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Divergent responses of evergreen needle-leaf forests in Europe to the 2020 warm winter

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Abstract

Relative to drought and heat waves, the effect of winter warming on forest CO_2 fluxes during the dormant season has less been investigated, despite its relevance for net CO_2 uptake in colder regions with higher carbon content in soils. Our objective was to test the effect of the exceptionally warm winter in 2020 on the winter CO_2 budget of cold-adapted evergreen needle-leaf forests across Europe, and identify the contribution of soil and air temperature to changes in winter CO_2 fluxes in response to warming. Our hypothesis was that warming in winter leads to higher emissions across colder sites due to increased ecosystem respiration. To test this hypothesis, we used 98 site-year eddy covariance measurements across 14 evergreen needle-leaf forests (ENFs) distributed from north to south of Europe (from Sweden to Italy). We used a data-driven approach to quantify the effect of air and soil temperature on changes in net ecosystem productivity (NEP) during the warm winter of 2020. Our results showed that the impact of warming was different across sites, as in the lower altitude and lower latitude sites positive soil temperature anomalies were larger, while positive air temperature anomalies were larger in the northern latitude and high-altitude sites. Warming in winter led to a divergent

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response across the sites. Out of 14 sites only in 3 sites net ecosystem productivity declined in winter significantly in response to warming. In addition, we observed that in the colder sites daytime NEP (that is dominated by photosynthesis) declined with warming of the air in winter, whereas in the warmer sites daytime NEP increased with warming of the soil. While warming increases ecosystem respiration, it might not trigger productivity in winter if the soil within the rooting zone remains frozen. Forests within the same plant functional type category can exhibit differing reactions to winter warming and to predict their responses accurately it is crucial to account for variations in local climate, physiology, and structure simultaneously.

Keywords: eddy covariance, respiration, productivity, long-term, extremes, carbon flux

Introduction

One of the largest sources of uncertainties in understanding how forests can mitigate climate change is the variation of forest CO_2 fluxes in response to extreme climatic conditions. Forests absorb a large part of anthropogenic CO_2 emissions (Friedlingstein et al. 2023), but extreme climatic conditions compromise the capacity of forests for carbon sequestration (Shekhar et al. 2023). While a large body of research focuses on extreme events during the growing season, effects of warming winters remain understudied (Kreyling et al. 2019). In northern latitudes and higher altitudes where evergreen conifers dominate, warming events are especially pronounced during the winter months (IPCC 2014). In 2020, Europe experienced its warmest winter on record since 1981 and the largest difference relative to the reference period (1981–2020) was observed in winter over northeastern Europe (Copernicus Climate Change Service 2020). However, it is not clear yet how such winter warming affected winter CO_2 fluxes particularly where forests are covered by snow and with high soil C content. Understanding the impact of winter warming on forest net CO_2 uptake requires high temporal resolution observations (sub-seasonal, daily) across many regions, as mechanisms that control forest carbon fluxes are complex and show different responses to changes in climatic conditions, depending on the region and forest type.

At the tree level, winter warming could increase CO_2 uptake in temperature-limited forests. While little of this uptake is expected to be allocated to stem growth (Krejza et al. 2022), this increased activity can impact physiological development of plants that are adapted to long cold periods. Plant CO_2 uptake is controlled by a range of physiological responses to light, temperature and CO_2 concentrations. In addition to these external drivers, physiological factors (e.g., photosynthetic parameters such as light-use efficiency, maximum rate of electron

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transport, maximum carboxylation rate, formation of carbohydrate reserves) and structural characteristics (e.g., leaf area index) which vary across different evergreen needle-leaf forests (ENF), directly affect how productivity and CO_2 uptake might be affected by warming in winter (Martinez Vilalta et al. 2016; Stocker et al. 2018).

Importance of winter period for evergreen needle-leaf forests (ENF)

Forests adapted to cold environments require a persistent number of days with low temperatures for building hardiness. Sudden warming during winter months can promote vegetation activity in response to a condition similar to a "false spring" which can interrupt the cold hardiness process (Laube et al. 2014). Additionally, increased respiration due to warming can deplete stored non-structural carbohydrates (NSC) and tree hydraulic functioning (if combined with drought) and affect tree functioning in spring (Sperling et al. 2015). Winter warming also affects phenological development of trees and increases the chance of photo-oxidative frost damage during earlier stages of the growing season (Gu et al. 2008; Chamberlain et al. 2019). All of this would compromise the capacity of the forest for CO_2 uptake throughout the year (Desai et al. 2016).

Environmental cues such as temperature, photoperiod, and light quality control a network of signalling pathways that coordinate cold acclimation and cold hardiness in trees that ensure survival during long periods of low temperature and freezing (Öquist and Hüner 2003; Ensminger et al. 2006). These signalling pathways include the gating of cold responses by the circadian clock, the interaction of light quality and photoperiod, and the involvement of phytohormones in low temperature acclimation (Chang et al. 2021). Soluble carbohydrates, including sucrose (most abundant) accumulate in response to low temperatures, starting from late autumn throughout winter (Strimbeck & Schaberg 2009; Chang et al. 2015). Persistent uninterrupted cold periods thus play an important role in forming the photosynthetic capacity of the trees and their functioning under extreme climatic conditions. Experimental evidence from temperature-sensitive conifers shows that warm spells in winter can induce premature dehardening of buds, and result in stunted shoot development in the following spring (Nørgaard Nielsen & Rasmussen, 2008). In addition to damage from frost, earlier dehardening can potentially affect the capacity of trees to cope with a range of extreme climatic conditions such as cold spells, drought and heat waves.

Effect of warming on forest carbon fluxes

Forest net ecosystem productivity (NEP) depends on the balance between gross ecosystem CO_2 uptake (gross primary productivity, GPP) and ecosystem respiration (Reco). Both these flux components are highly sensitive to climate drivers (e.g., air and soil temperature, solar

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radiation), and thus when canopy structural changes from one year to another are negligible, the interannual variations can be predominantly explained by changes in the climatic conditions (Hui et al. 2003). Net ecosystem productivity can increase or decrease with changes in air temperature. In temperature-limited ecosystems for example, increase in air temperature increases photosynthesis which leads to a larger gross productivity and potentially increased net CO_2 uptake (if respiration does not increase more). However with warming and increased temperatures, respiration (autotrophic and heterotrophic) can also increase, and the balance of this with changes in gross productivity could lead to an increase, no change, or a reduction in net CO_2 uptake (Gharun et al. 2020). In the presence of winter warming, despite more favourable conditions for photosynthesis, factors such as water stress or photoinhibition caused by high photon flux densities in combination with low air temperatures could downregulate photochemical efficiency and negatively affect net photosynthesis which could decline gross primary productivity (Troeng and Linder 1982).

