Effects of Climate Change on CH_4 and N_2O Fluxes from Temperate and Boreal Forest Soils

Eugenio Díaz-Pinés, Christian Werner, and Klaus Butterbach-Bahl

1 Introduction

Boreal and temperate forests cover 1210 and 680 million ha, respectively (Keenan et al. 2015). In contrast to tropical forests, whose extent is decreasing due to current deforestation activities resulting in huge emissions of greenhouse gases (Roman-Cuesta et al. 2016), the area of boreal forests remained constant, while the area of temperate forests slightly increased in the last 25 years at an average rate of 2.7 million ha a^{-1} (Keenan et al. 2015). In total, boreal and temperate forests cover approximately 13% of the global terrestrial land surface.

Temperate and boreal forests are known to provide a wide range of ecosystem services (e.g., Gamfeldt et al. 2013), including timber production, water regulation, soil protection and erosion control, support of biodiversity, or recreation. The role of forests in regulating the climate has been also well acknowledged, due to their strong potential for sequestering atmospheric CO_2 in its biomass and soils (De Vries et al. 2003; Vesterdal et al. 2008). In contrast to CO_2, the role of forests as both significant sinks and sources of other powerful greenhouse gases, i.e., CH_4 and N_2O has received comparatively little attention. The crucial role played by forests in

E. Díaz-Pinés (✉)
Institute of Soil Research, University of Natural Resources and Life Sciences (BOKU), Vienna, Austria

Institute of Meteorology and Climate Research, Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany
e-mail: eugenio.diaz-pines@boku.ac.at

C. Werner
Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt, Germany

K. Butterbach-Bahl
Institute of Meteorology and Climate Research, Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany

regulating nutrient cycling is only possible due to the microbial-mediated transformation processes of the soil organic matter, which make nutrients available again for plant metabolism while also resulting in a substantial release of CO_2, as well as CH_4 and N_2O, to the atmosphere.

Temperate and boreal forests represent one of the major global pools of carbon (C) and nitrogen (N), with more than half of the C being stored in soils (Batjes 1996). Pan et al. (2011) estimated that boreal forest ecosystems store approximately 271 ± 22 Pg C, distributed in the living (54 Pg C) and dead biomass (43 Pg C) and in the soils (down to 1 m) (175 Pg C). This estimate excludes some deep organic boreal forest soils, which explains the significant difference with a recent estimate by Bradshaw and Warkentin (2015) (average: 1096 Pg C, range: 367–1715 Pg C), who included peats, or assessments from IPCC (2007) (471 Pg C). However, all estimates agree that 2/3 to ¾ of all C is stored in soils and peats. For temperate forests, Pan et al. (2011) estimated that the living and dead biomass pool is 62 Pg C, approximately equal to the amount of C stored in soils down to 1 m (57 Pg). Global amounts of N in soils down to 1 m are estimated to be 133–140 Pg (Batjes 1996), while only 10 Pg of N is held in the global plant biomass (Davidson 1994). Figure 1 shows the distribution of forests (Fig. 1A), the soil N stocks down to 1 m (Fig. 1B), and the C:N ratio of these soils (Fig. 1C) for the temperate and boreal zones of the
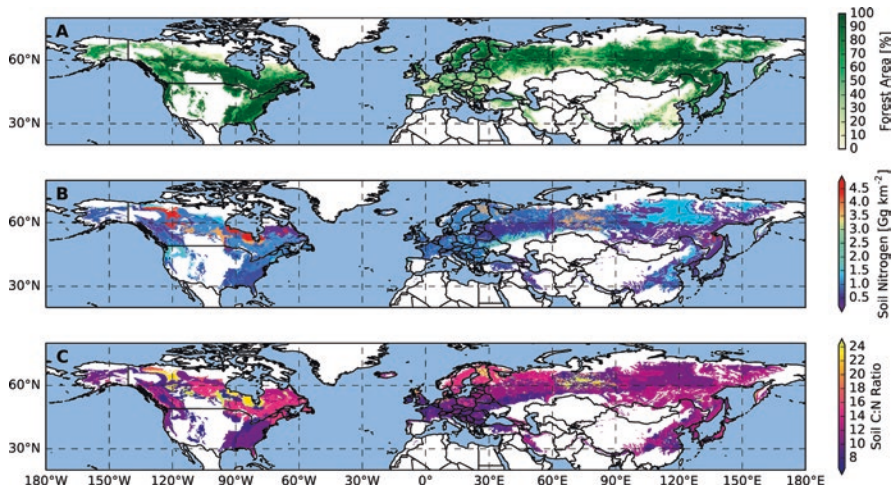
Fig. 1 Distribution of boreal and temperate forests (Panel A), the total nitrogen in soils (Panel B), and C:N ratio of soils (Panel C). The areal extent considered is based on the Olson ecoregions "temperate broadleaf and mixed forests" and "temperate coniferous forest" (Olson et al. 2001). The relative forest cover percentage is based on GlobCover 2009 v2.3 (Bontemps et al. 2011) including the following classes: "mosaic vegetation," "closed to open broadleaf (B) evergreen (E) forest," "closed B deciduous (D) forest," "open BD forest," "closed needleleaf (N) E forest," "open NE/ or BE forest," "closed to open mixed BD/ND forest," "mosaic forest," "closed to open B regularly flooded," "closed B forest permanently flooded." Spatially explicit soil C and N stocks were derived from the ISRIC-WISE soil map (Batjes 2012)

northern hemisphere. The areal extent considered is based on the Olson ecoregions (Olson et al. 2001), and the relative forest cover percentage (Fig. 1A) is based on the GlobCover 2009 (Bontemps et al. 2011). Spatially explicit soil C and N stocks were derived from the ISRIC-WISE soil map (Batjes 2012). According to this approach, the total soil N stocks in boreal and temperate forest soils are 10.4 Pg N and 7.2 Pg N, respectively.

Globally, both boreal and temperate forest soils have been identified as a source of atmospheric N$_2$O and as a net sink for atmospheric CH$_4$. The IPCC 2001 report listed the source strength of temperate forests for atmospheric N$_2$O with 1.0 Tg N$_2$O-N a^{-1} (0.1–2.0 Tg N$_2$O-N a^{-1}), while for boreal forest soils, an estimate was missing. More recently, Dalal and Allen (2008) estimated that boreal forests are a weak source for N$_2$O (0.33 ± 0.27 Tg N$_2$O-N a^{-1}) and confirmed earlier estimates for temperate forests (1.05 ± 0.37 Tg N$_2$O-N a^{-1}). With regard to atmospheric CH$_4$, Dutaur and Verchot (2007) estimated the sink strength of boreal and temperate forests to be 3.4 ± 5.0 Tg CH$_4$-C a^{-1} and 2.5 ± 2.6 Tg CH$_4$-C a^{-1}, respectively. However, since wetland forests were excluded from the study, this estimate is likely biased, because wetlands show net CH$_4$ emissions at the annual scale. Dalal and Allen (2008) estimated a smaller, more variable sink strength of boreal forest soils (2.0 ± 4.0 Tg CH$_4$-C a^{-1}), whereas the estimated CH$_4$ sink strength of temperate forests was with 3.7 ± 0.5 Tg CH$_4$-C a^{-1} higher and highly constrained.

