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Perspectives: Effect of global change drivers on carbon fluxes and resilience of European forests

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ABSTRACT

European forests play a central role for meeting the EU’s climate targets, but the declining carbon sink has left them trailing behind climate goals. Reversing this trend requires a systematic understanding of forest responses

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Nitrogen deposition
Drought
Heatwave

to shifting global change drivers, explicitly integrating aboveground and belowground processes. Here, we provide our perspective on the effects of multiple global change drivers on ecosystem-scale carbon fluxes (including both carbon dioxide (CO_2) and methane (CH_4)) and the resilience of these fluxes, based on direct flux observations (e.g., from eddy covariance towers). First, we present changes in several key drivers (warming, drought, atmospheric CO_2, nitrogen deposition, winter warming, excess precipitation, late frost), over recent decades, some of which (winter warming, windthrow, excess precipitation, late frost) have received limited attention in forest carbon assessments. Some of these—such as winter warming—are expected to become increasingly frequent in the future. We then explicitly summarize how the four (more-frequently studied) key drivers affect carbon fluxes (i.e., CO_2 and CH_4 fluxes). The response of the net CO_2 sink (i.e., net ecosystem productivity) is presented through its two component processes: gross primary productivity (GPP) and ecosystem respiration (Reco). When considered individually, global change drivers often produce relatively predictable responses in forest carbon fluxes: warming tends to enhance both GPP and Reco, elevated atmospheric CO_2 generally stimulates photosynthesis, and moderate nitrogen (N) inputs can enhance productivity in N-limited systems. However, when drivers interact, ecosystem responses frequently become non-linear, amplified, or even reversed relative to single-driver expectations. For example, warming alone may extend the growing season and increase GPP, but in combination with drought, elevated vapor pressure deficit suppresses stomatal conductance, reduces GPP, and can increase respiration losses during rewetting events. Similarly, the positive effect of rising CO_2 on productivity may be constrained by nutrient limitation or drought stress, while historical N deposition can temporarily sustain CO_2 fertilization effects but also increase vulnerability to climatic stressors. Under compound disturbances—such as drought followed by extreme precipitation or winter warming—ecosystem respiration pulses and structural damage can further reduce net ecosystem productivity (NEP). Collectively, these findings indicate that forest carbon dynamics cannot be reliably inferred from single-driver responses alone; instead, interacting drivers shape ecosystem resilience through feedbacks among physiological processes, soil biogeochemistry, and disturbance regimes, often leading to thresholds or tipping points in carbon sink strength.

1. Background

Forests play a vital role in the global carbon (C) budget. Covering nearly 40% of the European Union's (EU) land area, they sequester approximately 280 million tons of carbon dioxide (CO_2) equivalent ($MtCO_2eq$) annually (as of 2023) (EEA, 2025). However, despite a steadily growing carbon stock, the overall carbon sink is weakening; between 2010 and 2020, the sequestration capacity of EU forests declined by nearly one-third, from 466 to 295 $MtCO_2eq$ per year, based on national inventories (EEA, 2025). Consequently, EU forests are struggling to meet their role as a key C sink essential for achieving EU climate targets (Korosuo et al., 2023). Projections suggest that between 2026 and 2030, the land use, land-use change, and forestry (LULUCF) sector will fall short of the EU target of reducing emissions by 42 $MtCO_2eq$ compared to the average C sink of 2016–2018, as set by the LULUCF Regulation (Regulation (EU) 2018/841, 2018). To reverse this trend, it is critical to better understand and predict the impact of changing climate and air pollution on forest sector mitigation potential (McDowell et al., 2021; Migliavacca et al., 2025; Gruenig et al., 2026). Moreover, maintaining forest biodiversity is key to enhancing ecosystem stability and function (Jucker et al., 2014; Musavi et al., 2017). Immediate action is needed to protect and restore forest biodiversity to sustain forest resilience and maintain their long-term capacity for C sequestration and storage (Di Sacco et al., 2021; Imbert et al., 2021; Mahecha et al., 2024; Naudts et al., 2016).

Increasing global temperatures, primarily driven by greenhouse gas emissions from anthropogenic activities and land-use changes, are raising concerns about the stability and functioning of forest ecosystems (McDowell et al., 2020). Under ongoing climate change, forests are expected to experience shifts in productivity, composition and structure (Aber et al., 2001; Boisvenue and Running, 2006; Clark et al., 2016). At the same time, forests are simultaneously influenced by multiple interacting global change drivers, including nitrogen (N) deposition, increasing atmospheric CO_2 concentrations, and intensifying drought and heat. However, research on how these factors collectively affect ecosystem C fluxes remains limited. Understanding these links is crucial for predicting the future dynamics of the EU forest C sink. Accurately forecasting forest responses to these multiple stressors, including the interplay between stressors and forest structure (i.e., tree height, age structure), is essential for guiding adaptive forest management strategies (Dalmonech et al., 2022; McDowell et al., 2021). To maintain and enhance the EU forest C sink under global change, policy and management strategies must focus on ecological resilience (Holling, 1973), which is a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables (Gunderson, 2000; Holling, 1973; Ingrisch and Bahn, 2018; Nicotra et al., 2010). The resilience of trees and forest functioning (e.g., growth, water-use efficiency) has been extensively investigated, especially in response to disturbances (e.g., drought, fire, insect outbreaks); but the long-term and large-scale dynamics of C fluxes and forest net C sink remain largely unexplored. A fundamental challenge remains to determine how the components of forest C fluxes, and consequently the net C sink, respond to the complex interplay of multiple global change drivers, for example, climate extremes and air pollution. In this context, the term C flux specifically refers to the exchange of C between ecosystems and the atmosphere, primarily in the form of greenhouse gases, mainly CO_2 and methane (CH_4). Other forms of C transfer, such as dissolved organic carbon (DOC), particulate carbon (POC), or black C fluxes, are not considered in this study unless explicitly stated.

The capacity of forests for C uptake is determined by Net ecosystem productivity (NEP) which is the balance between gross primary productivity (GPP) and ecosystem respiration (Reco) (i.e., NEP = GPP - Reco). This balance determines if a forest is a source (negative NEP) or sink of CO_2 (positive NEP). In accordance with flux terminology and the focus of this paper, GPP represents the ecosystem-level photosynthesis, including trees and ground vegetation, while Reco consists of the sum of heterotrophic respiration (R_h, i.e., during decomposition) and autotrophic respiration from vegetation and soil (Brüggemann et al., 2011). Autotrophic respiration, including growth (R_g) and maintenance respiration (R_m), is primarily controlled by mean annual temperature (MAT) and biomass (Banbury Morgan et al., 2021; Collalti et al., 2020a, 2020b; Luo et al., 2025; Piao et al., 2010). Heterotrophic respiration is a significant component of Reco, represents the C losses from the decomposition of litter detritus and soil organic matter by microorganisms, and depends on (soil) temperature and soil moisture (Tang et al., 2020). Soil respiration, which is the largest component of Reco, remains also tightly linked to aboveground C fluxes and vegetation productivity (Brüggemann et al., 2011; Migliavacca et al., 2011; Ryan and Law, 2005). Because NEP is determined by the balance of GPP and Reco, uncertainties in the response of each of these two components can lead to divergent trajectories in the forest C sink. Reducing these uncertainties requires a thorough evaluation of how GPP and Reco respond to individual and combined global change drivers, and how these responses propagate to affect NEP.

At the same time, the forest C–climate balance is not governed by CO_2 exchange only but also by Methane (CH_4) fluxes. Forests can act as both sources and sinks of CH_4 (Saunois et al., 2024; Gauci, 2025), yet the environmental controls, process-understanding, and quantitative constraints on CH_4 flux responses to global change still remain very limited compared to CO_2 (Covey and Megonigal, 2019; Ni and Groffman, 2018; Barba et al., 2024; Gauci, 2025). Integrating CH_4 fluxes into assessments of forest C dynamics is therefore essential for a comprehensive understanding of ecosystem responses to global change, particularly for forests with organic soil at the northern latitudes and forested wetlands in temperate zone, where shifts in water table strongly affect CH_4 flux dynamics (e.g., Jurasinski et al., 2024).

Similar to forest CO_2 exchange, net forest ecosystem CH_4 exchange is a result of simultaneous exchange of gases from the forest soil, tree stems and canopies, herbaceous plants, cryptogamic covers, deadwood, and water bodies (in case of forested wetlands). Temperate forest soils are estimated to be the strongest sinks of CH_4 ($-4.79\ \mathrm{kg\ ha^{-1}\ yr^{-1}}$) among natural forest ecosystems (Dalal and Allen, 2008). In upland forest soils with predominant aerobic conditions, CH_4 can be oxidized by methanotrophs, leading to CH_4 uptake from the atmosphere (Krebs et al., 2024). In contrast, soils of wetland forests characterised by anaerobic conditions, can be sources of CH_4 due to methanogenesis (Smith et al., 2003). Plants including trees might substantially contribute to the forest CH_4 exchange by transporting soil-produced CH_4 via stems and leaves into the atmosphere (e.g., Pangala et al., 2017; Machacova et al., 2023), by producing and oxidising CH_4 in plant tissues (e.g., Wang et al., 2026), by consuming CH_4 from the atmosphere (e.g., Machacova et al., 2021), and by modifying C turnover processes in the adjacent soil (Covey and Megonigal, 2019). Cryptogamic covers might additionally contribute to the forest CH_4 exchange by their CH_4 emission or uptake depending on the environmental conditions (Lenhart et al., 2015; Machacova et al., 2021). Deadwood as an important biomass pool and C storage within forests might be another source of CH_4 in forests, thus showing internal CH_4 concentrations well above the ambient CH_4 concentrations (Covey et al., 2016). Unfortunately, the CH_4 exchange within forest ecosystems appears to be much more complex than previously thought, involving a combination of simultaneously running processes of production, consumption, transport, and emission and uptake of CH_4 by plants, soils and microbes (Barba et al., 2024). These processes, particularly their contribution to the net forest CH_4 exchange remain poorly understood, let alone quantified.

Recent research has revealed that besides commonly studied forest soils, also tree stems can be significant sources of atmospheric CH_4 (e.g., Barba et al., 2024). Some upland tree species can even take up CH_4 from the atmosphere (Gauci et al., 2024); however, the extent of this newly revealed process requires more investigation. Moreover, leaves of mature trees are still almost completely excluded from field flux measurements, but with first studies showing possible substantial leaf contribution to the tree and forest CH_4 exchange (e.g., Machacova et al., 2016; Vainio et al., 2022; Karim et al., 2024). Hence, the common lack of leaf CH_4 fluxes in ecosystem greenhouse gas flux calculations introduces substantial uncertainty in forest ecosystem CH_4 (and C) budget estimates. Further, rarely studied widespread cryptogamic covers have been excluded in previous greenhouse gas flux studies, even though they may be equally important in forest CH_4 exchange as soil and trees (Machacova et al., 2021).

The gas exchange capacity of trees and their contributions to ecosystem CH_4 exchange appear to depend on many aspects, such as on soil and site parameters, environmental conditions, tree size, age and health conditions, plant tissues parameters, and seasonal dynamics (e.g., Machacova et al., 2023; Barba et al., 2024; Wang et al., 2026). As a result, a high spatial variability in tree CH_4 exchange is frequently observed not only at inter-species, but also at intra-species and even at intra-individual levels (e.g., Covey and Megonigal, 2019; Moldaschl et al., 2021; Machacova et al., 2023; Mochidome and Epron, 2024; Wang et al., 2026). However, the underlying causes remain largely unexplained in most cases. The lack of causes behind the high spatial gas flux variability prevents the correct tree stem and leaf gas flux upscaling to the tree and ecosystem level, and thus the correct estimation of the overall forest ecosystem CH_4 exchange. Moreover, the temporal variability at diurnal, seasonal and inter-annual level is also typical for tree and forest CH_4 fluxes (e.g., Schindler et al., 2021; Mander et al., 2022; Machacova et al., 2023; Klaus et al., 2024; Bréchet et al., 2025). Without continuous long-term measurements of CH_4 exchange collected across a variety of tree species and site conditions, it remains extremely difficult to quantify the CH_4 fluxes from trees and therefore from forest ecosystems at daily, seasonal and annual time scales. In this perspective article, we assess the effects of multiple global change drivers on forest C fluxes and their resilience as C sinks. Specifically, Section 2 provides an overview of how global change drivers have varied across Europe over the last 50 years; Section 3 assesses their effects on C fluxes—both CO_2 and CH_4—at the ecosystem-scale, and C sink dynamics on various temporal scales. Section 4 then discusses ecosystem C fluxes under global change, highlighting the role of forest management, biodiversity and forest structure diversity on the European forest C sink under multiple interacting global change drivers. Section 5 concludes by synthesizing the key findings presented above.

2. Key global change drivers

The main global change drivers selected in this study and their observed variations over the past five decades are summarized in Table 1. The four main drivers of change include warming (both gradual trends as well as events), drought, atmospheric CO_2 concentrations, and N deposition. We also included understudied extremes such as winter warming, excess precipitation, and late frost to reflect both well-established and relatively unexplored pressures on forest functioning.

Europe has experienced a steady rise in air temperature, with statistically significant increases of around 0.1°C per year since 1990

Table 1
Overview of global change drivers and their changes in Europe over the past 40 years (the longest period of direct C flux observations in Europe).

Global change driver	Past changes in Europe
Warming	Since 1985, air temperature in Europe has risen steadily, with the strongest warming observed in spring ($0.061\ ^\circ\mathrm{C\ yr^{-1}}$) and the least pronounced in autumn ($0.045\ ^\circ\mathrm{C\ yr^{-1}}$) (Twardosz et al., 2021).
Drought	Droughts have increased, particularly since 2015 (Büntgen et al., 2021), as indicated by increased vapor pressure deficits (VPD) resulting from higher air temperatures and additionally in some regions reduced precipitation (Grossiord et al., 2020).
Atmospheric CO_2	Mean ΔCO_2 has increased by $1\text{–}2\ \mathrm{yr^{-1}}$ (~30% growth between 1990–1995 and 2000–2005) (Ramonet et al., 2010).
N deposition	Inorganic N deposition has decreased since the mid 1990s, particularly for NOx from measurements of wet deposition (Schmitz et al., 2019) and from modelled estimates of total N deposition (Schwede et al., 2018), but still exceeds the 'critical load' in some regions in Europe ($10\text{–}20\ \mathrm{kg\ N\ ha^{-1}\ yr^{-1}}$ for deciduous forests and $5\text{–}15\ \mathrm{kg\ N\ ha^{-1}\ yr^{-1}}$ for coniferous forests (Bobbink et al., 2022))
Understudied extremes	
Winter warming	In 2020, Europe experienced the warmest winter on record since 1981, with the most pronounced warming observed in northeastern Europe (Copernicus Climate Change Service, 2021).
Excess precipitation	Increase in recent decades, particularly in northern and central regions extreme precipitation events have increased (André et al., 2024)
Late frost	Increase of frost days during the growing season (Liu et al., 2018a)

particularly evident in northern regions and in countries surrounding the Black Sea (Fig. 1a). In contrast, precipitation trends since 1990 show spatial heterogeneity, with significant declines limited to specific regions (Fig. 1b). Atmospheric drought, reflected by increasing vapor pressure deficit (VPD), has intensified across large parts of Europe (Fig. 1c), while significant declines in soil moisture are primarily observed in areas exhibiting reduced precipitation (Fig. 1d). Over the same period, anthropogenic nitrogen and sulfur emissions have significantly decreased across the continent due to emission reduction policies and economic transformations (Erisman et al., 2003; Vestreng et al., 2007). This has led to substantial declines in atmospheric deposition of these elements on terrestrial ecosystems (Fig. 1e–f). In the following sections we provide an overview of temporal trends in each of the drivers responses of forests to these drivers, in terms of C fluxes, are outlined in Section 3).

2.1. *Extreme warming*

Rising global temperatures have led to an increase in the number of hot days, and a decline in the number of cold and frost days across nearly all land areas. Additionally, global warming has significantly increased the likelihood of climate extremes (Nasong et al., 2025). For instance, Stott et al. (2004) estimated that human-induced climate change has likely doubled the risk of heatwaves similar in magnitude to the extreme 2003 European heatwave. Particularly in Europe, a recent analysis shows a remarkably fast rate of change in the characteristics of extreme warming, especially in summer, leading both the ecosystems and the human population to experience unfamiliar warm conditions (Dosio et al., 2025; Jordan et al., 2024).

2.2. *Drought*

Tree-ring isotope records reveal that European forests have experienced unprecedented droughts since 2015 (Büntgen et al., 2021), with prominent droughts in the summer of 2018 (Buitink and Swank, 2020; Gharun et al., 2020; Smith et al., 2020) and 2022 (Gharun et al., 2024; van der Woude et al., 2023). While trends in relative humidity (RH) between 1979 and 2014 have varied regionally, with no single factor identified as the dominant driver (Vicente-Serrano et al., 2018), rising air temperatures have increased atmospheric dryness by elevating saturation vapor pressure and thereby increasing VPD, even where RH changes are modest. Elevated VPD, intensifies atmospheric drought stress on vegetation (Grossiord et al., 2020). Climate projections indicate that this trend will persist, with compounded soil and atmospheric dryness expected to triple in Europe by the end of the century (Shekhar et al., 2024).

2.3. *Elevated CO_2*

Global atmospheric CO_2 concentrations have risen from approximately 250 ppm in pre-industrial times to around 430 ppm today, primarily driven by fossil fuel combustion and land-use change (IPCC, 2023). This increase has been partially offset by CO_2 uptake from the terrestrial biosphere and the oceans (Friedlingstein et al., 2025). Beyond its role in radiative forcing—contributing to climate change and associated warming and drought trends—elevated CO_2 levels can have a more direct physiological impact on trees, with cascading impacts on their C sequestration (Walker et al., 2022).

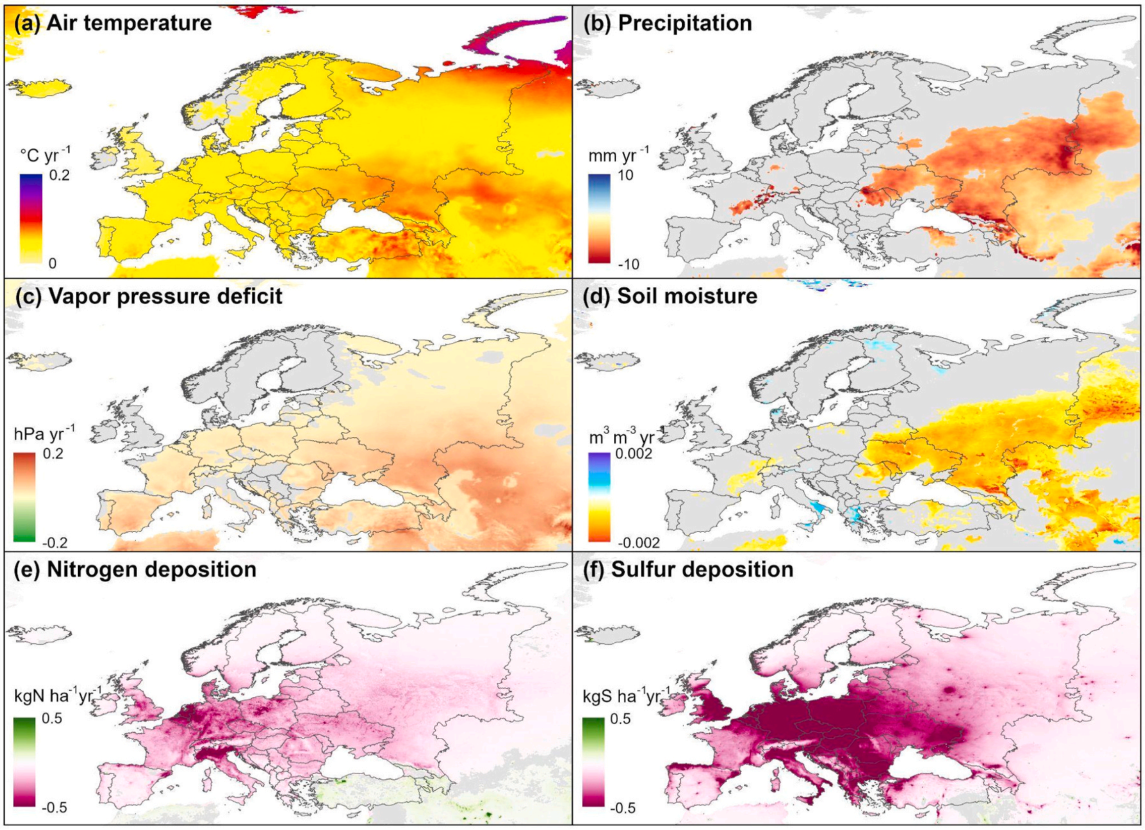

Fig. 1. Annual trend of global change drivers. Air temperature (a), precipitation (b), vapor pressure deficit (c), and soil moisture (d) are derived from ERA5-Land for the period 1990–2023. Nitrogen (e) and sulfur (f) deposition are derived from the EMEP product for the period 1990–2023. Grey areas indicate a nonsignificant temporal trend.