The temperature sensitivity of ecosystem respiration regulates how the terrestrial CO_2 emissions respond to a warming climate. Within naturally occurring temperature ranges, ecosystem respiration (sum of autotrophic and heterotrophic respirations) typically shows an exponential increase with temperature (Lloyd and Taylor 1994). While previous studies have shown an increase in Q_{10} (times of increased soil respiration with a 10 °C increase of temperature) with decrease in site mean temperature (e.g., Chen et al. 2020), the temperature sensitivity of ecosystem respiration incorporates both the direct response of ecosystem respiration to temperature and indirect influences from other climatic and physiological variables such as moisture, leaf area index, photosynthate input, litter quality, microbial community (Reichstein et al. 2002; Fierer et al. 2005; Lindroth et al. 2008; Migliavacca et al. 2011; Karhu et al. 2014; Collalti et al. 2020). These factors change across species composition and climatic regions and make predicting changes in forest carbon fluxes in response to warming challenging.

The winter of 2019-2020 was reported as the hottest on record (1981-2022) across Europe (Copernicus Climate Change Service/ECMWF). When compared to the average conditions, up to 45 less winter ice days were detected in eastern Europe Russe (C3S/KNMI). In Finland, for example, the average air temperature for January and February was over 6 degrees higher than the 1981-2010 mean (Copernicus Climate Change Service/ECMWF). In this study we investigated how the exceptionally warm winter of 2019-2020 affected ENFs in Europe. Our objectives were to:

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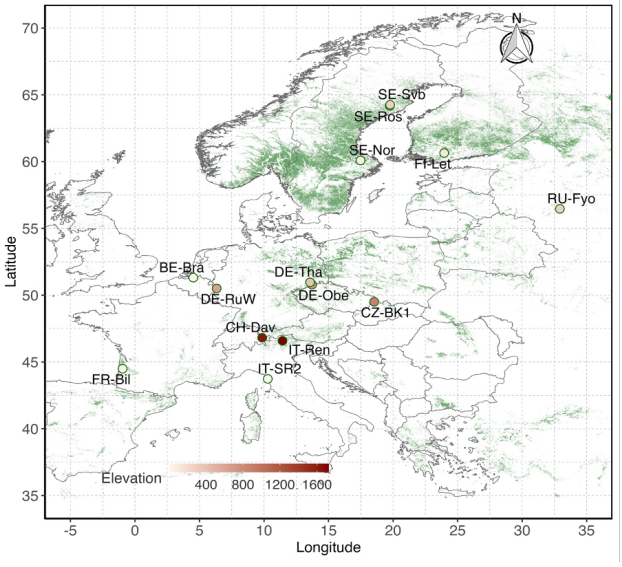
1) evaluate the relative change in air and soil temperature during the winter 2019-2020, compared to a 6-year reference period of 2014-2019, 2) quantify the relative changes in the winter CO_2 fluxes across coniferous sites with available ecosystem-level CO_2 flux measurements, and 3) identify the contribution of climatic drivers (air temperature, soil temperature, solar radiation) to changes in CO_2 fluxes during the warm winter. Our hypothesis was that warming in winter leads to a larger negative effect on net CO_2 balance (i.e., higher emissions) across colder forests. We addressed these objectives and tested our hypothesis by exploring ecosystem-level CO_2 fluxes measured with eddy covariance over 98 site-years in 14 evergreen needle-leaf forests distributed from the Boreal to the Mediterranean regions.

Material and Methods

Site description

We selected 14 evergreen needle-leaf forests where continuous CO_2 fluxes and meteorological measurements were available for at least six years until the end of 2020. Selected sites were located from the northern to the southern edge of ENF forest distribution in Europe (Figure 1).

Figure 1 Location of the 14 Evergreen Needleleaf Forest (ENF) sites included in this study. Base-map is the MODIS Land Cover Product (MOD12Q1, 500m spatial resolution) showing the distribution of ENFs in Europe in 2020. Elevation of the sites ranges from 4 m a.s.l. (IT-SR2) to 1735 m a.s.l. (IT-Ren).



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The most northern site studied is located in Sweden at 64.2 °N (SE-Svb) and the most southern site in Italy at 43.7 °N (IT-SR2). Mean annual air temperature varies between 1.8 °C (in SE-Ros and SE-Svb) and 15.4 °C (in IT-SR2) across sites. Mean annual total precipitation varies from 527 mm (in SE-Nor) to 1316 mm (in CZ-BK1). Elevation ranges from 4 m a.s.l. (IT-SR2) to 1730 m a.s.l. (IT-Ren). Table 1 summarizes the description of sites including their dominant canopy species.

Table 1 Description of the 14 ENF study sites. Mean annual temperature and total precipitation refer to the 2014-2019 period. Mean number of days with snow cover for each site is based on the MODIS satellite observations. Sites are listed in a decreasing order in the mean annual temperature.

Site ID	Lat. (º)	Long. (º)	Altitude (m a.s.l.)	Canopy species (dominant first)	Mean annual temperature (ºC)	Mean annual precipitation (mm)	Nr days with snow cover
IT-SR2	43.702	10.290	4	*Pinus pinea*	15.7	950	0
FR-Bil	44.493	-0.956	39	*Pinus pinaster*	14.1	930	11
BE-Bra	51.307	4.519	16	*Pinus sylvestris*	11.5	750	20
DE-Tha	50.962	13.565	385	*Picea abies*	10.2	843	41
DE-RuW	50.504	6.331	610	*Picea abies*	8.7	1250	50
DE-Obe	50.786	13.721	734	*Picea abies*	7.4	996	90
SE-Nor	60.086	17.479	45	Mixed (*Pinus sylvestris*, *Picea abies*)	7.2	527	89
CZ-Bk1	49.502	18.536	875	*Picea abies*	7.1	1316	71
RU-Fyo	56.461	32.922	265	Mixed (*Picea abies, Betula pubescens*)	6.1	711	58
FI-Let	60.641	23.959	111	Mixed (*Pinus sylvestris*, *Picea abies*, *Betula pubescens*)	5.9	627	99
IT-Ren	46.586	11.433	1735	*Picea abies*	5.5	809	112
CH-Dav	46.815	9.855	1639	*Picea abies*	4.8	1062	139
SE-Ros	64.172	19.738	160	*Pinus sylvestris*	4.0	614	102
SE-Svb	64.256	19.774	267	Mixed (*Pinus sylvestris*, *Picea abies*, *Betula pubescens*)	3.2	614	106

Dataset

We used the Warm Winter 2020 eddy covariance dataset processed with FLUXNET pipeline (compatible with the FLUXNET2015 collection) in this study (Warm Winter 2020 Team, & ICOS Ecosystem Thematic Centre, 2022); https://www.icos-cp.eu/data-products/2G60-ZHAK) (Pastorello et al. 2020). We included the analysis of the spring season at each site to account for

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the responses immediately after the winter season. Winter months included December, January, and February and spring months included March, April, and May. The 6-year reference period was from 2014 to 2019. This period was selected to have sufficient temporal overlap between the sites. NEE quality-checked with a constant friction velocity (u*) threshold was used for all sites (NEE_CUT_REF)(Shekhar et al. 2023). For an easier interpretation, we present net ecosystem exchange as net ecosystem productivity (NEP = -NEE) where a negative NEP indicates that forest is a net source, and positive NEP indicates forest is a net sink of CO_2 (Chapin et al. 2006).

