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

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Abstract

Compared to drought and heat waves, the impact of winter warming on forest CO_2 fluxes has been less studies, despite its significant relevance in colder regions with higher soil carbon content. 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 climate factors to changes in winter CO_2 fluxes. 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 radiation, air temperature, and soil temperature on changes in CO_2 fluxes during the warm winter of 2020. Our results showed that warming in winter declined forest net ecosystem productivity (NEP) significantly across most sites. The contribution of climate variables to CO_2 fluxes varied across the sites: in southern regions with warmer mean temperatures, radiation had a greater influence

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on NEP. Conversely in colder sites, air temperature played a more critical role in affecting NEP. During the warm winter of 2020, colder sites experienced larger air temperature anomalies and given their greater sensitivity to these changes, NEP in these regions declined significantly with winter warming. At sites with deeper snow cover, soil temperature remained relatively stable during the warm winter, due to the insulating properties of the snow. Our study confirms that winter warming can significantly reduce NEP particularly in colder regions where ecosystems are more sensitive to changes in temperature. The divergent responses of NEP across different sites underscore the complex interplay between climate variables, such as air and soil temperature, and radiation. These findings emphasize the need to incorporate winter warming effects in order to better predict and mitigate the impacts of climate change on forest carbon dynamics.

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

Introduction

One of the key challenges in assessing the role of forests in mitigating climate change lies in understanding how forest CO_2 fluxes respond to extreme climatic conditions, particularly increases in air temperature. While forests serve as a significant sink for anthropogenic CO_2 emissions (Friedlingstein et al. 2023), extreme warming events can compromise their ability to sequester carbon effectively (Shekhar et al. 2023). Although much research has focused on extreme events during the growing season, the impacts of warming winters remain relatively understudied (Kreyling et al. 2019).

In regions where evergreen conifers predominate, such as northern latitudes or higher altitudes, winter warming events can be particularly pronounced (IPCC, 2014). For instance, in 2020, Europe witnessed its warmest winter on record since 1981, with the most significant deviation from the reference period (1981–2020) observed in northeastern Europe (Copernicus Climate Change Service, 2020). However, the specific effects of such winter warming on CO_2 fluxes, especially in forested areas covered by snow and rich in soil carbon content, remain unclear.

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 emission (ecosystem respiration, Reco). Both these flux components are highly sensitive to climate drivers (e.g., air temperature, soil

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temperature, solar radiation). 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 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).

Evergreen forests in the northern hemisphere contribute significantly to the terrestrial carbon (C) storage and exchange (Beer et al., 2010; Thurner et al., 2014). High-latitude evergreen forests have shown an increase in gross primary productivity (GPP) with increasing temperature largely due to longer growing seasons (Myneni et al., 1997; Randerson et al., 1999; Forkel et al., 2016). Multiple other changes under warming however could counter effect such increase for the overall CO_2 uptake capacity of the forest (e.g., due to an increase in ecosystem respiration). In the absence of soil moisture limitation, respiration increases exponentially with increase in temperature (Law et al. 1999).

Additionaly, 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 Q10 (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 (i.e., increased metabolic activity of plants and microorganisms), and indirect influences from other climatic and physiological variables such as moisture, leaf area index, photosynthate input, litter quality, microbial community. For example soil moisture affects the microbial activity and decomposition rates, which in turn influence respiration rates. In moist conditions, microbial activity increases, leading to increased decomposition and

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respiration rates. Conversely, in dry conditions, microbial activity slows down, reducing the respiration rates. The amount of organic matter produced through photosynthesis affects the availability of substrates for microbial decomposition, and higher photosynthate input results in increased carbon availability, stimulating microbial activity and respiration rates (Reichstein et al. 2002; Fierer et al. 2005; Lindroth et al. 2008; Migliavacca et al. 2011; Karhu et al. 2014; Collalti et al. 2020). The temperature response of net ecosystem productivity is the product of sensitivity of GPP and ecosystem respiration to temperature (Lloyd and Taylor 1994; Niu et al. 2011), and temperature sensitivity of respiration (Q10) changes proportionally with site mean temperature (e.g., higher Q10 in colder sites, Chen et al. 2020).

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

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 as warmer winter temperatures increases the chance of photo-oxidative frost damage during earlier stages of the growing season (Gu et al. 2008; Chamberlain et al. 2019) which would compromise the capacity of the forest for CO_2 uptake throughout the year (Desai et al. 2016). The risks of photo-oxidative frost damage increases with winter warming, as warmer winter temperatures can lead to an accumulation of photosynthetically active compounds in plants, and when sudden frost events occur during periods of high radiation, the combination of low temperatures and intense sunlight can induce photo-oxidative stress in plant tissues. This occurs because the photosynthetic machinery is still active, but the low temperatures impair the plant's ability to dissipate excess energy, leading to the production (and imbalance) of reactive oxygen species (ROS) that can damage cells and tissues. Photochemical damage can also happen in the case of high radiation, low water content in the leaf tissue and low temperature, when photosynthesis and protein turnover become inhibited by low temperatures and when non photochemical, heat dissipation mechanisms are insufficient to deal with excess excitation

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(hence the negative effect of freezing temperatures after de-hardening) (Anderson & Osmond 1987; Öquist & Huner 2003).

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). 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).

The winter of 2019-2020 was reported as the hottest winter in the last four decades (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 and whether increasing winter temperature increased or decreased the carbon uptake of the forest. Our objectives were to:

1) evaluate the relative change in air and soil temperature and incoming radiation 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, 3) identify the contribution of climatic drivers (air temperature, soil temperature, solar radiation) to changes in CO_2 fluxes during the warm winter, 4) test the sensitivity of CO_2 fluxes to each of the climatic drivers, and 5) test if the sensitivity of CO_2 fluxes to temperature changed during the warmer winter compared to previous years. Our hypothesis was that warming in winter will lead to a larger negative effect on net ecosystem productivity (i.e., higher CO_2 emissions) across colder forests due to increased ecosystem respiration. We addressed these objectives and tested our hypothesis by exploring ecosystem-level CO_2 fluxes measured with the eddy covariance method over 98 site-years in 14 evergreen needle-leaf forests distributed from the Boreal to the Mediterranean regions in Europe.

