How do forest fires affect soil greenhouse gas emissions in upland boreal forests? A review

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ABSTRACT

Wildfires strongly regulate carbon (C) cycling and storage in boreal forests and account for almost 10% of global fire C emissions. However, the anticipated effects of climate change on fire regimes may destabilize current C-climate feedbacks and switch the systems to new stability domains. Since most of these forests are located in upland soils where permafrost is widespread, the expected climate warming and drying combined with more active fires may alter the greenhouse gas (GHG) budgets of boreal forests and trigger unprecedented changes in the global C balance. Therefore, a better understanding of the effects of fires on the various spatial and temporal patterns of GHG fluxes of different physical environments (permafrost and nonpermafrost soils) is fundamental to an understanding of the role played by fire in future climate feedbacks. While large amounts of C are released during fires, postfire GHG fluxes play an important role in boreal C budgets over the short and long term. The timescale over which the vegetation cover regenerates seems to drive the recovery of C emissions after both low- and high-severity fires, regardless of fire-induced changes in soil decomposition. In soils underlain by permafrost, fires increase the active layer depth for several years, which may alter the soil dynamics regulating soil GHG exchange. In a scenario of global warming, prolonged exposition of previously immobilized C could result in higher carbon dioxide emission during the early fire succession. However, without knowledge of the contribution of each respiration component combined with assessment of the warming and drying effects on both labile and recalcitrant soil organic matter throughout the soil profile, we cannot advance on the most relevant feedbacks involving fire and permafrost. Fires seem to have either negligible effects on methane (CH_4) fluxes or a slight increase in CH_4 uptake. However, permafrost thawing driven by climate or fire could turn upland boreal soils into temporary CH_4 sources, depending on how fast the transition from moist to drier soils occurs. Most studies indicate a slight decrease or no significant change in postfire nitrous oxide (N_2O) fluxes. However, simulations have shown that the temperature sensitivity of denitrification exceeds that of soil respiration; thus, the effects of warming on soil N_2O emissions may be greater than on C emissions.

1. Introduction

The Boreal Zone covers about one-third of the global forested area (approximately 16 million km^2) and is primarily located in Canada, Alaska, Russia and Scandinavia (Conard et al., 2002; Deluca and Boisvenue, 2012). About 80% of these forests are located in upland soils (i.e. well-drained, oxic), of which the great majority grows in environments underlain by different types of permafrost (Helbig et al., 2016). The carbon (C) pool in boreal upland forest soils was estimated to range from 90 Pg to 230 Pg (Allison and Treseder, 2011), accounting for about 23–60% of the global forest soil C pool (383 ± 30 Pg C) (Pan et al., 2011). As the climate becomes warmer, 25% of the permafrost has been predicted to thaw by the end of this century, exposing substantial quantities of organic C and nitrogen (N) to decomposition and mineralization (Davidson and Janssens, 2006; Harden et al., 2012). Due to the large C pool of boreal soils, this could trigger unprecedented changes in the global C balance (Allison and Treseder, 2011). Additionally, changes in soil hydrological conditions following permafrost thawing will likely regulate carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) emissions, with their combined emissions affecting the permafrost C-climate feedback (Lawrence et al., 2015; Voigt et al., 2017). Furthermore, unusual fire or other disturbances may interact with the system by destabilizing current feedbacks and switching the system to a new stability domain (Johnstone et al., 2010).

Fire is the most important natural disturbance in boreal forests (de Groot et al., 2013a), making the entire boreal biome a complex mosaic

of postfire forest successional stages. Boreal forests are mainly spruce (*Picea* spp.)-, larch (*Larix* spp.)- and pine (*Pinus* spp.)-dominated. Extensive nonstand-replacing fires of low and high intensity dominate the fire regime in larch- and pine-dominated forests, mostly in Scandinavia and Russia, while stand-replacing fires of high intensity predominate in the spruce forests of Canada (Rogers et al., 2015). The mean fire return interval in these areas varies between 53 years and 180 years, with Siberia in the lower end and North America in the upper (de Groot et al., 2013b). Thus, fire temporally regulates the regional C balance of all these areas (Kashian et al., 2006; Kasischke et al., 1995). At the time of burning, large amounts of C are released to the atmosphere through the combustion of plant biomass and soil organic matter (SOM). However, while some parts of the SOM are released through combustion, the remaining SOM accumulates over time across multiple fire events (Walker et al., 2019). Similarly, incomplete combustion of biomass results in thermally altered products, known as pyrogenic C, which is significantly more resistant to decomposition than its precursors (Deluca and Boisvenue, 2012; Jones et al., 2019). Furthermore, C pools also recover during the postfire succession through vegetation regrowth (Goulden et al., 2011). Each of these processes contributes to a long-term legacy C sink that is currently estimated to balance fire-related C emissions in boreal forests (Yue et al., 2016). However, the anticipated effects of climate change on several fire regime metrics (e.g. fire weather, fire season length, fire intensity, area burned, spread days etc.) may lead to more active future fire regimes (Coogan et al., 2019), while concomitantly threatening some of the boreal soils' legacy C, especially of that in dry young (< 60 years old) forest stands (Walker et al., 2019).