Climate change refers here to the human-induced alteration of weather patterns, such as temperature and rainfall (amount, frequency, seasonal distribution). Climate change affects soil environmental conditions, as well as landscape hydrology, vegetation cover, and substrate supply. Indirect effects of climate change on land use (e.g., it is expected an agricultural expansion further north (Kicklighter et al. 2014)) are not covered here. Different climate models indicate that the temperate and boreal zones will experience warming in the range of 1.4–5.8 °C by 2100 (Hanewinkel et al. 2013), accompanied by an increase in extreme weather events, which will provoke the shrinkage of permafrost, and the reduction of the snow cover period (IPCC 2013). This will result in changing environmental conditions in both forest canopies and soils, along with shifts of vegetation zones, i.e., upward and northward expansion of the temperate and boreal forest biomes. Alterations of forest species composition, forest growth, and vitality of natural and managed forest landscapes will result in modification of the ecosystem services sustained by forests. While synthesis on the contribution of forests to several ecosystem services is already available (e.g., Millennium Ecosystem Assessment 2005), comprehensive studies linking forests and the exchange of non-CO$_2$ greenhouse gases between forests and the atmosphere are much more scarce. This chapter aims at evaluating the role of temperate and boreal forests as providers of climate regulation services. Special emphasis is given to the production and consumption of non-CO$_2$ greenhouse gases by forest soils under changing environmental conditions. Specifically, this chapter assesses how the changes in climate and associated effects may affect temperate and boreal forest soils N$_2$O and CH$_4$ fluxes, thereby summarizing existing knowledge and identifying research gaps.

2 Governing Processes and Mechanisms of Forest Soil-Atmosphere CH₄ and N₂O Exchange

Nitrous oxide is mainly produced by the microbial processes of nitrification and denitrification, i.e., an oxidative process converting ammonia/ammonium (NH_3/NH_4^+, classical nitrification) or organic N (heterotrophic nitrification) to nitrate (NO_3^-) and a reductive process, which uses NO_3^- as an electron acceptor for C oxidation to finally convert it to N_2 (denitrification) (Butterbach-Bahl et al. 2013). In these key microbial processes, N_2O is either a facultative (nitrification) or obligate (denitrification) intermediate, which can be released to the soil air, consumed in other parts of the soil profile or finally be emitted to the atmosphere. Although denitrification is considered the most important source of N_2O in forest soils at the European level, nitrification activity also drives total soil N_2O emissions (Ambus et al. 2006). Other microbial processes such as NO_3^- ammonification or physicochemical processes, e.g., chemical decomposition of reactive inorganic N species such as hydroxylamine (NH_2OH) or nitrite (NO_2^-), can lead to N_2O formation too (Butterbach-Bahl et al. 2013). The major controls for N_2O production in forests soils are substrate availability, i.e., NH_3/NH_4^+ and/ or NO_3^- as well as easily degradable C availability (Butterbach-Bahl et al. 2012), temperature (with sensitivity for N_2O emission varying widely) (Brumme 1995; Butterbach-Bahl et al. 1997; Díaz-Pinés et al. 2014; Sitaula and Bakken 1993; Zhang et al. 2016), and soil moisture and soil aeration, as both affect the soil redox potential and thus the preference of reductive processes such as denitrification (Butterbach-Bahl et al. 2013). In addition, soil N_2O emissions are indirectly controlled by tree and associated plant species, forest stand characteristics, and their effects on the abovementioned parameters, soil C:N ratios (Klemedtsson et al. 2005) and soil microbial community composition (Philippot et al. 2009). Finally, the occurrence of extreme events, such as wildfires and pronounced freeze-thaw and soil drying-rewetting cycles (Borken and Matzner 2009; Butterbach-Bahl et al. 2013), strongly affects microbial activity and availability of substrates for N_2O-producing processes.

Methane is predominantly produced in anaerobic, organic-matter-rich microsites of forest soils as a final step of the anaerobic decomposition of organic matter (Conrad 1996). CH_4 production has been observed in both the forest floor and the mineral soil (Butterbach-Bahl and Papen 2002). Forest soils can predominantly function as weak sources of CH_4 (0–20 kg CH_4-C ha^{-1} a^{-1}) if soils are poorly drained or seasonally flooded due to their topographic position in the landscape, such as many aspen or alder stands (Mander et al. 2015; Matson et al. 2009). In upland soils, CH_4 produced at anaerobic microsites or in deeper soil layers is likely to be oxidized while passing through aerobic soil layers. This implies that the observed CH_4 flux at the forest soil-atmosphere interface is the net result of simultaneously occurring production and consumption processes (Conrad 1996). Most of the temperate and boreal forest soils are upland soils, which predominantly function at annual scales as weak sinks for atmospheric CH_4 (0–5 kg CH_4-C ha^{-1} a^{-1}) (Dutaur and Verchot 2007). However, topographically complex ecosystems may

lead to spatial fragmentation at the landscape level, with specific locations being net CH$_4$ sinks while others being strong "hotspot" CH$_4$ emitters (Nykänen et al. 2003). The CH$_4$-oxidizing microbial communities are mostly using O$_2$ – but under certain circumstances also use sulfate or NO$_3^-$ – as electron acceptors (Conrad 2009). High-affinity methanotrophic bacteria found in most forest soils are capable to gain energy from soil atmosphere CH$_4$ concentrations lower than 1.7 ppmv. Climate change interacts in several ways with CH$_4$ production and consumption processes in soils. On the one hand, climate change directly affects soil environmental conditions, namely, moisture and temperature, and by this the balance between oxidative and reductive processes, e.g., temperature increases, will – as long as water availability is not limiting – likely result in an increase in aerobic respiration, thus decreasing soil oxygen (O$_2$) availability and the CH$_4$ oxidizing capacity of upland soils. On the other hand, global change and increases in atmospheric CO$_2$ concentration affect plant biomass production and its aboveground-to-belowground ratio, root exudation, and litter quality. All these changes finally modify ecosystem CH$_4$ exchange, with results being different across different ecosystem types and climatic zones. Finally, climate change also affects regional water balances and thus landscape groundwater levels. This will ultimately control the future distribution of wetlands and emission magnitudes of CH$_4$ at the landscape scale (Jungkunst and Fiedler 2007).

3   Forest Composition and N$_2$O and CH$_4$ Fluxes

Forest tree species composition and tree species richness are of high significance with regard to the provision of economic and ecological services by forests (Gamfeldt et al. 2013). While extensive research has been conducted to elucidate the effect of tree species on biomass production (De Vries et al. 2003), biodiversity (Barbier et al. 2008), water regulation (Ewers et al. 2002), or soil C sequestration (Vesterdal et al. 2008; Díaz-Pinés et al. 2014), our knowledge is rather limited with regard to the relationship between forest composition and its importance for the function of forests as climate regulators, specifically in view of the importance of forest soils as sink or sources of non-CO$_2$ greenhouse gases.