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

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located from the northern to the southern edge of ENF forest distribution in Europe (Figure 1). 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). CZ-BK1 has the largest LAI (4.52 ± 0.09 se) and SE-Ros the smallest (2.59 ± 0.09). Table 1 summarizes the description of sites including their dominant canopy species.

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 soil and air temperature during the spring season at each site to check for any significant changes in the climate 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 the forest is a net source, and positive NEP indicates that the forest is a net sink of CO_2 (Chapin et al. 2006).

In terms of climatic variables we selected those that overlapped in data availability across all sites during the study period. These included incoming shortwave radiation (R_g), air temperature (T_{air}), soil temperature at 5cm (T_{soil}), and 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)

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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 quality check, we compared the measured snow depth against the remotely-sensed snow depth for one site (DE-Tha) where these measurements were available during the study period and found a reasonable agreement between the two datasets (r = 0.86, p < 0.001). 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. Start of the net carbon uptake period was defined as when daily NEP crosses from negative to positive, and end is the inverse following Shekhar et al. (2023).

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 were 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 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). For training the random forest model of Reco, we additionally used GPP as an explanatory variable. In addition to the influence of abiotic drivers, the empirical relationship between photosynthesis (and thus GPP) and ecosystem respiration in forests has been established by a large body of research (Brüggemann et al., 2011; Koerner, 2013; Migliavacca et al., 2011; Shekhar et al. 2024). Soil water content (SWC) was removed from the drivers analysis 1) because of its negligible effect on the overall model (see details below), 2) since not all sites had complete measurements throughout the study period, 3) and because soil water content measurements at freezing soil temperature levels are not reliable, and we observed that for several sites soil temperature in winter remained near or below zero (Supplementary Figure 1). The effect of soil water content on the RF model was negligible after we compared the random forest results once with, and once without including SWC. The comparison showed that the difference in the variance explained (r^2) was less than 3% (negligible improvement in results based on the %variance explained of the model, Supplementary Figure 2).

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)

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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.

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

$$\Delta v_a = v_{2020} - v_{reference} \qquad \text{Equation4}$$

To further understand how (absolute) anomalies of different variables (Rg, T_{air}, T_{soil}) explained the variation in 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 (r^2) 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 was also drier than normal (Supplementary Figure 3). Positive air temperature anomalies in winter 2020 were significantly larger in sites with a lower mean (2014-2019) air temperature ($p < 0.05$, $r = -0.53$) with largest significant anomaly of 4.79 °C in RU-Fyo and lowest significant positive anomaly of 0.87 °C observed in IT-SR2 (Figure 2). Incoming shortwave radiation did not change significantly across any of the sites during the warm winter (data not shown here).

The average number of snow cover days per year was highly variable across the study sites. (Table 1). The southernmost site studied here (IT-SR2) has no snow cover in winter, while the

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subalpine forest in Switzerland (CH-Dav) has a snow cover on 139 days per year in average (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 this reduction was considerable in FI-Let, RU-Fyo, SE-Nor, DE-Obe, DE-Ruw, and DE-Tha (Figure 3). In SE-Svb, FI-Let and DE-Obe soil temperature at 5 cm was continuously above the freezing level in winter 2020 (Supplementary Figure 1), 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 2), which is the reason why we focus on the effect of winter warming on CO_2 fluxes.

Effect of climate drivers on winter CO_2 fluxes

The annual NEP of the ENFs varied from 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). Except FR-Bil and DE-RuW, all sites were a CO_2 source in winter under reference conditions (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 4). 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 SE-Nor, CZ-BK1, and RU-Fyo forest shifted towards being a smaller source for CO_2 and IT-SR2 turned into a net sink in winter 2020 (Figure 4, Supplementary Table 1). IT-SR2 showed the largest increased daily NEP in winter (331%) and BE-Bra showed the largest decline in daily NEP (-98%) (Figure 4). During the warm winter ecosystem respiration (approximated by nighttime NEP) increased significantly across 10 out of 14 sites, indicated by a negative anomaly in nighttime NEP (Figure 4). Daytime NEP however (dominated by productivity) increased significantly with warming in only 5 sites, and mainly in the warmer sites (Figure 4).

Figure 5-7 shows the relationship between air temperature, soil temperature and incoming shortwave radiation with NEP. While the response of NEP to Rg was more consistent across sites, the effect of soil and air temperature on NEP varied largely across sites. Average variable

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explained by the random forest regression for NEP in winter was 78% (Supplementary Figure 4). 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 8). For example, in the three coldest 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 8). When looking into partitioned fluxes, radiation dominated the effect on winter GPP and temperature dominated the effect on winter respiration fluxes (Figure 8). Particularly in the colder sites the effect of radiation was the least important (Figure 8).

Effect of warming on NEP anomalies

Across the colder sites (low latitude or altitude < 1000 m a.s.l.) where NEP changed significantly in winter 2020 (IT-SR2, BE-Bra, DE-Obe), average NEP anomaly was +75%. In the warmer 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% (i.e., reduced net uptake) (Figure 4). Changes in NEP are attributed only to changes in climatic factors because except in FI-Let the forests did not undergo significant changes in the canopy density. 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).

Figure 9 shows the sensitivity of NEP anomalies to anomalies of air temperature, soil temperature and radiation across different sites. Overall, the sensitivity of NEP anomalies to soil temperature anomalies was larger than to anomalies of air temperature and radiation, as shown by the test of the slope of change in NEP anomalies (Figure 9).