Over the short term (years to decades), fires turn boreal forests into C sources, due to soil decomposition rates becoming higher than gross primary production (GPP) (Goulden et al., 2011; Kashian et al., 2006). Thus, the balance between C inputs from vegetation recovery and C lost through soil respiration (R_s) — heterotrophic respiration (R_h) plus autotrophic respiration (R_a) — represents the most substantial effect of fire on C balance and will dictate most of the initial net CO_2 emissions after fire (Kashian et al., 2006). The projected increase in fire frequency and severity are of particular concern to this balance, because it may result in a larger fraction of forests that are C sources (Kashian et al., 2006; O'Neill et al., 2003). However, due to the uncertainties associated with fire effects on the driving mechanisms of R_s, the progress and regulation of soil CO_2 emissions after the fire are still under debate. Numerous studies suggest increased initial emissions (compared with prefire), due to favourable postfire abiotic conditions for decomposition, such as increased soil temperature combined with availability of labile C (Burke et al., 1997; Kim and Tanaka, 2003) or increased active layer depth (O'Neill et al., 2002; Yi et al., 2010). In contrast, some studies indicate that R_s recovery is dependent on the microbiota recovery, which may require over a decade to return to prefire conditions (Holden et al., 2012, 2015, 2016; Treseder et al., 2004).

Time after a fire (i.e. time since disturbance) is often used to determine the ecosystem C balance in boreal forests (Seedre et al., 2011). Additionally, fire severity and the presence or absence of permafrost are defining factors for field studies within the fire discipline and interact with drivers of greenhouse gas (GHG) emissions (Wang et al., 2012), thereby affecting C budgets. For instance, dissimilarity within microbial communities increased with fire severity (Whitman et al., 2019), while the soil fungal community was most diverse soon after fire, showing signs of decline over time (Sun et al., 2015). Moreover, stronger fire effects are expected on the microbiota of nonpermafrost soils than those of permafrost soils (Allison and Treseder, 2011). What is less clear is the nature of the CH_4 and N_2O fluxes in relation to these variables. Recent evidence suggests that increases in fire severity and frequency threaten current boreal CH_4 sinks (McNamara et al., 2015). Meanwhile, the N_2O fluxes from forest soils are highly heterogeneous, challenging regional budget predictions. However, fire-induced changes that control N availability for nitrification and denitrification have strong controls on

N_2O fluxes (Huang and Gerber, 2015).

Despite the currently growing number of studies analysing the effects of fire on GHG emissions from boreal soils, there is no consensus on the progress of soil GHG emissions after fire or on the emissions' responses to the main drivers at different fire severities and physical environments (permafrost and nonpermafrost soils). Given the expected changes in fire regimes and fire-induced thawing of permafrost in the Boreal Zone, the postfire C sink (budget) recovery will determine the future role of fires in the C-climate feedbacks. Thus, this review aimed to address the following questions: (i) What are the current trends in soil GHG emissions in upland boreal forests in light of fire intensity and severity, time after fire and physical environment? (ii) What are the gaps and shortcomings of current research? (iii) How can we advance our understanding of CO_2, CH_4 and N_2O cycling under a changing climate system?

2. Methods

We used the Helka electronic libraries, which search through major databases (e.g. Scopus, Web of Science, SpringerLink etc) to gather published peer-reviewed articles. The search parameters included the terms wildfire, fire, boreal forest, soil respiration, CO_2, CH_4 and N_2O. The final dataset consisted of articles that reported the effects of fire on soil CO_2, CH_4 and/or N_2O in upland boreal forests (in total 38 articles) (Table S1). Since this study was intended as a literature review, we selected all studies that were relevant to the topic regardless of their success in reporting fire severity, age class of the control forest (age of unburned forest) and mean GHG fluxes. When available, we extracted the mean soil GHG flux values, age class (years), fire severity (high-, low-severity) and physical environment (permafrost, nonpermafrost soil) from the final dataset and generated a subset consisting of 32 studies (Table S1). The degree of fire severity from studies was determined as follows — (highly) intense or severe fires, crown fires and stand-replacing fires were considered of high severity, whereas weakly and moderately severe fires and surface fires were considered of low severity. When none of these terms was reported, the severity degree was set as not available. A web-based tool (WebPlotDigitizer v. 4.2; Ankit Rohatgi, San Francisco, CA, USA) (Rohatgi, 2019) was used to extract numerical values from figures in which mean GHG fluxes were only graphically available. We converted the CO_2, CH_4 and N_2O mean fluxes to g CO_2 m^{-2} d^{-1}, mg CH_4 m^{-2} d^{-1} and mg N_2O m^{-2} d^{-1}, respectively.