Individual trees strongly interact with the surrounding environment by, e.g., reducing the amount of light reaching the soil surface, intercepting water in their canopies, taking up water and nutrients from the soil, and returning organic matter back to the soil. Specific tree species usually behave differently (due to, e.g., different growth rates, water or nutritional requirements, or canopy and root system structure) and therefore create distinct ecological conditions and biogeochemical characteristics in both the canopy (radiation levels, microclimate) and the soil (moisture, pH value, or availability of nutrients). Consequently, microbial processes responsible for production and consumption of N$_2$O and CH$_4$ in both the forest floor and the mineral soil are usually tree-species-dependent (e.g., Borken et al. 2003; Butterbach-Bahl et al. 2002; Díaz-Pinés et al. 2014).

Litter is an inherent part of nutrient and C cycling in forest ecosystems. Aboveground litter regulates microclimatic conditions by forming a protective layer on the soil surface (Sayer 2006). Litter material from conifers contains high amounts of lignin and tannins, which are mainly decomposed by fungi (Dix and Webster 1995), as opposed to litter originated from deciduous trees (e.g., beech). The latter has simpler chemical structures and can be decomposed by broader spectra of soil microorganisms. This usually provokes that coniferous forests develop a thicker forest floor, which both produces and consumes CH_4 (Butterbach-Bahl and Papen 2002) and probably limits the transport of atmospheric CH_4 into the mineral soil (Borken and Beese 2006; Borken et al. 2003). At the same time, the usually compact and moist litter layer developed under deciduous forest can lead to high N_2O production rates (Pilegaard et al. 2006).

Belowground, rhizodeposition and root decay supply soil microorganisms with C to sustain further microbial decomposition (Cheng and Kuzyakov 2005). This, along with root respiration and water and nutrient uptake, significantly alters important biochemical properties (i.e., soil moisture, pH, O_2 and CO_2 concentrations, and labile C and N concentrations) in the rhizosphere. In a rhizotron experiment, it has been recently found that roots from different tree species affect soil microorganisms and C dynamics in different ways, with *Fraxinus excelsior* showing a higher CH_4 sink and a lower N_2O source strength compared with *Fagus sylvatica* or root-free soil (Fender et al. 2013), underpinning the possible tree-species-dependent root effects on trace gas production in soils.

In addition to the inherent variation of greenhouse gas fluxes along the landscape due to changing environmental conditions, trees can also pose a strong effect on the spatial pattern of N_2O and CH_4 exchange between the soil and the atmosphere (Butterbach-Bahl et al. 2002). It has been observed that fundamental soil properties (e.g., C and N contents, O_2 availability, microbial activity, moisture) strongly vary with distance from the stem (Chang and Matzner 2000) or from the canopy edge (Simón et al. 2013), and this pattern has been found to be tree-species-dependent (Butterbach-Bahl et al. 2002; Van Haren et al. 2010). Further, tree stems can be major conduits for soil-produced CH_4 and N_2O into the atmosphere. The transport may take place through aerenchymous tissues (extra-large intercellular spaces intended to facilitate aeration in the root system) as has been described for alder trees (Rusch and Rennenberg 1998) but also as dissolved gases in the water stream of the xylem. The contribution of tree trunks and tree leaves to the total ecosystem release of N_2O has been estimated to range from 1% to 3% in temperate beech forests (Díaz-Pinés et al. 2015) to 8% in boreal pine forests (Machacova et al. 2016). With regard to CH_4, *Alnus glutinosa* and *Betula pubescens* trees were found to contribute up to 27% of the ecosystem flux of temperate forested wetlands (Pangala et al. 2015). To our knowledge, information on the contribution of trees to the release of N_2O and CH_4 in boreal forested peatlands is not available.

Coniferous forests are predominant in temperate and boreal biomes (Douglas et al. 2014). In the frame of a changing climate, tree species better adapted to warmer temperatures and more tolerant to summer drought are supposed to have an adaptive advantage compared with other more water-sensitive tree species.

Drought-induced decline of Scots pine (*Pinus sylvestris*) stands has been observed already in the Alps (Rebetez and Dobbertin 2004) or in the Pyrenees (Galiano et al. 2010), at the extent of *Quercus* species. In the Rocky Mountains, drought-induced mortality of *Abies* and *Picea* species has also been observed (Bigler et al. 2007). In addition to the vegetation succession in view of changing environmental conditions, forest managers have promoted mixed forests or broadleaf species in the last decades, under the belief of having higher stability against disturbances (Jandl et al. 2007). It has been predicted the areal contribution of coniferous forests will shrink at the extent of broadleaf forests (Hanewinkel et al. 2013), even if we lack a clear understanding of how drought- and heat-induced tree mortality will impact the composition of most forests (Anderegg et al. 2013).

Following the change of forest composition, environmental conditions and soil microbial communities are expected to change, along with the organic matter transformation processes, ultimately leading to different end-, co-, and by-products during microbial N turnover (e.g., N$_2$O, NO, N$_2$). There is a substantial number of publications showing higher N$_2$O emissions in soils under deciduous forests than under coniferous ones (Ambus et al. 2006; Brumme et al. 1999; Butterbach-Bahl et al. 2002; Díaz-Pinés et al. 2014). This has been associated to larger NO losses in conifer forests (Butterbach-Bahl et al. 1997), resulting in higher N$_2$O:NO ratios (Papen et al. 2003). Recent results from forest floor incubations in European forests support higher NO emissions from coniferous forests but also a N$_2$O sink potential in the forest floor of deciduous species (Gritsch et al. 2016). Other authors have associated the lower N$_2$O emissions under conifer forests to a decoupling between N$_2$O production and reduction processes, resulting in decreased N$_2$O:N$_2$ ratios (Menyailo and Hungate 2005). With regard to CH$_4$, broadleaf forests usually show higher atmospheric CH$_4$ oxidation rates compared with coniferous ones (Butterbach-Bahl et al. 2002; Maurer et al. 2008), probably due to the distinct CH$_4$ diffusivity of the forest floor developed under each type of forest (Borken and Beese 2006; Borken et al. 2003). However, direct tree species effects on CH$_4$ fluxes can interact with soil moisture effects (Menyailo and Hungate 2005).