While the relationship between air temperature and soil temperature was stronger than the relationship between radiation and air temperature during the winter, we observed large variability in the strength of the relationship between soil and air temperature across the sites, as it is shown in Table 3. Nevertheless the relationship between air and soil temperature was stronger across warmer sites (Table 3).

Discussion

Warming of the air and the soil in winter

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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 colder sites (Figure 2, Supplementary Figure 11).

The strength of the coupling between the air and the soil temperature was not similar across all sites. In forests, topsoil temperature is directly affected by changes in air temperature; however, several underlying processes and properties modify the magnitude of decoupling between air and soil temperatures. This decoupling can reach up to 10 degrees, depending on the season and the properties of the biome type (Lembrechts et al. 2022). These underlying factors and processes 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). 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 ($p < 0.05$, r = 0.69, Table 3) as forest canopy structure influences the coupling of air and soil temperature in forest ecosystems, for example by shading the soil and reducing the snow depth beneath denser canopies (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, winter warming was concurrent with increased net CO_2 emissions (Figure 4). Except in the southernmost forest site, winter warming decreased net ecosystem productivity of the coniferous forests albeit to varying degrees. 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 air temperatures, and CO_2

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uptake increases. Warming of the air - if not translated into a direct warming of the soil– might not interrupt the dormant season (Bowling et al. 2024) 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 (Supplementary Figure 1).

CO_2 fluxes are sensitive to changes in both temperature and light (Supplementary Figures 5-9), and site baseline climate conditions showed to be a good proxy of how changes in light and air temperature lead to changes in NEP. 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 and temperature is no longer limiting, radiation becomes a larger constraint on NEP (Figure 9) (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, meaning that soil respiration increases faster in response to warming (Wang et al., 2014), however microbial C limitation can reduce expected increase in respired CO_2, if not countered by greater labile C inputs from plant material and root exudates (Sullivan et al., 2020). In addition, aboveground productivity increases with increase in temperature (Supplementary Figure 6, 7) and this can enhanc 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 (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). In our study sensitivity of Reco to air temperature (Q10) remained did not change significantly during the warm winter, and was copmarabale to the Q10 during the reference peorpiod (Supplementary Figure 10).

A decrease in the snowpack and increased soil freezing has short-term immediate impacts on plant CO_2 uptake, but it can also leave a long-lasting negative impact on the functioning of trees (Repo et al. 2021). Particularly, sites with prolonged cold winter seasons could be significantly

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negatively affected by winter warming. Trees growing in northern latitudes and higher altitudes could be more adversely impacted by winter warming, as optimal temperatures in these trees are regulated by short-term temperature changes. In contrast, in ecosystems where temperature fluctuations are seasonally larger, the 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). Studies that combine ecosystem-scale flux measurements with tree-level observations have the potential to closely examine the adverse effects of winter warming on cold-adapted forests.

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 forest CO_2 fluxes. Data on the responses of photosynthetic traits on a

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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 processes to investigate the effect of extreme climatic conditions across all seasons. We further 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 effects of the warm 2019-2020 winter on CO2 fluxes in evergreen needle-leaf forests across Europe. We observed increased net CO2 emissions, especially in colder sites, due to enhanced soil respiration and reduced net ecosystem productivity. However, responses varied among sites, with factors such as forest structure and local climatic conditions creating microclimates that either buffered or amplified the impact of warming on CO2 fluxes. By integrating long-term eddy covariance data with plant-level experiments, we can gain crucial insights into how winter warming affects forest ecosystems. Future research should focus on the carryover effects of winter warming on tree responses to seasonal climatic extremes, as understanding these processes in cold-adapted ecosystems is essential for predicting how forests will respond to future winter warming.

Acknowledgements

MG acknowledges funding from the Swiss National Science Foundation project ICOS-CH Phase 3 (20F120_198227). TG acknowledges funding from Free State of Saxony (project 'Sicherstellung des Treibhausgasmonitorings an sächsischen ICOS-Standorten') and BMBF (project ICOS-D building phase), A.V. was supported by the Russian Science Foundation (grant no. 21-14-00209). BG and RM acknowledge the Research Foundation Flanders (FWO) for the support of ICOS research infrastructure. NB acknowledges funding from the SNF for ICOS-CH Phase 2 (20FI20_173691), and EcoDrive (IZCOZ0_198094). LŠ was supported by the Ministry of Education, Youth and Sports of CR within the CzeCOS program, grant number LM2023048. AS acknowledges funding from SNF project EcoDrive (IZCOZ0_198094). We acknowledge the ICOS research infrastructure for data provision.

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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	Latitude (degrees)	Longitude (degrees)	Altitude (m a.s.l.)	Canopy species (dominant first)	Mean annual temperature (ºC)	Mean annual precipitation (mm)	Number of days with snow cover
IT-SR2	43.7020	10.2909	4	*Pinus pinea*	15.7	950	0
FR-Bil	44.4936	-0.9560	39	*Pinus pinaster*	14.1	930	11
BE-Bra	51.3076	4.5198	16	*Pinus sylvestris*	11.5	750	20
DE-Tha	50.9625	13.5651	385	*Picea abies*	10.2	843	41
DE-RuW	50.5049	6.3310	610	*Picea abies*	8.7	1250	50
DE-Obe	50.7866	13.7212	734	*Picea abies*	7.4	996	90
SE-Nor	60.0864	17.4795	45	Mixed (*Pinus sylvestris*, *Picea abies*)	7.2	527	89
CZ-Bk1	49.5020	18.5368	875	*Picea abies*	7.1	1316	71
RU-Fyo	56.4615	32.9220	265	Mixed (*Picea abies, Betula pubescens*)	6.1	711	58
FI-Let	60.6418	23.9595	111	Mixed (*Pinus sylvestris*, *Picea abies*, *Betula pubescens*)	5.9	627	99
IT-Ren	46.5868	11.4336	1735	*Picea abies*	5.5	809	112
CH-Dav	46.8153	9.8559	1639	*Picea abies*	4.8	1062	139
SE-Ros	64.1725	19.738	160	*Pinus sylvestris*	4.0	614	102