2.4. N deposition

Human activities, especially agriculture and industry, have greatly changed the global N cycle, increasing atmospheric reactive N and its deposition on land by 46 Tg N yr^{-1} compared to pre-industrial levels (Schlesinger, 2009). European N emissions and corresponding deposition increased from pre-industrial times till the mid-1980s, followed by a decrease since the 1990s (Engardt et al., 2017). Data from the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) have identified central Europe as a hotspot for wet N deposition, with rates around 10–20 kg N ha^{-1} yr^{-1}. In contrast, the continental parts of Fennoscandia experience some of the lowest deposition rates, below 5 kg N ha^{-1} yr^{-1} (Schmitz et al., 2019). Over the past three decades, inorganic N deposition has declined, with nitrate levels decreasing more rapidly than ammonium (Beachley et al., 2024; Schmitz et al., 2019; Waldner et al., 2014). This difference is largely attributed to effective policies targeting oxidized nitrogen emissions, whereas reducing ammonia emissions across the European continent is still a challenge (European Environment Agency, 2024; Sutton et al., 2013). Despite the overall reduction, N deposition in many forests still exceeds the critical load—estimated at 10–20 kg N ha^{-1} yr^{-1} for deciduous forests and 5–15 kg N ha^{-1} yr^{-1} for coniferous forests (Bobbink et al., 2022). Exceeding these thresholds can lead to cascading negative effects on forest functioning and health, including tree growth, soil acidification, nutrient imbalances, and increased susceptibility to stressors (Etzold et al., 2020; Galloway et al., 2003).

2.5. Understudied extremes

2.5.1. Winter warming

While much research has focused on extreme climate events during the growing season, the effects of winter warming remain understudied (see however Gharun et al., 2025; Kreyling et al., 2019). In northern latitudes and high-altitude regions dominated by evergreen conifers, winter warming trends are particularly pronounced (IPCC, 2023). Europe experienced its warmest winter on record in 2020, with the greatest temperature anomalies observed over northeastern Europe relative to the 1981–2020 reference period (Copernicus Climate Change Service, 2021). This record-breaking event underscores the increasing frequency of winter warming anomalies and highlights the need to better understand its implications for forest C dynamics (Copernicus Climate Change Service, 2021).

2.5.2. Excess precipitation

Beyond rising temperatures, future climate scenarios project an increase in precipitation extremes (Thackeray et al., 2022). Extreme rainfall can negatively impact tree growth and survival, particularly in regions prone to waterlogged soils, where prolonged saturation may impair root function and increase susceptibility to pathogens (Kramer et al., 2008; O'Brien et al., 2024).

2.5.3. Late frost

Despite overall warming trends, late frost events remain a persistent threat to forests. Observations indicate an increase in frost days during the growing season across the Northern Hemisphere, particularly in Europe (D'Andrea et al., 2020; Liu et al., 2018). Model projections suggest that more than one-third of European forest areas are increasingly threatened by frost damage (Zohner et al., 2020). However, the risk is not uniform across landscapes and tree species. A study analyzing data from 50 locations in Switzerland between 1975 and 2016 found a significant increase in frost risk at elevations above 800 m, while lower elevations showed little to no change (Vitasse et al., 2018). These findings underscore the need for region-specific assessments of frost-related damage to better inform forest management strategies.

3. Response of forest C fluxes to global change drivers

Forests absorb large amounts of atmospheric CO_2 through GPP. However, they also release CO_2 back through Reco. These two large fluxes, operating in opposite directions, determine how much C is taken up by the ecosystem or released back to the atmosphere. We identify three pathways through which global change drivers influence net C uptake in forests: (1) modifications in instantaneous rates of C uptake and release, (2) shifts in the balance between GPP and Reco, as well as CH_4, and (3) variations in the duration of the net C uptake period due to alterations in the length of the growing season.

3.1. Response to warming and drought

3.1.1. CO_2 fluxes

The effects of warming and drought on C fluxes are strongly interlinked and can be substantially altered when they interact. It is assumed that future changes in climate will decrease land C uptake with medium confidence (Canadell et al., 2021). Heatwaves alter the ability of European ecosystems to act as a C sink. The frequent dry summers experienced in recent years (e.g., Gharun et al., 2024; Smith et al., 2020), especially in Europe's central and southeastern regions, caused a severe decrease in net forest C uptake (a reduction by 56–62 Tg C) over the drought-affected areas.

Studies conducted at the European FLUXNET sites showed that GPP was relatively insensitive to short-term heat anomalies or droughts as single drivers, while it considerably declined when the two drivers (drought and warming) interacted (Buttlar et al., 2017). Furthermore, the impact of heatwaves and drought on GPP is dependent not only on the magnitude of the events but also on their duration (Buttlar et al., 2017). For example, the 2003 European heatwave event reduced forest GPP by 30% across Europe (195 g C m^{-2} yr^{-1}), an unprecedented drop compared to the last century (Ciais et al., 2005). Similarly, a more severe heatwave and drought in 2018 decreased forest GPP by 10% (98 g C m^{-2} $season^{-1}$) across Europe compared to the reference year 2016 (Fu et al., 2020). When a moderate drought occurred in a mixed oak and maple forest during the period between leaf bud break and full expansion, forest GPP declined by 16% (200 g C m^{-2} yr^{-1}) (Noormets et al., 2008) suggesting that drought effects depend on the timing of the event relative to phenological development.

The above-mentioned decline in forest GPP during the 2018 drought likely resulted from the combined effect of a strong negative influence of air temperature and VPD, a reduced positive contribution of radiation (photosynthetic photon flux density), and an intensification of water stress as soil water deficit increased (Fu et al., 2020). During the 2018 heatwave, reductions in GPP were closely linked to decreased stomatal conductance observed across eleven Nordic forests (Lindroth et al., 2020). While GPP responses in these forests were predominantly negative, two northern sites exhibited increased GPP, likely due to temperature-driven stimulation of GPP (Lindroth et al., 2020). Evidence from ecosystem-scale observations shows that, depending on the local climatic conditions, spring drought can increase GPP, as found for an evergreen forest in Switzerland (Gharun et al., 2020; Wolf et al., 2013) and a floodplain forest in the Czech Republic (Kowalska et al., 2020).

When warming is considered as a single driver, independent of drought, it generally leads to an extension of the growing season. However, when combined with drought, this effect can be reversed. Menzel and Fabian (1999) estimated an average total increment of 10.8 days for European forests from 1959 to 1993, and this trend was confirmed by other studies (Kolářová et al., 2014), but an opposite trend in the 2011–2020 decade was found due to an increase in atmospheric evaporative demand (Rahmati et al., 2023). A longer growing season may imply an enhancement of C uptake (increased GPP), especially through the autumn season (Zohner et al., 2019). However, evidence from both observational and modeling studies presents a more nuanced picture. Using one of the longest continuous records of CO_2 fluxes (collected in Switzerland), Krebs et al. (2025) found that changes in the length of the growing season did not account for the non-linear trend in annual NEP between 1997 and 2023. Similarly, model simulations across European forests predict a consistent decline in the C sink strength under climate change, even if the number of days with net C uptake has increased in evergreen needle-leaf forests. This suggests a decoupling between the duration of the C sink period and the total annual C uptake. In deciduous forests, the number of C sink days has remained relatively stable throughout the century, yet a reduction in annual C uptake is still projected (Morichetti et al., 2024).

The effect of warming and drought on forest NEP largely depends on respiration responses. Plant respiration (R_a) is directly influenced by photosynthesis at the individual plant level (Collalti et al., 2020b; Högberg et al., 2001) and also at the ecosystem level (Larsen et al., 2007). Moreover, photosynthesis and plant productivity are important drivers of both soil respiration (e.g., Janssen et al., 2001), and Reco (e.g., Migliavacca et al., 2011), and in some cases may outweigh the influence of temperature (García-Palacios et al., 2021; Morichetti et al., 2024; Quan et al., 2019).

Consistent evidence shows that, warming can accelerate both autotrophic and heterotrophic respiration associated with soil decomposition, leading to C losses and a positive climate feedback, provided that moisture does not limit respiration (García-Palacios et al., 2021; Morichetti et al., 2024). However, confidence in model projections of warming-induced increases in global autotrophic and heterotrophic respiration remains low due to the misrepresentation of key processes. These include temperature acclimation of autotrophic respiration (Smith and Dukes, 2013) and several processes affecting soil carbon dynamics in land surface models, such as microbial dynamics, permafrost thaw, the role of photosynthetic inputs in enhancing soil respiration, and peatland drainage (Canadell et al., 2021). During heatwaves, the causal effect strength of GPP on respiration is enhanced, with spatial heterogeneity driven by local climate and vegetation properties (Ping et al., 2023). However, respiration does not increase indefinitely with temperature but instead tends to saturate or decline beyond an optimum, consistent with enzyme-kinetic constraints such as those described by Michaelis–Menten substrate-based frameworks and thermal acclimation processes, whereby increases in growth temperature are partly offset by reduced respiration sensitivity to baseline temperature (Reich et al., 2016; Smith and Dukes, 2013). Recent evidence further suggests that under extreme climate conditions, Reco can be substantially reduced by severe root-zone soil moisture deficits, highlighting the strong limiting role of drought on respiratory fluxes, particularly when high temperatures exceed physiological optima (Dong et al., 2026). While excess water generally exerts limited influence on increasing soil respiration, severe drought typically constrains microbial and root activity, thereby reducing respiration rates (Metcalfe et al., 2010). Similarly, warming does not increase decomposition rates when soil and litter are dry (e.g., Orchard and Cook, 1983); instead, dryland-specific mechanisms of litter decay—such as photochemical degradation and humidity-enhanced microbial degradation—become increasingly important (Grünzweig et al., 2022; Wang et al., 2022). Following prolonged dry periods, subsequent rewetting by rainfall often triggers a sharp increase in Reco, commonly referred to as the "Birch effect" (Barnard et al., 2020; Birch, 1958; Jarvis et al., 2007). This pulse in Reco is associated with the reactivation of soil microbial communities, decomposition of accumulated dead biomass and necromass, and a range of physical and chemical processes in the soil (Schimel, 2018).

3.1.2. *CH_4 fluxes*

Forest CH_4 exchange is strongly regulated by soil water content. Upland forest soils typically act as sinks for atmospheric CH_4 (Krebs et al., 2024; Ni and Groffman, 2018). CH_4 uptake in these soils is closely linked to hydrological conditions; moderate drought often enhances uptake, but extremely low soil water content can suppress methanotrophic activity and thereby reduce CH_4 oxidation (Liu et al., 2019). A meta-analysis by Liu et al. (2019) found no consistent effect of ecosystem warming on CH_4 uptake in forest soils. By contrast, soils in wetland forests (e.g., floodplain, riparian, or peatland forests) with persistently high water-content or frequent flooding can act as significant sources of CH_4. Their exchange potential, however, is highly sensitive to soil water status and secondarily to temperature. Notably, a reduction in soil water content can often shift wetland soils from being net sources of CH_4 to functioning as net sinks (e.g., Mander et al., 2022).

In general, upland trees growing under low soil water conditions are predominantly low or negligible emitters of CH_4 or even sinks of CH_4, whereas wetland trees can show substantial CH_4 emissions (e.g., Covey and Megonigal, 2019; Moldaschl et al., 2021; Schindler et al., 2020). However, the contribution of trees depends on many aspects, such as forest type, tree species, tree and environmental parameters and seasonal dynamics, leading to high spatial and temporal variability in tree and ecosystem CH_4 fluxes (e.g., Barba et al., 2019; Machacova et al., 2023). The combined influence of drought and warming on soil CH_4 fluxes remains poorly understood, and available evidence is still limited.

Warming alone generally exerts a positive effect on CO_2 fluxes by enhancing both GPP and Reco. However, when warming interacts with drought, both CO_2 uptake and Reco tend to decline (Fig. 2). To improve estimates of tree- and forest-level CH_4 fluxes, there is an urgent need for long-term measurements of CH_4 exchange across a wide range of tree species and forest ecosystems. These measurements should be coupled with investigations of the underlying processes and mechanisms driving the frequently observed high spatio-temporal variability in CH_4 fluxes, as well as the response of these fluxes to global change drivers.

The processes described above are synthesised conceptually in Fig. 2, which integrates the responses of GPP, Reco, NEP, and CH_4 fluxes to individual global change drivers, illustrating the relative direction (e.g., decrease or increase) and perceived magnitude of change in carbon fluxes.

3.2. *Response to increasing atmospheric CO_2*

Elevated atmospheric CO_2 reduces stomatal conductance in trees, a response that is well supported across many species and can enhance water-use efficiency (e.g., Keenan et al., 2013; Montibeller et al., 2022; Treml et al., 2022). While CO_2 fertilization can promote forest growth and strengthen the C sink, emerging evidence suggests that it may also contribute to forest degradation by altering biodiversity and modifying moisture availability under certain conditions (Lapola et al., 2025).

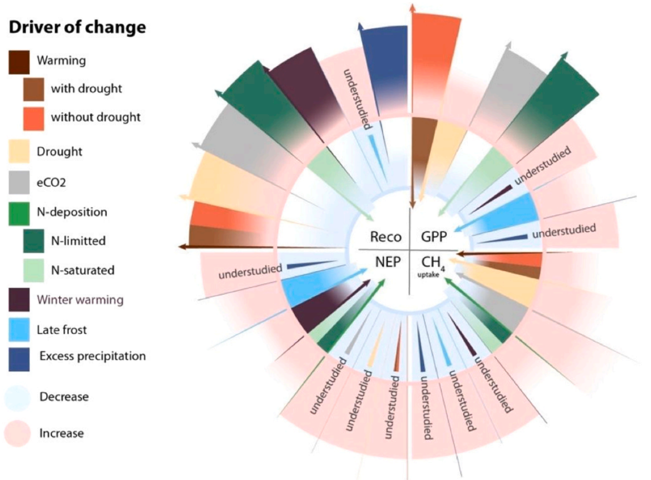

Fig. 2. Conceptual synthesis of response of C fluxes to global drivers of change. Red color marks the increasing response, and blue color marks a decreasing response. Bar sizes are illustrative and represent the relative direction and perceived magnitude of responses, not quantitatively derived values.

3.2.1. CO_2 fluxes

Rising atmospheric CO_2 concentration has been identified as a major driver of the increase in forest photosynthesis and GPP observed in recent decades at regional to continental scales (Chen et al., 2022; Fernández-Martínez et al., 2017). Its role is generally attributed to a combination of structural factors such as increase in leaf area index (LAI) as well as physiological controls such as enhanced photosynthetic efficiency and changes in stomatal regulation (Keenan et al., 2023). Experimental evidence from individual forest sites supports these mechanisms. For example, Gardner et al., (2022) reported an average of 23% increase in leaf-level photosynthetic CO_2 uptake in ~180-year-old English oak canopies following several years of elevated CO_2 exposure at a temperate forest Free Atmospheric CO2 enrichment (FACE) experiment, in central England. While such site-level experiments provide mechanistic insight, their responses may vary across species, stand structures, and environmental conditions. A comprehensive process-based land surface model (i.e., QUINCY) showed that increasing GPP due to CO_2 fertilization is evident at most forest sites in Europe, whereas responses at grassland sites are less clear due to high interannual variability in GPP (Zhan et al., 2022). However, the magnitude and persistence of the CO_2 fertilization effect on forests remain uncertain, due to concurrent changes in climate conditions - particularly increasing aridity, nutrient availability, and in some regions, stand aging (Peñuelas et al., 2017). There is also evidence suggesting a saturation and potential decline of the CO_2 fertilization effect on global forest productivity (Wang et al., 2020), although the magnitude and extent of this saturation remains under debate (Sang et al., 2021; Frankenberg et al., 2021).

Despite growing evidence for CO_2-driven stimulation of photosynthesis, isolating its contribution to observed increases in forest productivity remains challenging (Norby, 2025) because of potential confounding factors particularly phenological changes and lengthening of the growing season. Long-term trends in GPP inferred from eddy-covariance measurements and remote sensing products integrate the effects of multiple concurrent processes, including changes in growing-season length (Li et al., 2025), post-disturbance stand development (Cooper et al., 2017), shifts in forest demography, and alterations in nutrient supply (Yan et al., 2023). These factors can independently enhance canopy development and C uptake, potentially reinforcing or masking the influence of elevated atmospheric CO_2.

Evidence from tree-ring analyses also suggests that growth responses to increasing CO_2 are not universally expressed across species or regions (Gedalof and Berg, 2010; Zhang et al., 2026), and may weaken over time where nutrient or water availability become constraining (Gharun et al., 2021). Such discrepancies highlight the importance of considering ecosystem context and resource limitations when interpreting large-scale productivity trends. More broadly, the separation of CO_2 effects from those of climate variability, land-use history, and ecosystem recovery remains a key methodological challenge, particularly when relying on observational datasets (Brienen et al., 2012). Consequently, although multiple approaches indicate that rising atmospheric CO_2 has contributed to enhanced forest productivity at broad spatial scales, the magnitude of its contribution relative to other environmental drivers remains an active area of investigation.

Elevated atmospheric CO_2 influences forest respiration through complex interactions involving plant physiology, soil processes, and ecosystem acclimation (Liu et al., 2025). While there is no clear evidence that elevated CO_2 may directly increase enzymes kinetic, results from FACE experiments show that higher CO_2 levels enhance photosynthetic C assimilation (Ainsworth and Rogers, 2007) and stimulate belowground C allocation, leading to increased forest floor and soil respiration rates, particularly via greater root biomass and microbial activity (Leakey et al., 2009). Consistently, Suwa et al. (2004) observed a progressive increase in forest floor respiration under elevated CO_2, reaching a peak enhancement of 40%, before declining due to reduced soil CO_2 production and diffusivity constraints. However, this can vary with soil moisture and temperature conditions, sometimes leading to reduced respiration under very wet conditions (Barron-Gafford et al., 2005). Accordingly, regional differences in moisture availability influence the response magnitude, with elevated CO_2 effects on soil respiration typically being larger in humid regions than in arid regions (Liu et al., 2025).

3.2.2. CH_4 fluxes

Direct investigations of the effect of elevated atmospheric CO_2 concentrations on the forest and tree CH_4 exchange are still scarce and ongoing, and are connected to unique long-term manipulation experiments such as e.g., Birmingham Institute of Forest Research's Free Air CO_2 Enrichment (BIFoR-FACE) or The AmazonFACE programme (e.g., Gauci, 2025; Machacova et al., 2026).

In summary, increasing atmospheric CO_2 enhances GPP and soil respiration, though in this latter case, soil moisture can modulate CO_2 soil fluxes (Fig. 2), however the effect of increasing CO_2 on soil CH_4 uptake is much less consistent. Future research should prioritize disentangling indirect hydrological and plant-mediated pathways to CH_4 fluxes in forest, to better constrain forest C budgets under elevated CO_2.

3.3. Response to N deposition

3.3.1. CO_2 fluxes

Atmospheric N inputs are key drivers of the global forest C sink (Fernández-Martínez et al., 2017). While N deposition is estimated to contribute approximately 0.25 Pg C yr^{-1} to the global forest C sink, biological N fixation (BNF) plays a substantially larger role, contributing to around 1.58 Pg C yr^{-1}—more than six times the contribution from N deposition. Similarly, BNF supports 3.07 Pg C yr^{-1} of nitrogen-induced new net primary production (NPP), compared with only 0.41 Pg C yr^{-1} from N deposition, highlighting the dominant role of BNF in sustaining forest productivity and long-term C sequestration (Du et al., 2025; Du and Vries, 2018; Vries et al., 2014).