Tree species composition may change naturally in the course of ecological succession, but human interventions often also actively modulate stand composition and structures. Thus, forest management plays an active role for determining forest composition, which affects the benefits provided by forests in terms of ecosystem services, including its importance as climate regulators. However, the processes responsible for emitting or taking up N$_2$O or CH$_4$ are highly dynamic, and they are the result of complex biogeochemical processes and feedbacks and usually show a high temporal and spatial variability (e.g., Brumme et al. 1999; Butterbach-Bahl et al. 2002). Further, the forest composition is strongly influenced by the topography and landscape configuration, which in turn impacts the net exchange of CH$_4$ and N$_2$O. Finally, the relevant role of other parameters such as soil texture, precipitation (Borken and Beese 2005), or N limitation (Pilegaard et al. 2006), which may largely overwhelm the direct tree species effects on the net soil-atmosphere N$_2$O and CH$_4$ exchange, appeals for more comprehensive studies including not only different tree species but also soil types, N deposition rates, and climatic regions.

4 Effects of Tree Line and Forest-Tundra Ecotone Shifts on N_2O and CH_4 Fluxes

Effects of climate change (increasing temperatures, changing precipitation patterns) are particularly intense in temperate and boreal ecosystems compared with global averages, and it has been anticipated that the trend will continue in the coming years (Callaghan et al. 2005). Climatic changes are already affecting the location of the contact line between forest and grasslands or shrublands formation, the so-called tree line ecotone (Wieser 2010). Furthermore, the tree species composition of the forest is changing because of the natural adaptation to new environmental conditions, in addition to the forest management efforts to increase the forest resilience in the frame of global change and the succession after forest disturbances (e.g., wild-fires, windthrow). Finally, the spatial configuration and boundaries of temperate and boreal landscape units will probably change (Fig. 2), and the areal extent of the main land cover types (e.g., evergreen and deciduous forests, shrublands, woody wetlands) will vary following changing environmental conditions.

Both an upward shift of the tree line in mountainous areas (e.g., Kammer et al. 2009) and a northward migration of the forest-tundra ecotone in boreal latitudes (Serreze et al. 2000) have been detected, indicating an encroachment of forest areas into herbaceous and shrub communities. To our knowledge, there is no information available on the consequences of the movement of the mountainous tree line on the soil N_2O and CH_4 emissions. With regard to the forest encroachment in boreal latitudes, available studies are limited to individual case studies. When investigating the arctic tree line in Canada, Rouse et al. (2002) found significant releases of CH_4 in a fen compared with the negligible CH_4 fluxes in the forest (ca. 50 vs 8 kg CH_4-C ha^{-1} a^{-1}). Tupek et al. (2015) found higher CH_4 uptake in the upland forest than in the forest-mire transition, whereas no N_2O fluxes were observed in any of the ecosystems. In another tundra-forest comparison (Takakai et al. 2008), the forest was a small CH_4 sink compared with neutral or CH_4 sources from different grasslands. In the same study, the forest was a modest emitter of N_2O, whereas the magnitude of N_2O emitted by grasslands was highly dependent on water content. On the other hand, others have found no support for the hypothesis that conversion of tundra to forest or vice versa would result in a systematic change of net CH_4 fluxes in well-drained soils (Sjögersten and Wookey 2002). As it is usual that both CH_4 and N_2O emissions from tundra soils largely vary in space and time depending on local hydrological regimes (Zhu et al. 2014), with CH_4 annual fluxes from the same site ranging from 10 to 250 kg CH_4 ha^{-1} a^{-1} (Nykänen et al. 2003), prediction and assessment of CH_4 and N_2O emissions at the landscape or regional scale are highly challenging.

Due to the lack of a standardized terminology and methodology to locate, characterize, and observe changes, a general shift of the tree-grassland boundary was so far not detected at regional scales for northern latitudes (Callaghan et al. 2005). In addition, while climate change may promote forest encroachment through higher temperatures, human interventions lead to forest degradation and loss of forest-covered
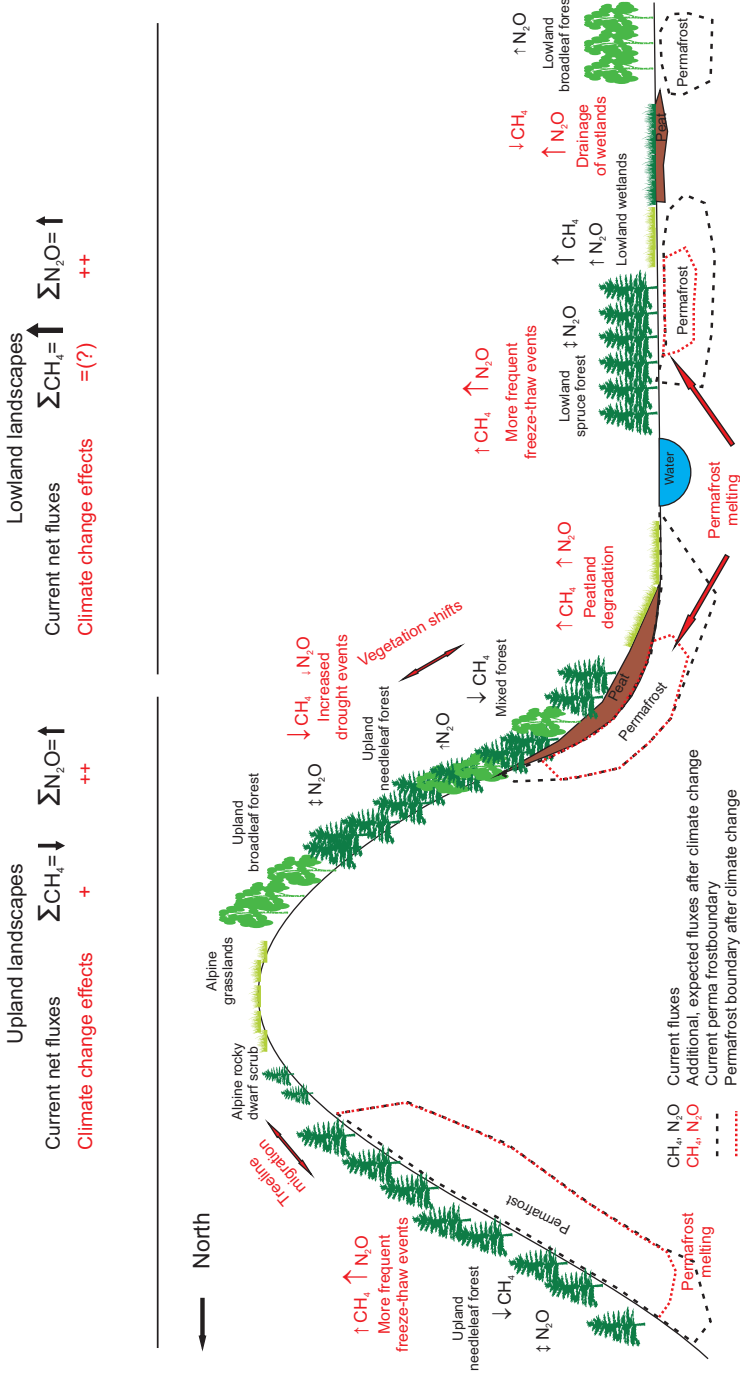
Fig. 2 Cross section representing the predominant upland and lowland landscape forms in boreal ecosystems. Size of vertical arrows is proportional to the magnitude of the fluxes (Adapted after Douglas et al. (2014) and Jorgenson et al. (2010)). Vegetation vectors designed by Natasha Sinegina and Bob Comix (creative commons license)

area. However, even in the scenario of no alteration of boundaries between ecosystem types, the soil-atmosphere balance of CH_4 and N_2O in the tree line ecotone is very sensitive to changing environmental conditions. Warming across an extensive northern gradient along the tundra-forest ecotone in Scandinavia consistently enhanced the soil CH_4 sink strength (Sjögersten and Wookey 2002), and in northern China, soil warming experiments in tundra resulted in increased uptake rates of both CH_4 and N_2O (Zhou et al. 2016). On the contrary, Karbin et al. (2015) have recently shown that soil warming does not affect soil CH_4 fluxes at the Alpine forest tree line, likely due to the negligible effect of warming on soil water contents.