SE-Svb	64.2561	19.774	267	Mixed (*Pinus sylvestris*, *Picea abies*, *Betula pubescens*)	3.2	614	106

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 (following Shekhar et al. 2023). 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	315	315
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

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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)

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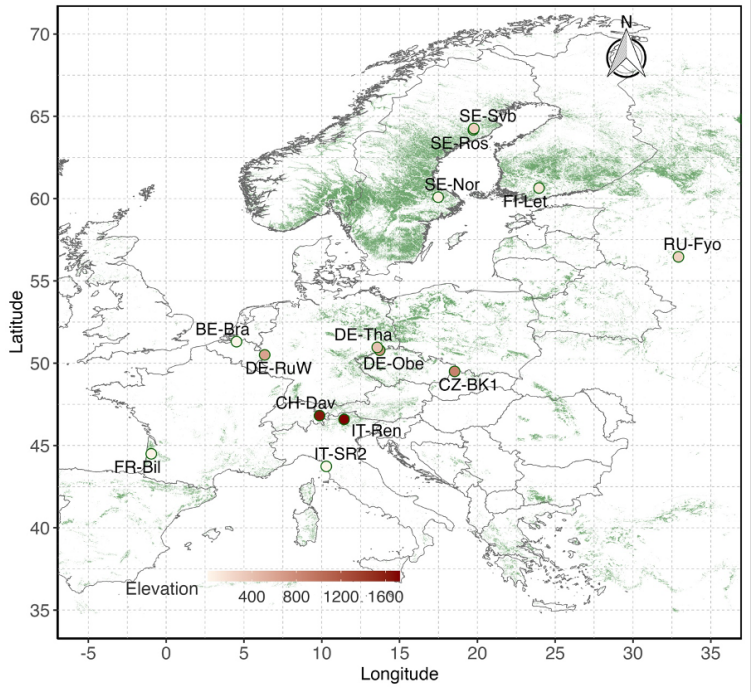

Figure 1 Location of the 14 Evergreen Needleleaf Forest (ENF) sites included in this study. Base-map is the MODIS Land Cover Product (MOD12Q1, 500m spatial resolution) showing the distribution of ENFs in Europe in 2020. Elevation of the sites ranges from 4 m a.s.l. (IT-SR2) to 1735 m a.s.l. (IT-Ren).

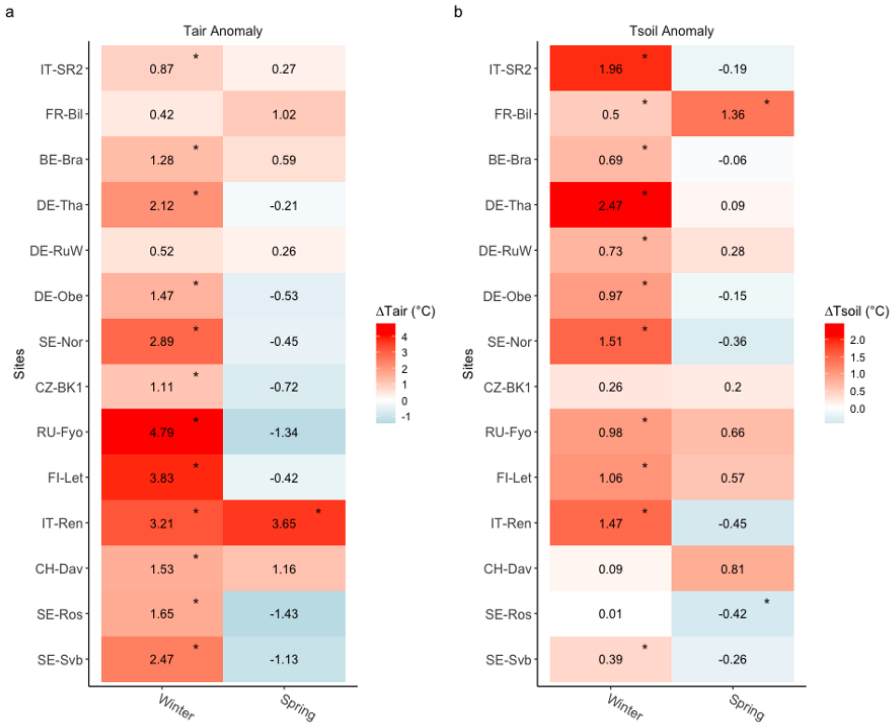

Figure 2 Seasonal changes in air temperature (T_{air}) and soil temperature (T_{soil}) in 2020 compared to the 6-year reference period (2014-2019). Asterisk marks where means in 2020 were significantly different from the reference period (p<0.05). Anomalies were calculated from daily values. Sites are listed from top to bottom in a decreasing order of site mean annual air temperature.

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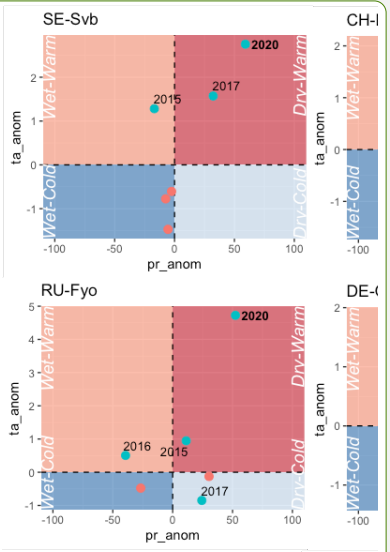