While the understanding of different driver effects on C fluxes is rapidly evolving, existing model projections expect that a decline in N deposition may partly offset an anticipated increase in forest growth in Europe between 2000 and 2050 due to rising atmospheric CO_2 concentrations, warming temperatures, and reduced exposure to phytotoxic ozone (Vries et al., 2017). However, such a decrease in N deposition has not yet led to observable changes in ecosystem CO_2 fluxes; for example, the decrease in N deposition between 1995 and 2011 did not significantly affect GPP and NEP across Europe and north America, whereas reduction in sulfur deposition and increasing atmospheric CO_2 were identified as stronger drivers of GPP enhancement (Fernández-Martínez et al., 2017). The relationship between GPP or NPP and N deposition appears to be non-linear (Flechard et al., 2020a, 2020b; Wang et al., 2021), which may help explain why recent overall declines in N deposition have not led to measurable changes in ecosystem CO_2 fluxes. For example, GPP or NEP estimated from eddy covariance forested sites across Europe tend to level off or even decline above a threshold ranging between 10 and 25 kg N ha^{-1} yr^{-1}, possibly indicating N saturation effects (Flechard et al., 2020b; van der Graaf et al., 2021; Wang et al., 2022).

In regions where N is not a limiting factor for forest growth, N deposition can suppress organic matter decomposition in the soil to an extent similar to the increased CO_2uptake by trees (Janssens et al., 2010). However, this effect is highly context-dependent. In N-limited forests, relatively low N deposition can actually increase soil respiration rather than suppress it (e.g., Hasselquist et al., 2016). Moreover, in Mediterranean mountain forests, the Reco response to N deposition varies seasonally, with the strongest effects observed between February and May (Fernández-Alonso et al., 2021). Increased soil respiration in N-limited sites may reduce NEP, while respiration suppression in N-rich soils could enhance it (e.g., Hasselquist et al., 2016; Janssens et al., 2010). On the other hand, N deposition can lead to soil acidification and changes in the soil C/N ratio, which are critical factors influencing soil respiration. Acidification can alter microbial communities and reduce microbial activity, potentially decreasing soil respiration rates (Rousseau et al., 2024).

Changes in N deposition can significantly affect plant–fungal interactions, notably by reducing the abundance of mutualistic fungi such as mycorrhizae (Dean et al., 2014; Ma et al., 2021). Many studies have shown that ectomycorrhizal species are more abundant at sites with lower N deposition, as observed in the case of oak (Suz et al., 2014), beech (De Witte et al., 2017) and pine tree species (Van Der Linde et al., 2018). Nitrogen deposition of 5.8 kg N ha^{-1} yr^{-1} has been identified as a tipping point, beyond which a steep decline in ectomycorrhizal fungi taxa associated with conifer species occurs (Van Der Linde et al., 2018). Shifts in soil microbial communities—typically marked by reduced diversity and a rise in nitrophilic species—can have significant implications for NEP in European forests (Baldrian et al., 2023). Addressing this knowledge gap should be a priority for future research, particularly to clarify how microbial transitions regulate forest carbon dynamics and shape NEP responses under changing nitrogen deposition regimes.

3.3.2. CH_4 fluxes

N deposition is generally thought to suppress CH_4 uptake by forest soils, although its effect depends on the level of N input. A meta-analysis of N-addition experiments by Xia et al. (2020) revealed a shift from positive to negative effects on forest soil CH_4 uptake with increasing N additions in both boreal and temperate forests. At current deposition levels, however, N inputs appear to have a neutral to slightly positive effect on CH_4 uptake in these regions (Xia et al., 2020). A recent global synthesis, including N manipulation experiments, estimated that N deposition has reduced forest soil CH_4 uptake by about 3% worldwide (Cen et al., 2024). Ni and Groffman (2018) however argue that soil CH_4 uptake is more strongly controlled by soil hydrology than by N deposition or rising temperatures. By contrast, the effects of N deposition on tree-mediated CH_4 exchange remain poorly understood and need future investigations.

In summary, N deposition can both enhance and suppress ecosystem CO_2 uptake and soil respiration, depending on whether forests have reached the critical empirical load for nitrogen. N deposition can also alter soil chemistry, microbial communities and plant-microbe interactions, with implications for long-term carbon dynamics (Fig. 2). N deposition generally reduces soil CH_4 uptake at higher levels, although current deposition rates show limited or slightly positive effects, with soil hydrology remaining a key controlling factor (Fig. 2).

3.4. Response to understudied extremes

3.4.1. CO_2 fluxes

Extreme weather events such as windthrow and excess precipitation can strongly affect forest GPP. For example, two Scots pine stands in Poland turned into significant CO_2 sources following a tornado-induced windthrow (Ziemblińska et al., 2018). Excess precipitation can also change ecosystem CO_2 dynamics: depending on the magnitude of the rain pulse, it may stimulate photosynthesis (López-Ballesteros et al., 2016), thereby altering GPP and the overall CO_2 balance. Such effects have been observed not only in Mediterranean forests (Bartsch et al., 2020; Unger et al., 2012) but also in temperate forests during dry summer periods (Ruehr et al., 2010). Heavy precipitation can cause extreme floods, which act as stressors to many tree species, reducing their aboveground productivity through a combination of lower germination rates and reduced growth as a result of physiological stress (Douda et al., 2009; Rodríguez-González et al., 2021). Excess precipitation can lead to waterlogging, affecting root-soil interactions and microbial activity. This, in turn, influences C mineralization rates, altering soil respiration and potentially impacting overall C sequestration (Wood et al., 2025). Future changes in the rainfall regime and net primary productivity will significantly alter the dynamics of the heterotrophic respiration (Rh) and the global C budget. In regions that are becoming more wet, R_h may increase faster than NPP, thereby reducing the C storage capacity of terrestrial ecosystems (Huang et al., 2021a).

Late frost events can have detrimental effects on forest ecosystems, impacting the photosynthetic process by damaging leaves, buds, and younger shoots. This damage disrupts C assimilation and, consequently, reduces the overall C uptake. Understanding the frost-phenology interactions is crucial for predicting the repercussions of climate-induced frost events on forest CO_2 fluxes (IPCC, 2023; Kreyling et al., 2019). Studies show that trees prioritize C allocation to storage and remobilization of recently stored reserves (starch and sugars) to support respiration rather than growth, to ensure immediate and future survival under negative CO_2 imbalance that may occur during critical periods of stress (Huang et al., 2021b). Beech trees, for example, survive complete defoliation due to spring late-frost damage and rapidly mobilize recent and old reserve C to survive strong source–sink imbalances (D`Andrea et al., 2019).

Winter warming increases Reco (and both autotrophic and heterotrophic), particularly in colder regions with higher soil C stocks (Gharun et al., 2025). During the exceptionally warm winter of 2020, elevated air and soil temperatures reduced NEP across many evergreen needleleaf forests in Europe, with the strongest effects observed at colder sites experiencing pronounced positive temperature anomalies. However, the associated increase in CO_2 fluxes across forests was not attributed to a single factor, reflecting complex interactions among air temperature, soil temperature, and radiation in regulating C dynamics (Gharun et al., 2025). This variability among sites suggests that additional mechanisms beyond temperature alone influence winter carbon responses. For instance, in a Scots pine–dominated boreal forest, the 2020 winter warming had negligible effects on CO_2 fluxes (Aslan et al., 2024). One such mechanism is snow dynamics, as warmer winters often reduce snow cover and accelerate snowmelt, with cascading effects on soil thermal regimes and carbon cycling during the subsequent growing season (Pongracz et al., 2024).

3.4.2. CH_4 fluxes

Extreme weather events such as excessive precipitation and winter warming can significantly alter forest CH_4 fluxes, yet their impacts remain understudied. Upland forest soils, typically CH_4 sinks, can shift to becoming sources of varying magnitude following prolonged heavy rainfall, highlighting the sensitivity of soil CH_4 dynamics to changes in moisture regimes (Korkiakoski et al., 2022). The frequency and intensity of precipitation events also play a role: in dryland ecosystems, more frequent but lower-intensity rain events have been shown to maximize CH_4 uptake, with effects varying depending on soil texture (Martins et al., 2021). In boreal forests, winter CH_4 dynamics are especially complex. While these ecosystems can act as CH_4 sinks during winter, the temperature controls on fluxes are nuanced. Experimental studies suggest that the effect of warming depends on whether it occurs at the surface or in deeper soil layers, with contrasting impacts on CH_4 fluxes (Mavrovic et al., 2024). This complexity underscores the need to improve model representations of winter CH_4 processes, particularly as Arctic-Boreal regions are warming up to four times faster than the global average (Rantanen et al., 2022).

In summary, overall, there is very limited information available on the effect of understudied extremes on forest C fluxes (Fig. 2). Site-level studies suggest that these additional drivers can alter carbon fluxes, though directionality really depends on environmental conditions.

3.5. Interacting effect of multiple drivers on C fluxes

3.5.1. Nutrient-based interactions

Since N can limit growth in boreal and temperate forests, it can affect tree responses to rising atmospheric CO_2, for example by amplifying or constraining a potential CO_2 fertilization effect (Luo et al., 2004; Wieder et al., 2015). Evidence from large-scale FACE experiments in young, replanted temperate sweetgum (ORNL-FACE) and pine forests (Duke-FACE) shows that elevated CO_2 stimulates growth only transiently, with

N limitation reducing CO_2 uptake within 3–5 years (Finzi et al., 2006; Norby et al., 2010). In contrast to young forest FACE experiments—often established on nutrient-rich former agricultural land—mature temperate forests are likely to exhibit stronger N limitations on C sequestration under elevated CO_2 (De Kauwe et al., 2014; Finzi et al., 2006).

Decades of reactive N deposition in European forests—often exceeding ecological thresholds—have enriched soil N stocks and enhanced N availability. This N legacy can temporarily sustain forest growth responses to rising atmospheric CO_2, prolonging the CO_2 fertilization effect until nutrient limitations re-emerge (Sgouridis et al., 2023). In contrast, forests receiving low N inputs (below 6–10 kg N ha^{-1} yr^{-1}) are expected to show weaker growth stimulation under elevated CO_2. Although elevated CO_2 generally promotes plant growth and forest productivity (Brienen et al., 2020; Ruehr et al., 2023), mature forests typically exhibit weaker responses than young stands, particularly when nutrient availability is constrained (Ellsworth et al., 2017; Körner et al., 2005). For example, at the EucFACE experiment in a mature *Eucalyptus* forest in Australia, no increase in net primary production (NPP) was observed under elevated CO_2, with responses limited by phosphorus (P) availability (Ellsworth et al., 2017).

3.5.2. *Climatic and nutrient-based interactions*

Beyond nutrient constraints, climate stressors also shape forest responses. Satellite-based models indicate widespread reductions in terrestrial GPP driven by rising VPD, offsetting potential CO_2 fertilization benefits (Mirabel et al., 2023; Yuan et al., 2019). Elevated VPD suppresses stomatal conductance, leading to lower photosynthesis and growth, increased transpiration up to a certain threshold, and heightened risks of hydraulic failure and C starvation (Grossiord et al., 2020). However, the net GPP response to elevated CO_2 under high VPD is strongly modulated by soil water availability (Preisler et al., 2023). Taken together, these findings highlight the need for experimental validation of the combined impacts of drought, pollution-driven nutrient enrichment, and elevated CO_2 to better constrain the C sequestration potential of European forests (Norby et al., 2016).

The interaction between N deposition and drought has been explored in various manipulation experiments with mixed outcomes. Some studies report that N addition can buffer drought effects by sustaining tree growth (Ibáñez et al., 2018; Wang et al., 2012), while others suggest that it may exacerbate drought sensitivity by reducing root biomass and thereby limiting water uptake (Dziedek et al., 2016), or by increasing the risk of uprooting (Braun et al., 2023). Observational evidence from FLUXNET sites across Europe similarly reveals no uniform effect of N deposition on forest productivity during drought, with responses varying by site and context (van der Graaf et al., 2021). Together, these findings emphasize the context dependency of N deposition effects and the complex interplay between nutrient enrichment and climatic stressors such as drought. To date, only one study has explicitly examined how N deposition interacts with drought to shape GPP across European forests based on direct flux observations (Wang et al., 2022). While confirming a generally positive relationship between GPP and N deposition up to a threshold of 10–15 kg N ha^{-1} yr^{-1}, this study found no consistent or significant effect of N deposition on forest GPP sensitivity to drought.

Looking forward, climate change is expected to intensify the challenges posed by drought–nutrient interactions. Air temperatures in Europe are projected to rise more rapidly than the global average, with increases of 1.2–3.4 °C under SSP1–2.6 and 4.1–8.5 °C under SSP5–8.5 by 2071–2100 (relative to 1981–2010), according to CMIP6 models. Compound soil and atmospheric drying events are anticipated to become up to three times more frequent across Europe (Shekhar et al., 2024). Concurrently, shifts in atmospheric chemistry are predicted: while emissions of oxidized N compounds are expected to decline by 2050, ammonia (NH_3) emissions may rise slightly (Simpson et al., 2014). Other climatic extremes are also likely to intensify. Snow-dominated regions are expected to face shorter snow cover duration, warmer winters and springs, and greater winter precipitation (Vitali et al., 2018). Excess precipitation events are projected to increase in frequency and intensity, particularly in northern and central Europe, under both RCP2.6 and RCP8.5 scenarios (Huo et al., 2021; Thackeray et al., 2022).

In summary, when considered individually, global change drivers often produce relatively predictable responses in forest carbon fluxes: warming tends to enhance both GPP and Reco, elevated atmospheric CO_2 generally stimulates photosynthesis, and moderate N inputs can enhance productivity in N-limited systems. However, when drivers interact, ecosystem responses frequently become non-linear, amplified, or even reversed relative to single-driver expectations. For example, warming alone may extend the growing season and increase GPP, but in combination with drought, elevated vapor pressure deficit suppresses stomatal conductance, reduces GPP, and can increase respiration losses during rewetting events. Similarly, the positive effect of rising CO_2 on productivity may be constrained by nutrient limitation or drought stress, while historical N deposition can temporarily sustain CO_2 fertilization effects but also increase vulnerability to climatic stressors. Under compound disturbances—such as drought followed by extreme precipitation or winter warming—ecosystem respiration pulses and structural damage can further reduce NEP. Collectively, these findings indicate that forest carbon dynamics cannot be reliably inferred from single-driver responses alone; instead, interacting drivers shape ecosystem resilience through feedbacks among physiological processes, soil biogeochemistry, and disturbance regimes, often leading to thresholds or tipping points in carbon sink strength.

4. Resilience of forest carbon fluxes to global change: roles of memory, management, biodiversity, and disturbance

Over recent decades, a number of studies have assessed forest resilience across spatial scales, using diverse observational approaches, ranging from leaf-level gas exchange measurements (Fürstenau Togashi et al., 2018) to drone-derived physiological indices (D'Odorico et al., 2021). Particularly with the increase in the frequency of extreme events during the past 30 years and the projected increase in frequency and intensity of such events until the end of the 21st century (Shekhar et al., 2024), the topic of forest resilience is becoming increasingly relevant. One approach to assessing tree and forest resilience to air pollution and climate extremes is the quantification of resistance (often referred to as stability), defined as the ability of ecosystem functioning to persist during an extreme event, and recovery, defined as the ability to return to pre-disturbance levels of performance (e.g., Ingrisch and Bahn, 2018; Nimmo et al., 2015). When considered together, resistance and recovery allow resilience to be quantified, provided that the system is capable of returning to pre-disturbance functioning (e.g., Schulze et al., 2019). A variety of different data sets and methodologies have been used so assess resistance, recovery, and resilience, e.g., satellite-based vegetation proxies (e.g., Huang & Xia, 2019; Khoury & Coomes, 2020), tree-ring width data (Fang & Zhang 2019; Gazol et al., 2018; Vitasse et al., 2019) or eddy covariance measurements of greenhouse gas flux between forests and the atmosphere (Reichstein et al., 2013; Musavi et al., 2017; Shekhar et al., 2023). The focus of this paper is however on resilience of C fluxes which entails assessing plot-scale flux observations.

Assessing the resilience of forest carbon (C) sink capacity requires not only identifying extreme events, but also understanding the processes that regulate carbon gain and water loss in trees and forest ecosystems across relevant spatial and temporal scales. Resilience can be quantified using a range of approaches, including variance-based metrics derived from detrended and deseasonalized fluxes, satellite-based observations, indicators of critical slowing down—although the robustness of these indicators has recently been questioned (Smith and Boers, 2023; Liu et al., 2026)—and measures of recovery time following climate or disturbance pulses (Ingrisch & Bahn, 2018). One of the key limitations of flux observations is the relatively short time series length, except for a subset of sites. Currently the typical assessments are done using variance-based methods. Nevertheless, as flux observation networks continue to mature, they are expected to play an increasingly central role in resilience assessments. Additionally, quantifying resilience in an ecological context is inherently challenging because the baseline climatic conditions against which responses are evaluated are themselves changing over time. Nevertheless, recent studies have demonstrated that machine-learning approaches applied to high-resolution flux measurements can be used to tackle this challenge and quantify forest resilience—in terms of fluxes—to increasing climate extremes (Shekhar et al., 2023).

Forests differ in their capacity for resilience to global change drivers, with ecosystem memory as well as lag and legacy effects playing key roles in shaping long-term C flux responses (Anderegg et al., 2016a; Forzieri et al., 2021; Liu et al., 2023; Müller and Bahn, 2022). Across much of temperate Europe, the resilience of NEP has declined over the past two decades, signaling increasing vulnerability of forests to environmental stressors (Gharun et al., 2024). This reduction in resilience is largely attributed to more frequent and severe natural and anthropogenic disturbances, which are expected to significantly diminish the future C uptake potential of European forests (Seidl et al., 2014; e.g., Turubanova et al., 2023; Gruenig et al., 2026). In the Mediterranean regions, the resilience of net biome production has already weakened in recent decades, reflecting the combined effects of increasing aridity, more frequent droughts, and higher temperatures that often trigger forest fires (Fernández-Martínez et al., 2023). Even boreal forests, traditionally considered more buffered, now show declining growth and C uptake (Henttonen et al., 2024; Laudon et al., 2024). In Fennoscandia, these declines are attributed not only to climate change but also to intensified harvesting pressures (e.g., Turubanova et al., 2023). Taken together, these patterns underscore the increasing vulnerability of forests and the need for improved resilience assessment frameworks.

4.1. Legacy effect on forest resilience in terms of C fluxes

Climate extremes can leave lasting impacts on forest growth and C uptake, with legacy effects persisting for several years (Pohl et al., 2023) and potentially leading to an increase in mortality (DeSoto et al., 2020). Ecosystem flux observations from monitoring sites in central Germany show that drought legacy effects on GPP can endure across multiple seasons and sometimes years, with reductions comparable to the immediate drought impact (Yu et al., 2022). These effects are partly explained by delayed leaf development, and vary with species composition, forest age, and stand structure, indicating that ecological characteristics and historical management shape the resilience of forests to past droughts and climate extremes. In fact, Vangi et al. (2024) showed that differences in age-class distribution - largely shaped by past management - can influence forest sensitivity and resilience even more strongly than climate.

Forests also display adaptive mechanisms that can buffer against extreme events. The resilience of C fluxes improves when trees draw on strategies common in dryland ecosystems (Grünzweig et al., 2022). For instance, foliar uptake of non-rainfall water (e.g., fog) has been shown to enhance seedling photosynthesis in temperate forests (Berry et al., 2014), while hydraulic redistribution during prolonged drought can maintain soil moisture and increase annual GPP by up to 30%, allowing forests to remain C sinks rather than becoming C sources (Domec et al., 2010).

Nevertheless, mounting evidence indicates a decline in forest C sink capacity under severe drought across diverse ecosystems (Lu and Yan, 2023; Nestola et al., 2018; Xu et al., 2020; Yao et al., 2023). In subalpine Norway spruce-dominated forests near Davos, Switzerland—typically strong C sinks—intensified drought has led to increased Reco and reduced GPP, turning the forest into a weaker C sink (Krebs et al., 2025). Long-term monitoring in the Amazon similarly reveals sharp, short-term declines in net C uptake during severe drought (Yao et al., 2023). In both cases, however, these shifts represent transient responses to extreme events rather than enduring legacy effects. By contrast, temperate mixed deciduous forests have maintained their sink function under drought stress more effectively than coniferous stands, suggesting that management strategies promoting mixed-species forests may enhance C sequestration under future climate extremes (Buchmann et al., 2025).