5   Extreme Events and Forest Soil N_2O and CH_4 Fluxes

Most climate projections show that temperature change will be highest in northern latitudes, accompanied by significant increases in precipitation (IPCC 2013). As much of the precipitation increase will be in the form of rain, including rain-on-snow, an accelerating rate of snowmelt can be expected (Callaghan et al. 2005), and a higher frequency of freeze-thaw events is forecasted in temperate and boreal regions (Fig. 2). Freeze-thaw events have been shown to result in major pulses of soil N_2O emissions, not only from agricultural but specifically from forest soils (De Bruijn et al. 2009). Luo et al. (2012) reported for the Höglwald Forest, a temperate forest in Southern Germany, freeze-thaw events in 5 out of 14 observational years, and that in those years, annual soil N_2O emissions were at least a factor of two higher than in other years due to the strong pulse of N_2O emissions associated with freeze-thaw events. In contrast, comparable effects on soil CH_4 fluxes were not observed.

Permafrost is perennially frozen ground, which underlies 20–25% of the exposed land surface in cold climates, and many boreal forests grow on permafrost (Serreze et al. 2000). Strong arctic warming forecasted in climate scenarios will provoke a strong collapse and shrinkage of permafrost (Callaghan et al. 2005). There is a growing body of research showing that permafrost thawing will yield increased C emissions due to the enhancement of both CO_2 and CH_4 emissions (e.g., Flessa et al. 2008; Schaefer et al. 2014; Schuur et al. 2015), as well as accelerated N losses following dramatic increases in soil N_2O fluxes (Abbott and Jones 2015).

Prolonged drought and following soil-rewetting events are also likely to exert a significant effect on annual soil N_2O and CH_4 fluxes of forest soils. For example, Borken et al. (2000) showed for a Norway spruce stand in Germany that a simulated drought period of 3–5 months resulted in an increase of the net sink capacity of the soil for atmospheric CH_4 by 40–100%. On the other hand, rewetting of soils after drought has been shown to result in pulses of soil N mineralization and soil N_2O emissions as a result of the release of accessible substrate from accumulated microbial and plant necromass, the lysis of live microbial cells, and the disruption of previously protected organic matter, allowing for accelerated microbial N turnover processes (Borken and Matzner 2009). However, pulse emissions due to soil rewet-

ting may compensate or not for reductions in soil N$_2$O emissions during the drought period compared with constantly wet scenarios, depending on the frequency of the drying-wetting cycles and the length of the drought periods and the magnitude of the priming effects following the wetting pulse (Borken and Matzner 2009). Moreover, it has been found that under drought conditions, soils might turn from a source to a sink of N$_2$O (Goldberg and Gebauer 2009), so that the expected future increases in drought periods may finally result in a decreasing atmospheric N$_2$O source strength of temperate and boreal forests.

The most important natural disturbances impacting the functioning of temperate and boreal forests are wildfires, windthrows, and insect and disease outbreaks. In a changing climate, the intensity and duration of extreme weather events will increase, with unexpected consequences for disaster, i.e., widespread damage and severe alteration in the normal functioning of ecosystems (IPCC 2012). As a result, ecosystem services provided by forests, including climate regulation, will be also affected. Studies have found a climate signal in the increased wildfire activity in North America (Gillett et al. 2004; Westerling et al. 2006). Enhanced drought in boreal forests is associated with higher frequency of defoliator outbreaks, while late-spring frost has a role in terminating outbreaks (Volney and Fleming 2000). Forest damages due to windthrows have also increased in Europe during the last century (Schelhaas et al. 2003). All these disturbances result in significant reductions or even complete losses of the canopy cover and an episodic, over-proportionated incorporation of plant litter and residues (e.g., ashes) on the forest floor. Reduced water interception and transpiration after forest disturbance has been shown to increase soil moisture levels (Huber et al. 2004), whereas reduced canopy cover leads to enhanced soil temperature amplitudes. Similar to clear-cutting effects, such disturbances usually result in strongly reduced CH$_4$ uptake activities (Strömgren et al. 2016; Wu et al. 2011) and in pulses of N$_2$O emissions during the growing season (e.g., Mcvicar and Kellman 2014; Zerva and Mencuccini 2005) as well as during freeze-thaw periods, due to accelerated organic matter mineralization, which provides substrate for soil microbial processes (Rosenkranz et al. 2010). However, the excess availability of N and the associated pulses seem to be limited to at most a few years, as N losses also increase along hydrological (NO$_3^-$ leaching; e.g., Huber et al. 2004, 2010) and gaseous pathways (N$_2$ emissions due to denitrification) and as the regrowing vegetation becomes quickly a strong competitor for the available soil N (Rosenkranz et al. 2010).

6   Synthesis

Temperate and boreal forests play a pivotal role in climate regulation, a critical ecosystem service. Dynamic changes in environmental conditions in the coming decades will likely affect the net forest-atmosphere balance of CH$_4$ and N$_2$O fluxes at different temporal and spatial scales, and these changes will feedback on chemical composition of the atmosphere and, thus, on the global climate.

Increasing temperature and changes in precipitation patterns are specifically expected for northern latitudes, with changes being more pronounced compared with tropical or temperate regions (IPCC 2013). This will affect the production and consumption of N_2O and CH_4 directly by changing the environmental conditions for microbial processes and indirectly through modifications of the landscape configuration, territory land use, and forest vegetation. A conversion of coniferous to broadleaf and mixed forests in response to climate change could lead to enhanced CH_4 uptake rates, whereas the overall effect on N_2O emissions is unclear if the role of increasing likeliness of summer droughts is taken into account. There is still insufficient empirical evidence of a direct and consistent link between tree species and the soil-atmosphere CH_4 and N_2O exchange rates, due to the complex interactions between tree species composition and site/soil characteristics. Soil drainage and more pronounced summer drought will increase the CH_4 oxidation strength of upland mineral soils, but this effect could be highly overwhelmed by the anticipated massive collapse of permafrost (Douglas et al. 2014), which is likely to result in the mobilization of currently frozen C and N stocks and years of high CH_4 and N_2O emissions. Furthermore, the lowering of the water table level will likely enhance soil N_2O emissions. Since shorter periods of snow-covered soil are expected, the occurrence and intensity of freeze-thaw events will increase, potentially leading to more frequent pulses of N_2O. Finally, acceleration of natural disturbances such as wildfires and pests will decrease the soil's capacity to uptake atmospheric CH_4 and will likely provoke further releases of N_2O as ecosystem N stocks are mobilized.