We used cubic smoothing splines (Eubank, 1999) to aid visualization and identification of trends of the expected value of the distribution of CO_2, CH_4 and N_2O mean fluxes over time. The trade-off between smoothness and model fit is governed by the parameter lambda (λ); if $\lambda = 0$, the smoothing spline interpolates the data, i.e. as the value of λ increases, the fit approaches a linear function (Perperoglou et al., 2019). In all of our model fits, λ was set to 0.05. Additionally, we used standardized age class values according to the equation: $z = \frac{X - \mu}{\sigma}$, where X is the age class, μ is the age class mean and σ is the standard deviation of the age class. Age classes reported as lower than 12 months were considered as zero. The maximum age class of the control forests was set to 100 years to match the average fire return interval in boreal forests (Giglio et al., 2006).

We considered studies that reported unusually high flux values compared with the subset dataset as outliers and thus omitted them from analysis. Figures including the mean fluxes from all the studies are available in the supplementary material (Figs. S2 and S3). The Mahalanobis distance was used as guidance to identify potential outliers. All statistical analyses were performed, using the JMP statistical software (JMP v. 14.3; SAS Institute Inc., Cary, NC, USA).

3. Characterization of soil greenhouse gas production and consumption

3.1. Carbon dioxide

Soil CO_2 emissions originate from the decomposition of SOM (both aerobic and anaerobic microbial respiration) and plant root respiration, R_h and R_a, respectively. Depending on the seasonal variability, R_a contributes between 10% and 95% to R_s (Hansen et al., 2000). A growing forest absorbs many tonnes of CO_2 each year, and despite significant amounts of respired CO_2, a mature boreal forest can continue to accumulate C and remain as a C sink (Luyssaert et al., 2008).

3.1.1. Fire severity

Fire severity is a metric of above- and belowground organic matter consumption from burning used to study ecosystem responses to fire (Keeley, 2009). The amount of energy released during a fire event determines the fire intensity. Often during a severe fire, high-intensity crown fires will occur, rapidly burning the canopy, while the soil organic layers may continue to burn over a longer period (Miyanishi and Johnson, 2002). Standard measures of fire severity include the depth of burned soil organic layers (Stocks et al., 2002) and tree mortality (Keeley, 2009). High-severity fires consume the organic horizon (Certini, 2005), directly reducing the active-labile soil C pool (Conant et al., 2011; Gonzalez-Perez et al., 2004; Tas et al., 2014). Such fires may, however, create new C forms and/or enhance the decomposition-resistance of existing forms (Gonzalez-Perez et al., 2004; Jones et al., 2019). For instance, Köster et al. (2016) stressed the importance of temporary increase in the amount of belowground litter after high-severity fires for the labile C pool of SOM. Moreover, the soil C stability was suggested to increase with fire severity and to be higher in burned than in unburned forest stands (Adkins et al., 2019). The immediate effects of low-severity fires on soil properties tend to be less evident (Jian et al., 2018), although such fires slow the microbial and enzymatic activity for several decades in the northern boreal forests of Finland (Köster et al., 2015b). Interestingly, the negative effects on R_s at the same sites were minor, lasting only a few years (Köster et al., 2015a). The authors suggested that surviving trees and quick recovery of vegetation could have compensated for R_h loss after such low-severity fires (Köster et al., 2015a).

In studies that examined the effects of fire severity on R_s, high-severity fires seemed to have a stronger impact on both respiration components than low-severity fires. For example, in the boreal forests of northeastern China, high-severity fires significantly reduced the annual R_s, whereas no effect was observed in low-severity fires (Hu et al., 2017a, 2017b). The decrease in R_s was attributed to fire-induced reduction of R_a rather than R_h. In contrast, no temporal variation in R_s was observed after low-severity fires, but rather an increase in spatial heterogeneity of R_s (Hu et al., 2016). Interestingly, in the study of Sawamoto et al. (2000), a decrease in R_s was found despite increased R_h after high-severity fires, whereas low-severity fires had no effect on either R_s component. This indicates that potential increases in R_h may not compensate for the loss in R_a, whereas as observed in Köster et al. (2015a), quick R_a recovery may offset microbial activity loss, at least after low-severity fires. It is important to bear in mind the possible bias in these responses, since a relatively low number of the studies reviewed investigated the effect of low-severity fires on R_h and R_a separately (Fig. 1). Yet, the balance between slow C turnover time and rapid recovery of net primary productivity (NPP) after high-severity fires in temperate forests may indicate a transition from a C source to a C sink driven by plant production rather than R_h (Adkins et al., 2019; Meigs et al., 2009). NPP in boreal forests may recover as quickly as 4 years after fire (Mack et al., 2008), whereas microbial biomass recovery is linked to the recovery of the humus layer and may require as long as 15 years (Dooley and Treseder, 2011). Thus, the fire effects on microbes also outlast the fire effects on the aboveground vegetation in boreal
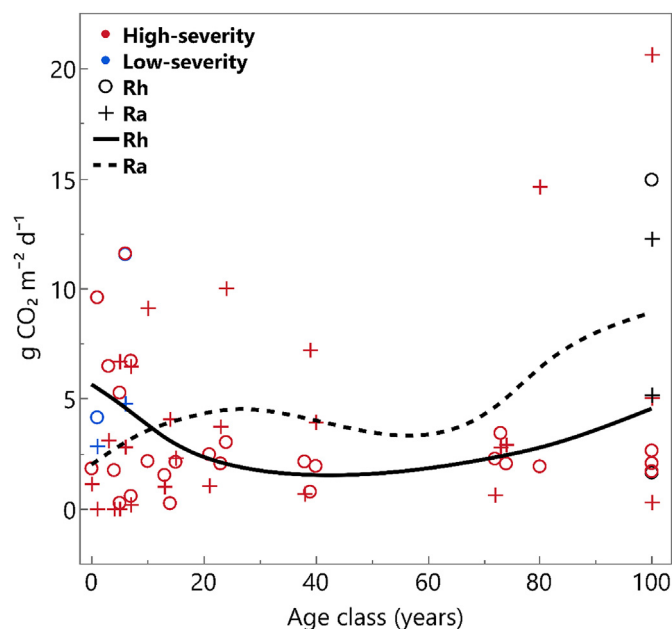