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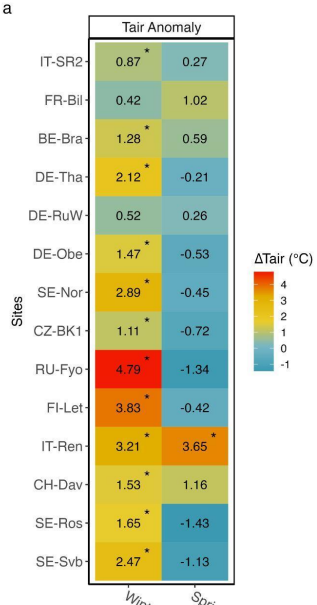

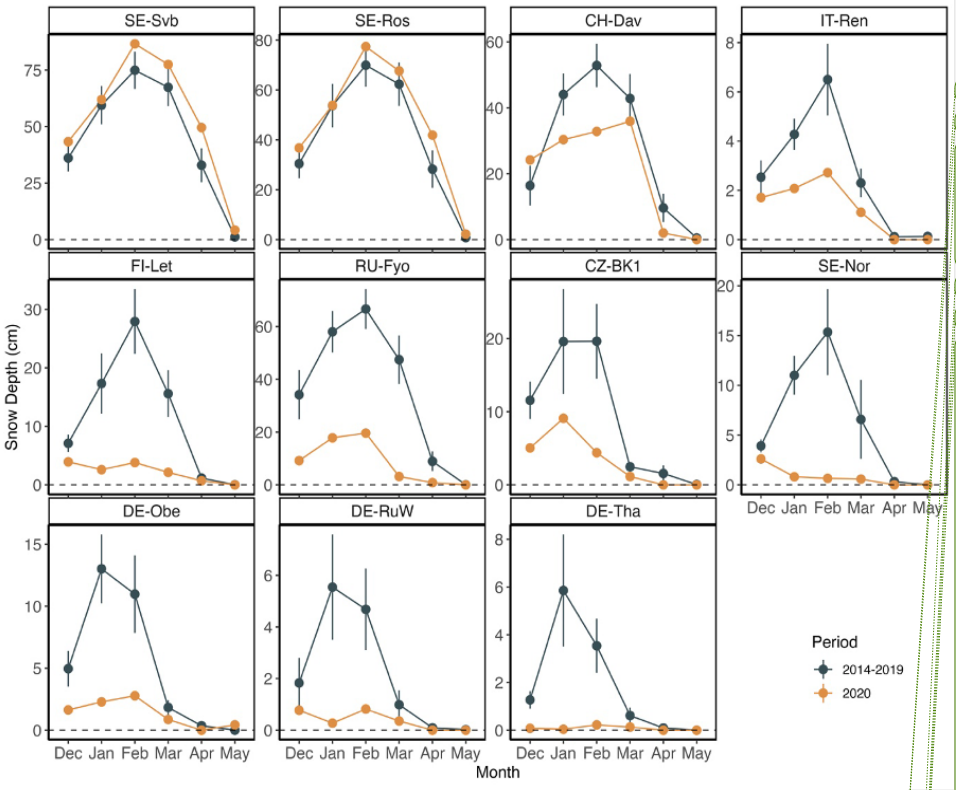

Figure 3 December to May snow depth changes in winter 2020 compared to the average winters during the reference period (2014-2019). Note that only 11 out of 14 sites have persistent snow cover in winter. Sites are ordered from top left to right, by increasing site mean temperature (SE-Svb coldest and DE-Tha warmest).

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Deleted: 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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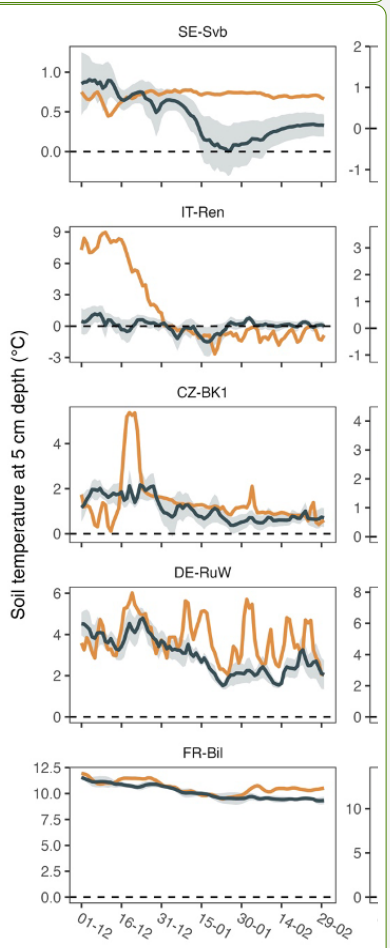

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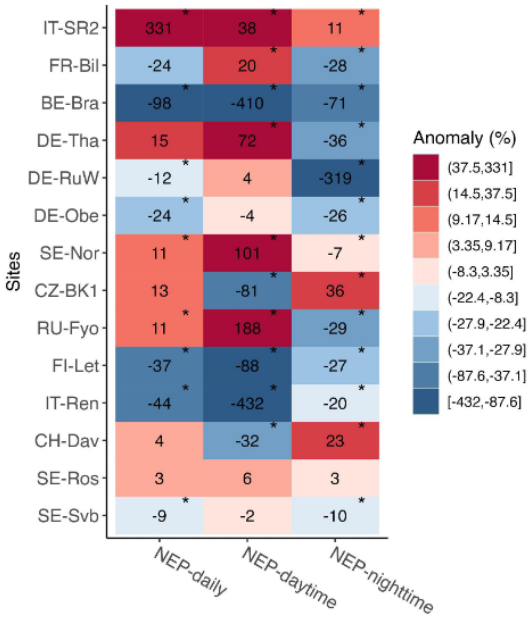

Figure 4 Relative change (anomaly, %) in mean daily, mean nighttime, and mean daytime NEP in winter 2020 compared to the 6-year reference winters (2014-2019). Asterisks mark where the mean in 2020 was significantly different from the reference period (p <0.05). Positive NEP change indicates increased 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 from top to bottom in a decreasing mean annual air temperature order.