In terms of climatic variables we selected those that overlapped across all sites during the study period. These included incoming shortwave radiation (R_g), air temperature (T_{air}), soil temperature at 5cm (T_{soil}), precipitation and top soil water content. Given that continuous long-term snow depth measurements were not available at all sites, we used remotely sensed snow depth products to quantify mean snow depth and snow depth anomalies in winter 2020. The snow depth data were derived from the simulation of the Famine Early Warning Systems Network (FEWS NET) Land Data Assimilation System (FLDAS) (McNally et al., 2017). FLDAS data are produced from the Noah version 3.6.1 Land Surface Model (LSM) at a monthly resolution with a global coverage at a spatial resolution of 0.1° × 0.1° (approx.10 km × 10 km) (Kumar et al., 2013) and has been used in the past to study global spatiotemporal patterns of snow depth and cover (Notarnicola 2022). For snow cover we used MODIS/Terra (MOD10A2) and MODIS/AQUA (MYD10A2) (Hall and Riggs, 2021) Snow Cover 8-Day L3 Global 500m SIN Grid, Version 6 dataset, which provides maximum snow cover extent at 8-day temporal resolution and 500m spatial resolution. For each forest site, we derived average (2014-2019) leaf area index (LAI) from the LAI Collection 300 m Version 1.1 product (LAI300) provided by the Copernicus Global Land Service (Fuster et al., 2020). Average LAI was estimated for each site during the mean net CO_2 uptake period (Supplementary Figure 2). Start of the net carbon uptake period was defined as when daily NEP crosses from negative to positive, and end is the inverse.

Statistical analysis

We compared average daily and daytime (when $R_g > 10$ W/m^2 and local time 8-18h) means of each variable (v; climate drivers, CO_2 fluxes) during the winter and spring of 2020 to the mean from a 6-year reference period (2014-2019) using a t-test ($p < 0.05$). Daily means of each variable was calculated only using the measured and good quality gap-filled half-hourly data (variable quality control = 0 or 1). To understand the major drivers of winter and spring NEP for each forest site, we derived conditional variable importance (CVI_v) of each predictor variable (R_g, T_{air}, and T_{soil}) based on a random forest regression model (Breiman, 2001). Soil water content was removed

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from the drivers analysis because of its negligible effect on the overall model. We tuned the random forest model by iterating 'ntree' parameter (number of trees to grow) from 100 to 500 with steps of 50, and 'mtry' parameter (number of variables to try at each split) from 1 to 3 with steps of 1, and chose the parameter (ntree = 300 and mtry = 2) with the minimum mean square error. CVI_v accounts for the correlation between the predictor variables, and was calculated using the *party* R-package (Hothorn et al., 2006). Based on a 7-day moving window (centered on the central value of the window) we calculated the mean daily (and daytime) NEP, T_{air}, R_g, and T_{soil}. To compare the CVI_v across sites, for each site we calculated the relative CVI (RCVI) for each variable as per equation 2.

$$RCVI_v\ (\%) = \frac{CVI_v}{\sum CVI_v} \times 100 \qquad \text{Equation 2}$$

Where $\sum CVI_v$ is the sum of CVI_v of all variables used in the model. We expressed changes in variable during 2020 (v_{2020}) and the reference period ($v_{reference}$) based on its relative anomaly (Δv_r) and absolute anomaly (Δv_a) as per equations 3 & 4.

$$\Delta v_r\ (\%) = \frac{v_{2020} - v_{reference}}{|v_{reference}|} \times 100 \qquad \text{Equation 3}$$

$$\Delta v_a = v_{2020} - v_{reference} \qquad \text{Equation 4}$$

To further understand the how (absolute) anomalies of different variables (daytime Rg, T_{air}, T_{soil}) explained the variation in daytime ΔNEP, we used the RCVI (as per equation 2) derived from (also) a random forest regression model with hyperparameters *ntree* = 100 and *mtry* = 3 (tuned for lowest mean squared error), for each site (number of data points at least 80 days). The % variance explained of the model was based on the out-of-bag estimates.

Results

Warm winter 2019-2020 conditions across different sites

According to the *in-situ* data, compared to the reference period (2014-2019), winter 2020 was the warmest winter across 10 sites. In seven sites, the winter also had lower precipitation than normal (Figure 2, and Supplementary Figure 1). Positive air temperature anomalies in winter 2020 were larger in the high latitude or high-altitude sites compared to the mid-latitude and low-elevation sites (Figure 3) with largest anomaly of 4.79 °C in RU-Fyo and lowest positive anomaly of 0.87 °C observed in IT-SR2 (Figure 3). The average number of snow cover days per year was highly

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variable across the study sites. (Table 1). The southernmost site studied here (IT-SR2) typically has no snow cover in winter, while the subalpine forest in Switzerland (CH-Dav) has on average 139 days with snow (Table 1). In those sites with consistent snow cover in winter (11 out of 14 sites) snow depth declined at 9 out of 11 sites during the warm winter of 2020 and reduction was considerable in FI-Let, RU-Fyo, SE-Nor, DE-Obe, DE-Ruw, and DE-Tha (Figure 4). In SE-Svb, FI-Let and DE-Obe soil temperature at 5 cm was continuously above the freezing level in winter 2020 (Figure 5), unlike the mean conditions at the sites where soil temperature fluctuates around zero in winter. Changes in winter temperature were more significant in winter than in spring (Figure 3), which is the reason why we focus on the effect of winter warming on CO_2 fluxes only.

Effect of climate drivers on winter CO_2 fluxes

The annual net productivity of ENFs varied from being a maximum sink (±sd) of 797 (± 320) g C m^{-2} yr^{-1} (CZ-BK1) to a maximum source of -311 (± 93) g C m^{-2} yr^{-1} (SE-Nor) during the six-year reference period (2014-2019) (Table 2). Inter-annual variation in NEP was largest in CZ-BK1 (320 gC m^{-2} y^{-1}) and lowest in SE-Svb (35 gC m^{-2} y^{-1}) (Table 2). The length of the net CO_2 uptake period was on average 178 days but varied between the sites from 105 days (in RU-Fyo) to 315 days (in DE-Ruw) (Table 2, Suppl. Figure 2). Except FR-Bil and DE-RuW all sites were a CO_2 source in winter under reference conditions, however in IT-SR2, the forest shifted from a CO_2 source into a CO_2 sink in winter 2020 (Supplementary Table 1).