Fig. 1. Distribution of soil respiration components (g carbon dioxide (CO_2) m^{-2} d^{-1}) over time according to fire severity. The solid line represents the trend of the heterotrophic respiration (R_h) after fires, the dotted line that of the autotrophic respiration (R_a) after fires. The circles represent the mean R_h after fires, the crosses the mean R_a after fires. The blue and red circles and crosses are low- and high-severity fires; the black circles and crosses indicate information not available regarding fire severity. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

forests (Dooley and Treseder, 2011).

When the experimental warmings were considered, a 20% increase in R_s was detected several years after fires of differing severity levels, implying transient positive feedback to global warming despite fire severity (Bergner et al., 2004). In contrast, when only high-severity fires were considered approximately 5 years later in the same area, elevated temperatures had no effect on R_s (Allison et al., 2010). Burke et al. (1997) showed that decomposition of thermally altered labile organic compounds can maintain CO_2 emissions for several months to several years after the fire. To determine the potential differences in C stability per severity level, future research should target the relationship between the various respiration components and (manipulated) soil temperature under several severity levels over time (long and short timescales).

3.1.2. Time after fire

The required amount of time after fire for forests to transition from C sources to sinks is dependent on fire severity (Meigs et al., 2009), geographical location (Wear and Coulston, 2015) and physical environment (permafrost or nonpermafrost). Moreover, the timescale over which the plant-soil system recovers from fire disturbances is an indicator for the significance of C losses during combustion and postfire succession to the C balance of terrestrial ecosystems (O'Neill et al., 2003). During recent decades, researchers have suggested that postfire soil C emissions can be as significant as, or even surpass, combustion emissions (Auclair and Carter, 1993; Kasischke et al., 1995; Richter et al., 2000). If proved correct, this could ultimately lead to a positive feedback to climate warming. However, recent studies have challenged this view by demonstrating that fire-induced effects on microbial biomass and function constrain decomposition (Allison and Treseder, 2011). Holden et al. (2015) hypothesized that reduced decomposition may eventually offset soil combustion emissions and contribute rather to a negative feedback to climate warming.

Based on our review of these compiled studies, many investigators
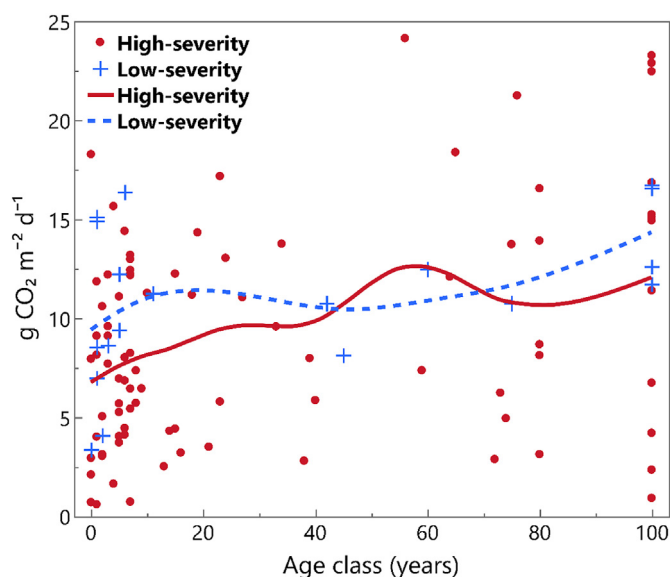
Fig. 2. Distribution of soil respiration (g carbon dioxide (CO_2) m^{-2} d^{-1}) over time according to fire severity. The solid line represents the trend of soil respiration after high-severity fires, the dotted line that of soil respiration after low-severity fires. The dots represent mean soil respiration after high-severity fires, the crosses that after low-severity fires.

found that CO_2 emissions increase as a function of time after fire (e.g. Czimczik et al., 2006; Goulden et al., 2011; Köster et al., 2014, 2016, 2017, 2018; O'Neill et al., 2003), as well as lower CO_2 emissions in burned compared with unburned sites (Kim and Tanaka, 2003; O'Neill et al., 2002; Pietikäinen and Fritze, 1995; Sun et al., 2014; Tas et al., 2014) (Figure S2). There were a few exceptions in which emissions in recently burned sites were similar to (Köster et al., 2015a; Takakai et al., 2008) or higher than (Song et al., 2017) those of unburned sites (Figure S2), with higher emissions associated with permafrost thawing following higher soil temperatures. Most often, emissions stabilize between 10 years and 30 years after fire, with low-severity fires at the lower end and high-severity fires at the upper end of this range (Fig. 2). This trend must be interpreted with caution, because very few study averages were used to determine the R_s smoother after low-severity fires. Moreover, despite lower initial postfire CO_2 emissions, boreal forests will remain C sources until NPP recovers (Bond-Lamberty et al., 2004b).