Recent advances in modeling further underscore the importance of ecosystem memory in shaping C dynamics. Studies show that incorporating lagged climate impacts into deep learning models improves the simulation of NEP and its interannual variability, demonstrating that past conditions strongly influence present-day fluxes (Liu et al., 2023). Similarly, machine learning approaches have shown that temporal context and stand age (time since last disturbance) improve NEP predictions (Besnard et al., 2019). Notably, the response of NEP to precipitation often lags behind that to temperature and radiation, with memory effects varying across ecosystems and seasons (Liu et al., 2019). These findings highlight the need to explicitly incorporate legacy and memory effects into forest ecosystem models to more accurately predict C balance and resilience under future climate and air pollution patterns.

4.2. Management effects on forest resilience in terms of C fluxes

Beyond legacy effects of climate extremes, forest management is a critical determinant of forest resilience to global change. Management directly shapes forest structure, stand age, and species composition, key attributes that regulate ecosystem productivity, sensitivity to drought, and recovery dynamics following disturbances, and ultimately influence CO_2 and CH_4 flux responses. By modifying age-class distributions, canopy complexity, and species diversity, management affects both ecosystem stability and C and water flux variability (Vangi et al., 2024; Yao et al., 2025). Similarly, management affects both ecosystem stability and the balance between GPP, NPP, and R_a, thereby ultimately controlling vegetation carbon-use efficiency (CUE = NPP/GPP; Luo et al., 2025) and water-use efficiency (Saponaro et al., 2026). Ameray et al. (2021) reviewed the impacts of contrasting management strategies—including intensive and extensive practices as well as old-growth conservation—on carbon sequestration and storage. Their analysis showed that old-growth conservation tends to promote higher soil carbon storage, whereas intensive approaches such as afforestation and nitrogen and phosphorus fertilization primarily enhance carbon sequestration in aboveground biomass. On this basis, the authors proposed a functional zoning framework that strategically integrates different management approaches. Such a framework could optimize forest management outcomes by reconciling industrial demands with climate change mitigation objectives, while simultaneously strengthening the resilience of carbon fluxes under global change. However, Dalmonech et al. (2022) showed that there is little or no leeway to increase both carbon sequestration and stock capacity by simply increasing intensity and frequency of thinning under climate change scenarios.

The role of forest management on modulating CH_4 fluxes is still rarely addressed, despite their potential to influence soil microclimate, substrate availability, and gas transport processes. For instance, Doukalianou et al. (2019) and Mazza et al. (2019) found that thinning in *Pinus* stands in Greece and Italy temporarily enhanced the soil's capacity to act as a CH_4 sink. Yet, these studies focused narrowly on soil fluxes, overlooking other potential CH_4 sources and sinks such as stems and woody tissues.

In boreal forests, where clear-cutting is still a dominant management practice, associated soil disturbance and altered hydrology can increase soil moisture, potentially shifting soils from net CH_4 sinks to net sources (Vestin et al., 2020). However, empirical evidence remains inconclusive, with studies reporting contrasting outcomes (Korkiakoski et al., 2019; Sundqvist et al., 2014). Conversely, historical drainage practices such as ditching, which lower groundwater tables, have been shown to suppress CH_4 emissions from both soils and stems and, in some cases, even promote CH_4 uptake (Klaus et al., 2024). The influence of forest management on non-CO_2 greenhouse gas (GHG) fluxes remain poorly understood, representing a major knowledge gap—particularly in Mediterranean ecosystems, where available studies are scarce and often limited to short-term observations.

4.3. Effect of biodiversity on forest resilience in terms of C fluxes

A robust positive relationship between biodiversity and forest productivity has been documented in both natural and managed forests, particularly in systems managed for timber production (Ammer, 2019; Jucker et al., 2014, 2016; Yang et al., 2023). Beyond enhancing productivity, biodiversity also contributes to soil health. For example, higher plant diversity has been associated with greater levels of extractable organic carbon and nitrogen in soils (Zuo et al., 2023). However, current forest stability does not preclude future biodiversity loss, as many ecosystems face an extinction debt—especially where climate change interacts with human-driven land-use change (Travis, 2003). These findings highlight the need to account not only for present biodiversity states, but also for their future trajectories when assessing forest resilience, since ongoing environmental pressures may outpace species' adaptive capacities.

Higher biodiversity has been consistently linked to greater ecosystem resilience, manifested in more stable productivity and enhanced carbon storage. Highly diverse forests are generally better able to withstand and recover from climatic extremes and anthropogenic disturbances (Ammer, 2019; Hisano et al., 2018; Mina et al., 2022; Thompson, 2009). Understanding the role of biodiversity in sustaining forest resilience and carbon dynamics requires consideration of the complex interactions between taxonomic, functional, and structural diversity, carbon cycling, and global change drivers (Forzieri et al., 2021). Such an understanding calls for an integrated perspective on ecosystem multifunctionality that incorporates both above- and belowground biodiversity (Bardgett and van der Putten, 2014; Cameron et al., 2019; Weiskopf et al., 2024), and explicitly addresses the interactions between biodiversity and forest management practices (Oettel and Lapin, 2021).

Studies indicate that forests with higher tree species diversity generally maintain greater carbon stocks than monocultures, as diverse ecosystems often benefit from complementary interactions that optimize light capture and nutrient use (Buotte et al., 2020; Chen et al., 2023). However, the magnitude of these positive complementarity effects can vary depending on species identity, limiting resources, and forest developmental stage (Ammer, 2019). Climate change further challenges the long-term viability of many species for management. Modeling of 69 European tree species suggests that 33–49% may become unsuitable for planting under moderate to severe climate scenarios, reducing the pool of climatically appropriate species and constraining mixed-forest management strategies (Wessely et al., 2024). This decline in species availability threatens forest resilience, particularly with regard to carbon storage.

Functional trait diversity, especially in hydraulic traits, has emerged as a key mediator of ecosystem carbon flux resilience. For example, greater diversity in tree hydraulic traits buffers carbon flux fluctuations during droughts across temperate and boreal forests (Anderegg et al., 2016b). Such hydraulic diversity is expected to play an increasingly important role in forest–atmosphere interactions under changing climates. Additionally, higher species and trait diversity mitigates the impacts of disturbances on carbon storage and uptake, thereby enhancing the robustness of forest carbon sequestration and strengthening their role in climate change mitigation (Hisano et al., 2018).

Additionally, soil biodiversity is a fundamental driver of forest resilience, with a single gram of soil harboring up to a billion bacteria and a vast array of fungal species (Basile-Doelsch et al., 2020). Microbial diversity, particularly among bacteria and fungi, strongly influences ecosystem responses to global change, including elevated CO_2, nitrogen deposition, and warming (Bardgett and van der Putten, 2014; García-Palacios et al., 2014). The soil microbiome is critical for forest ecosystem functioning, particularly in mediating responses to disturbances such as drought, warming, and nutrient enrichment. For instance, mycorrhizal fungi and saprotrophic communities exhibit distinct responses to environmental stressors, thereby affecting forest productivity and resilience (Eagar et al., 2022; Lenoir et al., 2016; Morera et al., 2022).

High ecological integrity in diverse forest patches not only enhances carbon storage but also provides habitats for wildlife, which can further support ecosystem stability, productivity, and resilience (Asbeck et al., 2021). However, achieving high levels of both biodiversity and aboveground carbon storage can be challenging in temperate forests, as prioritizing one often entails trade-offs with the other. Consequently, stand-scale management strategies that explicitly target either biodiversity or carbon are necessary to maximize co-benefits at landscape scales (Sabatini et al., 2019).

4.4. Effect of disturbance on resilience of forests in terms of C fluxes

The stand-replacing disturbances (wind, fire, insect, clear-cut) turn forests into a carbon source (Aslan et al., 2024; Rebane et al., 2019). The recovery of forest carbon sequestration can be defined by two terms, i.e., carbon compensation point (CCP - time required to turn from source to sink) and payback time (time required to compensate the cumulative carbon loss until reaching the compensation point) (Aguilos et al., 2014). Amiro et al. (2010) reported varying CCP between 2 and 20 years for North American forests, while Aguilos et al. (2014) estimated payback time as long as 88 years for an extended dataset covering also European and Asian boreal and temperate forests. A recent compilation of National Forest Inventory data showed a decadal decline in forest floor soil organic carbon after clear-cutting in Nordic and Canadian forests (Johannesson et al., 2024), while a comparison of previous clear-cut and natural forests in Norway did not reveal differences in present carbon balance (Madsen et al., 2025). One of the key factors influencing CCP duration is the availability of easily decomposable materials, which convert to CO_2 during fire. As a result, recovery time is expected to be shorter for fire disturbances compared to wind, insect, or clear-cut disturbances in on-site carbon balance evaluations (Amiro et al., 2010). As for thinning, it is often assumed that it reduces GPP and Reco, yet NEP would remain the same (Vesala et al., 2005; Wilkinson et al., 2016). Aslan et al., (2024) concluded that thinning generally reduces GPP due to foliage reduction, while the response of Reco is variable, i.e., either smaller reductions compared to GPP, remains neutral, or increases relative to pre-disturbance levels, mainly depending on the availability of easily decomposable material. Consequently, NEP tends to decline persistently, although the magnitude of this reduction varies, particularly in the boreal region, where similar management practices, species composition, and relatively low interannual weather variability prevail. In contrast, responses in the temperate region are more heterogenous, most likely reflecting greater variability in these factors.

5. Conclusions

Forest gross primary productivity (GPP) and ecosystem respiration (Reco) respond differently yet interdependently to global change drivers, collectively reshaping net carbon uptake across European forests. Drought-prone regions, particularly Central Europe and the Mediterranean, have emerged as climate impact hotspots, where increasing water limitations are already disrupting carbon cycling with long-term consequences for productivity and resilience. At the same time, declining atmospheric nitrogen deposition across much of Europe—resulting from improved air-quality policies—has altered nutrient availability and may constrain productivity gains previously supported by elevated nitrogen inputs, especially in nutrient-poor soils and aging stands with high nitrogen demand. Biodiversity remains a key component of resilience, as structurally and functionally diverse forests generally better withstand environmental stress while maintaining ecosystem functioning. Management effects on CO_2 and CH_4 fluxes are strongly context-dependent and mediated by interacting drivers such as temperature, water availability, nutrient status, and disturbance regimes. This highlights the need for flexible, site-specific management approaches that consider how interventions modify ecosystem structure, carbon allocation, and belowground processes. Resilience to global change is therefore not uniform but varies with species composition, forest type, stand development, and climatic context, underscoring the importance of adaptive strategies that promote diversity and structural heterogeneity.

This perspective review highlights that interactions between carbon fluxes and global change drivers are multifaceted, necessitating integrated approaches for effective understanding and management. Maintaining and further intensifying long-term monitoring of ecosystem fluxes is crucial to capture both spatial and temporal variability in ecosystem responses to global change drivers, particularly those that remain understudied. Future research should therefore prioritize continuous, site-specific observations that account for the synergistic effects of multiple stressors and disturbances, as well as the role of management in mitigating their impacts. Additionally, greater attention should be given to carbon fluxes beyond CO_2, as our understanding remains limited regarding how different global change drivers influence both methane emissions and uptake at the ecosystem scale.

CRediT authorship contribution statement

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

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Data availability

Data will be made available on request.

References

Aber, J., Neilson, R.P., McNULTY, S., Lenihan, J.M., Bachelet, D., Drapek, R.J., 2001. Forest Processes and Global Environmental Change: Predicting the Effects of Individual and Multiple Stressors. BioScience 51 (9), 735. https://doi.org/10.1641/0006-3568(2001)051[0735:FPAGEC]2.0.CO;2.

Aguilos, M., Takagi, K., Liang, N., Ueyama, M., Fukuzawa, K., Nomura, M., Kishida, O., Fukazawa, T., Takahashi, H., Kotsuka, C., Sakai, R., Ito, K., Watanabe, Y., Fujinuma, Y., Takahashi, Y., Murayama, T., Saigusa, N., Sasa, K., 2014. Dynamics of ecosystem carbon balance recovering from a clear-cutting in a cool-temperate forest. Agric. For. Meteorol. 197, 26–39.

Ainsworth, E.A., Rogers, A., 2007. The response of photosynthesis and stomatal conductance to rising [CO_2]: Mechanisms and environmental interactions. Plant Cell & Environ. 30 (3), 258–270. https://doi.org/10.1111/j.1365-3040.2007.01641.x.

Ameray, A., Bergeron, Y., Valeria, O., Montoro Girona, M., Cavard, X., 2021. Forest Carbon Management: A Review of Silvicultural Practices and Management Strategies Across Boreal, Temperate and Tropical Forests. Curr. For. Rep. 7 (4), 245–266.

Amiro, B.D., Barr, A.G., Barr, J.G., Black, T.A., Bracho, R., Brown, M., Chen, J., Clark, K. L., Davis, K.J., Desai, A.R., Dore, S., Engel, V., Fuentes, J.D., Goldstein, A.H., Goulden, M.L., Kolb, T.E., Lavigne, M.B., Law, B.E., Margolis, H.A., Xiao, J., 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. J. Geophys. Res. Biogeosciences 115 (G4).

Ammer, C., 2019. Diversity and forest productivity in a changing climate. N. Phytol. 221 (1), 50–66, 15.06.2018.

Anderegg, W.R.L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A.F.A., Choat, B., Jansen, S., 2016b. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. Proc. Natl. Acad. Sci. USA 113 (18), 5024–5029, 18.04.2016.

Anderegg, W.R.L., Martinez-Vilalta, J., Cailleret, M., Camarero, J.J., Ewers, B.E., Galbraith, D., Gessler, A., Grote, R., Huang, C., Levick, S.R., Powell, T.L., Rowland, L., Sánchez-Salguero, R., Trotsiuk, V., 2016a. When a Tree Dies in the Forest: Scaling Climate-Driven Tree Mortality to Ecosystem Water and Carbon Fluxes. In. Ecosystems 19 (6), 1133–1147.

André, J., D'Andrea, F., Drobinski, P., Muller, C., 2024. Regimes of Precipitation Change Over Europe and the Mediterranean. J. Geophys. Res. Atmospheres 129 (15), e2023JD040413. https://doi.org/10.1029/2023JD040413.

Asbeck, T., Sabatini, F., Augustynczik, A.L.D., Basile, M., Helbach, J., Jonker, M., Knuff, A., Bauhus, J., 2021. Biodiversity response to forest management intensity, carbon stocks and net primary production in temperate montane forests. Sci. Rep. 11 (1), 1625. https://doi.org/10.1038/s41598-020-80499-4.

Aslan, T., Launiainen, S., Kolari, P., Peltola, O., Aalto, J., Bäck, J., Vesala, T., Mammarella, I., 2024. Thinning turned boreal forest to a temporary carbon source—Short term effects of partial harvest on carbon dioxide and water vapor fluxes. Agric. For. Meteorol. 353, 110061.

Baldrian, P., López-Mondéjar, R., Kohout, P., 2023. Forest microbiome and global change. Nat. Rev. Microbiol. 21 (8), 487–501, 20.03.2023.

Banbury Morgan, R., Herrmann, V., Kunert, N., Bond-Lamberty, B., Muller-Landau, H.C., Anderson-Teixeira, K.J., 2021. Global patterns of forest autotrophic carbon fluxes. Glob. Change Biol. 27 (12), 2840–2855. https://doi.org/10.1111/gcb.15574.

Barba, J., Brewer, P.E., Pangala, S.R., Machacova, K., 2024. Methane emissions from tree stems—Current knowledge and challenges: An introduction to a Virtual Issue. N. Phytol. 241 (4), 1377–1380.

Barba, J., Poyatos, R., Vargas, R., 2019. Automated measurements of greenhouse gases fluxes from tree stems and soils: Magnitudes, patterns and drivers. Sci. Rep. 9 (1), 4005 (08.03.2019.

Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515 (7528), 505–511.

Barnard, R.L., Blazewicz, S.J., Firestone, M.K., 2020. Rewetting of soil: Revisiting the origin of soil CO2 emissions. Soil Biol. Biochem. 147, 107819. https://doi.org/10.1016/j.soilbio.2020.107819.

Barron-Gafford, G., Martens, D., Grieve, K., Biel, K., Kudeyarov, V., McLain, J.E.T., Lipson, D., Murthy, R., 2005. Growth of Eastern Cottonwoods (*Populus deltoides*) in elevated [CO$_2$] stimulates stand-level respiration and rhizodeposition of carbohydrates, accelerates soil nutrient depletion, yet stimulates above- and belowground biomass production. Glob. Change Biol. 11 (8), 1220–1233. https://doi.org/10.1111/j.1365-2486.2005.00985.x.

Bartsch, S., Stegehuis, A.I., Boissard, C., Lathière, J., Peterschmitt, J.-Y., Reiter, I.M., Gauquelin, T., Baldy, V., Genesio, L., Matteucci, G., Fernandez, C., Guenet, B., 2020. Impact of precipitation, air temperature and abiotic emissions on gross primary production in Mediterranean ecosystems in Europe. Eur. J. For. Res. 139 (1), 111–126.

Basile-Doelsch, I., Balesdent, J., Pellerin, S., 2020. Reviews and syntheses: The mechanisms underlying carbon storage in soil. Biogeosciences 17 (21), 5223–5242.

Beachley, G.M., Fenn, M.E., Du, E., De Vries, W., Bauters, M., Bell, M.D., Kulshrestha, U. C., Schmitz, A., Walker, J.T., 2024. Monitoring nitrogen deposition in global forests. Atmospheric Nitrogen Deposition to Global Forests. Elsevier, pp. 17–38. https://doi.org/10.1016/B978-0-323-91140-5.00019-1.

Berry, Z.C., White, J.C., Smith, W.K., 2014. Foliar uptake, carbon fluxes and water status are affected by the timing of daily fog in saplings from a threatened cloud forest. Tree Physiol. 34 (5), 459–470. https://doi.org/10.1093/treephys/tpu032.

Besnard, S., Carvalhais, N., Arain, M.A., Black, A., Brede, B., Buchmann, N., Chen, J., Clevers, J.G.P.W., Dutrieux, L.P., Gans, F., Herold, M., Jung, M., Kosugi, Y., Knohl, A., Law, B.E., Paul-Limoges, E., Lohila, A., Merbold, L., Roupsard, O., Reichstein, M., 2019. Memory effects of climate and vegetation affecting net ecosystem CO2 fluxes in global forests. PLOS ONE 14 (2), e0211510. https://doi.org/10.1371/journal.pone.0211510.

Birch, H.F., 1958. The effect of soil drying on humus decomposition and nitrogen availability. Plant Soil 10 (1), 9–31.

Bobbink, R., Loran, C., & Tomassen, H. (2022). Review and revision of empirical critical loads and dose-response relationships. ⟨https://www.researchgate.net/publication/288936123_Review_and_revision_of_empirical_critical_loads_and_dose-response_relationships_National_Institute_for_Public_Health_and_the_Environment_RIVM⟩.

Boisvenue, C., Running, S.W., 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. Glob. Change Biol. 12 (5), 862–882.

Braun, S., Rihm, B., Tresch, S., Schindler, C., 2023. Long-term risk assessment of uprooting and stem breakage under drought conditions and at high N deposition in beech and Norway spruce. Agric. For. Meteorol. 341, 109669. https://doi.org/10.1016/j.agrformet.2023.109669.

Bréchet, L.M., Salomón, R.L., Machacova, K., Stahl, C., Burban, B., Goret, J.-Y., Steppe, K., Bonal, D., Janssens, I.A., 2025. Insights into the subdaily variations in methane, nitrous oxide and carbon dioxide fluxes from upland tropical tree stems. N. Phytol. 245, 2451–2466.

Brienen, R.J.W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., Ceccantini, G., Di Filippo, A., Helama, S., Locosselli, G.M., Lopez, L., Piovesan, G., Schöngart, J., Villalba, R., Gloor, E., 2020. Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. Nat. Commun. 11 (1), 4241, 08.09.2020.

Brienen, R.J.W., Gloor, E., Zuidema, P.A., 2012. Detecting evidence for CO2 fertilization from tree ring studies: The potential role of sampling biases. Glob. Biogeochem. Cycles 26, GB1025. https://doi.org/10.1029/2011GB004143.