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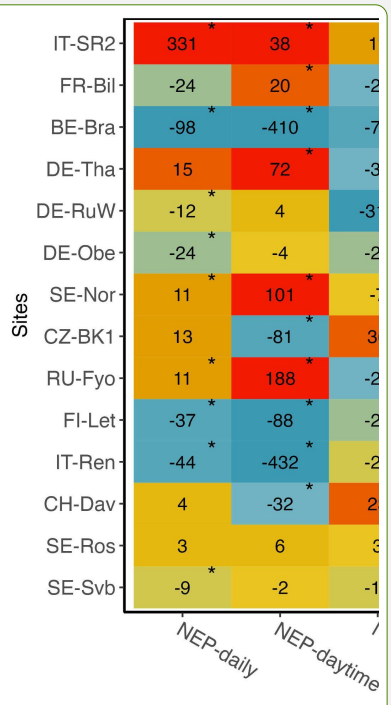

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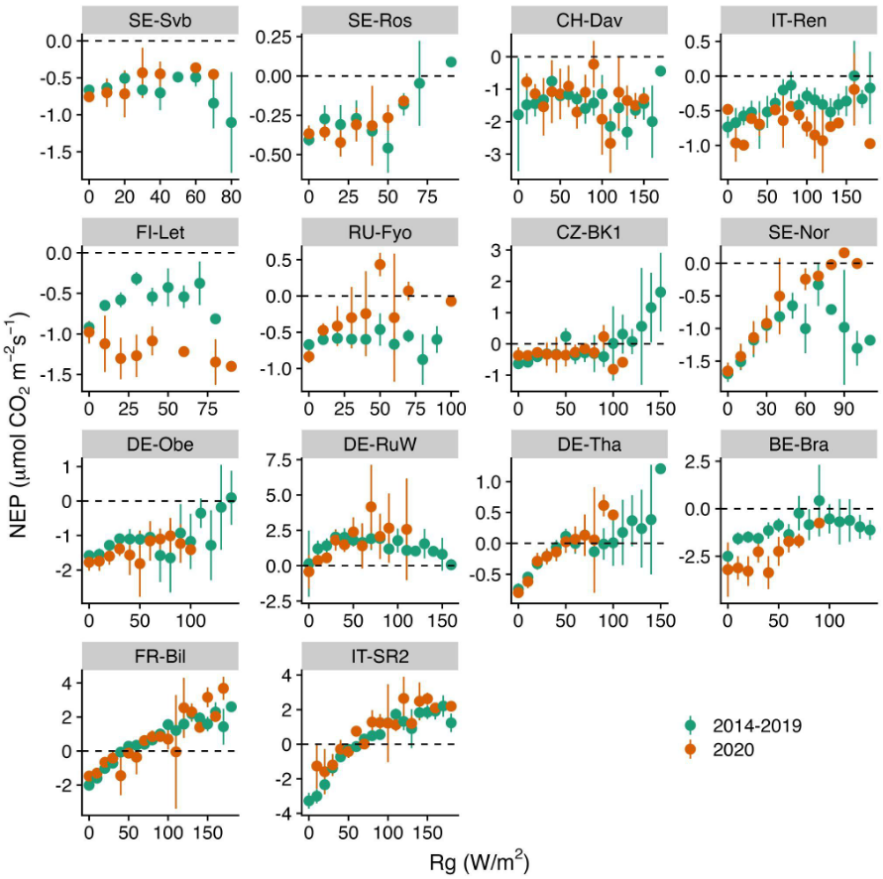

Figure 5 Comparison of NEP vs Rg (incoming shortwave radiation) binned response during the winters of the reference period (2014-2019) and winter 2020 across all sites (arranged from top left to bottom based on increasing mean air temperature). The daily mean NEP is aggregated (mean ± 95% CI as error bars) at 10 Wm^{-2} Rg bins.

