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Climate change triggered synchronous woody plants recruitment in the last two centuries in the treeline ecotone of the Northern Hemisphere

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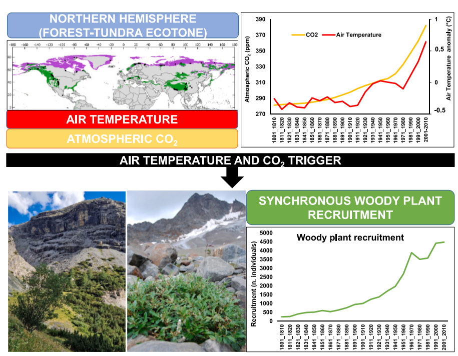
HIGHLIGHTS

- Woody plant recruitment shows a major change in the Earth's biophysical systems.
- We detected a synchronous recruitment trend since 1801 in the Northern Hemisphere.
- Atmospheric CO_2 and air temperature are the main drivers of woody plant recruitment.
- After 1950 air temperature became the main driver overcoming CO_2 fertilization.
- Evergreen and Pinaceae are the woody plants most sensitive to climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change triggers several ecosystem responses, including woody plant encroachment.

We analyse woody plant recruitment across the treeline ecotone (the forest-tundra ecotone) of the Northern Hemisphere (NH) over an extended period (1801–2010) and its relation with atmospheric CO_2 and air temperature.

We detected a synchronous trend of woody plant recruitment across the NH, indicating a major climatic and environmental change, triggered by a combination of CO_2 fertilization and air temperature changes.

The drivers of woody plant recruitment changed with time: CO_2 fertilization was the main driver in the period 1801–1950, while air temperature was the main driver after 1950, despite the drastic acceleration of CO_2 increase in the last decades. These data support the hypothesis that we are shifting from a fertilization-dominated to a warming-dominated period.

The temporal patterns of woody plant recruitment are consistent with the occurrence of the 1980 regime shift, a major change occurred in the Earth's biophysical systems. Indeed, the recruitment drop promoted by the 1960s–1980s air cooling, was followed by an intensive recruitment increase triggered by the restart of air warming in the last decades.

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The largest sensitivity and fastest resilience of evergreen and *Pinaceae* to the restart of air warming allows to hypothesize that, among the woody plant functional and taxonomic groups, they could perform the largest expansion also in future decades.

1. Introduction

Climate change has resulted in the global woody plant (trees and shrubs) encroachment (Harsch et al., 2009; Elmendorf et al., 2012a, 2012b; Myers-Smith and Hik, 2018; Rees et al., 2020; Lu et al., 2021, 2022). The most remarkable changes occurred at the treeline ecotone (or forest-tundra ecotone, here defined as the transition zone between the boreal or subalpine forests and the Arctic or alpine tundra) (Körner, 2012; Rees et al., 2020), located at high latitude (irrespective of elevation) and/or at high elevation in middle and low latitude, as these ecotones are particularly sensitive and vulnerable to climate change. In this context woody plant encroachment triggers ecosystem changes detectable from the species to the landscape level (Harsch et al., 2009; Myers-Smith et al., 2011; Elmendorf et al., 2012a, 2012b; Myers-Smith and Hik, 2018), with environmental feedbacks involving both the abiotic (e.g. changes in snow cover, albedo, soil moisture and temperature, surface energy balance) as well as the biotic components of ecosystems and their processes (e.g., ecosystem composition, structure, dynamics, biogeochemical cycles, C fluxes, C storage, etc.) (Chapin et al., 2005; Sturm et al., 2005; Loranty et al., 2011; Natali et al., 2011; Demarco et al., 2014). The assessment of woody plant encroachment has been performed by analysing the changes of treeline and shrubline, their spatial distribution as well as their temporal dynamics (i.e., tree and shrub recruitment) (e.g., Sturm et al., 2001; Harsch et al., 2009; Lu et al., 2021). The recruitment patterns of woody plants are considered one of the most sensitive indicators of climatic change (Myers-Smith et al., 2011; Lu et al., 2022), and the occurrence of synchronous and convergent trends of woody plant recruitment across geographically remote locations could be considered the result of climatic factors occurring at large scale (e.g. regional, continental, hemispheric) (Lu et al., 2022). However, few studies investigated at wide spatial scale and across an extended period of time (prior 1870) the recruitment of woody plants in the treeline ecotone at hemispheric scale (Harsch et al., 2009; Rees et al., 2020; Lu et al., 2022).

Woody plant encroachment could be triggered by the increase of atmospheric CO_2 through a process known as CO_2 fertilization (Wang et al., 2020). CO_2 fertilization enhances the physiological process of CO_2 uptake through the increase of the assimilation rates of CO_2 (through stomata) and of the intrinsic water use efficiency (iWUE, i.e. the rate of Carbon uptake for unit of water loss) (Soh et al., 2019; Wang et al., 2020, 2021). Physiological studies documented an increase of iWUE of woody plants in response to the increase of atmospheric CO_2 in the last decades (Soh et al., 2019), showing different sensitivity among plant functional (e.g. deciduous versus evergreen) and taxonomic groups (Soh et al., 2019). The combination of CO_2 fertilization and climate change may promote plant photosynthesis and enhance plant growth, thus increasing plant biomass stocks and land C storage (Peñuelas et al., 2020). However, CO_2 fertilization could be affected by nutrient limitations, which may induce a decline of the CO_2 enhancement of woody plants productivity (Norby et al., 2010; Wieder et al., 2015). To our knowledge, the impact of CO_2 fertilization on woody plant recruitment has not yet been addressed, and its assessment would allow to discriminate between the effect of climate change and CO_2 fertilization on the observed woody plant recruitment patterns, and improve our understanding.