Brüggemann, N., Gessler, A., Kayler, Z., Keel, S.G., Badeck, F., Barthel, M., Boeckx, P., Buchmann, N., Brugnoli, E., Esperschütz, J., Gavrichkova, O., Ghashghaie, J., Gomez-Casanovas, N., Keitel, C., Knohl, A., Kuptz, D., Palacio, S., Salmon, Y., Uchida, Y., Bahn, M., 2011. Carbon allocation and carbon isotope fluxes in the plant-soil-atmosphere continuum: A review. Biogeosciences 8 (11), 3457–3489. https://doi.org/10.5194/bg-8-3457-2011.

Buchmann, N., Baur, T., Burri, S., Etzold, S., Feigenwinter, I., Hörtnagl, L., Krebs, L., Meier, P., Scapucci, L., Shekhar, A., Zweifel, R., 2025. Forest ecosystem functioning in a changing climate: Fluxes, drivers, feedbacks at multiple scales. ARPHA Conf. Abstr. 8, e152042. https://doi.org/10.3897/aca.8.e152042.

Buitink, J., & Swank, A.M. (2020). Anatomy of the 2018 agricultural drought in The Netherlands using in situ soil moisture and satellite vegetation indices.

Büntgen, U., Urban, O., Krusic, P.J., Rybníček, M., Kolář, T., Kyncl, T., Ač, A., Koňasová, E., Čáslavský, J., Esper, J., Wagner, S., Saurer, M., Tegel, W., Dobrovolný, P., Cherubini, P., Reinig, F., Trnka, M., 2021. Recent European drought extremes beyond Common Era background variability. Nat. Geosci. 14 (4), 190–196.

Buotte, P.C., Law, B.E., Ripple, W.J., Berner, L.T., 2020. Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States. Ecol. Appl. 30 (2), e02039. https://doi.org/10.1002/eap.2039.

Buttlar, J. von, Zscheischler, J., Rammig, A., Sippel, S., Reichstein, M., Knohl, A., Jung, M., Menzer, O., Arain, M.A., Buchmann, N., Cescatti, A., Gianelle, D., Kieley, G., Law, B.E., Magliulo, V., Margolis, H., McCaughey, H., Merbold, L., Migliavacca, M., … Mahecha, M.D. (2017). Impacts of droughts and extreme temperature events on gross primary production and ecosystem respiration: A systematic assessment across ecosystems and climate zones.

Cameron, E.K., Martins, I.S., Lavelle, P., Mathieu, J., Tedersoo, L., Bahram, M., Gottschall, F., Guerra, C.A., Hines, J., Patoine, G., Siebert, J., Winter, M., Cesarz, S., Ferlian, O., Kreft, H., Lovejoy, T.E., Montanarella, L., Orgiazzi, A., Pereira, H.M., Eisenhauer, N., 2019. Global mismatches in aboveground and belowground biodiversity. Conserv. Biol. J. Soc. Conserv. Biol. 33 (5), 1187–1192, 26.04.2019.

Canadell, J.G., 2021. Global Carbon and Other Biogeochemical Cycles and Feedbacks. In: IPCC (Ed.), Climate Change 2021 – The Physical Science Basis. Cambridge University Press, pp. 673–816.

Cen, X., He, N., Li, M., Xu, L., Yu, X., Cai, W., Li, X., Butterbach-Bahl, K., 2024. Suppression of Nitrogen Deposition on Global Forest Soil CH$_4$ Uptake Depends on Nitrogen Status. Glob. Biogeochem. Cycles 38 (7), e2024GB008098. https://doi.org/10.1029/2024GB008098.

Chen, C., Riley, W.J., Prentice, I.C., Keenan, T.F., 2022. CO2 fertilization of terrestrial photosynthesis inferred from site to global scales. Proc. Natl. Acad. Sci. 119 (10), e2115627119. https://doi.org/10.1073/pnas.2115627119.

Chen, X., Taylor, A.R., Reich, P.B., Hisano, M., Chen, H.Y.H., Chang, S.X., 2023. Tree diversity increases decadal forest soil carbon and nitrogen accrual. Nature 618 (7963), 94–101. https://doi.org/10.1038/s41586-023-05941-9.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., Noblet, N. de, Friend, A.D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437 (7058), 529–533.

Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., D'Amato, A. W., Davis, F.W., Hersh, M.H., Ibanez, I., Jackson, S.T., Matthews, S., Pederson, N., Peters, M., Schwartz, M.W., Waring, K.M., Zimmermann, N.E., 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Glob. Change Biol. 22 (7), 2329–2352, 21.02.2016.

Collalti, A., Ibrom, A., Stockmarr, A., Cescatti, A., Alkama, R., Fernández-Martínez, M., Matteucci, G., Sitch, S., Friedlingstein, P., Ciais, P., Goll, D.S., Nabel, J.E.M.S., Pongratz, J., Arneth, A., Haverd, V., Prentice, I.C., 2020b. Forest production efficiency increases with growth temperature. Nat. Commun. 11 (1), 5322. https://doi.org/10.1038/s41467-020-19187-w.

Collalti, A., Tjoelker, M.G., Hoch, G., Mäkelä, A., Guidolotti, G., Heskel, M., Petit, G., Ryan, M.G., Battipaglia, G., Matteucci, G., Prentice, I.C., 2020a. Plant respiration: Controlled by photosynthesis or biomass? Glob. Change Biol. 26 (3), 1739–1753. https://doi.org/10.1111/gcb.14857.

Cooper, L.A., Ballantyne, A.P., Holden, Z.A., Landguth, E.L., 2017. Disturbance impacts on land surface temperature and gross primary productivity in the western United States. J. Geophys. Res. Biogeosci 122, 930–946. https://doi.org/10.1002/2016JG003622.

Copernicus Climate Change Service. (2021). Copernicus Climate Change Service (2021): European State of the Climate 2020 Summary.

Covey, K.R., et al., 2016. Greenhouse trace gases in deadwood. Biogeochemistry 130, 215–226.

Covey, K.R., Megonigal, J.P., 2019. Methane production and emissions in trees and forests. N. Phytol. 222 (1), 35–51.

D'Andrea, E., Rezaie, N., Battistelli, A., Gavrichkova, O., Kuhlmann, I., Matteucci, G., Moscatello, S., Proietti, S., Scartazza, A., Trumbore, S., Muhr, J., 2019. Winter's bite: Beech trees survive complete defoliation due to spring late-frost damage by mobilizing old C reserves. N. Phytol. 224 (2), 625–631.

D'Andrea, E., Rezaie, N., Prislan, P., Gričar, J., Collalti, A., Muhr, J., Matteucci, G., 2020. Frost and drought: Effects of extreme weather events on stem carbon dynamics in a Mediterranean beech forest. Plant Cell & Environ. 43 (10), 2365–2379. https://doi.org/10.1111/pce.13858.

Dalal, R.C., Allen, D.E., 2008. Greenhouse gas fluxes from natural ecosystems. Aust. J. Bot. 56, 369–407.

Dalmonech, D., Marano, G., Amthor, J.S., Cescatti, A., Lindner, M., Trotta, C., Collalti, A., 2022. Feasibility of enhancing carbon sequestration and stock capacity in temperate and boreal European forests via changes to management regimes. Agric. For. Meteorol. 327, 109203.

De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Walker, A.P., Dietze, M.C., Wang, Y., Luo, Y., Jain, A.K., El-Masri, B., Hickler, T., Wårlind, D., Weng, E., Parton, W.J., Thornton, P. E., Wang, S., Prentice, I.C., Asao, S., Smith, B., McCarthy, H.R., Norby, R.J., 2014. Where does the carbon go? A model–data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO_2 enrichment sites. N. Phytol. 203 (3), 883–899. https://doi.org/10.1111/nph.12847.

De Witte, L.C., Rosenstock, N.P., Van Der Linde, S., Braun, S., 2017. Nitrogen deposition changes ectomycorrhizal communities in Swiss beech forests. Sci. Total Environ. 605–606, 1083–1096. https://doi.org/10.1016/j.scitotenv.2017.06.142.

Dean, S.L., Farrer, E.C., Taylor, D.L., Porras-Alfaro, A., Suding, K.N., Sinsabaugh, R.L., 2014. Nitrogen deposition alters plant-fungal relationships: Linking belowground dynamics to aboveground vegetation change. Mol. Ecol. 23 (6), 1364–1378, 06.11.2013.

DeSoto, L., Cailleret, M., Sterck, F., Jansen, S., Kramer, K., Robert, E.M.R., Aakala, T., Amoroso, M.M., Bigler, C., Camarero, J.J., Čufar, K., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hereş, A.-M., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Martínez-Vilalta, J., 2020. Low growth resilience to drought is related to future mortality risk in trees. Nat. Commun. 11 (1), 545. https://doi.org/10.1038/s41467-020-14300-5.

Di Sacco, A., Hardwick, K.A., Blakesley, D., Brancalion, P.H.S., Breman, E., Cecilio Rebola, L., Chomba, S., Dixon, K., Elliott, S., Ruyonga, G., Shaw, K., Smith, P., Smith, R.J., Antonelli, A., 2021. Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. Glob. Change Biol. 27 (7), 1328–1348, 25.01.2021.

D'Odorico, P., Schönbeck, L., Vitali, V., Meusburger, K., Schaub, M., Ginzler, C., Zweifel, R., Velasco, V.M.E., Gisler, J., Gessler, A., Ensminger, I., 2021. Drone-based physiological index reveals long-term acclimation and drought stress responses in trees. Plant Cell & Environ. 44 (11), 3552–3570. https://doi.org/10.1111/pce.14177.

Domec, J., King, J.S., Noormets, A., Treasure, E., Gavazzi, M.J., Sun, G., McNulty, S.G., 2010. Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange. N. Phytol. 187 (1), 171–183. https://doi.org/10.1111/j.1469-8137.2010.03245.x.

Dong, G., Jiang, F., Zhang, Y., et al., 2026. Canadian net forest CO2 uptake enhanced by heat drought via reduced respiration. Nat. Geosci. 19, 145–152. https://doi.org/10.1038/s41561-025-01875-1.

Dosio, A., Migliavacca, M., Maraun, D., 2025. How fast is climate changing? One generation is sufficient for unfamiliar heatwave characteristics to emerge in Europe. Clim. Change 178 (2), 26. https://doi.org/10.1007/s10584-024-03855-7.

Douda, J., Čejková, A., Douda, K., Kochánková, J., 2009. Development of alder carr after the abandonment of wet grasslands during the last 70 years. Ann. For. Sci. 66 (7), 712.

Doukalianou, F., Radoglou, K., Agnelli, A.E., Kitikidou, K., Milios, E., Orfanoudakis, M., Lagomarsino, A., 2019. Annual Greenhouse-Gas Emissions from Forest Soil of a Peri-Urban Conifer Forest in Greece under Different Thinning Intensities and Their Climate-Change Mitigation Potential. For. Sci. 65 (4), 387–400.

Du, E., De Vries, W., Collalti, A., De Marco, A., 2025. Climate Warming Alters Nutrient Cycling and its Constraint on CO2 Fertilization in Global Forests. Curr. Clim. Change Rep. 11 (1), 3. https://doi.org/10.1007/s40641-025-00201-6.

Du, E., Vries, W. de, 2018. Nitrogen-induced new net primary production and carbon sequestration in global forests. In: Environmental pollution (Barking, Essex: 1987), 242, pp. 1476–1487, 14.08.2018.

Dziedek, C., Härdtle, W., Oheimb, G. von, Fichtner, A., 2016. Nitrogen Addition Enhances Drought Sensitivity of Young Deciduous Tree Species. Front. Plant Sci. 7, 1100 (22.07.2016.

Eagar, A.C., Mushinski, R.M., Horning, A.L., Smemo, K.A., Phillips, R.P., Blackwood, C. B., 2022. Arbuscular Mycorrhizal Tree Communities Have Greater Soil Fungal Diversity and Relative Abundances of Saprotrophs and Pathogens than Ectomycorrhizal Tree Communities. Appl. Environ. Microbiol. 88 (1), e01782-21. https://doi.org/10.1128/AEM.01782-21.

EEA. (2025). EEA, European Environmental Agency: Annual European Union greenhouse gas inventory 1990-2023 and inventory document 2025. ⟨https://www.eea.europa.eu/en/analysis/publications/⟩ (last access: 23 May 2025).

Ellsworth, D.S., Anderson, I.C., Crous, K.Y., Cooke, J., Drake, J.E., Gherlenda, A.N., Gimeno, T.E., Macdonald, C.A., Medlyn, B.E., Powell, J.R., Tjoelker, M.G., Reich, P. B., 2017. Elevated CO2 does not increase eucalypt forest productivity on a low-phosphorus soil. Nat. Clim. Change 7 (4), 279–282.

Engardt, M., Simpson, D., Schwikowski, M., Granat, L., 2017. Deposition of sulphur and nitrogen in Europe 1900–2050. Model calculations and comparison to historical observations. Tellus B Chem. Phys. Meteorol. 69 (1), 1328945. https://doi.org/10.1080/16000889.2017.1328945.

Erisman, J.W., Grennfelt, P., Sutton, M., 2003. The European perspective on nitrogen emission and deposition. Environ. Int. 29 (2–3), 311–325. https://doi.org/10.1016/S0160-4120(02)00162-9.

Etzold, S., Ferretti, M., Reinds, G.J., Solberg, S., Gessler, A., Waldner, P., Schaub, M., Simpson, D., Benham, S., Hansen, K., Ingerslev, M., Jonard, M., Karlsson, P.E., Lindroos, A.-J., Marchetto, A., Manninger, M., Meesenburg, H., Merilä, P., Nöjd, P., De Vries, W., 2020. Nitrogen deposition is the most important environmental driver of growth of pure, even-aged and managed European forests. For. Ecol. Manag. 458, 117762. https://doi.org/10.1016/j.foreco.2019.117762.

European Environment Agency. (2024). European Environment Agency (2024). Briefing no. 07/2024, Air pollution in Europe: 2024 reporting status under the National Emission reduction Commitments Directive, EN HTML: TH-AM-24-010-EN-Q - ISBN: 978-92-9480-651-2—ISSN: 2467-3196—Doi: ⟨10.2800/019282⟩.

Fang, O., Zhang, Q.-B., 2019. Tree resilience to drought increases in the Tibetan Plateau. Glob Change Biol. 25, 245–253. https://doi.org/10.1111/gcb.14470.

Fernández-Alonso, M.J., Díaz-Pinés, E., Rubio, A., 2021. Drivers of soil respiration in response to nitrogen addition in a Mediterranean mountain forest. Biogeochemistry 155 (3), 305–321.

Fernández-Martínez, M., Peñuelas, J., Chevallier, F., Ciais, P., Obersteiner, M., Rödenbeck, C., Sardans, J., Vicca, S., Yang, H., Sitch, S., Friedlingstein, P., Arora, V. K., Goll, D.S., Jain, A.K., Lombardozzi, D.L., McGuire, P.C., Janssens, I.A., 2023. Diagnosing destabilization risk in global land carbon sinks. Nature 615 (7954), 848–853, 22.02.2023.

Fernández-Martínez, M., Vicca, S., Janssens, I.A., Ciais, P., Obersteiner, M., Bartrons, M., Sardans, J., Verger, A., Canadell, J.G., Chevallier, F., Wang, X., Bernhofer, C., Curtis, P.S., Gianelle, D., Grünwald, T., Heinesch, B., Ibrom, A., Knohl, A., Laurila, T., Peñuelas, J., 2017. Atmospheric deposition, CO2, and change in the land carbon sink. Sci. Rep. 7 (1), 9632, 29.08.2017.

Finzi, A.C., Moore, D.J.P., DeLucia, E.H., Lichter, J., Hofmockel, K.S., Jackson, R.B., Kim, H.-S., Matamala, R., McCarthy, H.R., Oren, R., Pippen, J.S., Schlesinger, W.H., 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO2 in a warm-temperate forest. Ecology 87 (1), 15–25.

Flechard, C.R., Ibrom, A., Skiba, U.M., Vries, W. de, van Oijen, M., Cameron, D.R., Dise, N.B., Korhonen, J.F.J., Buchmann, N., Legout, A., Simpson, D., Sanz, M.J., Aubinet, M., Loustau, D., Montagnani, L., Neirynck, J., Janssens, I.A., Pihlatie, M., Kiese, R., Sutton, M.A., 2020a. Carbon–nitrogen interactions in European forests and semi-natural vegetation – Part 1: Fluxes and budgets of carbon, nitrogen and greenhouse gases from ecosystem monitoring and modelling. In. Biogeosciences 17 (6), 1583–1620.

Flechard, C.R., van Oijen, M., Cameron, D.R., Vries, W. de, Ibrom, A., Buchmann, N., Dise, N.B., Janssens, I.A., Neirynck, J., Montagnani, L., Varlagin, A., Loustau, D., Legout, A., Ziemblińska, K., Aubinet, M., Aurela, M., Chojnicki, B.H., Drewer, J., Eugster, W., Sutton, M.A., 2020b. Carbon–nitrogen interactions in European forests and semi-natural vegetation – Part 2: Untangling climatic, edaphic, management and nitrogen deposition effects on carbon sequestration potentials. Biogeosciences 17 (6), 1621–1654.

Forzieri, G., Girardello, M., Ceccherini, G., Spinoni, J., Feyen, L., Hartmann, H., Beck, P. S.A., Camps-Valls, G., Chirici, G., Mauri, A., Cescatti, A., 2021. Emergent vulnerability to climate-driven disturbances in European forests. Nat. Commun. 12 (1), 1081, 23.02.2021.

Frankenberg, et al., 2021. Comment on "Recent global decline of CO2 fertilization effects on vegetation photosynthesis. Science 373, eabg2947. https://doi.org/10.1126/science.abg2947.

Friedlingstein, P., O'Sullivan, M., Jones, M.W., Andrew, R.M., Hauck, J., Landschützer, P., Le Quéré, C., Li, H., Luijkx, I.T., Olsen, A., Peters, G.P., Peters, W., Pongratz, J., Schwingshackl, C., Sitch, S., Canadell, J.G., Ciais, P., Jackson, R.B., Alin, S.R., Zeng, J., 2025. Global Carbon Budget 2024. Earth Syst. Sci. Data 17 (3), 965–1039. https://doi.org/10.5194/essd-17-965-2025.

Fu, Z., Ciais, P., Bastos, A., Stoy, P.C., Yang, H., Green, J.K., Wang, B., Yu, K., Huang, Y., Knohl, A., Šigut, L., Gharun, M., Cuntz, M., Arriga, N., Roland, M., Peichl, M., Migliavacca, M., Cremonese, E., Varlagin, A., Koebsch, F., 2020. Sensitivity of gross primary productivity to climatic drivers during the summer drought of 2018 in Europe. Philos. Trans. R. Soc. B Biol. Sci. 375 (1810), 20190747. https://doi.org/10.1098/rstb.2019.0747.

Fürstenau Togashi, H., Prentice, I.C., Atkin, O.K., Macfarlane, C., Prober, S.M., Bloomfield, K.J., Evans, B.J., 2018. Thermal acclimation of leaf photosynthetic traits in an evergreen woodland, consistent with the coordination hypothesis. Biogeosciences 15, 3461–3474. https://doi.org/10.5194/bg-15-3461-2018, 2018.

Galloway, J.N., Aber, J.D., Erisman, J.W.N., Seitzinger, S.P., Howarth, R.W., Cowling, E. B., Cosby, B.J., 2003. The Nitrogen Cascade. BioScience 53 (4), 341.

García-Palacios, P., Crowther, T.W., Dacal, M., Hartley, I.P., Reinsch, S., Rinnan, R., Rousk, J., Van Den Hoogen, J., Ye, J.-S., Bradford, M.A., 2021. Evidence for large microbial-mediated losses of soil carbon under anthropogenic warming. Nat. Rev. Earth & Environ. 2 (7), 507–517. https://doi.org/10.1038/s43017-021-00178-4.

García-Palacios, P., Vandegehuchte, M.L., Shaw, E.A., Dam, M., Post, K.H., Ramirez, K.S., Sylvain, Z.A., Tomasel, C.M. de, Wall, D.H., 2014. Are there links between responses of soil microbes and ecosystem functioning to elevated CO2, N deposition and warming? A global perspective. Glob. Change Biol. 21 (4), 1590–1600, 12.12.2014.