During the warm winter 2020, mean daily NEP (i.e., annual winter CO_2 sink or source strength) changed significantly ($p < 0.05$) in 9 out of 14 sites (BE-Bra, CZ-BK1, DE-Obe, FI-Let, IT-Ren, IT-SR2, SE-Svb, SE-Nor, RU-Fyo, grouped as the “affected” sites) compared to the 2014-2019 reference period, with changes in both positive and negative directions (Figure 6). For example, in BE-Bra, DE-Obe, IT-Ren, SE-Svb and FI-Let, the forest became a significantly larger source of CO_2 in winter 2020, while in IT-SR2, SE-Nor, CZ-BK1, and RU-Fyo forest shifted towards being a smaller source for CO_2 in winter 2020 (Figure 6, Supplementary Table 1). IT-SR2 showed the largest increased daily NEP in winter (346%) and BE-Bra showed the largest negative anomaly in daily NEP (-97%) (Figure 6). During the warm winter ecosystem respiration (approximated by nighttime NEP) increased significantly across 10 out of 14 sites (Figure 6). Daytime NEP however (dominated by productivity) increased significantly with warming in only 5 sites, and mainly in the warmer sites (Figure 6).

The relative importance results of the random forest regression analysis showed that across tested variables, R_g generally had the largest control on NEP. However, with decrease in site baseline (i.e., mean) temperature, the effect of R_g declined (Figure 7). For example, in the three coldest

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sites (SE-Svb, CH-Dav, IT-Ren) R_g had a relative importance of 52%, 23% and 41% for the variations in NEP respectively, while in the three warmest sites (IT-SR2, FR-Bil and BE-Bra) R_g had a relative importance of 73%, 81% and 58% for NEP respectively (Figure 7). Radiation dominated the effect on winter GPP and temperature dominated the effect on winter respiration fluxes. Particularly in the colder sites the effect of radiation was the least (Figure 7).

Figure 2 Winter temperature and precipitation anomalies (x_anom = x-x_mean) in 2020 (between December 2019 and February 2020) at those sites where winter 2020 was the warmest and driest relative to winters during the reference period 2014-2019. Precipitation anomalies are converted to relative change (relative to mean) but temperature changes are in the original unit (°C). Anomalies are classified in four main classes of "wet-warm", "dry-warm", "wet-cold", and "dry-cold". Winter 2020 is marked in bold. Symbols are marked in blue and label (year) is displayed only if precipitation change was larger than 10% and at the same time temperature change more than 0.5 °C. Sites ordered by increasing mean temperature (SE-Svb coldest and IT-SR2 warmest).

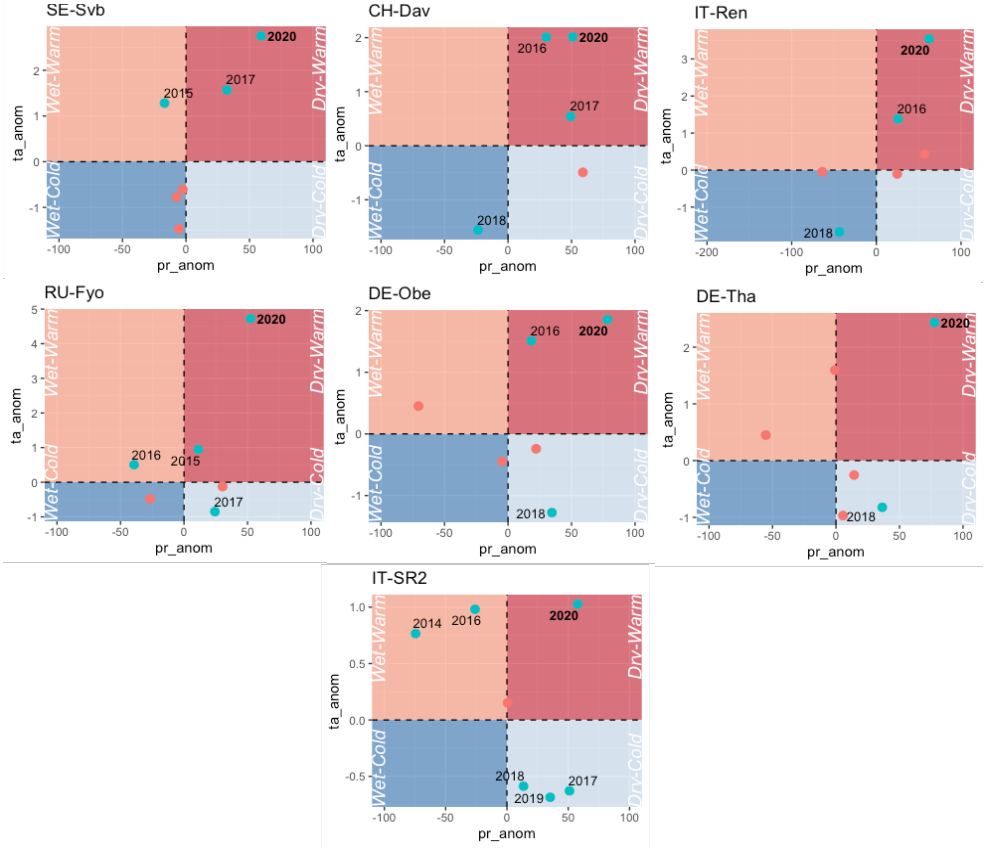

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Figure 3 Seasonal changes in air temperature (T_{air}) and soil temperature (T_s) in 2020 compared to the 6-year reference period (2014-2019). Asterisk marks where means in 2020 were significantly different from the reference period (p<0.05). Anomalies were calculated from daily values. Sites are listed in a decreasing order of mean annual air temperature.

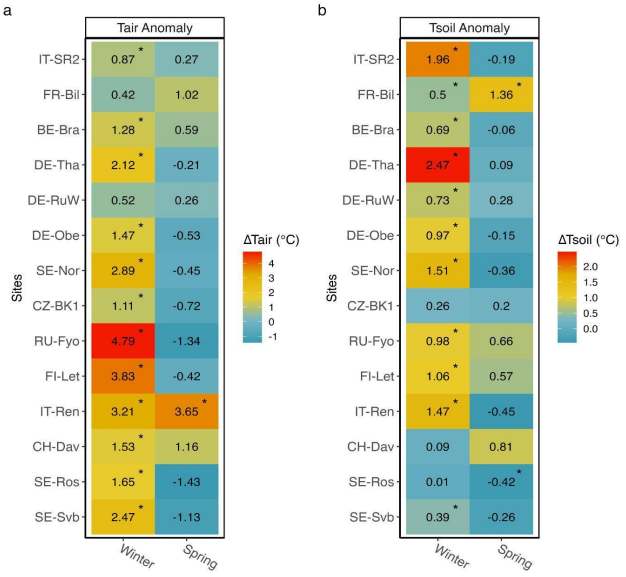

Figure 4 December to May snow depth changes (cm) in winter 2020 compared to the average winters during the reference period (2014-2019). Note that only 11 out of 14 sites have persistent snow cover in winter. Sites ordered by increasing mean temperature (SE-Svb coldest and DE-Tha warmest).

