bucher E, Carturan L, Mair V, Gabrielli P, Oeggl K (2015) A novel pollen-based method to detect seasonality in ice cores: a case study from the Ortles glacier, South Tyrol, Italy. J Glaciol 61(229):815–824

Festi D, Carturan L, Kofler W, Fontana GD, De Blasi F, Cazorzi F, Bucher E, Mair V, Gabrielli P, Oeggl K (2017) Linking pollen deposition and snow accumulation on the Alto dell'Ortles glacier (South Tyrol, Italy) for subseasonal dating of a firn temperate core. The Cryosphere 11(2):937–948

Festi D, Kofler W, Oeggl K (2019) Comments on Brugger and others (2019) "A quantitative comparison of microfossil extraction methods from ice cores. J Glaciol 65(250):344–346

Festi D, Schwikowski M, Maggi V, Oeggl K, Jenk TM (2021) Significant mass loss in the accumulation area of the Adamello glacier indicated by the chronology of a 46 m ice core. Cryosphere 15:4135–4143

Fordham DA, Jackson ST, Brown SC, Huntley B, Brook BW, Dahl-Jensen D et al (2020) Using paleo-archives to safeguard biodiversity under climate change. Science 369(6507):eabc5654

Fyfe R, Roberts N, Woodbridge J (2010) A pollen-based pseudobiomisation approach to anthropogenic land-cover change. The Holocene 20(7):1165–1171

Fyfe RM, Woodbridge J, Roberts N (2015) From forest to farmland: pollen-inferred land cover change across Europe using the pseudobiomization approach. Glob Chang Biol 21(3):1197–1212

Gabrielli P, Barbante C, Bertagna G, Bertó M, Binder D, Carton A, Carturan L et al (2016) Age of the Mt. Ortles ice cores, the Tyrolean Iceman and glaciation of the highest summit of South Tyrol since the Northern hemisphere climatic optimum. Cryosphere 10:2779–2797

Garbarino M, Morresi D, Urbinati C, Malandra F, Motta R, Sibona EM, Vitali A, Weisberg PJ (2020) Contrasting land use legacy effects on forest landscape dynamics in the italian Alps and the Apennines. Lands Ecol 35(12):2679–2694

Geburek T, Hiess K, Litschauer R, Milasowszky N (2012) Temporal pollen pattern in temperate trees: expedience or fate? Oikos 121(10):1603–1612

Gentili R, Gilardelli F, Bona E, Prosser F, Selvaggi A, Alessandrini A, Martini F, Nimis PL, Wilhalm T, Adorni M, Ardenghi NMG, Barni E, Bonafede F, Bonini M, Bouvet D, Buffa G, Ciappetta S, Giordana F, Faggi G et al (2017) Distribution map of *Ambrosia artemisiifolia* L. (Asteraceae) in Italy. Plant Biosyst 151(3):381–386

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

Grabherr G (2000) Rapid Biodiversity Assessment for the Alps Ecoregion. WWF Alpine programme. 77 pp

Helbing D (2013) Globally networked risks and how to respond. Nature 497(7447):51–59

IPCC (2014) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Barros VR et al (eds) (2014). Cambridge University Press, Cambridge, p 688

IPCC (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte VP, Zhai A, Pirani SL, Connors C, Péan S, Berger N, Caud Y, Chen L, Goldfarb MI, Gomis M, Huang K, Leitzell E, Lonnoy JBR, Matthews TK, Maycock T, Waterfield O, Yelekçi R, Yu and B Zhou (eds.)]. Cambridge University Press. In Press

ISTAT (2016) ; http://seriestoriche.istat.it/. Accessed 04 March 2022

ISTAT (2019) http://dati.istat.it/Index.aspx?QueryId=18462. Accessed 04 March 2022

Kandel P, Gurung J, Chettri N et al (2016) Biodiversity research trends and gap analysis from a transboundary landscape, Eastern Himalayas. J Asia-Pacific Biodivers 9:1–10

Kapfer J, Hédl R, Jurasinski G, Kopecký M, Schei FH, Grytnes JA (2017) Resurveying historical vegetation data–opportunities and challenges. Appl Veg Sci 20(2):164–171

Kelly D (1994) The evolutionary ecology of mast seeding. Trends in Ecol Evol 9(12):465–470

Lamontagne JM, Boutin S (2007) Local-scale synchrony and variability in mast seed production patterns of Picea glauca. J Ecol 95:991–1000

Lamprecht A, Semenchuk PR, Steinbauer K, Winkler M, Pauli H (2018) Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps. New Phytol 220(2):447–459

Lang, (1994) Quartäre Vegetationsgeschichte Europas Methoden und Ergebnisse. Gustav-Fischer- Verlag Jena, New York, p 462

Leuschner C, Ellenberg H (2017) Ecology f Central European Forests. Vegetation Ecology of Central Europe. Springer, Berlin. https://doi.org/10.1007/978-3-319-43042-3

Li K, Liao M, Ni J, Liu X, Wang Y (2019) Treeline composition and biodiversity change on the southeastern Tibetan Plateau during the past millennium, inferred from a high-resolution alpine pollen record. Quat Sci Rev 206:44–55

Liu KB, Reese CA, Thompson LG (2007) A potential pollen proxy for ENSO derived from the Sajama ice core. Geophys Res Lett 34(9):1–5

Lona F, Bertoldi R, Bonatti E (1965) Osservazioni preliminari sull'immigrazione del Quercus ilex nella zona del lago di Garda. Natura Alpina 16(3):39–45