Gardner, A., Ellsworth, D.S., Crous, K.Y., Pritchard, J., MacKenzie, A.R., 2022. Is photosynthetic enhancement sustained through three years of elevated CO2 exposure in 175-year-old Quercus robur? Tree Physiol. 42 (1), 130–144.

Gauci, V., et al., 2024. Global atmospheric methane uptake by upland tree woody surfaces. Nature 631, 796–803.

Gauci, V., 2025. Tree methane exchange in a changing world. Nat. Rev. Earth & Environ. 6, 471–483.

Gazol A, Camarero JJ, Vicente-Serrano SM, Sánchez-Salguero R, Gutiérrez E, de Luis M, Sangüesa-Barreda G, Novak K, Rozas V, Tíscar PA, Linares JC, Martín-Hernández N, Martínez Del Castillo E, Ribas M, García-González I, Silla F, Camisón A, Génova M, Olano JM, Longares LA, Hevia A, Tomás-Burguera M, Galván JD. Forest resilience to drought varies across biomes. Glob Chang Biol. 2018 May;24(5):2143-2158. doi: 10.1111/gcb.14082. Epub 2018 Feb 28. PMID: 29488293.

Gedalof, Z., Berg, A.A., 2010. Tree ring evidence for limited direct CO2 fertilization of forests over the 20th century. Glob. Biogeochem. Cycles 24, GB3027. https://doi.org/10.1029/2009GB003699.

Gharun, M., Hörtnagl, L., Paul-Limoges, E., Ghiasi, S., Feigenwinter, I., Burri, S., Marquardt, K., Etzold, S., Zweifel, R., Eugster, W., Buchmann, N., 2020. Physiological response of Swiss ecosystems to 2018 drought across plant types and elevation. Philos. Trans. R. Soc. B Biol. Sci. 375 (1810), 20190521. https://doi.org/10.1098/rstb.2019.0521.

Gharun, M., Klesse, S., Tomlinson, G., Waldner, P., Stocker, B., Rihm, B., Siegwolf, R., Buchmann, N., 2021. Effect of nitrogen deposition on centennial forest water- use efficiency. Environ. Res. Lett. 16, 114036. https://doi.org/10.1088/1748- 9326/ac30f9.

Gharun, M., Shekhar, A., Hörtnagl, L., Krebs, L., Arriga, N., Migliavacca, M., Roland, M., Gielen, B., Montagnani, L., Tomelleri, E., Šigut, L., Peichl, M., Zhao, P., Schmidt, M., Grünwald, T., Korkiakoski, M., Lohila, A., Buchmann, N., 2025. Impact of winter warming on CO_2 fluxes in evergreen needleleaf forests. Biogeosciences 22 (5), 1393–1411. https://doi.org/10.5194/bg-22-1393-2025.

Gharun, M., Shekhar, A., Xiao, J., Li, X., Buchmann, N., 2024. Effect of the 2022 summer drought across forest types in Europe. Biogeosciences 21 (23), 5481–5494. https://doi.org/10.5194/bg-21-5481-2024.

Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T.W., Sperry, J.S., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. N. Phytol. 226 (6), 1550–1566, 20.03.2020.

Grünig, et al., 2026. Climate change will increase forest disturbances in Europe throughout the 21st century. Science 391 (2026), eadx6329. https://doi.org/10.1126/science.adx6329.

Grünzweig, J.M., Boeck, H.J., de, Rey, A., Santos, M.J., Adam, O., Bahn, M., Belnap, J., Deckmyn, G., Dekker, S.C., Flores, O., Gliksman, D., Helman, D., Hultine, K.R., Liu, L., Meron, E., Michael, Y., Sheffer, E., Throop, H.L., Tzuk, O., Yakir, D., 2022. Dryland mechanisms could widely control ecosystem functioning in a drier and warmer world. Nat. Ecol. & Evol. (25. 07. 2022 6 (8), 1064–1076.

Gunderson, L.H., 2000. Ecological Resilience—In Theory and Application. Annu. Rev. Ecol. Syst. 31 (1), 425–439.

Hasselquist, N.J., Metcalfe, D.B., Inselsbacher, E., Stangl, Z., Oren, R., Näsholm, T., Högberg, P., 2016. Greater carbon allocation to mycorrhizal fungi reduces tree nitrogen uptake in a boreal forest. Ecology.

Henttonen, H.M., Nöjd, P., Mäkinen, H., 2024. Environment-induced growth changes in forests of Finland revisited—A follow-up using an extended data set from the 1960s to the 2020s. For. Ecol. Manag. 551, 121515. https://doi.org/10.1016/j.foreco.2023.121515.

Hisano, M., Searle, E.B., Chen, H.Y.H., 2018. Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. Biol. Rev. Camb. Philos. Soc. 93 (1), 439–456, 10.07.2017.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411 (6839), 789–792.

Holling, C.S., 1973. Resilience and Stability of Ecological Systems. Annu. Rev. Ecol. Syst. 4 (1), 1–23.

Huang, H., Calabrese, S., Rodriguez-Iturbe, I., 2021a. Variability of ecosystem carbon source from microbial respiration is controlled by rainfall dynamics. Proc. Natl. Acad. Sci. 118 (52), e2115283118. https://doi.org/10.1073/pnas.2115283118.

Huang, J., Hammerbacher, A., Gershenzon, J., van Dam, N.M., Sala, A., McDowell, N.G., Chowdhury, S., Gleixner, G., Trumbore, S., Hartmann, H., 2021b. Storage of carbon reserves in spruce trees is prioritized over growth in the face of carbon limitation. Proc. Natl. Acad. Sci. USA 118 (33).

Huang, K., Xia, J., 2019. High ecosystem stability of evergreen broadleaf forests under severe droughts. Global Change Biology 25, 3494–3503. https://doi.org/10.1111/gcb.14748.

Huo, R., Li, L., Chen, H., Xu, C.-Y., Chen, J., Guo, S., 2021. Extreme Precipitation Changes in Europe from the Last Millennium to the End of the Twenty-First Century. J. Clim. 34 (2), 567–588. https://doi.org/10.1175/JCLI-D-19-0879.1.

Ibáñez, I., Zak, D.R., Burton, A.J., Pregitzer, K.S., 2018. Anthropogenic nitrogen deposition ameliorates the decline in tree growth caused by a drier climate. Ecol. (17. 01. 2018 99 (2), 411–420.

Imbert, J.B., Blanco, J.A., Candel-Pérez, D., Lo, Y.-H., González de Andrés, E., Yeste, A., Herrera-Álvarez, X., Rivadeneira Barba, G., Liu, Y., Chang, S.-C., 2021. Synergies Between Climate Change, Biodiversity, Ecosystem Function and Services, Indirect Drivers of Change and Human Well-Being in Forests. In: Venkatramanan, In.V., Shah, S., Prasad, R. (Eds.), Exploring Synergies and Trade-offs between Climate Change and the Sustainable Development Goals. Springer, Singapore, pp. 263–320.

Ingrisch, J., Bahn, M., 2018. Towards a Comparable Quantification of Resilience. Trends Ecol. & Evol. 33 (4), 251–259. https://doi.org/10.1016/j.tree.2018.01.013.

IPCC. (2023). Climate Change 2022 – Impacts, Adaptation and Vulnerability. Cambridge University Press.

Janssens, I.A., Dieleman, W., Luyssaert, S., Subke, J.-A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A.J., Grace, J., Matteucci, G., Papale, D., Piao, S.L., Schulze, E.-D., Tang, J., Law, B.E., 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nat. Geosci. 3 (5), 315–322.

Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.-.-D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R. and Valentini, R. (2001), Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biology, 7: 269-278. https://doi.org/10.1046/j.1365-2486.2001.00412.x.

Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., Valentini, R., 2007. Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: The "Birch effect. Tree Physiol. 27 (7), 929–940. https://doi.org/10.1093/treephys/27.7.929.

Johannesson, C.-F., Ilvesniemi, H., Kjønaas, O.J., Larsen, K.S., Lehtonen, A., Nordén, J., Paré, D., Silvennoinen, H., Stendahl, J., Stupak, I., Vesterdal, L., & Dalsgaard, L. (2024). Decadal Decline in Forest Floor Soil Organic Carbon after Clear-Cutting in Nordic and Canadian Forests. SSRN. ⟨https://doi.org/10.2139/ssrn.5022374⟩.

Jordan, E., Shekhar, A., Gharun, M., 2024. Assessing the Volatility of Daily Maximum Temperature across Germany between 1990 and 2022. Atmosphere 15 (7), 838. https://doi.org/10.3390/atmos15070838.

Jucker, T., Avăcăriței, D., Bărnoaiea, I., Duduman, G., Bouriaud, O., Coomes, D.A., 2016. Climate modulates the effects of tree diversity on forest productivity. J. Ecol. 104 (2), 388–398.

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: Linking patterns and processes. Ecol. Lett. 17 (12), 1560–1569, 13.10.2014.

Jurasinski, G., Barthelmes, A., Byrne, K.A., Chojnicki, B.H., Christiansen, J.R., Decleer, K., Fritz, C., Günther, A.B., Huth, V., Joosten, H., Juszczak, R., Juutinen, S., Kasimir, Å., Klemedtsson, L., Koebsch, F., Kotowski, W., Kull, A., Lamentowicz, M., Lindgren, A., Couwenberg, J., 2024. Active afforestation of drained peatlands is not a viable option under the EU Nature Restoration Law. Ambio 53 (7), 970–983. https://doi.org/10.1007/s13280-024-02016-5.

Karim, M.R., Halim, M.A., Thomas, S.C., 2024. Foliar methane and nitrous oxide fluxes in tropical tree species. Sci. Total Environ. 954, 176503.

Keenan, T.F., Hollinger, D.Y., Bohrer, G., Dragoni, D., Munger, J.W., Schmid, H.P., Richardson, A.D., 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature 499 (7458), 324–327. https://doi.org/10.1038/nature12291.

Keenan, T.F., Luo, X., Stocker, B.D., De Kauwe, M.G., Medlyn, B.E., Prentice, I.C., Smith, N.G., Terrer, C., Wang, H., Zhang, Y., Zhou, S., 2023. A constraint on historic growth in global photosynthesis due to rising CO2. Nat. Clim. Change 13 (12), 1376–1381. https://doi.org/10.1038/s41558-023-01867-2.

Khoury, S., Coomes, D.A., 2020. Resilience of Spanish forests to recent droughts and climate change. Glob Change Biol. 26, 7079–7098. https://doi.org/10.1111/gcb.15268.

Klaus, M., Öquist, M., Macháčová, K., 2024. Tree stem-atmosphere greenhouse gas fluxes in a boreal riparian forest. Sci. Total Environ. 954, 176243. https://doi.org/10.1016/j.scitotenv.2024.176243.

Kolářová, E., Nekovář, J., Adamík, P., 2014. Long-term temporal changes in central European tree phenology (1946-2010) confirm the recent extension of growing seasons. Int. J. Biometeorol. 58 (8), 1739–1748, 05.01.2014.

Korkiakoski, M., Määttä, T., Peltoniemi, K., Penttilä, T., Lohila, A., 2022. Excess soil moisture and fresh carbon input are prerequisites for methane production in podzolic soil. Biogeosciences 19 (7), 2025–2041. https://doi.org/10.5194/bg-19-2025-2022.

Korkiakoski, M., Tuovinen, J.-P., Penttilä, T., Sarkkola, S., Ojanen, P., Minkkinen, K., Rainne, J., Laurila, T., Lohila, A., 2019. Greenhouse gas and energy fluxes in a boreal peatland forest after clear-cutting. Biogeosciences 16 (19), 3703–3723.

Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S.G., Peláez-Riedl, S., Pepin, S., Siegwolf, R.T.W., Zotz, G., 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO2. Science (New York N. Y.) 309 (5739), 1360–1362.

Korosuo, A., Pilli, R., Abad Viñas, R., Blujdea, V.N.B., Colditz, R.R., Fiorese, G., Rossi, S., Vizzarri, M., Grassi, G., 2023. The role of forests in the EU climate policy: Are we on the right track? In. Carbon Balance Manag. (30. 07. 2023 18 (1), 15.

Kowalska, N., Šigut, L., Stojanović, M., Fischer, M., Kyselova, I., Pavelka, M., 2020. Analysis of floodplain forest sensitivity to drought. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. (07. 09. 2020 375 (1810), 20190518.

Kramer, K., Vreugdenhil, S.J., van der Werf, D.C., 2008. Effects of flooding on the recruitment, damage and mortality of riparian tree species: A field and simulation study on the Rhine floodplain. For. Ecol. Manag. 255 (11), 3893–3903. https://doi.org/10.1016/j.foreco.2008.03.044.

Krebs, L., Burri, S., Feigenwinter, I., Gharun, M., Meier, P., Buchmann, N., 2024. Forest-floor respiration, N_2O fluxes, and CH_4 fluxes in a subalpine spruce forest: Drivers and annual budgets. Biogeosciences 21 (8), 2005–2028. https://doi.org/10.5194/bg-21-2005-2024.

Krebs, L., Hörtnagl, L., Scapucci, L., Gharun, M., Feigenwinter, I., Buchmann, N., 2025. Net Ecosystem CO_2 Exchange of a Subalpine Spruce Forest in Switzerland Over 26 Years: Effects of Phenology and Contributions of Abiotic Drivers at Daily Time Scales. Glob. Change Biol. 31 (7), e70371. https://doi.org/10.1111/gcb.70371.

Kreyling, J., Grant, K., Hammerl, V., Arfin-Khan, M.A.S., Malyshev, A.V., Peñuelas, J., Pritsch, K., Sardans, J., Schloter, M., Schuerings, J., Jentsch, A., Beierkuhnlein, C., 2019. Winter warming is ecologically more relevant than summer warming in a cool-temperate grassland. Sci. Rep. (10. 10. 2019 9 (1), 14632.

Lapola, D.M., Blanco, C.C., Cardeli, B.R., Esquivel-Muelbert, A., Martinelli, J.V., Quesada, C.A.N., Rius, B.F., Silva-Junior, C.H.L., 2025. Not just semantics: CO_2 fertilization can be a disturbance leading to worldwide forest degradation. PLANTS PEOPLE PLANET 7 (3), 638–643. https://doi.org/10.1002/ppp3.10601.

Larsen, K.S., Ibrom, A., Beier, C., Jonasson, S., Michelsen, A., 2007. Ecosystem respiration depends strongly on photosynthesis in a temperate heath. Biogeochemistry 85 (2), 201–213. https://doi.org/10.1007/s10533-007-9129-8.

Laudon, H., Mensah, A.A., Fridman, J., Näsholm, T., Jämtgård, S., 2024. Perspectives: Swedish forest growth decline: A consequence of climate warming? For. Ecol. Manag. 565, 122052. https://doi.org/10.1016/j.foreco.2024.122052.

Leakey, Andrew D.B., Elizabeth, A. Ainsworth, Bernacchi, Carl J., Rogers, Alistair, Long, Stephen P., Ort, Donald R., 2009. Elevated CO2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. Journal of Experimental Botany 60 (10), 2859–2876. https://doi.org/10.1093/jxb/erp096.

Lenhart, K., Weber, B., Elbert, W., Steinkamp, J., Clough, T., Crutzen, P., Pöschl, U., Keppler, F., 2015. Nitrous oxide and methane emissions from cryptogamic covers. Glob. Change Biol. 21, 3889–3900.

Lenoir, I., Fontaine, J., Lounès-Hadj Sahraoui, A., 2016. Arbuscular mycorrhizal fungal responses to abiotic stresses: A review. Phytochemistry 123, 4–15. https://doi.org/10.1016/j.phytochem.2016.01.002.

Li, M.W., Zhang, J., Wu, Z.F., Fu, Y.S., 2025. Effect of growing season length on gross primary productivity increased in the Jinsha River watershed. J. Plant Ecol. 18 (1), rtae108. https://doi.org/10.1093/jpe/rtae108.

Lindroth, A., Holst, J., Linderson, M.-L., Aurela, M., Biermann, T., Heliasz, M., Chi, J., Ibrom, A., Kolari, P., Klemedtsson, L., Krasnova, A., Laurila, T., Lehner, I., Lohila, A., Mammarella, I., Mölder, M., Löfvenius, M.O., Peichl, M., Pilegaard, K., Nilsson, M., 2020. Effects of drought and meteorological forcing on carbon and water fluxes in Nordic forests during the dry summer of 2018. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. (07. 09. 2020 375 (1810), 20190516.

Liu, et al., 2026. Data gaps and outliers distort critical-slowing-down-based resilience indicators. Sci. Adv. 12, eaee1916. https://doi.org/10.1126/sciadv.aee1916.

Liu, L., Estiarte, M., Peñuelas, J., 2019. Soil moisture as the key factor of atmospheric CH4 uptake in forest soils under environmental change. Geoderma 355, 113920.

Liu, J., Fan, B., Sun, Z., Dai, L., Duan, A., 2025. A global meta-analysis of soil respiration in response to elevated CO2. Soil Biol. Biochem. 203, 109734. https://doi.org/10.1016/j.soilbio.2025.109734.

Liu, W., He, H., Wu, X., Ren, X., Zhang, L., shi, L., Feng, L., Wang, Y., Lv, Y., 2023. Importance of the memory effect for assessing interannual variation in net ecosystem exchange. Agric. For. Meteorol. 341, 109691.

Liu, S., Ji, C., Wang, C., Chen, J., Jin, Y., Zou, Z., Li, S., Niu, S., Zou, J., 2018. Climatic role of terrestrial ecosystem under elevated CO2: A bottom-up greenhouse gases budget. Ecol. Lett. (07. 05. 2018 21 (7), 1108–1118.

Liu, Q., Piao, S., Janssens, I.A., Fu, Y., Peng, S., Lian, X., Ciais, P., Myneni, R.B., Peñuelas, J., Wang, T., 2018a. Extension of the growing season increases vegetation exposure to frost. Nat. Commun. (30. 01. 2018 9 (1), 426.

López-Ballesteros, A., Serrano-Ortiz, P., Sánchez-Cañete, E.P., Oyonarte, C., Kowalski, A. S., Pérez-Priego, Ó., Domingo, F., 2016. Enhancement of the net CO 2 release of a semiarid grassland in SE Spain by rain pulses. In. J. Geophys. Res. Biogeosciences 121 (1), 52–66.

Lu, J., Yan, F., 2023. The Divergent Resistance and Resilience of Forest and Grassland Ecosystems to Extreme Summer Drought in Carbon Sequestration. Land 12 (9), 1672. https://doi.org/10.3390/land12091672.

Luo, X., Zhao, R., Chu, H., Collalti, A., Fatichi, S., Keenan, T.F., Lu, X., Nguyen, N., Prentice, I.C., Sun, W., Yu, K., Yu, L., 2025. Global variation in vegetation carbon use efficiency inferred from eddy covariance observations. Nat. Ecol. & Evol. 9 (8), 1414–1425. https://doi.org/10.1038/s41559-025-02753-0.

Ma, X., Zhu, B., Nie, Y., Liu, Y., Kuzyakov, Y., 2021. Root and mycorrhizal strategies for nutrient acquisition in forests under nitrogen deposition: A meta-analysis. Soil Biol. Biochem. 163, 108418. https://doi.org/10.1016/j.soilbio.2021.108418.

Machacova, K., Bäck, J., Vanhatalo, A., Halmeenmäki, E., Kolari, P., Mammarella, I., Pumpanen, J., Acosta, M., Urban, O., Pihlatie, M., 2016. Pinus sylvestris as a missing source of nitrous oxide and methane in boreal forest. Sci. Rep. 6, 23410. https://doi.org/10.1038/srep23410.

Machacova, K., Borak, L., Agyei, T., Schindler, T., Soosaar, K., Mander, Ü., Ah-Peng, C., 2021. Trees as net sinks for methane (CH$_4$) and nitrous oxide (N$_2$O) in the lowland tropical rain forest on volcanic Réunion Island. N. Phytol. 229 (4), 1983–1994. https://doi.org/10.1111/nph.17002.

Machacova, K., Klem, K., Medňanský, T., Warlo, H., Ullah, S., 2026. Effect of elevated atmospheric CO2 concentration on greenhouse gas exchange of common hazel trees and soils. EGU Gen. Assem. 2026 Abstr. EGU 26–2737.