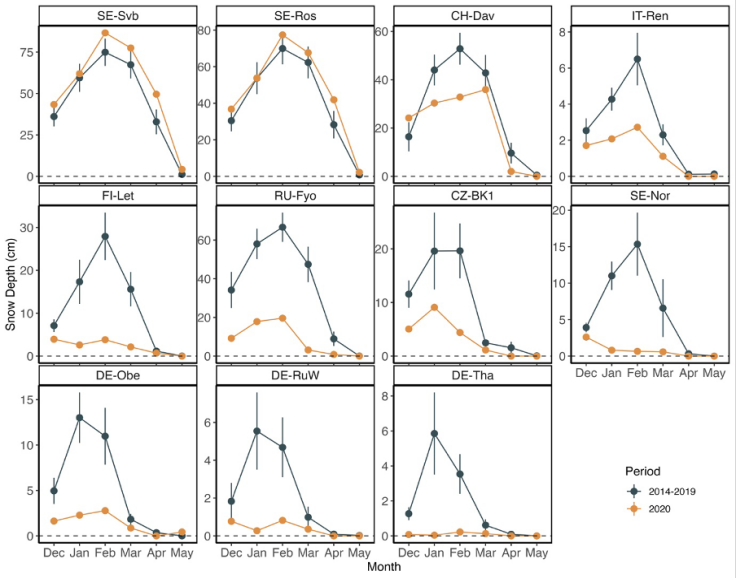

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Table 2 Mean total annual net ecosystem productivity (NEP) and the standard deviation (inter-annual variation) during the reference period (2014 and 2019). Start of the net carbon uptake period (SOS, day of year, DOY) is when daily NEP changes from negative to positive and end (EOS) is the inverse (see Suppl. Figure 2). Sites are listed in a decreasing order in mean annual air temperature.

Site ID	NEP (±sd) (g C m^{-2} y^{-1})	SOS (DOY)	EOS (DOY)	Net carbon uptake period (days)
IT-SR2	197 (±67)	35	200	165
FR-Bil	324 (±103)	20	215	195
BE-Bra	279 (±158)	95	270	175
DE-Tha	484 (±88)	55	305	250
DE-Ruw	597 (±155)	1	365	365
DE-Obe	251 (±147)	75	265	190
SE-Nor	-311 (±93)	90	200	110
CZ-Bk1	797 (±320)	70	310	240
RU-Fyo	25 (±50)	95	200	105
FI-Let	-113 (±123)	100	230	130
IT-Ren	675 (±70)	75	305	230
CH-Dav	231 (±139)	80	280	200
SE-Ros	320 (±136)	95	255	160
SE-Svb	163 (±35)	95	240	145

Effect of warming on NEP anomalies

Across the low latitude or low altitude (< 1000 m a.s.l.) sites where NEP changed significantly in winter 2020 (IT-SR2, BE-Bra, DE-Obe), average NEP anomaly was +75%. In the high-latitude-high elevation sites where NEP was significantly different in winter 2020 (SE-Nor, CZ-BK1, RU-Fyo, FI-Let, IT-Ren, SE-Svb) the average NEP anomaly was -8.8% (reduced net uptake) (Figure 6, Supplementary Figure 5). Average variable explained by the random forest regression for daytime ΔNEP when abiotic drivers were included in winter was 72% in winter (Figure 8). Across the affected sites, changes in the air temperature dominated the effect on NEP anomalies (Figure 8). While FI-Let was affected by a partial cut in 2016 (Korkiakoski et al. 2019; Korkiakoski et al. 2020), winter fluxes remained relatively stable in all pre- and post-harvest years as the partial cut affected mostly the summer fluxes (data not shown here).

The relationship between air and soil temperature was stronger than radiation and air temperature across sites and the relationship between air and soil temperature was stronger in warmer sites (Table 3). In addition to snow cover, leaf area index and the degree of canopy closure (directly related to LAI) affect the relationship between air and soil temperature through a stronger shading of the soil in dense forests. CZ-BK1 had the largest LAI (4.52 ± 0.09 se)

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and SE-Ros the smallest (2.59 ± 0.09). FI-Let had the largest inter-annual variation (± 0.27) in LAI and IT-Ren and FR-Bil smallest inter-annual variation (± 0.08) (Table 3).

Table 3 Pearson correlation coefficient between mean daily incoming shortwave radiation (Rg), air temperature (T_{air}) and soil temperature at 5m (T_{soil}) at each site during the reference period (2014-2019). Sites are ordered by a decreasing mean air temperature. Leaf area index (LAI) values are shown as mean across the study period ± standard error of the mean.

Site ID	R_g-T_{air}	T_{air}-T_{soil}	LAI ± se
IT-SR2	0.69	0.97	3.12 (0.11)
FR-Bil	0.65	0.76	3.50 (0.08)
BE-Bra	0.67	0.92	4.42 (0.13)
DE-Tha	0.73	0.96	4.04 (0.19)
DE-RuW	0.59	0.83	2.99 (0.22)
DE-Obe	0.72	0.94	3.69 (0.21)
SE-Nor	0.71	0.90	3.08 (0.09)
CZ-Bk1	0.72	0.92	4.52 (0.09)
RU-Fyo	0.74	0.78	4.06 (0.14)
FI-Let	0.66	0.88	3.29 (0.27)
IT-Ren	0.64	0.84	3.54 (0.08)
CH-Dav	0.63	0.87	3.25 (0.12)
SE-Ros	0.69	0.77	2.59 (0.09)
SE-Svb	0.71	0.84	2.79 (0.12)

Figure 5 Soil temperature (at 5cm) changes in winter 2020 compared to the reference period (2014-2019). Shaded bands around the mean show the 95% confidence interval of mean soil temperature. Sites are ordered (top and right to left) by increasing baseline temperature (SE-Svb coldest and IT-SR2 warmest).