Here we analyse the recruitment of woody plants of the treeline ecotone across the Northern Hemisphere (NH) over more than two centuries (1801–2010). We hypothesize that increased atmospheric CO_2 and air temperature changes triggered a synchronous woody plant recruitment trend across the NH representing a major change at hemispheric scale. Considering the recent hypothesis that the effect of CO_2 fertilization on plant growth would slow down due to nutrient constraints “shifting from a fertilization-dominated to a warming-dominated period” (Peñuelas et al., 2020), we tested whether during the selected study period, and especially in the last decades, CO_2 fertilization could be less effective than air temperature in promoting woody plant recruitment. We also tested whether the recruitment of woody plants follows different patterns among key functional (evergreen vs deciduous) and taxonomic (*Pinaceae*, *Betulaceae*, *Salicaceae*) groups coherently with their physiological sensitivity and responsiveness to climate change drivers.

2. Materials and methods

2.1. Data collection

We collected the available recruitment data of woody plants of the treeline ecotone based on temporal and spatial high-resolution, quantitative data. To identify the most appropriate studies, the assembled data were searched in ISI Web of Science using several keywords including, among all, “shrub”, “tree”, “recruitment”, “dynamic”, “expansion”, “encroachment”, “establishment”, “tundra” as well as 46 different combinations of keywords.

The selected recruitment studies were based on samples of woody plants of different size classes (see the original references for detailed information on the threshold between classes, for references see Tables 1SM, 2SM), with reported ages, heights, stem basal diameters and/or diameters at breast height of single individuals with the following ranges: age between 1 and 423 yrs, height between 0.015 and 18 m, stem basal diameter from 0.5 to −460 mm and stem diameter at breast height >4 cm, respectively.

Totally 289 studies referred to the treeline ecotone were analysed.

We selected 46 of the 289 studies for further analyses (Fig. 1, Tables 1SM, 2SM, 5SM) as they fulfilled the following criteria:

(a) quantitative information and recruitment curves were clearly stated and available and were obtained using dendrochronology;
(b) recruitment curves were expressed in absolute values (number of individuals);
(c) observation period exceeded 50 years and with age-clusters of 1-yr, or 5-yr or 10-yrs.

As the recruitment data provided different age-clusters (1-, or 5-, or 10- years), to use the whole dataset we computed all recruitment data as decadal means. For studies involving more than one species per site, we included one site per each species when data were given separately (Rees et al., 2020). The recruitments were species-specific for 137 curves and multispecies for 24 curves, for a total of 161 recruitment curves referred to 49 species (28 deciduous, 21 evergreen) of four main families (*Pinaceae*, *Betulaceae*, *Salicaceae* and *Ericaceae*), from 46 studies performed in Europe, Asia and North America (Fig. 1, Tables 1SM, 2SM, 3SM). All the 6 species of *Betulaceae* (from 8 studies, Table 1SM) and the 14 species of *Salicaceae* (from 5 studies, Table 1SM) were deciduous. Among *Pinaceae*, 20 species were evergreen (belonging to *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, from 27 studies, Table 1SM) and 8 species were deciduous (all belonging to the genus *Larix*, from 11 studies, Table 1SM), while the only species of *Ericaceae* (1 study) was evergreen (Table 1SM).

As different functional and taxonomic groups of woody plants may show different sensitivity to elevated atmospheric CO_2 (Soh et al., 2019) and climate change, we analysed the relation between woody plant recruitment and the climatic and environmental variables as follows: a) whole dataset; b) functional groups (deciduous versus evergreen); c) taxonomic groups (*Betulaceae*, *Pinaceae*, *Salicaceae*). We did not perform specific analyses on *Ericaceae* due to the low number of individuals.

Concerning the study period, we included recruitment data between 1801 and 2010, excluding he decade 2011–2020 to avoid potential artefacts, as the recruitment after 2011 could be underestimated due to the small size of the young individuals (Büntgen et al., 2015; Myers-Smith and Hik, 2018; Cannone et al., 2022a).

For each site, the following general information were recorded from the original study (Table 3SM): coordinate; elevation; species; number of sampled individuals; investigated period (assumed as the duration between the first and the last year of data); age-class clusters of the recruitment curves (i.e. 1, 5, 10 yrs); recruitment rates for each age-class (number of individuals established for each age-class cluster, as reported by the original studies). When the recruitment rates were not provided in digital form (i.e. dataset, tables), a plot digitizer program (http://plotdigitizer.sourceforge.net) was used to extract the data from the figures published in the studies (Lu et al., 2021).

To analyse the relation between woody plant recruitment and the climatic and environmental drivers, we collected from the available long-term monitoring and reconstruction studies the data referred to the Northern Hemisphere (NH) of the following parameters in the period 1801–2010:

- NH mean annual atmospheric CO_2 concentration (www.co2.earth/historical-co2-datasets; period 1801–2010, compiled by the Institute for Atmospheric and Climate Science (IAC) at Eidgenossische Technische Hochschule in Zurich, Switzerland);
- NH mean annual air temperature anomaly (MAAT, °C) (period 1801–2010);
- seasonal air temperature anomaly (°C) (DJF = winter; MAM = spring; JJA = summer; SON = autumn; period 1851–2010) (relative to the 1961–1990 mean).