We should mention that there is already a reasonable understanding on how single climate change parameters such as temperature or moisture affect soil environmental conditions, C and N cycling, and associated soil N_2O and CH_4 emissions. However, we still do not understand how interacting effects of environmental condition changes, i.e., combined changes in tree species composition, atmospheric chemistry (i.e., CO_2, ozone, or reactive N concentrations), or enhanced and more severe extreme weather events will jointly affect the soil-atmosphere CH_4 and N_2O flux. Only a few experiments have tried to tackle this problem comprehensively (e.g., Carter et al. 2012). Even though the fact that gaining this knowledge is fundamental for predicting future feedbacks of soil N_2O and CH_4 fluxes from temperate and boreal forest soils in response to environmental changes, we are lacking suitable experimental approaches. Moreover, research has been mainly focused on plot to ecosystem scale, without confronting the issue of how landscape fluxes may change due to specific changes in environmental drivers. For example, changes in groundwater table levels, lateral water flows, and flooding events will occur at landscape scales and provoke huge changes in hydrological regimes. Those alterations may exert for many landscapes a more pronounced effect specifically on forest soil N_2O fluxes as, e.g., changes in temperature (Butterbach-Bahl and Dannenmann 2011). Here, manipulation experiments of groundwater table levels in combination with other climate change factors and a better fine-scale mapping of the affected territory offer a way forward to get a better insight in forest soil greenhouse gas fluxes in the frame of global change.

References

Abbott BW, Jones JB (2015) Permafrost collapse alters soil carbon stocks, respiration, CH$_4$, and N$_2$O in upland tundra. Glob Chang Biol 21:4570–4587

Ambus P, Zechmeister-Boltenstern S, Butterbach-Bahl K (2006) Sources of nitrous oxide emitted from European forest soils. Biogeosciences 3:135–145

Anderegg WRL, Kane JM, Anderegg LDL (2013) Consequences of widespread tree mortality triggered by drought and temperature stress. Nat Clim Chang 3:30–36

Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. For Ecol Manag 254:1–15

Batjes NH (1996) Total carbon and nitrogen in the soils of the world. Eur J Soil Sci 47:151–163

Batjes NH (2012) ISRIC-WISE derived soil properties on a 5 by 5 arc-minutes global grid (ver 1.2). Report 2012/01. ISRIC – World Soil Information, Wageningen

Bigler C, Gavin DG, Gunning C, Veblen TT (2007) Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. Oikos 116:1983–1994

Bontemps S, Defourny P, Van Bogaert E, Arino O, Kalogirou V, Ramos Perez J (2011) GLOBCOVER 2009. Products description and validation report. Université Catholique de Louvain & ESA Team

Borken W, Beese F (2005) Control of nitrous oxide emissions in European beech, Norway spruce and scots pine forests. Biogeochemistry 76:141–159

Borken W, Beese F (2006) Methane and nitrous oxide fluxes of soils in pure and mixed stands of European beech and Norway spruce. Eur J Soil Sci 57:617–625

Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob Chang Biol 15:808–824

Borken W, Xu YJ, Beese F (2003) Conversion of hardwood forests to spruce and pine plantations strongly reduced soil methane sink in Germany. Glob Chang Biol 9:956–966

Borken W, Xu YJ, Brumme R (2000) Effects of prolonged soil drought on CH$_4$ oxidation in a temperate spruce forest. J Geophys Res Atmos 105:7079–7088

Bradshaw CJA, Warkentin IG (2015) Global estimates of boreal forest carbon stocks and flux. Glob Planet. Change 128:24–30

Brumme R (1995) Mechanisms of carbon and nutrient release and retention in beech forest gaps. Plant Soil 168:593–600

Brumme R, Borken W, Finke S (1999) Hierarchical control on nitrous oxide emission in forest ecosystems. Glob Biogeochem Cycles 13:1137–1148

Butterbach-Bahl K, Baggs EM, Dannenmann M, Kiese R, Zechmeister-Boltenstern S (2013) Nitrous oxide emissions from soils: how well do we understand the processes and their controls? Phil Trans R Soc B Biol Sci 368:20130122

Butterbach-Bahl K, Dannenmann M (2011) Denitrification and associated soil N$_2$O emissions due to agricultural activities in a changing climate. Curr Opin Environ Sustain 3:389–395

Butterbach-Bahl K, Díaz-Pinés E, Dannenmann M (2012) Soil trace gas emissions and climate change. In: Freedman B (ed) Global environmental change. Berlin/Heidelberg, Springer, pp 325–334

Butterbach-Bahl K, Gasche R, Breuer L, Papen H (1997) Fluxes of NO and N$_2$O from temperate forest soils: impact of forest type, N deposition and of liming on the NO and N$_2$O emissions. Nutr Cycl Agroecosyst 48:79–90

Butterbach-Bahl K, Papen H (2002) Four years continuous record of CH$_4$-exchange between the atmosphere and untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany. Plant Soil 240:77–90

Butterbach-Bahl K, Rothe A, Papen H (2002) Effect of tree distance on N$_2$O and CH$_4$-fluxes from soils in temperate forest ecosystems. Plant Soil 240:91–103

Callaghan TV, Björn LO, Chapin FS III et al (2005) Arctic tundra and polar desert ecosystems. In: Symon C, Arris L, Heal B (eds) Arctic climate impact assessment. Cambridge University Press, New York, pp 243–352

Carter MS, Larsen KS, Emmett B et al (2012) Synthesizing greenhouse gas fluxes across nine European peatlands and shrublands – responses to climatic and environmental changes. Biogeosciences 9:3739–3755

Chang S-C, Matzner E (2000) Soil nitrogen turnover in proximal and distal stem areas of European beech trees. Plant Soil 218:117–125

Cheng W, Kuzyakov Y (2005) Root effects on soil organic matter decomposition. In: Zobel R, Wright S (eds) Roots and soil management: interactions between roots and the soil. ASA-SSSA, Madison, pp 119–144

Conrad R (1996) Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH_4, OCS, N_2O, and NO). Microbiol Rev 60:609–640

Conrad R (2009) The global methane cycle: recent advances in understanding the microbial processes involved. Environ Microbiol Rep 1:285–292

Dalal RC, Allen DE (2008) Greenhouse gas fluxes from natural ecosystems. Aust J Bot 56:369–407

Davidson EA (1994) Climate change and soil microbial processes: secondary effects are hypothesised from better known interacting primary effects. In: Rounsevell MDA, Loveland PJ (eds) Soil responses to climate change. Springer, Berlin/Heidelberg, pp 155–168