Since the studies reviewed seldom quantified each respiration component separately, the recognized tendency for soil CO_2 emissions to increase with time after fire was mostly based on R_s. A systematic literature review performed in Hanson et al. (2000) concluded that the average R_h of multiple forest ecosystems accounted for about 50% of R_s, but to date there has been little agreement on the temporal and spatial patterns of R_a and R_h in postfire boreal forests. An increase or decrease in the heterotrophic component of R_s may lead to a corresponding decrease or increase in C turnover time (Hanson et al., 2000). For example, in Köster et al. (2014), decline in R_h mimicking a very slow fungal biomass recovery, resulted in higher C turnover time. Therefore, clarifying the contribution of decomposition to soil CO_2 emissions during the postfire succession is paramount to determining the fire C-climate feedback.

The studies reviewed that quantified each component's contribution describe competing patterns of heterotrophic and autotrophic contributions to R_s. On one hand, after an R_a decline during the first months postfire (Sun et al., 2014), it surpassed R_h during early stand development (5–40 years after fire), increasing with time (70–80 years after fire) (Czimczik et al., 2006; Goulden et al., 2011). The trend we identified, based on the distribution of mean R_a and R_h rates over time, partially reflected the patterns described above (Czimczik et al., 2006;

Goulden et al., 2011; Sun et al., 2014), but with a time lag of 5 years (Fig. 1). On the other hand, R_h predominated during the first decade after fire (O'Neill et al., 2006), or even throughout the entire fire succession (Bond-Lamberty et al., 2004a). Such inconsistencies in respiration patterns could have resulted from differences in measurement methods and experimental design, i.e. which component of respiration was included as rhizosphere respiration (Czimczik et al., 2006; Sun et al., 2014), and how much variability existed between successional age classes. For instance, in the study of O'Neill et al. (2006), the burn severity of age classes above 10 years after the fire is unknown. Moreover, assuming zero R_a immediately after the fire may lead to overestimation of R_h, since roots could remain active before dying entirely (Allison and Treseder, 2011). Similarly, in quantifying the effects of fires on soil emissions, fire severity, as well as the presence of permafrost, will likely affect respiration components differently over time. Therefore, we should consider and report these aspects when designing experiments and disseminating results.

3.1.3. Environmental conditions in permafrost and nonpermafrost areas

While the R_a is driven mainly by recently found photosynthates (Collalti et al., 2019; Pumpanen et al., 2015), R_h is primarily regulated by environmental factors (e.g. soil temperature, soil moisture), microbiota and substrate quality (Flannigan et al., 2009). These are affected temporally by fire (Czimczik et al., 2006; Holden et al., 2015; Holden and Treseder, 2013; Köster et al., 2015a). Climate change is expected to alter fire regimes through changes in parts of the climate system (e.g. temperature, precipitation, humidity) (Coogan et al., 2019), which in turn also play a role in regulating R_s and the permafrost ground thermal regime (Karjalainen et al., 2019). Hence, potential interactions and new feedbacks involving fire and permafrost can be expected under a changing climate (Allison and Treseder, 2011).

Fires are known to increase soil temperature for several years by increasing the postfire absorption of solar radiation in the ground through depletion of vegetation cover and insulating moss layer, as well as the decrease in surface albedo during summer (O'Neill et al., 2006; Yoshikawa et al., 2002). In soils underlain by permafrost, these changes additionally increase the active layer depth for approximately 3–5 years after fire, depending on fire severity and site conditions (Morishita et al., 2015; O'Neill et al., 2006; Yoshikawa et al., 2002), until the vegetation begins to regenerate, allowing the active layer depth to recover to prefire conditions (Köster et al., 2018; Zhou et al., 2018). Increases in the depth of the seasonally thawed active layer could further result in enhanced decomposition of previously immobilized C (Grosse et al., 2011; O'Donnell et al., 2011; O'Neill et al., 2002). Unfortunately, none of the studies reviewed has directly investigated the role of soil microbial communities in the release of CO_2 from permafrost soils during a fire succession. This is a significant shortcoming, because fire is a major factor controlling the long-term dynamics of soil C and permafrost stability in boreal ecosystems (Jafarov et al., 2013), while microbial communities mediate major processes of the C cycle (Holden et al., 2012).