2.2. Data analysis

Concerning the climatic data, the CDIAC dataset (www.cdiac.ess-dive.lbl.gov/) (Jones et al., 2016) provided the mean annual air temperature anomaly (relative to the 1961–1990 mean) for the period 1851–2010. To extend our study period back to 1801, we integrated the CDIAC MAAT anomaly with the MAAT anomaly provided by the reconstruction of PAGES 2 k (relative to the 1961–1990 mean) (PAGES 2K, 2019). For this aim, we computed the regression equation between the MAAT anomaly of PAGES and CDIAC for the period 1851–2000 (common to both datasets). As the relation between the two datasets was statistically significant ($r = 0.9443$; $p < 0.01$), we could recalculate the MAAT anomaly for the period 1801–1850 applying to the PAGES dataset the following regression equation:

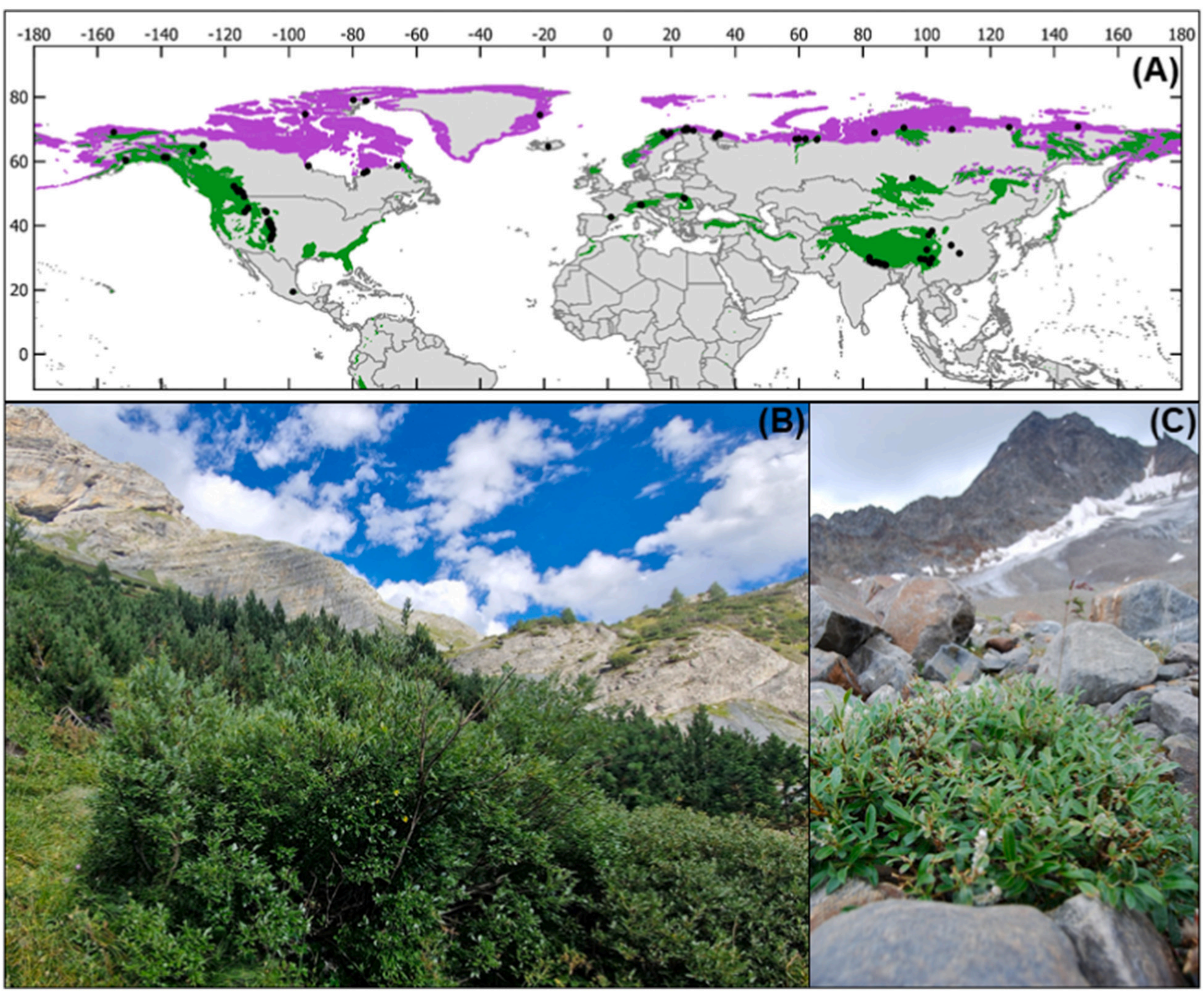

Fig. 1. (A) Location of the study sites (black dots) providing the recruitment curves of woody plants at the treeline ecotone in the period 1801–2010 across the northern Hemisphere; and some examples of (B) woody plant functional groups (deciduous and evergreen) and (C) taxonomic groups (*Salicaceae*). Legend: purple areas = high latitude irrespective of elevation; green areas = high elevation at middle and low latitudes.

$MAAT_{PAGES} = 0.907*MAAT_{CDIAC} - 0.1643$

The selected environmental and climatic parameters were averaged on a 10-yrs basis.

Concerning the recruitment data, to compare the recruitment rates with different time-resolutions, the recruitment data with age-clusters of 1-yr (n = 30) and 5-yrs (n = 62) were computed on a 10-yrs basis and treated with the 69 curves with age cluster of 10-yrs, for a total of 161 recruitment curves (all on a 10-yrs basis).