De Bruijn AMG, Butterbach-Bahl K, Blagodatsky S, Grote R (2009) Model evaluation of different mechanisms driving freeze–thaw N_2O emissions. Agric Ecosyst Environ 133:196–207

De Vries W, Reinds GJ, Posch M et al (2003) Intensive monitoring of forest ecosystems in europe, 2003 technical report. EC, UN/ECE, Brussels

Díaz-Pinés E, Heras P, Gasche R, Rubio A, Rennenberg H, Butterbach-Bahl K, Kiese R (2015) Nitrous oxide emissions from stems of ash (Fraxinus angustifolia Vahl) and European beech (Fagus sylvatica L.) Plant Soil 398:35–45

Díaz-Pinés E, Schindlbacher A, Godino M, Kitzler B, Jandl R, Zechmeister-Boltenstern S, Rubio A (2014) Effects of tree species composition on the CO_2 and N_2O efflux of a Mediterranean mountain forest soil. Plant Soil 384:243–257

Dix NJ, Webster J (1995) Fungal ecology. Chapman & Hall, London

Douglas TA, Jones MC, Hiemstra CA, Arnold JR (2014) Sources and sins of carbon in boreal ecosystems of interior Alaska: a review. Elementa: Science of the Anthropocene 2:000032

Dutaur L, Verchot LV (2007) A global inventory of the soil CH_4 sink. Glob Biogeochem Cycles 21:GB4013

Ewers BE, Mackay DS, Gower ST, Ahl DE, Burrows SN, Samanta SS (2002) Tree species effects on stand transpiration in northern Wisconsin. Water Resour Res 38:8–1-8-11

Fender A-C, Gansert D, Jungkunst HF et al (2013) Root-induced tree species effects on the source/sink strength for greenhouse gases (CH_4, N_2O and CO_2) of a temperate deciduous forest soil. Soil Biol Biochem 57:587–597

Flessa H, Rodionov A, Guggenberger G et al (2008) Landscape controls of CH_4 fluxes in a catchment of the forest tundra ecotone in northern Siberia. Glob Chang Biol 14:2040–2056

Galiano L, Martinez-Vilalta J, Lloret F (2010) Drought-induced multifactor decline of scots pine in the pyrenees and potential vegetation change by the expansion of co-occurring oak species. Ecosystems 13:978–991

Gamfeldt L, Snäll T, Bagchi R et al (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. Nat Commun 4:1340

Gillett NP, Weaver AJ, Zwiers FW, Flannigan MD (2004) Detecting the effect of climate change on Canadian forest fires. Geophys Res Lett 31:L18211

Goldberg SD, Gebauer G (2009) Drought turns a Central European Norway spruce forest soil from an N_2O source to a transient N_2O sink. Glob Chang Biol 15:850–860

Gritsch C, Egger F, Zehetner F, Zechmeister-Boltenstern S (2016) The effect of temperature and moisture on trace gas emissions from deciduous and coniferous leaf litter. J Geophys Res Biogeo 121:1339–1351

Hanewinkel M, Cullmann DA, Schelhaas M-J, Nabuurs G-J, Zimmermann NE (2013) Climate change may cause severe loss in the economic value of European forest land. Nat Clim Chang 3:203–207

Huber C, Aherne J, Weis W, Farrell EP, Göttlein A, Cummins T (2010) Ion concentrations and fluxes of seepage water before and after clear cutting of Norway spruce stands at Ballyhooly, Ireland, and Höglwald, Germany. Biogeochemistry 101:7–26

Huber C, Weis W, Baumgarten M, Göttlein A (2004) Spatial and temporal variation of seepage water chemistry after femel and small scale clear-cutting in a N-saturated Norway spruce stand. Plant Soil 267:23–40

IPCC (2001) In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (eds) Climate change 2001: the scientific basis. Contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK/New York

IPCC (2007) Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the fourth assessment report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, Geneva

IPCC (2012) In: Field CB, Barros V, Stocker TF, Qin D, Dokken DJ, Ebi KL, Mastrandrea MD, Mach KJ, Plattner GK, Allen SK, Tignor M, Midgley PM (eds) Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK/New York

IPCC (2013) Climate change 2013: the physical science basis. Contribution of Working Group I to the fifth assessment of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK/New York

Jandl R, Lindner M, Vesterdal L et al (2007) How strongly can forest management influence soil carbon sequestration? Geoderma 137:253–268

Jorgenson MT, Romanovsky V, Harden J et al (2010) Resilience and vulnerability of permafrost to climate change. Can J For Res 40:1219–1236

Jungkunst HF, Fiedler S (2007) Latitudinal differentiated water table control of carbon dioxide, methane and nitrous oxide fluxes from hydromorphic soils: feedbacks to climate change. Glob Chang Biol 13:2668–2683

Kammer A, Hagedorn F, Shevchenko I et al (2009) Treeline shifts in the Ural mountains affect soil organic matter dynamics. Glob Chang Biol 15:1570–1583

Karbin S, Hagedorn F, Dawes MA, Niklaus PA (2015) Treeline soil warming does not affect soil methane fluxes and the spatial micro-distribution of methanotrophic bacteria. Soil Biol Biochem 86:164–171

Keenan RJ, Reams GA, Achard F, De Freitas JV, Grainger A, Lindquist E (2015) Dynamics of global forest area: results from the FAO global forest resources assessment 2015. For Ecol Manag 352:9–20

Kicklighter DW, Cai Y, Zhuang Q et al (2014) Potential influence of climate-induced vegetation shifts on future land use and associated land carbon fluxes in Northern Eurasia. Environ Res Lett 9:035004

Klemedtsson L, Von Arnold K, Weslien P, Gundersen P (2005) Soil CN ratio as a scalar parameter to predict nitrous oxide emissions. Glob Chang Biol 11:1142–1147

Luo GJ, Brüggemann N, Wolf B, Gasche R, Grote R, Butterbach-Bahl K (2012) Decadal variability of soil CO$_2$, NO, N$_2$O, and CH$_4$ fluxes at the Höglwald Forest, Germany. Biogeosciences 9:1741–1763

Machacova K, Bäck J, Vanhatalo A et al (2016) Pinus sylvestris as a missing source of nitrous oxide and methane in boreal forest. Sci Rep 6:23410

Mander Ü, Maddison M, Soosaar K, Teemusk A, Kanal A, Uri V, Truu J (2015) The impact of a pulsing groundwater table on greenhouse gas emissions in riparian grey alder stands. Environ Sci Pollut Res 22:2360–2371

Matson A, Pennock D, Bedard-Haughn A (2009) Methane and nitrous oxide emissions from mature forest stands in the boreal forest, Saskatchewan, Canada. For Ecol Manag 258:1073–1083

Maurer D, Kolb S, Haumaier L, Borken W (2008) Inhibition of atmospheric methane oxidation by monoterpenes in Norway spruce and European beech soils. Soil Biol Biochem 40:3014–3020