Recent research indicates that the loss of SOM-derived C should be considered together with the change in SOM quality. Aaltonen et al. (2019a) showed that the fire-induced reduction in the labile fraction (active and slow pool) of the SOM of the humus layer coincided with an increasing proportion of the recalcitrant fraction (very slow pool). The authors identified active layer depth as the main driver in the above-mentioned changes. Conversely, despite fire exposing mineral soil as low as 50 cm deep to thawing, changes in the SOM fractions were minor at this layer. Therefore, it seems that despite increasing the active layer depth, fires simultaneously increase the sources for recalcitrant SOM in the humus layer, while only weakly affecting the mineral soil below 50 cm. Moreover, fire reduced the microbial biomass in the same areas in soil layers down to 10 cm, but not at 30 cm (Zhou et al., 2018). These changes in SOM quality and microbial biomass were reflected in reduced R_s rates, whilst R_h remained similar under prefire conditions at

the same sites 3 years after fire (Aaltonen et al., 2019b; Köster et al., 2017). These findings are consistent with the dynamics regarding CO_2 production potential captured in Tas et al. (2014) 7 years after fire.

Assuming that during the first few years after fire soil CO_2 emissions correspond mainly to R_h, the above findings suggest that the lack of strong fire effects on deeper previously frozen mineral layers curbs the R_s rates in the first years after fire. Given the large size of the C reservoir of boreal forests, with the expected increase in fire frequency and the resulting increase in the number of young forest stands, microbial recovery and fire-induced changes in SOM quality will become a central issue in accurately predicting global change feedbacks. Therefore, in addition to clarifying the contribution of decomposition to soil CO_2 emissions, future research should verify whether R_h reflects the patterns described in SOM and microbial biomass throughout the soil profile and estimate what the timeframe of these patterns is. An even more urgent research question is whether these considerations apply under future climatic conditions, in other words, how the combined effects of fire and a warmer climate affect the temperature sensitivity (Q_{10}) of SOM decomposition in different soil layers. Despite the growing body of literature on the Q_{10} of soil respiration after boreal fires, findings are still controversial (Aaltonen et al., 2019b). Furthermore, of the three studies that analysed R_s responses to warmer and/or drier climate in a postfire environment, only one was undertaken in soils underlain by permafrost (Song et al., 2018). The authors attributed the higher R_s observed during warming and drying manipulations to soil nutrient availability and enzymatic activity 7–8 years after fire. These results contrast with those of Allison et al. (2010), who suggested that labile C was depleted 7–9 years after fires in boreal forests not underlain by permafrost. Among the issues emerging from this comparison is the possibility that exposure of previously frozen SOM to a warmer climate will trigger higher C emissions during the early fire succession than in those areas not underlain by permafrost (Allison and Treseder, 2011). However, in the study of Song et al. (2018), R_s after fire was already higher than under the prefire conditions prior to the warming experiment, which goes against most of the previous published studies (Köster et al., 2018; O'Neill et al., 2003; O'Neill et al., 2006; Sawamoto et al., 2000). Without knowledge of the contribution of each respiration component combined with assessment of the warming and drying effects on both labile and recalcitrant SOM throughout the soil profile, we cannot advance on the most relevant feedbacks involving fire and permafrost. Further studies, which take these variables into account, will need to be undertaken.

Stronger postfire effects of soil temperature over moisture on the temporal variability of R_s is commonly reported in both permafrost (Morishita et al., 2015; Song et al., 2017) and nonpermafrost areas (Hu et al., 2017b). However, fire-induced changes in soil properties may temporarily alter the temperature-moisture dynamics controlling R_s and increase the R_s dependence on the most limiting factor at the postfire sites (O'Neill et al., 2002). For example, O'Neill et al. (2002) observed that the loss of the insulating organic matter layer and vegetation cover after an extremely severe fire made previously poorly drained black spruce (*Picea mariana* (Mill.) BSP) stands drier, which made R_s more sensitive to soil moisture. On the other hand, increased soil temperature may directly enhance R_h (Kim and Tanaka, 2003), but the fire-induced reduction in R_a may mask the low gains in R_h (O'Neill et al., 2003). Soil moisture is also an important factor regulating the respiration from the moss layer, which may contribute about 10–55% of the total CO_2 emissions (O'Neill et al., 2006). In forest areas underlain by permafrost, the most important factors predicting R_s are the successional stages of the forest (measured in time after fire) (Köster et al., 2017), pH of the organic layer, biomass of the trees and ground vegetation (Köster et al., 2018), soil temperature, organic C content (Sawamoto et al., 2000, 2001), soil moisture, thawing depth, landscape cover (upland vs. wetland) and an interaction between soil temperature, soil moisture and fire severity (O'Donnell et al., 2009).

The spatial variation in R_s after fire has not been closely examined,

but Hu et al. (2016) showed that fire may change its driving factors. Boreal fires tend to initially create a patchy mosaic of forest floor with burned and unburned areas that will then be homogenized as the succession proceeds (Lavoie and Mack, 2012). However, the heterogeneity of R_s and R_h could continue to increase with time, due to decreasing variability in soil temperature and moisture (Das Gupta and Mackenzie, 2016).