Machacova, K., Warlo, H., Svobodová, K., Agyei, T., Uchytilová, T., Horáček, P., Lang, F., 2023. Methane emission from stems of European beech (Fagus sylvatica) offsets as much as half of methane oxidation in soil. N. Phytol. 238, 584–597. https://doi.org/10.1111/nph.18726.

Madsen, R.L., Asplund, J., Nybakken, L., Biong, R., Kjønaas, O.J., 2025. Harvesting history affects soil respiration and litterfall but not overall carbon balance in boreal Norway spruce forests. For. Ecol. Manag. 578, 122485. https://doi.org/10.1016/j.foreco.2024.122485.

Mahecha, M.D., Bastos, A., Bohn, F.J., Eisenhauer, N., Feilhauer, H., Hickler, T., Kalesse-Los, H., Migliavacca, M., Otto, F.E.L., Peng, J., Sippel, S., Tegen, I., Weigelt, A., Wendisch, M., Wirth, C., Al-Halbouni, D., Deneke, H., Doktor, D., Dunker, S., Quaas, J., 2024. Biodiversity and Climate Extremes: Known Interactions and Research Gaps. Earth'S. Future 12 (6), e2023EF003963. https://doi.org/10.1029/2023EF003963.

Mander, Ü., Krasnova, A., Schindler, T., Megonigal, J.P., Escuer-Gatius, J., Espenberg, M., Machacova, K., Maddison, M., Pärn, J., Ranniku, R., Pihlatie, M., Kasak, K., Niinemets, Ü., Soosaar, K., 2022. Long-term dynamics of soil, tree stem and ecosystem methane fluxes in a riparian forest. Sci. Total Environ. 809, 151723. https://doi.org/10.1016/j.scitotenv.2021.151723.

Martins, C.S.C., Nazaries, L., Delgado-Baquerizo, M., Macdonald, C.A., Anderson, I.C., Singh, B.K., 2021. Rainfall frequency and soil water availability regulate soil methane and nitrous oxide fluxes from a native forest exposed to elevated carbon dioxide. Funct. Ecol. 35 (8), 1833–1847. https://doi.org/10.1111/1365-2435.13853.

Mavrovic, A., Sonnentag, O., Lemmetyinen, J., Voigt, C., Aurela, M., Roy, A., 2024. Winter methane fluxes over boreal and Arctic environments. Preprints. https://doi.org/10.22541/essoar.170542245.58670859/v1.

Mazza, G., Agnelli, A.E., Cantiani, P., Chiavetta, U., Doukalianou, F., Kitikidou, K., Milios, E., Orfanoudakis, M., Radoglou, K., Lagomarsino, A., 2019. Short-term effects of thinning on soil CO2, N2O and CH4 fluxes in Mediterranean forest ecosystems. Science total environment (20. 09. 2018 651 (Pt 1), 713–724.

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science (New York N. Y.) 368 (6494).

McDowell, G., Stevens, M., Lesnikowski, A., Huggel, C., Harden, A., DiBella, J., Morecroft, M., Kumar, P., Joe, E.T., Bhatt, I.D., Initiative, the G.A.M., 2021. Closing the Adaptation Gap in Mountains. Mt. Res. Dev. 41 (3).

Menzel, A., Fabian, P., 1999. Growing season extended in Europe. Nature 397 (6721), 659.

Metcalfe, D.B., Meir, P., Aragão, L.E.O.C., Lobo-do-Vale, R., Galbraith, D., Fisher, R.A., Chaves, M.M., Maroco, J.P., Da Costa, A.C.L., De Almeida, S.S., Braga, A.P., Gonçalves, P.H.L., De Athaydes, J., Da Costa, M., Portela, T.T.B., De Oliveira, A.A.R., Malhi, Y., Williams, M., 2010. Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. N. Phytol. 187 (3), 608–621. https://doi.org/10.1111/j.1469-8137.2010.03319.x.

Migliavacca, M., Grassi, G., Bastos, A., Ceccherini, G., Ciais, P., Janssens-Maenhout, G., Lugato, E., Mahecha, M.D., Novick, K.A., Peñuelas, J., Pilli, R., Reichstein, M., Avitabile, V., Beck, P.S.A., Barredo, J.I., Forzieri, G., Herold, M., Korosuo, A., Mansuy, N., Cescatti, A., 2025. Securing the forest carbon sink for the European Union's climate ambition. Nature 643 (8074), 1203–1213. https://doi.org/10.1038/s41586-025-08967-3.

Migliavacca, M., Reichstein, M., Richardson, A.D., Colombo, R., Sutton, M.A., Lasslop, G., Tomelleri, E., Wohlfahrt, G., Carvalhais, N., Cescatti, A., Mahecha, M.D., Montagnani, L., Papale, D., Zaehle, S., Arain, A., Arneth, A., Black, T.A., Carrara, A., Dore, S., Van Der Molen, M.K., 2011. Semiempirical modeling of abiotic and biotic factors controlling ecosystem respiration across eddy covariance sites: SEMIEMPIRICAL MODELING OF ECOSYSTEM RESPIRATION. Glob. Change Biol. 17 (1), 390–409. https://doi.org/10.1111/j.1365-2486.2010.02243.x.

Mina, M., Messier, C., Duveneck, M.J., Fortin, M.-J., Aquilué, N., 2022. Managing for the unexpected: Building resilient forest landscapes to cope with global change. Glob. Change Biol. (25. 04. 2022 28 (14), 4323–4341.

Mirabel, A., Girardin, M.P., Metsaranta, J., Way, D., Reich, P.B., 2023. Increasing atmospheric dryness reduces boreal forest tree growth. Nat. Commun. (30. 10. 2023 14 (1), 6901.

Mochidome, T., Epron, D., 2024. Drivers of intra-individual spatial variability in methane emissions from tree trunks in upland forest. Trees 38, 625–636.

Moldaschl, E., Kitzler, B., Machacova, K., Schindler, T., Schindlbacher, A., 2021. Stem CH4 and N2O fluxes of Fraxinus excelsior and Populus alba trees along a flooding gradient. Plant Soil 461 (1–2), 407–420. https://doi.org/10.1007/s11104-020-04818-4.

Montibeller, B., Marshall, M., Mander, Ü., Uuemaa, E., 2022. Increased carbon assimilation and efficient water usage may not compensate for carbon loss in European forests. Commun. Earth & Environ. 3 (1), 194. https://doi.org/10.1038/s43247-022-00535-1.

Morera, A., Martínez De Aragón, J., De Cáceres, M., Bonet, J.A., de-Miguel, S., 2022. Historical and future spatially-explicit climate change impacts on mycorrhizal and saprotrophic macrofungal productivity in Mediterranean pine forests. Agric. For. Meteorol. 319, 108918. https://doi.org/10.1016/j.agrformet.2022.108918.

Morichetti, M., Vangi, E., Collalti, A., 2024. Predicted Future Changes in the Mean Seasonal Carbon Cycle Due to Climate Change. Forests 15 (7), 1124. https://doi.org/10.3390/f15071124.

Müller, L.M., Bahn, M., 2022. Drought legacies and ecosystem responses to subsequent drought. Glob. Change Biol. (23. 06. 2022 28 (17), 5086–5103.

Musavi, T., Migliavacca, M., Reichstein, M., Kattge, J., Wirth, C., Black, T.A., Janssens, I., Knohl, A., Loustau, D., Roupsard, O., Varlagin, A., Rambal, S., Cescatti, A., Gianelle, D., Kondo, H., Tamrakar, R., Mahecha, M.D., 2017. Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity. Nat. Ecol. & Evol. 1 (2), 0048. https://doi.org/10.1038/s41559-016-0048.

Nasong, D., Zhou, S., Kornhuber, K., Yu, B., 2025. Concurrent heat extremes in relation to global warming, high atmospheric pressure and low soil moisture in the Northern Hemisphere. Earth's. Future 13, e2024EF005256. https://doi.org/10.1029/2024EF005256.

Naudts, K., Chen, Y., McGrath, M.J., Ryder, J., Valade, A., Otto, J., Luyssaert, S., 2016. Europe's forest management did not mitigate climate warming. Science 351 (6273), 597–600. https://doi.org/10.1126/science.aad7270.

Nestola, E., Scartazza, A., Di Baccio, D., Castagna, A., Ranieri, A., Cammarano, M., Mazzenga, F., Matteucci, G., Calfapietra, C., 2018. Are optical indices good proxies of seasonal changes in carbon fluxes and stress-related physiological status in a beech forest? Sci. Total Environ. 612, 1030–1041. https://doi.org/10.1016/j.scitotenv.2017.08.167.

Ni, X., Groffman, P.M., 2018. Declines in methane uptake in forest soils. Proc. Natl. Acad. Sci. 115 (34), 8587–8590. https://doi.org/10.1073/pnas.1807377115.

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F., van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. Trends plant science (21. 10. 2010 15 (12), 684–692.

Nimmo, D.G., Mac Nally, R., Cunningham, S.C., Haslem, A., Bennett, A.F., 2015. Vive la résistance: reviving resistance for 21st century conservation. Trends in Ecology & Evolution 30 (9), 516–523. https://doi.org/10.1016/j.tree.2015.07.008.

Noormets, A., McNulty, S.G., DeForest, J.L., Sun, G., Li, Q., Chen, J., 2008. Drought during canopy development has lasting effect on annual carbon balance in a deciduous temperate forest. N. Phytol. (05. 06. 2008 179 (3), 818–828.

Norby, R.J., 2025. Forest productivity response to elevated CO2 in free-air CO2 enrichment experiments: the 23 % solution, revisited. N. Phytol. 246, 1952–1959. https://doi.org/10.1111/nph.70162.

Norby, R.J., Kauwe, M.G., de, Domingues, T.F., Duursma, R.A., Ellsworth, D.S., Goll, D. S., Lapola, D.M., Luus, K.A., MacKenzie, A.R., Medlyn, B.E., Pavlick, R., Rammig, A., Smith, B., Thomas, R., Thonicke, K., Walker, A.P., Yang, X., Zaehle, S., 2016. Model-data synthesis for the next generation of forest free-air CO2 enrichment (FACE) experiments. N. Phytol. (06. 08. 2015 209 (1), 17–28.

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., McMurtrie, R.E., 2010. CO2 enhancement of forest productivity constrained by limited nitrogen availability. Proc. Natl. Acad. Sci. USA 19368–19373, 25.10.2010, Vol. 107, Issue 45.

O'Brien, M.J., Hector, A., Ong, R., Philipson, C.D., 2024. Tree growth and survival are more sensitive to high rainfall than drought in an aseasonal forest in Malaysia. Commun. Earth & Environ. 5 (1), 179. https://doi.org/10.1038/s43247-024-01335-5.

Oettel, J., Lapin, K., 2021. Linking forest management and biodiversity indicators to strengthen sustainable forest management in Europe. Ecol. Indic. 122, 107275.

Orchard, V.A., Cook, F.J., 1983. Relationship between soil respiration and soil moisture. Soil Biol. Biochem. 15 (4), 447–453. https://doi.org/10.1016/0038-0717(83)90010-X.

Pangala, S.R., et al., 2017. Large emissions from floodplain trees close the Amazon methane budget. Nature 552, 230–234.

Peñuelas, J., Ciais, P., Canadell, J.G., Janssens, I.A., Fernández-Martínez, M., Carnicer, J., Obersteiner, M., Piao, S., Vautard, R., Sardans, J., 2017. Shifting from a fertilization-dominated to a warming-dominated period. Nat. Ecol. & Evol. 1 (10), 1438–1445. https://doi.org/10.1038/s41559-017-0274-8.

Piao, S., Luyssaert, S., Ciais, P., Janssens, I.A., Chen, A., Cao, C., Fang, J., Friedlingstein, P., Luo, Y., Wang, S., 2010. Forest annual carbon cost: A global-scale analysis of autotrophic respiration. Ecology 91 (3), 652–661. https://doi.org/10.1890/08-2176.1.

Ping, J., Cui, E., Du, Y., Wei, N., Zhou, J., Wang, J., Niu, S., Luo, Y., Xia, J., 2023. Enhanced causal effect of ecosystem photosynthesis on respiration during heatwaves. Sci. Adv. 9 (43), eadi6395, 25.10.2023.

Pohl, F., Werban, U., Kumar, R., Hildebrandt, A., Rebmann, C., 2023. Observational evidence of legacy effects of the 2018 drought on a mixed deciduous forest in Germany. Sci. Rep. 05 (07), 10863, 2023, Vol. 13, Issue 1.

Pongracz, A., Wårlind, D., Miller, P.A., Gustafson, A., Rabin, S.S., Parmentier, F.-J.W., 2024. Warming-induced contrasts in snow depth drive the future trajectory of soil carbon loss across the Arctic-Boreal region. Commun. Earth & Environ. 5 (1), 684. https://doi.org/10.1038/s43247-024-01838-1.

Preisler, Y., Grünzweig, J.M., Ahiman, O., Amer, M., Oz, I., Feng, X., Muller, J.D., Ruehr, N., Rotenberg, E., Birami, B., Yakir, D., 2023. Vapour pressure deficit was not a primary limiting factor for gas exchange in an irrigated, mature dryland Aleppo pine forest. Plant Cell & Environ. 46 (12), 3775–3790, 07.09.2023.

Quan, Q., Tian, D., Luo, Y., Zhang, F., Crowther, T.W., Zhu, K., Chen, H.Y.H., Zhou, Q., Niu, S., 2019. Water scaling of ecosystem carbon cycle feedback to climate warming. Sci. Adv. 5 (8), eaav1131. https://doi.org/10.1126/sciadv.aav1131.

Rahmati, M., Graf, A., Poppe Terán, C., Amelung, W., Dorigo, W., Franssen, H.-J.H., Montzka, C., Or, D., Sprenger, M., Vanderborght, J., Verhoest, N.E.C., Vereecken, H., 2023. Continuous increase in evaporative demand shortened the growing season of European ecosystems in the last decade. Commun. Earth & Environ. 4 (1).

Ramonet, M., Ciais, P., Aalto, T., Aulagnier, C., Chevallier, F., Cipriano, D., Conway, T.J., Haszpra, L., Kazan, V., Meinhardt, F., Paris, J.-D., Schmidt, M., Simmonds, P., Xueref-Rémy, I., Necki, J.N., 2010. A recent build-up of atmospheric CO_2 over Europe. Part 1: Observed signals and possible explanations. Tellus B Chem. Phys. Meteorol. 62 (1), 1. https://doi.org/10.1111/j.1600-0889.2009.00442.x.

Rantanen, M., Karpechko, A.Y., Lipponen, A., et al., 2022. The Arctic has warmed nearly four times faster than the globe since 1979. Commun Earth Environ 3 (168). https://doi.org/10.1038/s43247-022-00498-3.

Rebane, S., Jõgiste, K., Põldveer, E., Stanturf, J.A., Metslaid, M., 2019. Direct measurements of carbon exchange at forest disturbance sites: A review of results with the eddy covariance method. Scand. J. For. Res. 34 (7), 585–597.

Regulation (EU) 2018/841. (2018). Regulation (EU) 2018/841 of the European Parliament and of the Council of 30 May 2018 on the inclusion of greenhouse gas emissions and removals from land use, land use change and forestry in the 2030 climate and energy framework, and amending Regulation (EU) No 525/2013 and Decision No 529/2013/EU. 〈https://eur-lex.europa.eu/eli/reg/2018/841/oj/eng〉.

Reich, P.B., Sendall, K.M., Stefanski, A., Wei, X., Rich, R.L., Montgomery, R.A., 2016. Boreal and temperate trees show strong acclimation of respiration to warming. Nature 531 (7596), 633–636. https://doi.org/10.1038/nature17142.

Reichstein, M., Bahn, M., Ciais, P., et al., 2013. Climate extremes and the carbon cycle. Nature 500, 287–295. https://doi.org/10.1038/nature12350.

Rodríguez-González, P.M., Colangelo, M., Sánchez-Miranda, Á., Sánchez-Salguero, R., Campelo, F., Rita, A., Gomes Marques, I., Albuquerque, A., Ripullone, F., Camarero, J.J., 2021. Climate, drought and hydrology drive narrow-leaved ash growth dynamics in southern European riparian forests. For. Ecol. Manag. 490, 119128.

Rousseau, M., Siegenthaler, A., Skidmore, A.K., De Groot, G.A., Laros, I., 2024. Further reduction in soil bacterial diversity under severe acidification in European temperate forests. Eur. J. Soil Sci. 75 (6), e70005. https://doi.org/10.1111/ejss.70005.

Ruehr, S., Keenan, T.F., Williams, C., Zhou, Y., Lu, X., Bastos, A., Canadell, J.G., Prentice, I.C., Sitch, S., Terrer, C., 2023. Evidence and attribution of the enhanced land carbon sink. Nat. Rev. Earth & Environ. 4 (8), 518–534.

Ruehr, N.K., Knohl, A., Buchmann, N., 2010. Environmental variables controlling soil respiration on diurnal, seasonal and annual time-scales in a mixed mountain forest in Switzerland. Biogeochemistry 98 (s 1–3), 153–170.

Ryan, M.G., Law, B.E., 2005. Interpreting, measuring, and modeling soil respiration. Biogeochemistry 73 (1), 3–27. https://doi.org/10.1007/s10533-004-5167-7.

Sabatini, F.M., De Andrade, R.B., Paillet, Y., Ódor, P., Bouget, C., Campagnaro, T., Gosselin, F., Janssen, P., Mattioli, W., Nascimbene, J., Sitzia, T., Kuemmerle, T., Burrascano, S., 2019. Trade-offs between carbon stocks and biodiversity in European temperate forests. Glob. Change Biol. 25 (2), 536–548. https://doi.org/10.1111/gcb.14503.

Sang, et al., 2021. Comment on “Recent global decline of CO_2 fertilization effects on vegetation photosynthesis. Science 373, eabg4420. https://doi.org/10.1126/science.abg4420.

Saponaro, V., et al., 2026. Climate change, more than management, drives short- and long-term changes in iWUE in a sub-Alpine beech forest. J. For. Res. 37, 16. https://doi.org/10.1007/s11676-025-01942-8.

Saunois, M., Martinez, A., Poulter, B., Zhang, Z., Raymond, P., Regnier, P., Canadell, J.G., Jackson, R.B., Patra, P.K., Bousquet, P., Ciais, P., Dlugokencky, E.J., Lan, X., Allen, G.H., Bastviken, D., Beerling, D.J., Belikov, D.A., Blake, D.R., Castaldi, S., Zhuang, Q., 2024. Global Methane Budget 2000–2020. ESSD Atmosphere/Atmos. Chem. Phys. https://doi.org/10.5194/essd-2024-115.

Schimel, J.P., 2018. Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes. Annu. Rev. Ecol. Evol. Syst. 49 (1), 409–432.

Schindler, T., Machacova, K., Mander, Ü., Escuer-Gatius, J., Soosaar, K., 2021. Diurnal tree stem CH4 and N2O flux dynamics from a riparian alder forest. Forests 12, 863.

Schindler, T., Mander, Ü., Machacova, K., Espenberg, M., Krasnov, D., Escuer-Gatius, J., Veber, G., Pärn, J., Soosaar, K., 2020. Short-term flooding increases CH4 and N2O emissions from trees in a riparian forest soil-stem continuum. Sci. Rep. 10 (1), 3204. https://doi.org/10.1038/s41598-020-60058-7.

Schlesinger, W.H., 2009. On the fate of anthropogenic nitrogen. Proc. Natl. Acad. Sci. USA (31. 12. 2008 106 (1), 203–208.

Schmitz, A., Sanders, T.G.M., Bolte, A., Bussotti, F., Dirnböck, T., Johnson, J., Peñuelas, J., Pollastrini, M., Prescher, A.-K., Sardans, J., Verstraeten, A., Vries, W. de, 2019. Responses of forest ecosystems in Europe to decreasing nitrogen deposition. In: Environmental pollution (Barking, Essex: 1987), 244, pp. 980–994, 26.10.2018.

Schulze, E.-D., Beck, E., Buchmann, N., Clemens, S., Müller-Hohenstein, K., & Scherer-Lorenzen, M., 2019. Plant Ecology. Berlin: Springer. https://doi.org/10.1007/978-3-662-56233-8.

Schwede, D.B., Simpson, D., Tan, J., Fu, J.S., Dentener, F., Du, E., deVries, W., 2018. Spatial variation of modelled total, dry and wet nitrogen deposition to forests at global scale. In: Environmental pollution (Barking, Essex: 1987) (20.09.2018, 243, pp. 1287–1301.

Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nat. Clim. Change 4 (9), 806–810. https://doi.org/10.1038/nclimate2318.

Sgouridis, F., Reay, M., Cotchim, S., Ma, J., Radu, A., Ullah, S., 2023. Stimulation of soil gross nitrogen transformations and nitrous oxide emission under Free air CO2 enrichment in a mature temperate oak forest at BIFoR-FACE. Soil Biol. Biochem. 184, 109072.

Shekhar, A., Buchmann, N., Humphrey, V., Gharun, M., 2024. More than three-fold increase in compound soil and air dryness across Europe by the end of 21st century. Weather Clim. Extrem. 44, 100666.

Shekhar, A., Hörtnagl, L., Buchmann, N., Gharun, M., 2023. Long-term changes in forest response to extreme atmospheric dryness, 00, 1 Glob. Change Biol. (18). https://doi.org/10.1111/gcb.16846.

Simpson, D., Andersson, C., Christensen, J.H., Engardt, M., Geels, C., Nyiri, A., Posch, M., Soares, J., Sofiev, M., Wind, P., Langner, J., 2014. Impacts of climate and emission changes on nitrogen deposition in Europe: A multi-model study. Atmos. Chem. Phys. 14 (13), 6995–7017. https://doi.org/10.5194/acp-14-6995-2014.

Smith, K.A., Ball, T., Conen, F., Dobbie, K.E., Massheder, J., Rey, A., 2003. Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. Eur. J. Soil Sci. 54, 779–791.

Smith, T., Boers, N., 2023. Reliability of vegetation resilience estimates depends on biomass density. Nat. Ecol. Evol. 7, 1799–1808. https://doi.org/10.1038/s41559-023-02194-7.

Smith, N.G., Dukes, J.S., 2013. Plant respiration and photosynthesis in global-scale models: Incorporating acclimation to temperature and CO_2. Glob. Change Biol. 19 (1), 45–63. https://doi.org/10.1111/j.1365-2486.2012.02797.x.

Smith, N.E., Kooijmans, L.M.J., Koren, G., Van Schaik, E., Van Der Woude, A.M., Wanders, N., Ramonet, M., Xueref-Remy, I., Siebicke, L., Manca, G., Brümmer, C., Baker, I.T., Haynes, K.D., Luijkx, I.T., Peters, W., 2020. Spring enhancement and summer reduction in carbon uptake during the 2018 drought in northwestern Europe. Philos. Trans. R. Soc. B Biol. Sci. 375 (1810), 20190509. https://doi.org/10.1098/rstb.2019.0509.

Stott, P.A., Stone, D.A., Allen, M.R., 2004. Human contribution to the European heatwave of 2003. Nature 432 (7017), 610–614.

Sundqvist, E., Vestin, P., Crill, P., Persson, T., Lindroth, A., 2014. Short-term effects of thinning, clear-cutting and stump harvesting on methane exchange in a boreal forest. Biogeosciences 11 (21), 6095–6105.

Sutton, M.A., Reis, S., Riddick, S.N., Dragosits, U., Nemitz, E., Theobald, M.R., Tang, Y.S., Braban, C.F., Vieno, M., Dore, A.J., Mitchell, R.F., Wanless, S., Daunt, F., Fowler, D., Blackall, T.D., Milford, C., Flechard, C.R., Loubet, B., Massad, R., Vries, W. de, 2013. Towards a climate-dependent paradigm of ammonia emission and deposition. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 368 (1621), 20130166.

Suwa, M., Katul, G.G., Oren, R., Andrews, J., Pippen, J., Mace, A., Schlesinger, W.H., 2004. Impact of elevated atmospheric CO_2 on forest floor respiration in a temperate pine forest. Glob. Biogeochem. Cycles 18 (2), 2003GB002182. https://doi.org/10.1029/2003GB002182.

Suz, L.M., Barsoum, N., Benham, S., Dietrich, H.P., Fetzer, K.D., Fischer, R., García, P., Gehrman, J., Kristöfel, F., Manninger, M., Neagu, S., Nicolas, M., Oldenburger, J., Raspe, S., Sánchez, G., Schröck, H.W., Schubert, A., Verheyen, K., Verstraeten, A., Bidartondo, M.I., 2014 Nov. Environmental drivers of ectomycorrhizal communities in Europe's temperate oak forests. Mol Ecol. 23 (22), 5628–5644. https://doi.org/10.1111/mec.12947. Epub 2014 Nov 7. PMID: 25277863.

Tang, X., Du, J., Shi, Y., Lei, N., Chen, G., Cao, L., Pei, X., 2020. Global patterns of soil heterotrophic respiration – A meta-analysis of available dataset. Catena 191, 104574. https://doi.org/10.1016/j.catena.2020.104574.

Thackeray, C.W., Hall, A., Norris, J., Chen, D., 2022. Constraining the increased frequency of global precipitation extremes under warming. Nat. Clim. Change 12 (5), 441–448.

Thompson, I.D., 2009. Forest resilience, biodiversity, and climate change: A synthesis of the biodiversity / resiliende / stability relationship in forest ecosystems. CBD technical series. Secretariat of the Convention on Biological Diversity, p. 67.

Travis, J.M.J., 2003. Climate change and habitat destruction: A deadly anthropogenic cocktail. Proc. Biol. Sci. 270 (1514), 467–473.

Treml, V., Tumajer, J., Jandová, K., Oulehle, F., Rydval, M., Čada, V., Treydte, K., Mašek, J., Vondrovicová, L., Lhotáková, Z., Svoboda, M., 2022. Increasing water-use efficiency mediates effects of atmospheric carbon, sulfur, and nitrogen on growth variability of central European conifers. Sci. Total Environ. 838, 156483. https://doi.org/10.1016/j.scitotenv.2022.156483.

Turubanova, S., Potapov, P., Hansen, M.C., Li, X., Tyukavina, A., Pickens, A.H., Hernandez-Serna, A., Arranz, A.P., Guerra-Hernandez, J., Senf, C., Häme, T., Valbuena, R., Eklundh, L., Brovkina, O., Navrátilová, B., Novotný, J., Harris, N., Stolle, F., 2023. Tree canopy extent and height change in Europe, 2001–2021, quantified using Landsat data archive. Remote Sens. Environ. 298, 113797. https://doi.org/10.1016/j.rse.2023.113797.

Twardosz, R., Walanus, A., Guzik, I., 2021. Warming in Europe: Recent Trends in Annual and Seasonal temperatures. Pure Appl. Geophys. 178 (10), 4021–4032. https://doi.org/10.1007/s00024-021-02860-6.

Unger, S., Máguas, C., Pereira, J.S., David, T.S., Werner, C., 2012. Interpreting post-drought rewetting effects on soil and ecosystem carbon dynamics in a Mediterranean oak savannah. Agric. For. Meteorol. . 154–155, 9–18.

Vainio, E., Haikarainen, I.P., Machacova, K., Putkinen, A., Santalahti, M., Koskinen, M., Fritze, H., Tuomivirta, T., Pihlatie, M., 2022. Soil tree atmosphere CH4 flux dynamics of boreal birch and spruce trees during spring leaf out. Plant Soil 478, 391–407.

van der Graaf, S.C., Janssen, T.A.J., Erisman, J.W., Schaap, M., 2021. Nitrogen deposition shows no consistent negative nor positive effect on the response of forest productivity to drought across European FLUXNET forest sites. Environ. Res. Commun. 3 (12), 125003.

Van Der Linde, S., Suz, L.M., Orme, C.D.L., Cox, F., Andreae, H., Asi, E., Atkinson, B., Benham, S., Carroll, C., Cools, N., De Vos, B., Dietrich, H.-P., Eichhorn, J., Gehrmann, J., Grebenc, T., Gweon, H.S., Hansen, K., Jacob, F., Kristöfel, F., Bidartondo, M.I., 2018. Environment and host as large-scale controls of ectomycorrhizal fungi. Nature 558 (7709), 243–248. https://doi.org/10.1038/s41586-018-0189-9.

van der Woude, A.M., Peters, W., Joetzjer, E., Lafont, S., Koren, G., Ciais, P., Ramonet, M., Xu, Y., Bastos, A., Botía, S., Sitch, S., Kok, R., de, Kneuer, T., Kubistin, D., Jacotot, A., Loubet, B., Herig-Coimbra, P.-H., Loustau, D., Luijkx, I.T., 2023. Temperature extremes of 2022 reduced carbon uptake by forests in Europe. Nat. Commun. (06. 10. 2023 14 (1), 6218.

Vangi, E., Dalmonech, D., Cioccolo, E., Marano, G., Bianchini, L., Puchi, P.F., Grieco, E., Cescatti, A., Colantoni, A., Chirici, G., Collalti, A., 2024. Stand age diversity (and more than climate change) affects forests' resilience and stability, although unevenly. J. Environ. Manag. 366, 121822. https://doi.org/10.1016/j.jenvman.2024.121822.

Vesala, T., Suni, T., Rannik, Ü., Keronen, P., Markkanen, T., Sevanto, S., Grönholm, T., Smolander, S., Kulmala, M., Ilvesniemi, H., Ojansuu, R., Uotila, A., Levula, J., Mäkelä, A., Pumpanen, J., Kolari, P., Kulmala, L., Altimir, N., Berninger, F., Hari, P., 2005. Effect of thinning on surface fluxes in a boreal forest. Glob. Biogeochem. Cycles 19 (2).

Vestin, P., Mölder, M., Kljun, N., Cai, Z., Hasan, A., Holst, J., Klemedtsson, L., Lindroth, A., 2020. Impacts of Clear-Cutting of a Boreal Forest on Carbon Dioxide, Methane and Nitrous Oxide Fluxes. Forests 11 (9), 961.

Vestreng, V., Myhre, G., Fagerli, H., Reis, S., & Tarrason, L. (2007). Twenty-five years of continuous sulphur dioxide emission reduction in Europe. Atmos. Chem. Phys.

Vicente-Serrano, S.M., Nieto, R., Gimeno, L., Azorin-Molina, C., Drumond, A., El Kenawy, A., Dominguez-Castro, F., Tomas-Burguera, M., Peña-Gallardo, M., 2018. Recent changes of relative humidity: Regional connections with land and ocean processes. Earth Syst. Dyn. 9 (2), 915–937. https://doi.org/10.5194/esd-9-915-2018.

Vitali, V., Büntgen, U., Bauhus, J., 2018. Seasonality matters—The effects of past and projected seasonal climate change on the growth of native and exotic conifer species in Central Europe. Dendrochronologia 48, 1–9. https://doi.org/10.1016/j.dendro.2018.01.001.

Vitasse, Y., Bottero, A., Cailleret, M., et al., 2019. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Glob Change Biol. 25, 3781–3792. https://doi.org/10.1111/gcb.14803.

Vitasse, Y., Schneider, L., Rixen, C., Christen, D., Rebetez, M., 2018. Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. Agric. For. Meteorol. 248, 60–69.

Vries, W., de, Du, E., Butterbach-Bahl, K., 2014. Short and long-term impacts of nitrogen deposition on carbon sequestration by forest ecosystems. Curr. Opin. Environ. Sustain. . 9–10, 90–104.

Vries, W. de, Posch, M., Simpson, D., Reinds, G.J., 2017. Modelling long-term impacts of changes in climate, nitrogen deposition and ozone exposure on carbon sequestration of European forest ecosystems. Sci. Total Environ. 19 (07), 1097–1116, 2017, Vols. 605–606.

Waldner, P., Marchetto, A., Thimonier, A., Schmitt, M., Rogora, M., Granke, O., Mues, V., Hansen, K., Pihl Karlsson, G., Žlindra, D., Clarke, N., Verstraeten, A., Lazdins, A., Schimming, C., Iacoban, C., Lindroos, A.-J., Vanguelova, E., Benham, S., Meesenburg, H., Lorenz, M., 2014. Detection of temporal trends in atmospheric deposition of inorganic nitrogen and sulphate to forests in Europe. Atmos. Environ. 95, 363–374. https://doi.org/10.1016/j.atmosenv.2014.06.054.

Walker, W.S., Gorelik, S.R., Cook-Patton, S.C., Baccini, A., Farina, M.K., Solvik, K.K., Ellis, P.W., Sanderman, J., Houghton, R.A., Leavitt, S.M., Schwalm, C.R., Griscom, B. W., 2022. The global potential for increased storage of carbon on land. Proc. Natl. Acad. Sci. U.S.A. 119 (23), e2111312119. https://doi.org/10.1073/pnas.2111312119.

Wang, et al., 2020. Recent global decline of CO2 fertilization effects on vegetation photosynthesis. Science 370, 1295–1300. https://doi.org/10.1126/science.abb7772.

Wang, Y.-R., Buchmann, N., Hessen, D.O., Stordal, F., Erisman, J.W., Vollsnes, A.V., Andersen, T., Dolman, H., 2022. Disentangling effects of natural and anthropogenic drivers on forest net ecosystem production. Sci. Total Environ. 30 (05), 156326, 2022, Vol. 839.

Wang, Z.P., Jeffrey, L.C., Barba, J., Machacova, K., Zhang, X.M., Li, A., Han, S.J., 2026. Aboveground living plant-based methane production does not dominate methane emissions in terrestrial ecosystems. Planta 263 (9).

Wang, Q., Pieristè, M., Liu, C., Kenta, T., Robson, T.M., Kurokawa, H., 2021. The contribution of photodegradation to litter decomposition in a temperate forest gap and understorey. N. Phytol. 229 (5), 2625–2636. https://doi.org/10.1111/nph.17022.

Wang, M., Shi, S., Lin, F., Hao, Z., Jiang, P., Dai, G., 2012. Effects of soil water and nitrogen on growth and photosynthetic response of Manchurian ash (Fraxinus mandshurica) seedlings in northeastern China. PloS One 08 (02), e30754, 2012, Vol. 7, Issue 2.

Weiskopf, S.R., Isbell, F., Arce-Plata, M.I., Di Marco, M., Harfoot, M., Johnson, J., Lerman, S.B., Miller, B.W., Morelli, T.L., Mori, A.S., Weng, E., Ferrier, S., 2024. Biodiversity loss reduces global terrestrial carbon storage. Nat. Commun. 15 (1), 4354. https://doi.org/10.1038/s41467-024-47872-7.

Wessely, J., Essl, F., Fiedler, K., Gattringer, A., Hülber, B., Ignateva, O., Moser, D., Rammer, W., Dullinger, S., Seidl, R., 2024. A climate-induced tree species bottleneck for forest management in Europe. Nat. Ecol. & Evol. 8 (6), 1109–1117. https://doi.org/10.1038/s41559-024-02406-8.

Wieder, W.R., Grandy, A.S., Kallenbach, C.M., Taylor, P.G., Bonan, G.B., 2015. Representing life in the Earth system with soil microbial functional traits in the MIMICS model. Geoscientific Model Development 8, 1789–1808. https://doi.org/10.5194/gmd-8-1789-2015.

Wilkinson, M., Crow, P., Eaton, E.L., Morison, J.I.L., 2016. Effects of management thinning on CO2 exchange by a plantation oak woodland in south-eastern England. Biogeosciences 13 (8), 2367–2378.

Wolf, S., Eugster, W., Ammann, C., Häni, M., Zielis, S., Hiller, R., Stieger, J., Imer, D., Merbold, L., Buchmann, N., 2013. Contrasting response of grassland versus forest carbon and water fluxes to spring drought in Switzerland. Environ. Res. Lett. 8 (3), 035007.

Wood, T.E., Tucker, C., Alonso-Rodríguez, A.M., et al., 2025. Warming induces unexpectedly high soil respiration in a wet tropical forest. Nat. Commun. 16, 8222. https://doi.org/10.1038/s41467-025-62065-6.

Xia, N., Du, E., Wu, X., Tang, Y., Wang, Y., Vries, W. de, 2020. Effects of nitrogen addition on soil methane uptake in global forest biomes. In: Environmental pollution (Barking, Essex: 1987) (08.05.2020, 264, 114751.

Xu, B., Arain, M.A., Black, T.A., Law, B.E., Pastorello, G.Z., Chu, H., 2020. Seasonal variability of forest sensitivity to heat and drought stresses: A synthesis based on carbon fluxes from North American forest ecosystems. Glob. Change Biol. 26 (2), 901–918. https://doi.org/10.1111/gcb.14843.

Yan, P., Zhang, J., He, N., Zhang, W., Liu, C., Fernández-Martínez, M., 2023. Functional diversity and soil nutrients regulate the interannual variability in gross primary productivity. J. Ecol. 111, 1094–1106. https://doi.org/10.1111/1365-2745.14082.

Yang, L., Zhang, J., Wang, J., Gu, Y., Han, S., 2023. A linear positive relationship between tree species diversity and forest productivity across forest-dominated natural reserves on a large spatial scale. For. Ecol. Manag. 548, 121409.

Yao, Y., Ciais, P., Viovy, N., Joetzjer, E., Chave, J., 2023. How drought events during the last century have impacted biomass carbon in Amazonian rainforests. Glob. Change Biol. 29 (3), 747–762. https://doi.org/10.1111/gcb.16504.

Yao, Y., Sieber, P., Hauser, M., et al., 2025. Conversion from coniferous to broadleaved trees can make European forests more climate-effective. Nat Commun 16, 9536. https://doi.org/10.1038/s41467-025-64580-y.

Yiqi Luo, Bo Su, William S. Currie, Jeffrey S. Dukes, Adrien Finzi, Ueli Hartwig, Bruce Hungate, Ross E. McMurtrie, Ram Oren, William J. Parton, Diane E. Pataki, Rebecca M. Shaw, Donald R. Zak, Christopher B. Field, Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide, BioScience, Volume 54, Issue 8, August 2004, Pages 731–739, https://doi.org/10.1641/0006-3568(2004)054[0731:PNLOER]2.0.CO;2.

Yu, X., Orth, R., Reichstein, M., Bahn, M., Klosterhalfen, A., Knohl, A., Koebsch, F., Migliavacca, M., Mund, M., Nelson, J.A., Stocker, B.D., Walther, S., Bastos, A., 2022. Contrasting drought legacy effects on gross primary productivity in a mixed versus pure beech forest. Biogeosciences 19 (17), 4315–4329.

Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong, W., Hu, Z., Jain, A.K., Jiang, C., Kato, E., Li, S., Lienert, S., Liu, S., Nabel, J.E.

M.S., Qin, Z., Quine, T., Yang, S., 2019. Increased atmospheric vapor pressure deficit reduces global vegetation growth. Science advances (14. 08. 2019 5 (8), eaax1396.

Zhan, C., Orth, R., Migliavacca, M., Zaehle, S., Reichstein, M., Engel, J., Rammig, A., Winkler, A.J., 2022. Emergence of the physiological effects of elevated CO2 on land-atmosphere exchange of carbon and water. Glob. Change Biol. 13 (09), 7313–7326, 2022, Vol. 28, Issue 24.

Zhang, et al., 2026. Increased efficiency of water use does not stimulate tree productivity. Nat. Clim. Chang 16 (2026), 87–94.

Ziemblińska, K., Urbaniak, M., Merbold, L., Black, T.A., Jagodziński, A.M., Herbst, M., Qiu, C., Olejnik, J., 2018. The carbon balance of a Scots pine forest following severe windthrow: Comparison of reforestation techniques. Agric. For. Meteorol. . 260–261, 216–228.

Zohner, C.M., Mo, L., Renner, S.S., Svenning, J.-C., Vitasse, Y., Benito, B.M., Ordonez, A., Baumgarten, F., Bastin, J.-F., Sebald, V., Reich, P.B., Liang, J., Nabuurs, G.-J., de-Miguel, S., Alberti, G., Antón-Fernández, C., Balazy, R., Brändli, U.-B., Chen, H.Y.H., Crowther, T.W., 2020. Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. Proc. Natl. Acad. Sci. USA (11. 05. 2020 117 (22), 12192–12200.

Zohner, C.M., Rockinger, A., Renner, S.S., 2019. Increased autumn productivity permits temperate trees to compensate for spring frost damage. N. Phytol. 221 (2), 789–795. https://doi.org/10.1111/nph.15445.

Zuo, H., Xu, W., Liu, Z., Smaill, S.J., Zhou, X., 2023. Long-term plant diversity increases soil extractable organic carbon and nitrogen contents in a subtropical forest. Sci. Total Environ. 28 (03), 163118, 2023, Vol. 878.