Mcvicar K, Kellman L (2014) Growing season nitrous oxide fluxes across a 125+ year harvested red spruce forest chronosequence. Biogeochemistry 120:225–238

Menyailo OV, Hungate B (2005) Tree species effects on potential production and consumption of carbon dioxide, methane and nitrous oxide: the Siberian afforestation experiment. In: Binkley D, Menyailo OV (eds) Tree species effects on soils: implications for global change. Springer, Dordrecht, pp 293–305

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC

Nykänen H, Heikkinen JEP, Pirinen L, Tiilikainen K, Martikainen P (2003) Annual CO_2 exchange and CH_4 fluxes on a subarctic palsa mire during climatically different years. Glob Biogeochem Cycles 17:18–11

Olson DM, Dinerstein E, Wikramanayake ED et al (2001) Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. Bioscience 51:933–938

Pan Y, Birdsey RA, Fang J et al (2011) A large and persistent carbon sink in the world's forests. Science 333:988–993

Pangala SR, Hornibrook ERC, Gowing DJ, Gauci V (2015) The contribution of trees to ecosystem methane emissions in a temperate forested wetland. Glob Chang Biol 21:2642–2654

Papen H, Rosenkranz P, Butterbach-Bahl K, Gasche R, Willibald G, Brüggemann N (2003) Effects of tree species on C- and N- cycling and biosphere-atmosphere exchange of trace gases in forests. In: Binkley D, Menyailo O (eds) Tree species effects on soils: implications for global change. Springer, Dordrecht, pp 165–172

Philippot L, Cuhel J, Saby NBA et al (2009) Mapping field-scale spatial patterns of size and activity of the denitrifier community. Environ Microbiol 11:1518–1526

Pilegaard K, Skiba U, Ambus P et al (2006) Factors controlling regional differences in forest soil emissions of nitrogen oxides (NO and N_2O). Biogeosciences 3:651–661

Rebetez M, Dobbertin M (2004) Climate change may already threaten Scots pine stands in the Swiss Alps. Theor Appl Climatol 79:1–9

Roman-Cuesta RM, Rufino MC, Herold M et al (2016) Hotspots of gross emissions from the land use sector: patterns, uncertainties, and leading emission sources for the period 2000–2005 in the tropics. Biogeosciences 13:4253–4269

Rosenkranz P, Dannenmann M, Brüggemann N, Papen H, Berger U, Zumbusch E, Butterbach-Bahl K (2010) Gross rates of ammonification and nitrification at a nitrogen-saturated spruce (Picea abies (L.) Karst.) stand in southern Germany. Eur J Soil Sci 61:745–758

Rouse WR, Bello RL, Souza A, Griffis TJ, Lafleur PM (2002) The annual carbon budget for fen and forest in a wetland at Arctic treeline. Arctic 55:229–237

Rusch H, Rennenberg H (1998) Black alder (Alnus Glutinosa (L.) Gaertn.) trees mediate methane and nitrous oxide emission from the soil to the atmosphere. Plant Soil 201:1–7

Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol Rev 81:1–31

Schaefer K, Lantuit H, Romanovsky VE, Schuur EG, Witt R (2014) The impact of the permafrost carbon feedback on global climate. Environ Res Lett 9:085003

Schelhaas M-J, Nabuurs G-J, Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th centuries. Glob Chang Biol 9:1620–1633

Schuur EG, Mcguire AD, Schädel C et al (2015) Climate change and the permafrost carbon feedback. Nature 520:171–179

Serreze MC, Walsh JE, Chapin FS et al (2000) Observational evidence of recent change in the northern high-latitude environment. Clim Chang 46:159–207

Simón N, Montes F, Díaz-Pinés E, Benavides R, Roig S, Rubio A (2013) Spatial distribution of the soil organic carbon pool in a Holm oak dehesa in Spain. Plant Soil 366:537–549

Sitaula BK, Bakken LR (1993) Nitrous oxide release from spruce forest soil: relationships with nitrification, methane uptake, temperature, moisture and fertilization. Soil Biol Biochem 25:1415–1421

Sjögersten S, Wookey PA (2002) Spatio-temporal variability and environmental controls of methane fluxes at the forest–tundra ecotone in the Fennoscandian mountains. Glob Chang Biol 8:885–894

Strömgren M, Hedwall PO, Olsson BA (2016) Effects of stump harvest and site preparation on N$_2$O and CH$_4$ emissions from boreal forest soils after clear-cutting. For Ecol Manag 371:15–22

Takakai F, Desyatkin AR, Lopez CML, Fedorov AN, Desyatkin RV, Hatano R (2008) CH$_4$ and N$_2$O emissions from a forest-alas ecosystem in the permafrost taiga forest region, eastern Siberia, Russia. J Geophys Res Biogeosci 113:G02002

Tupek B, Minkkinen K, Pumpanen J, Vesala T, Nikinmaa E (2015) CH$_4$ and N$_2$O dynamics in the boreal forest–mire ecotone. Biogeosciences 12:281–297

Van Haren JLM, De Oliveira RC, Restrepo-Coupe N, Hutyra L, De Camargo PB, Keller M, Saleska SR (2010) Do plant species influence soil CO$_2$ and N$_2$O fluxes in a diverse tropical forest? J Geophys Res Biogeosci 115:G03010

Vesterdal L, Schmidt IK, Callesen I, Nilsson LO, Gundersen P (2008) Carbon and nitrogen in forest floor and mineral soil under six common European tree species. For Ecol Manag 255:35–48

Volney WJA, Fleming RA (2000) Climate change and impacts of boreal forest insects. Agric Ecosyst Environ 82:283–294

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943

Wieser G (2010) Lessons from the timberline ecotone in the Central Tyrolean Alps: a review. Plant Ecol Div 5:127–139

Wu X, Brüggemann N, Gasche R, Papen H, Willibald G, Butterbach-Bahl K (2011) Long-term effects of clear-cutting and selective cutting on soil methane fluxes in a temperate spruce forest in southern Germany. Environ Pollut 159:2467–2475

Zerva A, Mencuccini M (2005) Short-term effects of clearfelling on soil CO$_2$, CH$_4$, and N$_2$O fluxes in a Sitka spruce plantation. Soil Biol Biochem 37:2025–2036

Zhang J, Peng C, Zhu Q et al (2016) Temperature sensitivity of soil carbon dioxide and nitrous oxide emissions in mountain forest and meadow ecosystems in China. Atmos Environ 142:340–350

Zhou Y, Hagedorn F, Zhou C, Jiang X, Wang X, Li M-H (2016) Experimental warming of a mountain tundra increases soil CO$_2$ effluxes and enhances CH$_4$ and N$_2$O uptake at Changbai Mountain, China. Sci Rep 6:21108

Zhu R, Ma D, Xu H (2014) Summertime N$_2$O, CH$_4$ and CO$_2$ exchanges from a tundra marsh and an upland tundra in maritime Antarctica. Atmos Environ 83:269–281