As seed germination may require long time periods (Bernareggi et al., 2015) and does not ensure individual survival and persistence (Holtmeier and Broll, 2005), we analysed the relationship between climate and the ten (t-10) years before the recruitment (MAAT-10).

As recruitment is sustained by seed production, we analysed also the relationship between recruitment and the climatic conditions ten years after recruitment (MAAT+10), allowing to reach the age of reproductive maturity, which is ≤5 years (modal class 1–5 y) for woody Angiosperms, and ≥5 years for Gymnosperms (modal class 6–20 y) (Verdù, 2002).

The trends with time of the recruitment of woody plants as well as of the main climatic (mean annual and seasonal air temperature) and environmental variables (atmospheric CO_2) were tested by linear and exponential regression using the software StatSoft©.

Multivariate analysis (redundancy analysis, RDA) was performed to analyse the relationships between the recruitment of woody plants (referring to the whole dataset, named "all", as well as to each selected functional type category) and the main climatic (decadal means of the anomalies of annual air temperatures), MAAT (same decade), MAAT-10 (previous decade), MAAT+10 (following decade) (period 1801–2010); decadal means of seasonal air temperatures, DJF, MAM, JJA, SON (period 1851–2010) and environmental (decadal means of atmospheric CO_2) parameters.

As the trends with time of atmospheric CO_2 exhibited a drastic acceleration after 1950s'compared to the previous period, we performed three separate multivariate analyses (RDAs) to assess whether the climatic and environmental drivers of woody plant recruitment changed during time, referring to the following time periods: 1801–2010 (whole study period); 1801–1950 (period before CO_2 acceleration); 1951–2010 (period of CO_2 acceleration).

The variables showing collinearity, identified by the inflation factor >20, were deleted from the analysis to avoid redundancy. In particular, we deleted the following variables to avoid collinearity: a) from the RDA 1801–1950 we excluded DJF, MAM, SON; b) from the RDA 1801–1950 we excluded DJF, MAM, SON; c) from the RDA 1951–2010 we excluded MAAT, DJF, MAM, JJA, SON.

Each RDA was performed with the square-root transformation of species data, scaling through inter-species correlation, species scores divided by standard deviation, centered and standardized by samples,

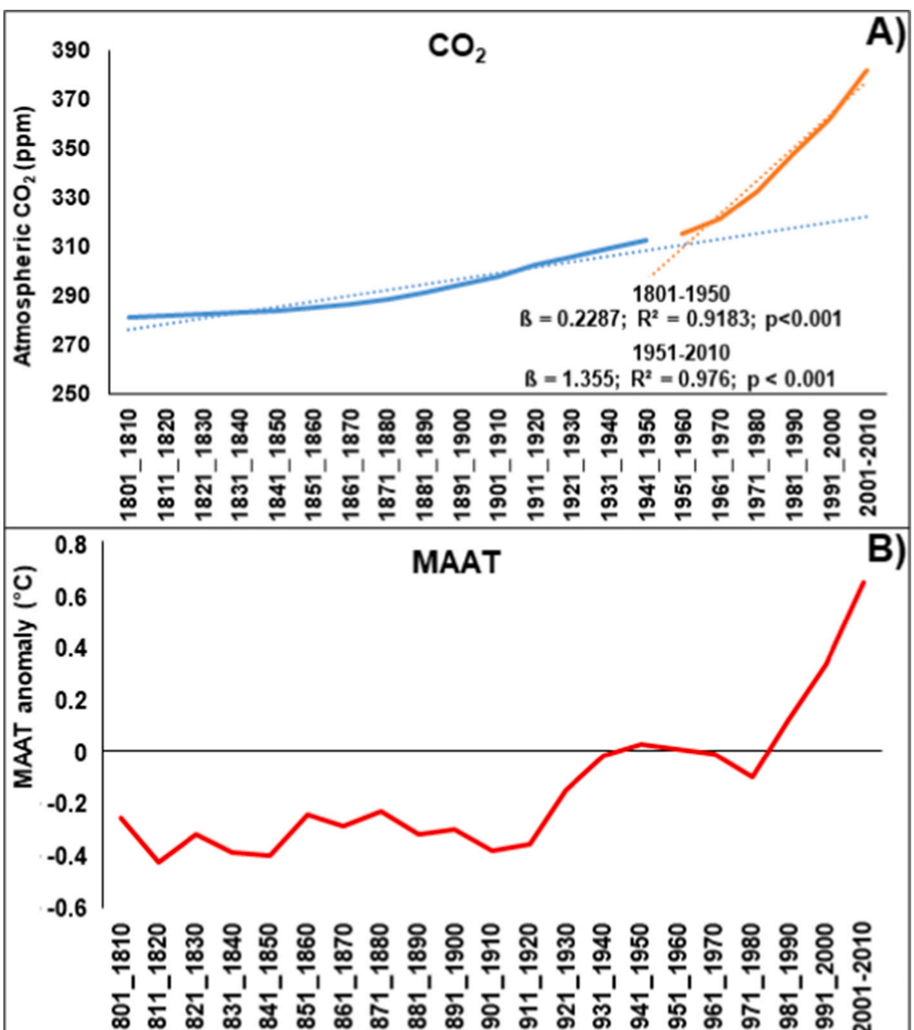

Fig. 2. Trends with time in the Northern Hemisphere in the period 1801–2010 of the decadal means of: A) atmospheric concentration of CO_2 (ppm) showing a statistically significant acceleration since 1950s' (blue line: period 1801–1950; orange line: period 1951–2010); B) mean annual air temperature anomaly (MAAT) (°C).

centered by species, and performing the Monte Carlo permutation test on all ordination axes.