Makra L, Matyasovszky I, Thibaudon M, Bonini M (2011) Forecasting ragweed pollen characteristics with

nonparametric regression methods over the most polluted areas in Europe. Int J Biometeorology 55:361–371
Marchesoni V (1958) Aspetti mediterrranei lungo il margine meridionale delle alpi con particolare riguardo al settore prealpino antistante al bacino atesino. Studi Trentini Scienze Naturali 35:47–49
Matteodo M, Wipf S, Stöckli V, Rixen C, Vittoz P (2013) Elevation gradient of successful plant traits for colonizing alpine summits under climate change. Environ Res Lett. https://doi.org/10.1088/1748-9326/8/2/024043
Mauri A, Caudullo G (2016) Alnus viridis in Europe: distribution, habitat, usage and threats. In: San Miguel-Ayanz J, De Rigo D, Caudullo G, Houston Durrant T, Mauri A (eds) European Atlas of Forest Tree Species. Publication Office of the European Union, Luxembourg, p 68
Moore PD, Webb JA, Collinson ME (1991) Pollen analysis. Blackwell, Oxford
Nowak A, Świerszcz S, Nowak S, Hisorev H, Klichowska E, Wróbel A, Nobis A, Nobis M (2020) Red list of vascular plants of Tajikistan – the core area of the mountains of Central Asia global biodiversity hotspot. Sci Rep 10:6235. https://doi.org/10.1038/s41598-020-63333-9
Papina T, Blyakharchuk T, Eichler A, Malygina N, Mitrofanova E, Schwikowski M (2013) Biological proxies recorded in a Belukha ice core, russian Altai. Clim Past 9(5):2399–2411
Paul F, Rastner P, Azzoni RS, Diolaiuti G, Fugazza D, Le Bris R et al (2020) Glacier shrinkage in the Alps continues unabated as revealed by a new glacier inventory from Sentinel-2. Earth Syst Sci Data 12(3):1805–1821
Pauli H, Gottfried M, Grabherr G (2003) Effects of climate change on the alpine and nival vegetation of the Alps. J Mountain Ecol 7(Suppl):9–12
Pavlova A, Jenk TM, Schmid P, Bogdal C, Steinlin C, Schwikowski M (2015) Polychlorinated Biphenyls in a temperate Alpine Glacier: 1. Effect of percolating meltwater on their distribution in Glacier Ice. Environ Sci Technol 49(24):14085–14091
Payne D, Spehn EM, Snethlage M, Fischer M (2017) Opportunities for research on mountain biodiversity under global change. Curr Opin Environ Sustain 29:40–47
Picotti S, Francese R, Giorgi M, Pettenati F, Carcione JM (2017) Estimation of glacier thicknesses and basal properties using the horizontal-to-vertical component spectral ratio (HVSR) technique from passive seismic data. J Glaciol 63(238):229–248
Pisetta M, Montecchio L, Longa CMO, Salvadori C, Zottele F, Maresi G (2012) Green alder decline in the italian Alps. For Ecol Manage 281:75–83
Raffl C, Mallaun M, Mayer R, Erschbamer B (2006) Vegetation succession pattern and diversity changes in a Glacier Valley, Central Alps, Austria. Arct Antarc Alp Res 38(3):421–428
Reese CA, Liu KB, Thompson LG (2013) An ice-core pollen record showing vegetation response to late-glacial and holocene climate changes at Nevado Sajama, Bolivia. Ann Glaciol 54(63):183–190
Reille M (1992) Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de botanique historique et palynologie
Robbins P (2007) “Hydropower”. Encyclopedia of Environment and Society. https://doi.org/10.4135/9781412953924
Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. J veg sci 20(4):596–602
Romano B, Zullo F, Fiorini L, Marucci A, Ciabò S (2017) Land transformation of Italy due to half a century of urbanization. Land Use Policy 67:387–400
Scherrer D, Schmid S, Körner C (2011) Elevational species shifts in a warmer climate are overestimated when based on weather station data. Int J Biometeorol 55(4):645–654
Schneeberger N, Bürgi M, Kienast PDF (2007) Rates of landscape change at the northern fringe of the Swiss Alps: historical and recent tendencies. Landsc Urban Plan 80(1–2):127–136
Smiraglia C, Diolaiuti G (2015) Il nuovo Catasto dei Ghiacciai Italiani. Ev-K2-CNR. ed., Bergamo (Italy)
Smith M, Cecchi L, Skjøth CA, Karrer G, Šikoparija B (2013) Common ragweed: a threat to environmental health in Europe. Environ Int 61:115–126
Steinbauer MJ, Grytnes JA, Jurasinski G, Kulonen A, Lenoir J, Pauli H, Rixen C, Winkler M, Bardy-durchhalter M, Barni E et al (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. Nature 556:231–234
Steinbauer K, Lamprecht A, Semenchuk P, Winkler M, Pauli H (2020) Dieback and expansions: species-specific responses during 20 years of amplified warming in the high Alps. Alp Bot 130:1–11
Tasser E, Walde J, Tappeiner U, Teutsch A, Noggler W (2007) Land use changes and natural reforestation in the Eastern Central Alps. Agric Ecosyst Environ 118:115–129
Tichý L (2002) JUICE, software for vegetation classification. J Veg Sci 13(3):451–453
Vareschi V (1934) Pollenanalysen aus Gletschereis. Ber Geobot Inst Rübel 1934:81–99
Verde S, Assini S, Andreis C (2010) Le serie di vegetazione della Regione Lombardia. In: La vegetazione d'Italia. Ed. Blasi C. - Roma: Palombi, 2010. - ISBN 9788860602909. pp. 52–81
Vignolo-Lutati F (1934) L'Ambrosia artemisiifolia L. in Italia. N Giorn Bot Ital 41:172–173
Woodbridge J, Fyfe RM, Roberts N (2014) A comparison of remotely sensed and pollen-based approaches to mapping Europe's land cover. J Biogeogr 41(11):2080–2092