3.1.4. Temperature sensitivity

Previous studies have found that fires either increase (Aaltonen et al., 2019b; Muñoz-Rojas et al., 2016) or decrease (O'Neill et al., 2002; Song et al., 2017; Takakai et al., 2008) the Q_{10} of the CO_2 efflux in soils. The Q_{10} values observed in these studies have varied around 2–4, which may have resulted from the various measurement techniques used. For example, studies using chamber measurements (thus measuring R_s) mostly observed decreasing Q_{10} values (O'Neill et al., 2002; Song et al., 2017; Takakai et al., 2008), while studies using the incubation method (measuring R_h) observed increases (Aaltonen et al., 2019b). However, some studies using the chamber method have also observed increased Q_{10} values and *vice versa* (De Baets et al., 2016; Muñoz-Rojas et al., 2016).

The decrease in postfire Q_{10} of soil respiration may have been associated with the loss of root activity (O'Neill et al., 2002), while increased values may have been associated with the decreased substrate quality after the fire (Aaltonen et al., 2019a, 2019b), since fires may decrease the quality of SOM (Certini, 2005; Knicker, 2007). The change in Q_{10} values of soil respiration are also dependent on fire severity. Hu et al. (2017a, 2017b) found that Q_{10} increased after low-severity fires, but decreased after high-severity fires. Since fire severity denotes the direct effect of fire on vegetation and soil, it may also have variable effects on both R_a and R_h. While R_a peaks decades after the fire (Gower et al., 2001), R_h is highest shortly after the fire, due to the high temperatures and presence of fire residues (Litvak et al., 2003; Wang et al., 2003). Therefore, the postfire Q_{10} also reflects which respiration component is currently peaking.

3.2. Methane

The CH_4 flux exchange between soil and the atmosphere is described as a balance between the metabolisms of methanogenic microbes (i.e. CH_4 production) and methanotrophic bacteria (i.e. CH_4 consumption) (Borken and Beese, 2006; Smith et al., 2000) regulated by soil diffusivity (Wang et al., 2015). CH_4 production occurs under anoxic conditions, although there is evidence of less significant CH_4 production in oxic environments as well (Dean et al., 2018). Conversely, CH_4 consumption can be done by aerobic and anaerobic methanotrophs. Upland boreal forest soils are aerobic and well-drained environments and usually act as sinks for atmospheric CH_4 (Hanson and Hanson, 1996), with an average uptake of 1.94 kg CH_4 ha^{-1} yr^{-1} (Dalal and Allen, 2008). CH_4 emissions also occur in upland soils, but at low rates (von Fischer and Hedin, 2007). Even though permafrost areas are C sinks, they are currently a source of CH_4, ranging between 4 and 17 Tg CH_4 yr^{-1} (including peatlands), and these emissions are expected to increase with a warmer climate (Dean et al., 2018).

3.2.1. Fire severity

Based on the distribution of mean CH_4 fluxes over time according to fire severity, high-severity fires may lead to a postfire succession characterized by lower CH_4 uptake (Fig. 3). However, the low-severity fire trend from midsuccession onwards is mostly determined by one study, which hinders our ability to speculate on differences between fire severity classes. When studies directly compared fire severity classes, the results were conflicting. A larger CH_4 uptake was observed after high-severity (than after low-severity) fires in Alaska (Morishita et al., 2015). In contrast, a larger CH_4 uptake after low-severity (than after high-severity) fires was observed in Siberia (Sawamoto et al., 2001).
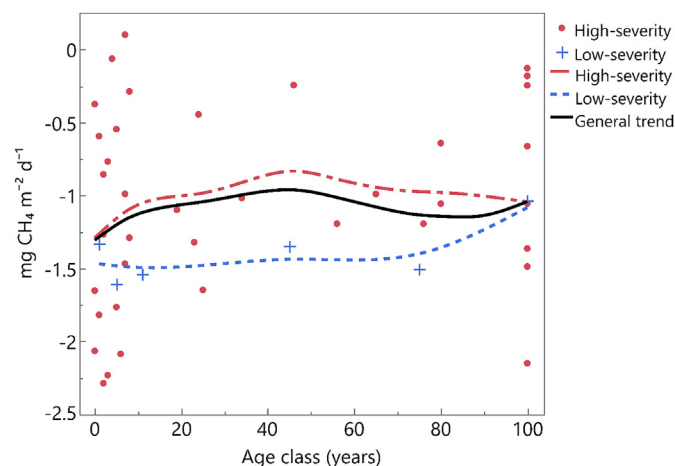
Fig. 3. Distribution of methane (CH_4) flux (mg CH_4 m^{-2} d^{-1}) over time according to fire severity. The solid line represents the general trend of the CH_4 flux after fires. The dot dashed line represents the trend of the flux after high-severity fires, the dotted line the trend after low-severity fires. The dots represent the mean CH_4 fluxes after high-severity fires, the crosses the mean fluxes after low-severity fires.

Fig. 4. Distribution of methane (CH_4) flux (mg CH_4 m^{-2} d^{-1}) over time according to presence or absence of permafrost ground. The solid line represents the trend of the CH_4 flux in nonpermafrost areas, the dotted line the trend in permafrost areas. The empty dots represent the mean CH_4 fluxes in nonpermafrost areas, the crosses the mean fluxes in permafrost areas.