3. Results

3.1. Climatic and environmental trends across the study period

During the study period in the Northern Hemisphere the concentration of atmospheric CO_2 exhibited a striking and statistically significant exponential trend ($p < 0.001$; $R = 0.92$; $CO_2 = 83.1264*\exp(0.0116*x)$) (Fig. 2A), characterized by a drastic acceleration since 1950's from +0.2 per decade in the period 1801–1950, to +1.3 ppm per decade in the period 1951–2010, as tested by linear regression (Fig. 2A).

Mean annual air temperature (Fig. 2B, Table 4SM) as well as seasonal air temperatures (Table 4SM, Fig. 1A Supplementary material) exhibited a significant increase, especially since the second part of the XIX century (i.e., the period 1801–1900), although there was a short period of cooling between 1961 and 1980 (culminating in 1971–1980), followed by the restart of a very intensive warming (Fig. 2B, Fig. 1SM), with a time lag between the exponential increase of atmospheric CO_2 and the major increase of air temperature.

3.2. Recruitment trends of woody plants

We detected a synchronous trend of woody plant recruitment (whole dataset): between 1801 and 1961 the recruitment had a statistically significant exponential trend ($r = 0.87$; $p < 0.001$), then it suffered a striking decrease between 1961 and 1990 following the observed air temperature cooling, and started again to increase after 1991 (Fig. 3A). Analysing the single functional and taxonomic woody plant groups, a statistically significant exponential increase between 1801 and 1970 was evident for evergreen ($r = 0.83$; $p < 0.001$; Fig. 3B) and *Pinaceae* ($r = 0.99$; $p < 0.001$; Fig. 3C), followed by a strong decrease and a recent restart. The exponential pattern was evident also for deciduous ($r = 0.86$; $p < 0.001$; Fig. 3B) and *Betulaceae* ($r = 0.88$; $p < 0.001$; Fig. 3C) but with a different timing, reaching its maximum in the decade 1991–2000, and then followed by a drastic decrease in the last decade (2001–2010). An exponential increase characterized also *Salicaceae* ($r = 0.614$; $p = 0.005$; Fig. 3C) reaching their maximum earlier (1981–1990) and then followed by a decrease. According to the observed trends, evergreen and *Pinaceae* are the functional and taxonomic groups characterized by the largest sensitivity and fastest resilience to the restart of warming (Fig. 3C). Within the *Pinaceae* the evergreen species (*Abies*, *Picea*, *Pinus*, *Pseudotsuga*) exhibited a slightly different recruitment trend and abundance compared to deciduous *Pinaceae* (*Larix*) (Fig. 3D). Evergreen *Pinaceae* were generally much more abundant and their recruitment trends followed strictly the air temperature trends, with a statistically significant exponential increase over the whole period ($r = 0.90$; $p < 0.001$; Fig. 3D). this trend was continuous until 1961–70, followed by a sharp decrease reaching the minimum recruitment in 1981–1990, and then restarting the increase in the last decades. Deciduous *Pinaceae* were less abundant (also because this category was represented only by one genus, *Larix*), and exhibited a statistically significant exponential trend over the whole study period ($r = 0.88$; $p < 0.001$; Fig. 3D), characterized by an alternance of large increases and small decreases since 1950s (Fig. 3D).

3.3. Environmental and climatic drivers of woody plant recruitment: period 1801–2010

The multivariate analysis (redundancy analysis, RDA) performed on the whole study period (1801–2010) was statistically significant and