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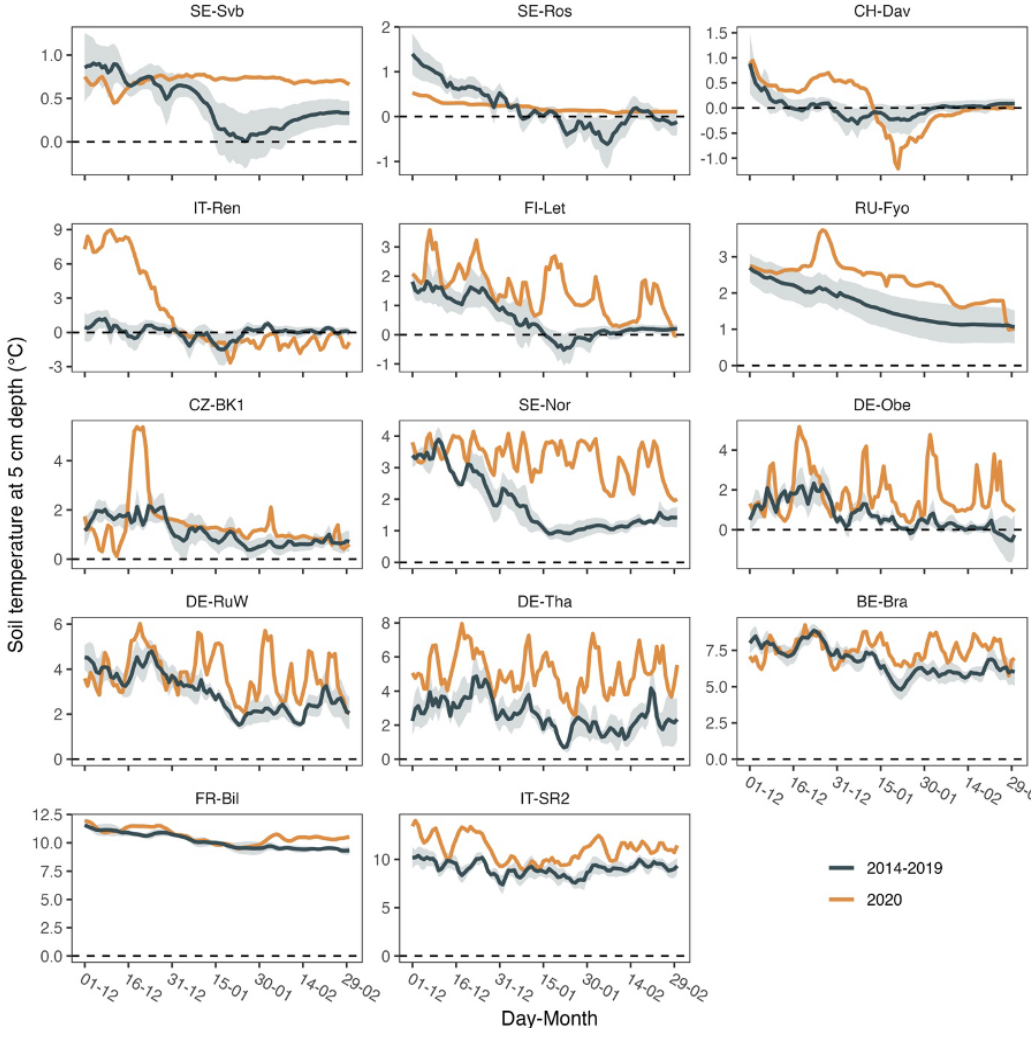

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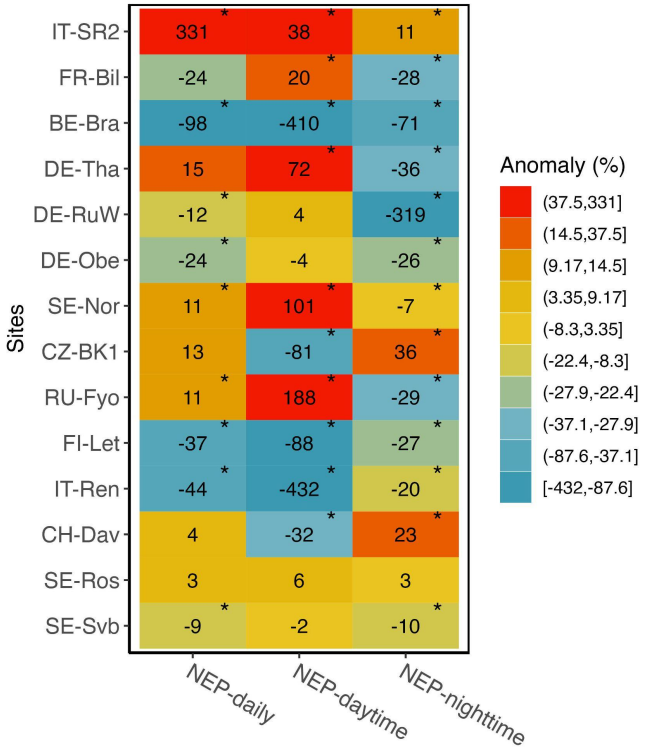
Figure 6 Relative changes (%) in mean daily, nighttime, and daytime NEP in winter 2020 compared to the 6-year reference winters (2014-2019). Asterisks mark where means in 2020 were significantly different from the reference period (p <0.05). Positive NEP change indicates increased net uptake (due to increased uptake or reduced emission) and negative change indicates decreased net uptake (due to reduced uptake or increased emission). Sites are listed in a decreasing mean annual air temperature order.



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394 **Figure 7** Relative conditional variable importance (RCVI, %) of three climatic variables for
395 daily winter NEP, GPP and Reco, and the overall variable explained (marked with red
396 triangles) estimated from the random forest regression analysis. The RFR model was trained
397 on winter observations during the reference period (2014-2019). The sites are ordered by
398 decreasing mean annual temperature (top to bottom).