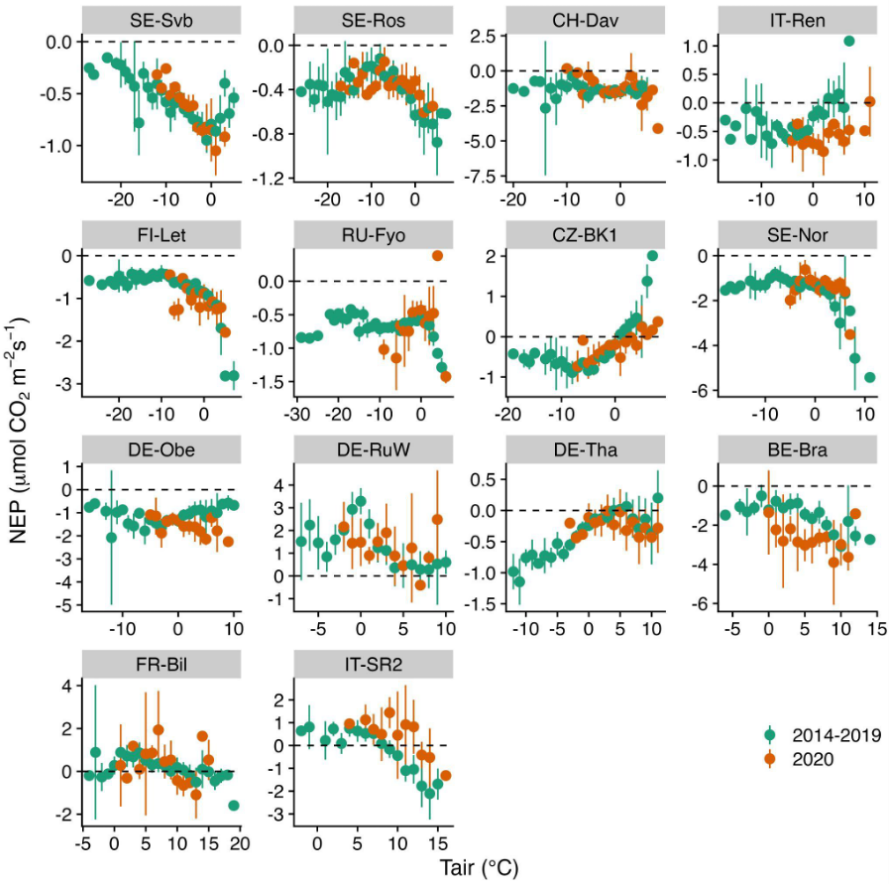

Figure 6 Comparison of NEP vs Tair (air temperature) binned response during the winters of the reference period (2014-2019) and winter 2020 across all sites (arranged from top left to bottom based on increasing mean air temperature). The daily mean NEP is aggregated (mean ± 95% C.I as error bars) at 1°C Tair bins.

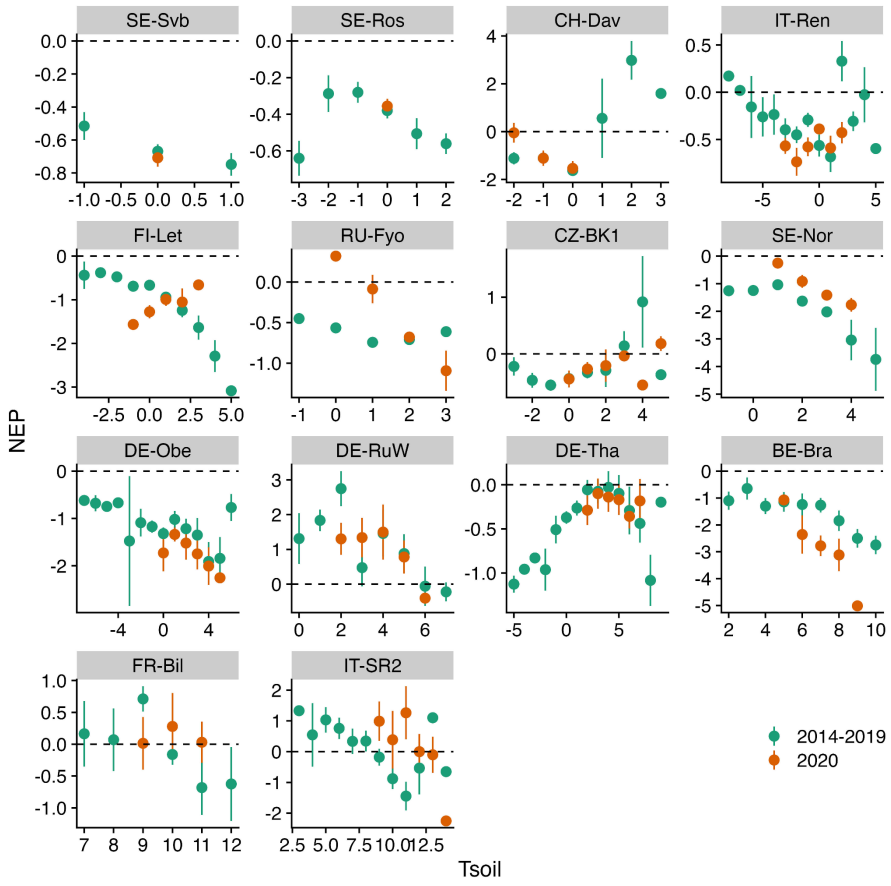

Figure 7 Comparison of NEP vs Tsoil (soil temperature) binned response during the winters of the reference period (2014-2019) and winter 2020 across all sites (arranged from top left to bottom based on increasing mean air temperature). The daily mean NEP is aggregated (mean ± 95% CI as error bars) at 1°C Tsoil bins.

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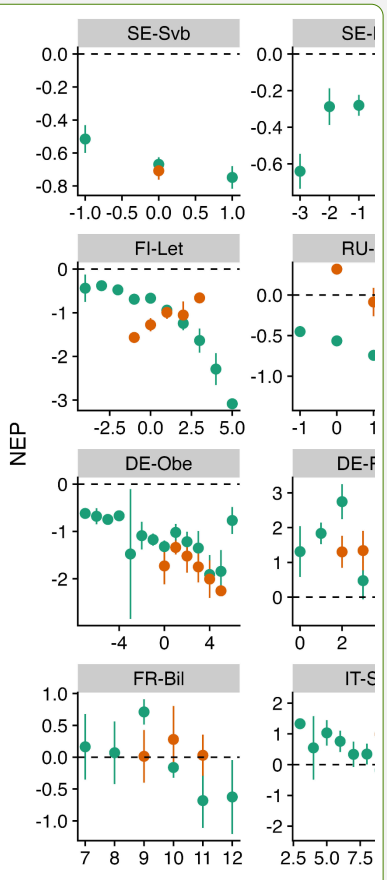

Figure 6 Comparison of NEP vs Tsoil (soil temperature) (binned) response curve during the winter of reference period (2014-2019) and 2020 across all the sites (arranged from top to bottom based on increasing mean air temperature). The daily mean NEP is aggregated (mean ± 95% CI as error bars) at 1°C Tair bins.