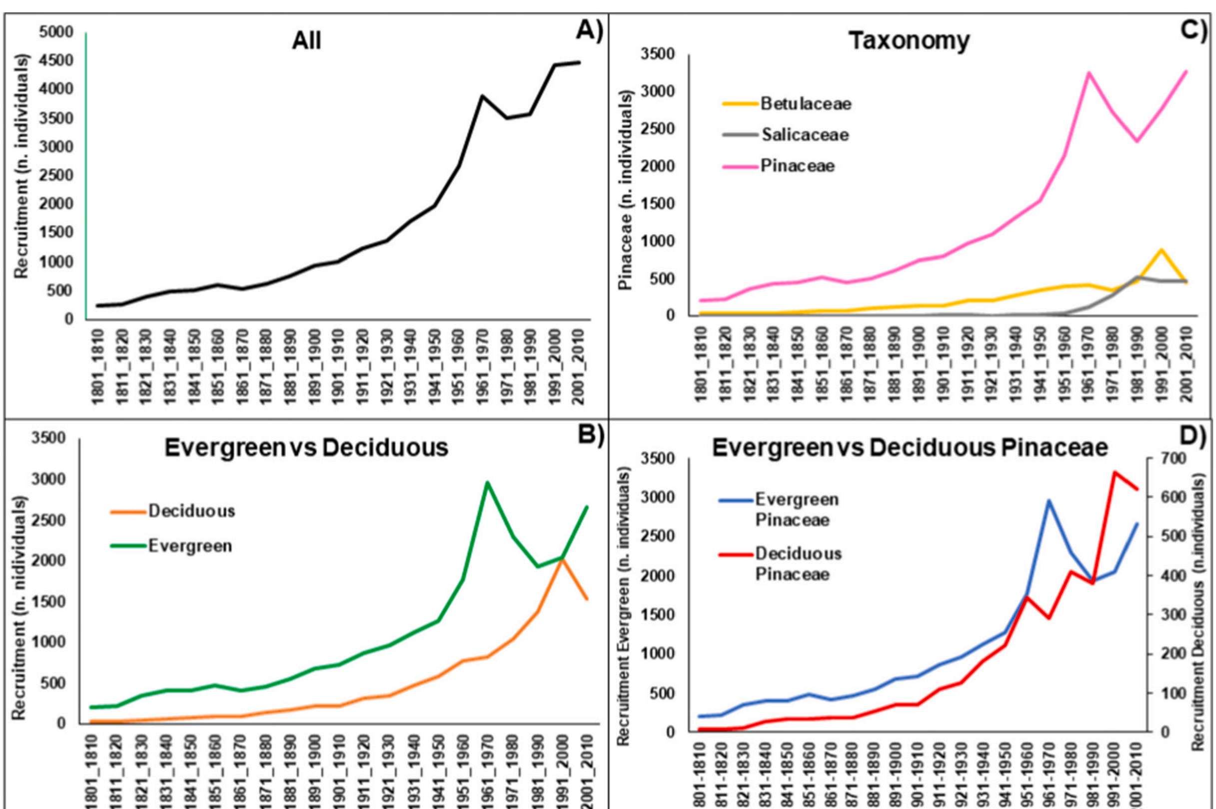

Fig. 3. Decadal means of the recruitment of woody plants referring to (A) the whole dataset, and to key functional and taxonomic groups: B) deciduous (orange line) and evergreen (green line); C) *Betulaceae* (yellow line), *Pinaceae* (pink line) and *Salicaceae* (grey line); D) evergreen *Pinaceae* (blue line) versus deciduous *Pinaceae* (red line).

explained 99.6 % of the total variance (Fig. 4A, Table 1). The RDA indicated that the most important driver of woody plant recruitment was atmospheric CO_2, followed by air temperature in the following decade (MAAT+10) and summer temperature (JJA) (Fig. 4A, Table 1). The RDA emphasized that before 1900 woody plant recruitment was mainly associated to evergreen and *Pinaceae* (with 20 of the 28 species selected of this family being evergreen), whose recruitment started since the beginning of the study period when the warming trend and the increase of atmospheric CO_2 was still limited (Figs. 2, 3), while deciduous, *Salicaceae* and *Betulaceae* were mainly recruited after 1900.

3.4. Change of woody plant recruitment drivers: 1801–1950 vs 1951–2010

According to the observed drastic acceleration of atmospheric CO_2 after 1950s' (Fig. 2A), we performed two separate RDAs to assess whether the climatic and environmental drivers of woody plant recruitment changed comparing the period 1801–1950 with the period 1951–2010.

The RDA referred to the period 1801–1950 (Fig. 4B, Table 1) was statistically significant and explained 99.5 % of the total variance. As for the whole study period (Fig. 4A), also the RDA 1801–1950 confirmed that the most important and the only statistically significant driver of woody plant recruitment was atmospheric CO_2 (Table 1). This RDA further emphasized the differences of evergreen and *Pinaceae* (whose recruitment occurred since the beginning of the study period between 1801 and 1880), while the other woody plant groups started to exhibit a larger recruitment mainly after 1881 (Fig. 4B).

The RDA referred to the period 1951–2010 was statistically significant and explained 99.8 % of the total variance, highlighting an interesting change, with air temperature of the following decade (MAAT+10) becoming the most important and the only statistically significant factor as driver of woody plant recruitment (Fig. 4D, Table 1).

4. Discussion

4.1. Drivers of woody plant recruitment

Here we show the occurrence of a synchronous trend of woody plant recruitment at the treeline ecotone across the NH driven by a combination of CO_2 fertilization and air temperature changes, indicating a major climatic and environmental change at hemispheric scale (Myers-Smith et al., 2011; Lu et al., 2022).

In the last two centuries our planet experienced a strong air warming and the exponential increase of atmospheric CO_2 (Fig. 2A), reaching in <150 years the highest concentrations observed in the last 650,000 years (Petit et al., 1999; Lüthi et al., 2008) (382 ppm as mean concentration in 2001–2010). We demonstrated that CO_2 fertilization combined with air temperature changes (warming and cooling) influences also woody plant recruitment (Fig. 3), integrating the existing knowledge of CO_2 fertilization effects on plant photosynthesis, growth, biomass stocks and land C storage (Soh et al., 2019; Wang et al., 2020, 2021). Moreover, our data show that the drivers of woody plant recruitment changed with time, with CO_2 fertilization being the main driver in the period 1801–1950, while after 1951 the main driver was air temperature (Table 1), despite the further acceleration of atmospheric CO_2 increase (>360 ppm) (Fig. 2A). These data are compatible with the observation of a recent global decline of CO_2 fertilization on vegetation photosynthesis since 1982 (Wang et al., 2020), and also with the results of manipulative experiments indicating that soil warming was more effective than CO_2 enrichment in enhancing plant growth, and emphasizing the occurrence of species-specific responses (Dawes et al., 2013, 2015). These results are coherent with the hypothesis that we are shifting from a fertilization-dominated to a warming-dominated period likely due to the potential saturation of the fertilization effect on tree growth and/or to emerging nutrient constraints (Peñuelas et al., 2020).