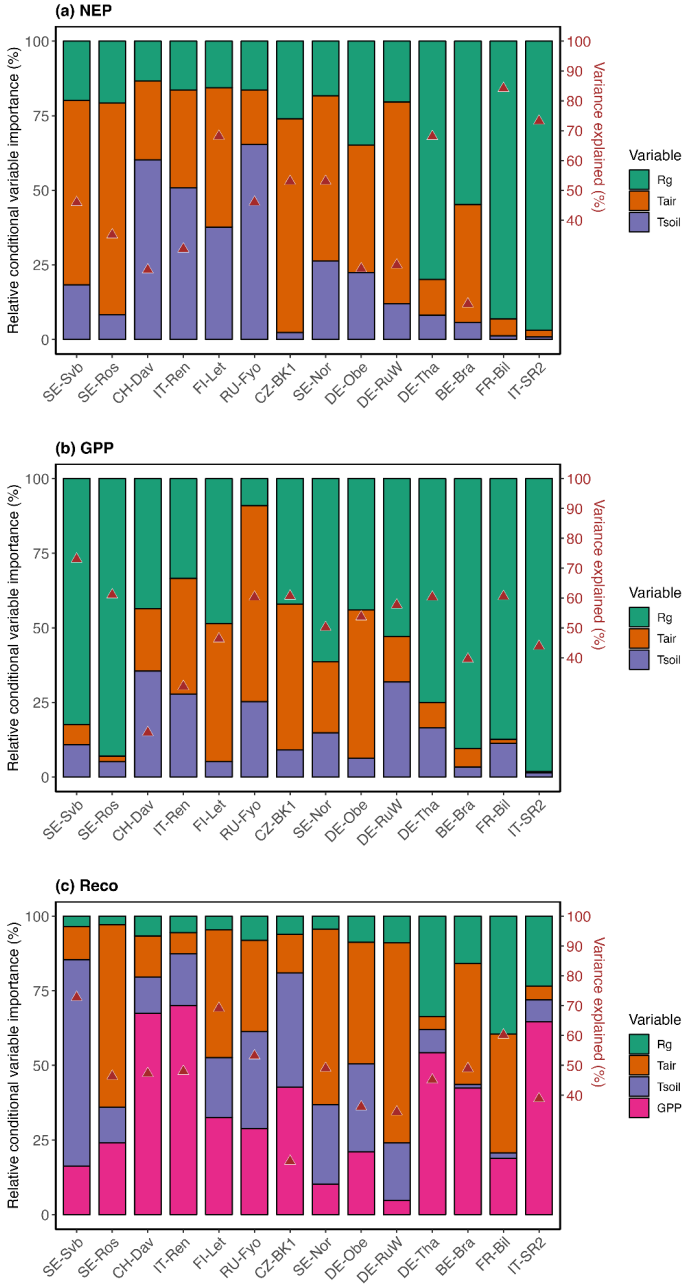

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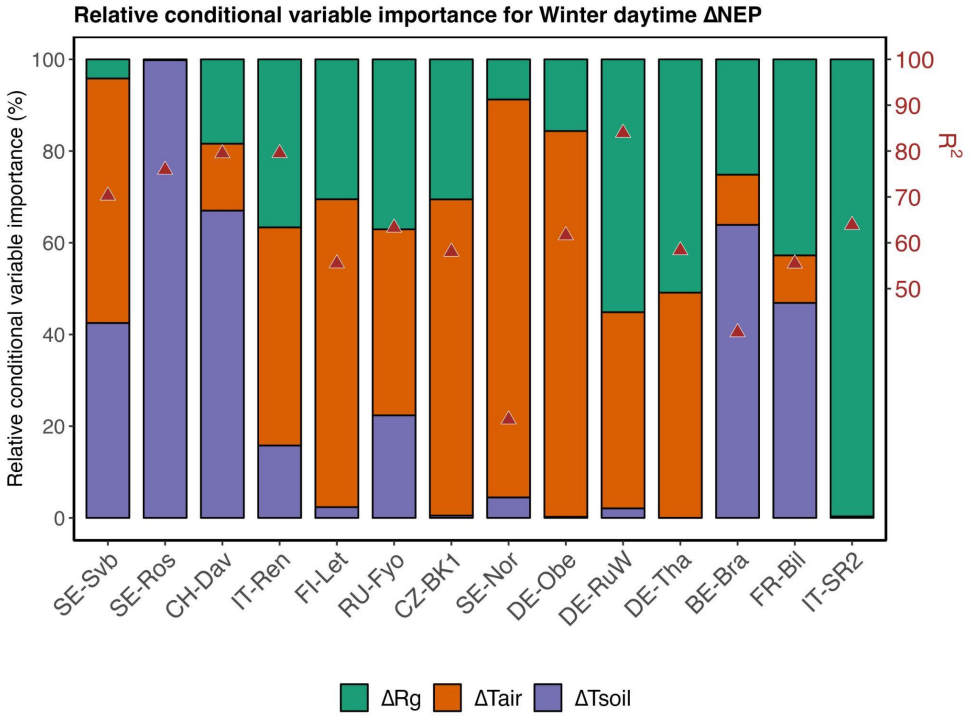
Figure 8 Comparison of the relative importance of abiotic (T_{air}, R_g, T_s) variables, for NEP changes (**ΔNEP**) in winter 2020. R^2 of the RFR model that was used to explain the variation in daytime ΔNEP (i.e., when PPFD > 0) is shown on the secondary (right) y-axis and marked with red triangles. Sites are ordered by increasing mean air temperature (from left to right).



Discussion

Warming of the air and the soil in winter

We tested how climate variables and CO_2 fluxes deviated from a reference period (2014-2019) during the warm winter of 2020 , across 14 evergreen needle-leaf forest sites distributed from north to south of Europe (from Sweden to Italy). The sites where winter 2020 was particularly warm and dry were not clustered in a certain climatic region, however we observed a consistent pattern that warming of the air was more pronounced in the northern latitude and on high altitudes sites, while in lower latitudes and altitudes warming of the soil was more pronounced (Figure 3). While in forests top soil temperature is directly affected by changes in the air temperature, several underlying processes and properties modify the magnitude of decoupling of air and soil temperature which could reach up to 10 degrees, depending on the season and properties of the biome type (Lembrechts et al. 2022). These underlying factors and processes

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include for example 1) a vertically complex and horizontally continuous forest structure that leads to higher decoupling of the soil temperature from air temperature, 2) soil moisture content as moisture increases the soil heat storage, 3) insulation by the litter or snow cover, 4) cloud cover, ground surface albedo, and rate of evapotranspiration which collectively affect the radiation balance and energy exchange between the soil and the air, and 5) microtopography that affects the drainage of air (e.g., cool air drains in low-lying areas) (Guan et al., 2009; Lozano-Parra et al., 2018; De Frenne et al., 2021; Gril et al., 2023). Given that in our study the type of forest was similar across sites (all sites were dominated by evergreen needle-leaf forests) and given that our focus was on the warming during the winter season, we attribute the main source of difference in the soil and air temperature to two main factors. First the snow depth that ranged from no snow to over 100 cm across sites (Table 1, Figure 4), and second, differences in forest structure (e.g, LAI) which varied between 2.59 to 4.52 across the sites (Table 3). We observed that the sites with the smaller snow depth showed a larger warming of the soil during the warm winter of 2020 perhaps because the insulating effect of snow cover was weaker here (Friesen et al. 2021) (Figure 2, Figure 4). At the sites where snow depth declined significantly in winter 2020, soil temperatures increased substantially with large fluctuations over the season, whereas in other sites with greater snow depth such soil temperature fluctuations were absent (Figure 5). The link between warming of the air and warming of the soil was also controlled by the canopy structure as we found a significant positive relationship between the two ($p < 0.05$, $r = 0.69$). Although the direct effect of canopy closure on snow distribution, accumulation and melting at different periods was not tested here, it was evident that sites that had a larger LAI also showed a tighter coupling between air temperature and soil temperature as forest canopy closure reduces snow depth (Table 3)(Woods et al. 2006; Gao et al. 2022).