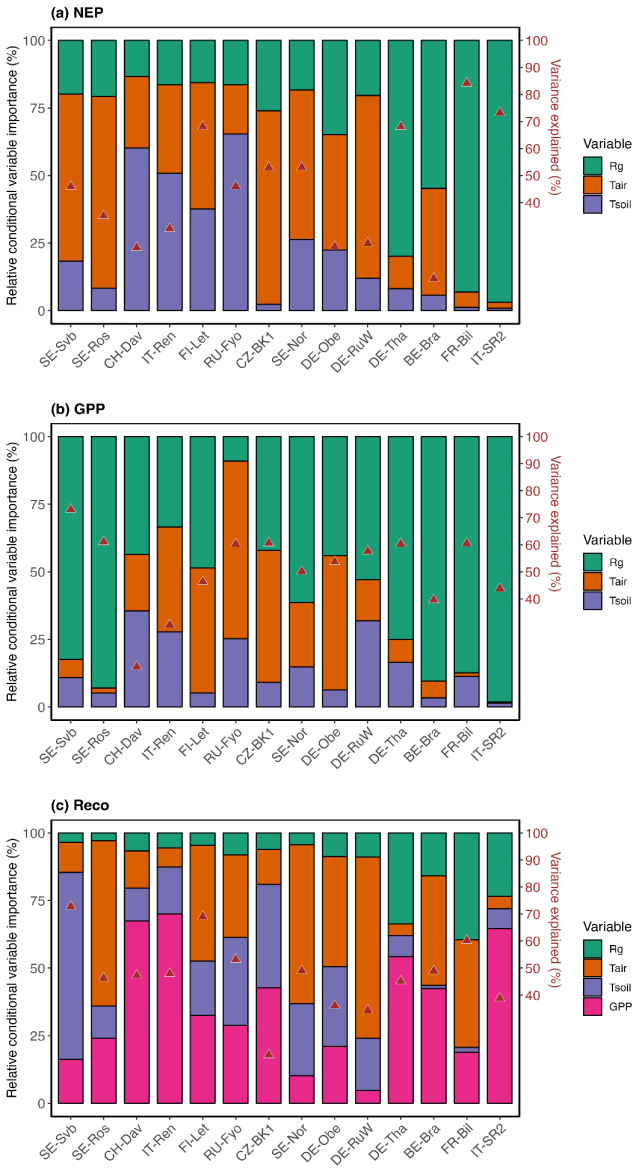

Figure 8 Relative conditional variable importance (RCVI, %) of three climatic variables for explaining the variance in daily winter NEP, GPP and Reco, and the overall variability explained (r^2) (marked with red triangles) estimated from the random forest regression analysis. The RFR model was trained on winter observations during the reference period (2014-2019). Sites are ordered by increasing site mean annual temperature (from left to right). For modelling Reco, GPP was used as an additional predictor (see the Methods section for more detail).

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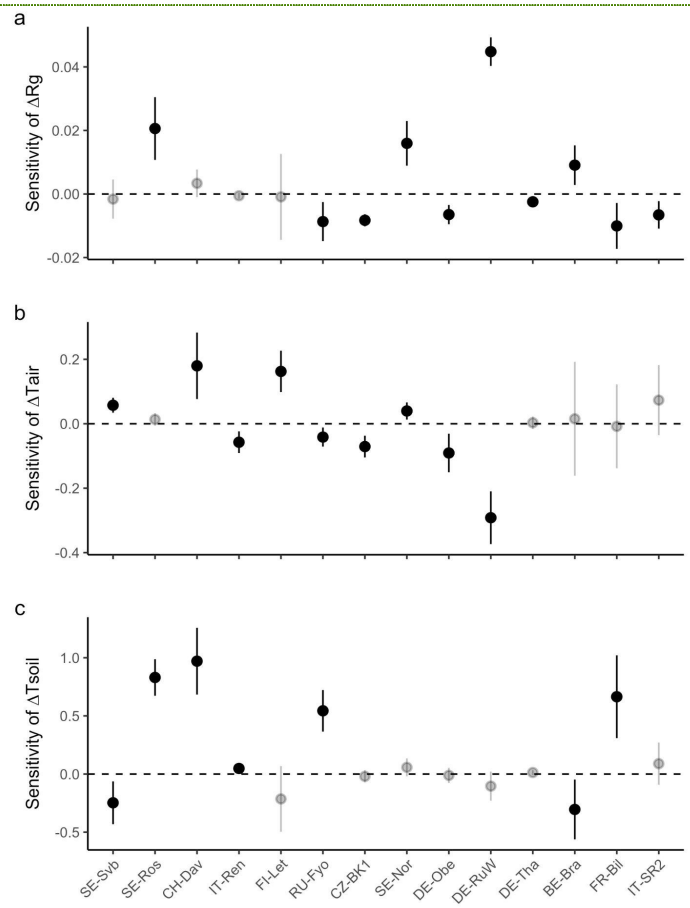

Figure 9 Sensitivity of NEP anomalies in winter (ΔNEP) to (a) anomalies of incoming solar radiation (ΔRg) (b) anomalies of air temperature (ΔTair), and (c) anomalies of soil temperature (ΔTsoil). The sensitivities represent the slope of ΔRg, ΔTair, and ΔTsoil when regressed with ΔNEP using a multivariate linear regression (ΔNEP ~ ΔRg + ΔTair + ΔTsoil). The non-significant ($p<0.05$) sensitivity is shown as a transparent point. Error-bar shows the 95% CI of the slope obtained from the multivariate linear regression. Sites are ordered by increasing site mean air temperature (from left to right).

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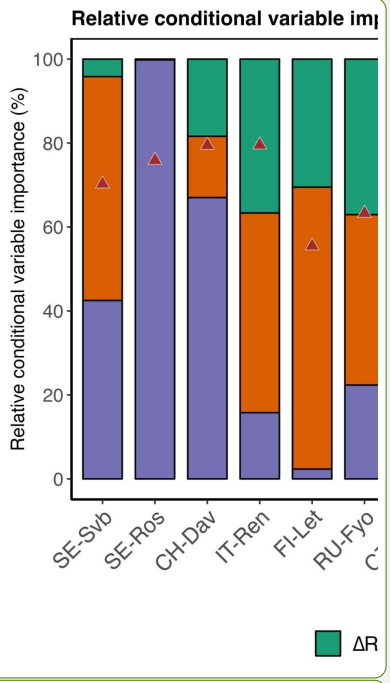

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