Across the whole study period, warming persistence (referring to air temperature of the following and/or previous decade) may be a factor contributing to achieve and sustain woody plant recruitment (Table 1), confirming at hemispheric scale the patterns observed at local scale for the recruitment of alpine trees and shrubs (Malfasi and Cannone, 2020; Cannone et al., 2022a). Warming persistence in the years before recruitment provides suitable conditions for seed production and germination, which may require several years (Bernareggi et al., 2015). Warming persistence in the years following the recruitment is crucial to achieve the age of reproductive maturity, both for Gymnosperms (6–20 y) and Angiosperms (1–5 y) (Verdù, 2002), sustaining plant recruitment through sexual reproduction and seed production.

4.2. Recruitment trends with time

According to our data the recruitment of woody plants appeared to be not constant with time, with an almost exponential increase until 1961–70, followed by a sharp decrease with a minimum in 1981–1990, and then a large increase in the last decades (Fig. 3). However, high mortality rates may affect young seedlings and saplings (due to different factors, including competitive pressures, herbivory, avalanches, etc.), so that the patterns that we can obtain by our actual sampling could underestimate the past recruitment occurred in the first part of the study period, of which we can detect now only the survival rate. Moreover, specific patterns and timing were evident based on the selected functional and taxonomic groups (Fig. 3), with the most rapid response provided by evergreen and *Pinaceae*, showing a large sensitivity both to air cooling as well as to air warming.

The temporal trends of woody plant recruitment (Fig. 3) reflected air temperature trends (Fig. 2B) especially in the last decades, with a recruitment drop promoted by the 1960s–1980s air cooling (despite the continuous increase of atmospheric CO_2), followed by the intensive increase triggered by the air warming restart (Figs. 2A, B, 3).

These patterns are consistent with the occurrence of the 1980 regime shift (i.e., abrupt, substantial and persistent changes in the state of natural systems), representing a major change in the Earth's biophysical systems, triggered by rapid global warming from anthropogenic plus the natural forcing associated with the recovery from the El Chichón volcanic eruption (Reid et al., 2016), which was more intensive for land surface temperatures (compared to sea) and for the Northern Hemisphere (see Fig. 5b from Reid et al., 2016). Our data indicate a different sensitivity and responsiveness of woody plants functional and taxonomic groups, with more intensive and faster responses detected in evergreen compared to deciduous, and in *Pinaceae* compared to *Salicaceae* and *Betulaceae* (Fig. 3).

The recruitment trends observed in the last decades (in particular for evergreen and *Pinaceae*) provide further evidence of the acceleration of biotic responses to climate change, previously detected by changes of species richness (Steinbauer et al., 2018) and community dynamics (Cannone et al., 2022b) of non-woody plants of the alpine and polar tundra.

Among functional and taxonomic groups, the largest sensitivity and fastest resilience to the restart of warming of evergreen and *Pinaceae* (Fig. 3C) allows to hypothesize that they could perform the largest expansion also in the future decades. This is in agreement with the observation of very recent (post 2010) rapid range expansion of conifer tree species (Brodie et al., 2019; Ali et al., 2022; Dial et al., 2022), compatible with a boreal forest biome shift (Berner and Goetz, 2022), assuming that the trend of air warming and increasing atmospheric CO_2 would prosecute in the future. The slightly different responses recorded comparing evergreen versus deciduous *Pinaceae* (Fig. 3D) could also reflect their different ecology, as most *Larix* are pioneer species, while most of the evergreen *Pinaceae* are late-successional species with more restrictive ecological requirements. In particular, evergreen *Pinaceae* are characterized by larger drought resistance compared to Angiosperms due to their lower stomatal sensitivity to vapour pressure deficit and