Winter warming effect on forest CO_2 fluxes

Our general observation was that across sites with a lower mean average temperature (i.e., high altitude or high latitude sites) winter warming was concurrent with increased net CO_2 emissions. In the warmer sites however (low altitude or low latitude sites) winter warming also increased the productivity and CO_2 uptake (Supplementary Figure 5). This difference can generally be explained by the balance of changes in the warming of the soil versus warming of the air (Bond-Lamberty and Thomson 2010) which affects both soil respiration and tree CO_2 uptake. Where soil becomes proportionally warmer and soil temperature reaches above freezing levels, root activity is enhanced and tree productivity responds directly to the increased

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air temperatures, and CO_2 uptake increases. Warming of the air - if not translated into a direct warming of the soil– might not enhance productivity if the soil within the rooting zone remains frozen. In IT-Ren for example where daytime NEP declined significantly in the warm winter, air temperature increased to over 3.5 degrees more than normal, however soil temperature remained at freezing levels (Figure 5).

CO_2 fluxes are sensitive to changes in both temperature and light (e.g., incoming radiation) and site baseline climate conditions showed to be a good proxy of how changes in light and air temperature lead to changes in NEP (Figure 7). There is however evidence that temperature responses of biochemical processes are a function of plant growth temperature, and not just instantaneous temperature (Fürstenau Togashi et al. 2018). In addition, response of NEP to similar temperature can be different across seasons (i.e., an evident hysteresis), depending on other environmental factors such as solar radiation and soil water content (Niu et al. 2011). While across different sites sensitivity of NEP to temperature increases with a decrease in site mean temperature, as site mean temperature increases (temperature is no longer limiting) radiation becomes a larger constraint on NEP (Running et al. 2004).

Chamber-based observations from boreal forests show that snow-depth and soil moisture affect temperature sensitivity of soil CO_2 fluxes as the freeze-thaw cycles abruptly change the moisture content of the soil (Du et al., 2013). In that sense, warmer winters can trigger larger respiration (and availability of nutrients to trees) because of higher Q_{10} of thawed than frozen soils (Wang et al., 2014), however microbial C limitation can reduce expected increase in respired CO_2, if not countered by greater labile C inputs (Sullivan et al., 2020). In addition, aboveground productivity increases with increase in temperature (Supplementary Figure 3) and enhances the autotrophic respiration. Warming in winter also affects the microbial community that control labile and stable organic carbon decomposition in the soil that would offset respiration response to temperature and lead to a reduction of soil respiration under warming (Tian et al., 2021). The magnitude of increase in belowground autotrophic respiration in response to warming and the supply of labile substrate through rhizodeposition and root exudate also affects net CO_2 fluxes under warming (Nyberg et al., 2020). Decrease in the snow pack and increased soil freezing has short-term immediate impacts on plant CO_2 uptake, but can also leave a long-lasting negative impact on functioning of trees (Repo et al. 2021). Particularly sites with prolonged cold winter seasons could be rather negatively affected by the warming in winter, as we observed through reduced daytime NEP which is an indication of stress from warming during winter. Trees growing in northern latitudes and higher altitudes could be more negatively affected by warming in winter as optimal temperatures in trees are

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regulated by the short-term changes in temperature, whereas in ecosystems where temperature fluctuations are seasonally larger, optimal temperature for growth has a broader range (Weng et al. 2010; Liu 2020).

Winter tree physiology effect on CO_2 fluxes

Responses of coniferous species to soil warming can vary largely depending on the species' adaptive traits, the overall ecosystem context, and interactions with other environmental factors such as precipitation, temperature, and nutrient availability (Dawes et al. 2017; Oddi et al. 2022). The sites we studied here, although all were dominated by evergreen needle-leaf species, consisted of different canopy species and some sites were dominated by a mixture of species (Table 1). There can be significant differences in photosynthetic parameters across different species of evergreen conifers that would affect tree and ecosystem response to warming (Fürstenau Togashi et al. 2018). The different responses of productivity to increased warming in ENFs can stem from differences in the quantity (and quality) of stored NSC in the roots, and the rate at which this C storage is mobilized within the tree during the warm winter (Bansal and Germino 2009). Warmer temperatures and dry conditions in winter lead to stomatal closure and depletion of carbohydrate reserves for trees that are adapted to ample precipitation and low VPD conditions in winter, and this effect leads to reduced CO_2 uptake of trees during warmer winters (Earles et al. 2018).

Low temperature is essential for signals that trigger the synthesis of soluble carbohydrates involved in osmotic and freezing protection against cold extremes (Chang et al. 2021) that otherwise impair the Calvin cycle by inhibiting the regeneration of ribulose bisphosphate (RuBP) and decrease the efficiency of Rubisco carboxylation (Ensminger et al. 2012; Crosatti et al. 2013). Non-structural carbohydrates (sugar and starch) that are accumulated during the growing season are utilized in winter to ensure survival of trees (Zhu et al. 2012; Tixier et al. 2020) and failure to develop overwintering defences can cause evergreen conifer needles to remain susceptible for example to photo-oxidative damage during frost events (Chang et al. 2016).

Our results provide the first analysis of the effect of winter warming on CO_2 fluxes of evergreen needle-leaf forests in Europe and point to the importance of understanding multiple underlying mechanisms that govern CO_2 fluxes. Data on the responses of photosynthetic traits on a timescale that is ecologically relevant (days to years) are scarce, but eddy covariance observations provide an opportunity for constructing long-term time series of canopy level

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processes to investigate the effect of extreme climatic conditions across all seasons. We encourage studies that combine long-term observations and plant-level experiments to investigate how changes in the functioning in winter might affect trees' response to extremes that occur earlier in the growing season (e.g., spring frost, spring drought) and to understand the consequences of such extremes for ecosystem carbon uptake.

Conclusion

Our study investigated the effect of winter warming on CO_2 fluxes of evergreen needle-leaf forests across Europe during the warm 2019-2020 winter. We found significant differences in the impact of warming across sites, with northern and higher-altitude locations experiencing more significant warming of the air, while southern and lower-altitude sites saw greater soil warming. Winter warming influenced forest CO_2 fluxes, with daytime Net Ecosystem Productivity (NEP) decreasing in colder sites due to lower soil temperature, while warmer sites experienced increased CO_2 uptake. However, responses were not similar across all sites, and factors such as forest structure, and local mean climatic conditions played a role in creating microclimates that buffer or enhance the impact of warming on CO_2 fluxes. Understanding these variations combined with tree ecophysiological functioning of cold-adapte ecosystems is crucial for predicting how forests will respond to future winter warming.

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Data availability: The dataset used in this study is openly available from the ICOS Carbon Portal. https://doi.org/10.18160/2G60-ZHAK

Author contributions: MG designed the study; MG and AS performed the data analysis; MG wrote the manuscript, and all authors commented on the analysis and contributed substantially to the writing of the manuscript.

Competing interests: The authors declare that they have no conflict of interests.

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