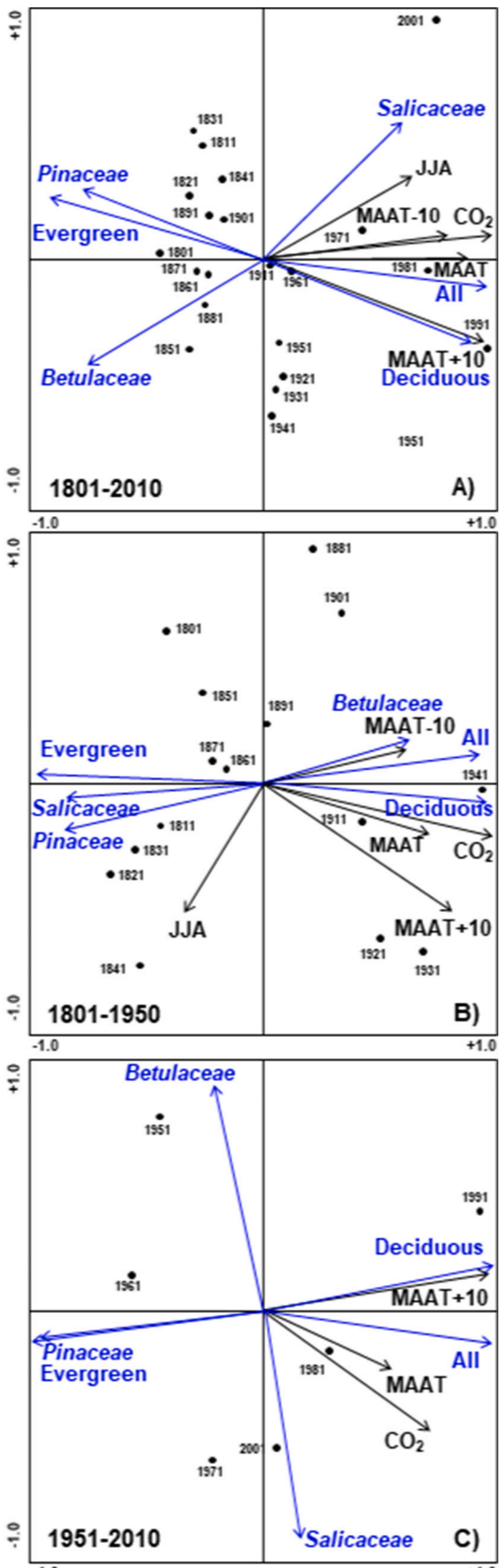

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Fig. 4. Redundancy analysis (RDA) showing the change of the environmental and climatic drivers triggering the recruitment of woody plants comparing: (A) the whole study period (1801–2010); (B) the first part of the study period (1801–1950); (C) the last decades characterized by the acceleration of atmospheric CO_2 increase (1951–2010). Legend: MAAT = mean annual air temperature of the decade (°C); MAAT+10 = mean annual air temperature of the following decade (°C); MAAT-10 = mean annual air temperature of the previous decade (°C); JJA = decadal mean of summer air temperature (June, July, August); CO_2 = decadal mean of the concentration of atmospheric CO_2 (ppm).

more cavitation-resistant xylem (Carnicer et al., 2013; Moran et al., 2017), reducing the exposition of evergreen conifers to water limitation. Also the large increase of needleleaf deciduous *Pinaceae* in the last decades is compatible with the potential saturation of CO_2 fertilization, as they can efficiently prevent water limitation by anticipating leaf senescence and leaf fall.

5. Conclusions

The detection of a synchronous trend of woody plant recruitment across the NH indicates a major climatic and environmental change occurring at hemispheric scale in response to a combination of CO_2 fertilization and air temperature changes.

The drivers of woody plant recruitment changed with time. CO_2 fertilization was the most important driver between 1801 and 1950 while, notably, after 1950 air temperature became the main recruitment driver, despite the acceleration of atmospheric CO_2 increase, supporting the hypothesis that we are shifting from a fertilization-dominated to a warming-dominated period. The temporal patterns of woody plant recruitment are consistent with occurrence of the 1980 regime shift, representing a major change in the Earth's biophysical systems. Indeed, the recruitment drop promoted by the 1960–1980 air cooling was followed by a rapid recruitment increase in response to warming restart.

The analyses based on functional and taxonomic groups of woody plants allowed assess their different sensitivity and responsiveness to climate change, with more intensive and faster responses provided by evergreen and *Pinaceae*, allowing to hypothesize that they could perform the largest expansion also in the future decades, with potential implications concerning the onset of different successional patterns and/or to shifts in dominance at the treeline, with several ecological feedbacks involving biodiversity, biogeochemical cycles, C fluxes, C storage, drought resistance, fire and pathogens' sensitivity. In particular, the different responses of evergreen versus deciduous *Pinaceae* may imply novel dynamics occurring at the treeline in the future decades involving also the forest management and the associated ecosystem services. These data improve our understanding of past and present dynamics at the treeline of woody plant responses to climatic changes, providing useful information for the management and active conservation of the treeline ecotone, and model its responses to future climate changes.

CRediT authorship contribution statement

N. Cannone: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization. **F. Malfasi:** Writing – review & editing, Methodology, Formal analysis.

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.

Data availability

The data on woody plant recruitment have been obtained by the studies reported in the supplementary materials (Tables 1–3 SM), the

Table 1
Eigenvalues, cumulative percentage variance of species-environment relation, test of significance of all canonical axes and conditional effects of the environmental variables of the Redundancy Analysis (RDA) carried out for the whole period (1801–2010) and for the two sub-periods (1801–1950 vs 1951–2010).

RDA 1801–2010					
Axes	1	2	3	4	Total variance
Eigenvalues	0.659	0.128	0.002	0.001	1
Cumulative variance of species-environment relation	83.4	99.6	99.9	100	
Test of significance of all canonical axes	P = 0.005	F-ratio = 11.3			
Conditional effects	**P**		**F**		
CO_2	0.005		29.9		
MAAT + 10	0.01		6.54		
JJA	0.04		3.87		
MAAT	0.2		1.3		
MAAT-10	0.8		0.23		

RDA 1801–1950					
Axes	1	2	3	4	Total variance
Eigenvalues	0.796	0.008	0.002	0.001	1
Cumulative variance of species-environment relation	98.6	99.6	99.9	100	
Test of significance of all canonical axes	P = 0.005	F-ratio = 7.557			
Conditional effects	**P**		**F**		
CO_2	0.005		38.56		
MAAT-10	0.4		0.81		
JJA	0.22		1.58		
MAAT + 10	0.63		0.4		
MAAT	0.76		0.3		

RDA 1951–2010					
Axes	1	2	3	4	Total variance
Eigenvalues	0.626	0.288	0.002	0.064	1
Cumulative variance of species-environment relation	68.4	99.8	100	100	
Test of significance of all canonical axes	P = 0.005	F-ratio = 7.259			
Conditional effects	**P**		**F**		
MAAT + 10	0.005		5.14		
CO_2	0.24		1.86		
MAAT	0.135		4.42		

climatic and atmospheric CO_2 data have been obtained by the studies reported in the methods' section. The recruitment, climatic and environmental data are reported in Table 6SM. Fig. 1. (A) Location of the study sites (black dots) providing the recruitment curves of woody plants at the treeline ecotone in the period 1801–2010 across the northern Hemisphere; and some examples of (B) woody plant functional groups (deciduous and evergreen) and (C) taxonomic groups (*Salicaceae*). Legend: purple areas = high latitude irrespective of elevation; green areas = high elevation at middle and low latitudes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.170953.

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