Several factors could have influenced such discrepancies, e.g. differences in study location. However, similar inconsistencies are often present in comparisons made across studies — where the conditions under which the study was conducted do not support such comparisons — and most certainly are almost unavoidable in fire chronosequence approaches. For example, both studies compared fire severity between different age classes, compromising the ability to statistically differentiate the effect of time after fire from fire severity on emissions. Another caveat in studies investigating CH_4 fluxes is the campaign-based approach, because important drivers of CH_4 fluxes that are time-dependent could be left out. For instance, despite soil moisture being a major driver in CH_4 fluxes, it tends to only strongly correlate with CH_4 fluxes during relatively long timespans (Morin, 2019).

3.2.2. Time after fire

Our literature review revealed that most studies have reported either negligible effects of fire on CH_4 fluxes or a slight postfire increase in CH_4 uptake (Fig. 3) (Köster et al., 2017, 2018; Kulmala et al., 2014; Tas et al., 2014). However, based on the distribution of the CH_4 flux over time, this increase may have been more prominent in non-permafrost areas (Fig. 4). In fact, a noticeable change in CH_4 uptake in areas underlain by permafrost occurs only after midstand development — once again, this increase seems to be driven by only one observation. Interestingly, the CH_4 uptake observed tends to oppose the changes in water availability described for white birch (*Betula pendula*) and Scots pine (*Pinus sylvestris* L.) mixed-forest stands in Leuschner (2002), which characterizes many of the sites where the studies reviewed were performed (Table S1). The authors reported that as the vegetation recovers, the increased leaf surface area and canopy cover lead to higher water uptake, which then tends to decrease towards late-successional stages (Leuschner, 2002). Moreover, during vegetation regeneration, the increased root exudation has been observed to increase substrate availability to methanogenic microbes (Dean et al., 2018). In addition, changes in species composition have been linked to shift from a CH_4 sink to source (Nauta et al., 2014). Thus, further studies with more focus on postfire CH_4 fluxes during midsuccession and links to species composition are suggested.

3.2.3. Environmental conditions in permafrost and nonpermafrost areas

Fire is known to influence the species composition and quantity of microbes through heat-induced mortality (Hamman et al., 2007; Hart et al., 2005; Sullivan et al., 2010). However, while the rapid recovery of
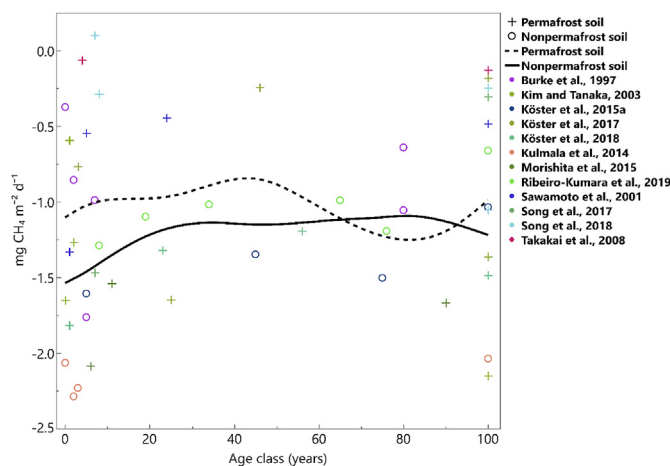
the microbial community is pointed out as the main reason for postfire recovery of the CH_4 uptake (Hamman et al., 2007; Kulmala et al., 2014), the activity and diversity of CH_4-oxidizing bacteria (methanotrophs) have not been perceived as significantly affected by fire (Jaatinen et al., 2004). In fact, soil diffusivity is more limiting to CH_4 uptake than the activity of methanotrophs (Fest et al., 2016), while the full potential for methanotrophic activity is only achieved given enough diffusivity between the soil and the atmosphere (von Fischer et al., 2009). Moreover, Certini (2005) showed that the fire effects on microorganisms are mainly a function of the soil moisture conditions at the time of burning; higher moisture facilitates heat transfer deeper into the soil profile, causing higher microbial mortality. Therefore, weak fire effects reported on the microbiota may have been attenuated by dry soil conditions at the time of fire, described at least in (Hamman et al., 2007).

The indirect impacts of fire on soil moisture and temperature were the most studied drivers of CH_4 fluxes throughout the literature reviewed. Reduction of evapotranspiration following fires is often accompanied by increased surface runoff. These two competing processes are the key to determining the water balance shortly after fire. Recent studies have shown that the new water balance reflects the reduction in evapotranspiration rather than the increased water runoff, resulting in wetter soils, unless fire severity is high enough to overcome the effect of reduced evapotranspiration, resulting in drier soils (Atchley et al., 2018). Previous research has established that CH_4 uptake declines with increasing bulk density and soil moisture content in coniferous and broad-leaved forests (Hashimoto et al., 2011; von Fischer and Hedin, 2007). Even though the average CH_4 flux of all the studies reviewed has revealed a fire succession characterized by a consistent CH_4 uptake (Fig. 3), several studies observed postfire CH_4 emissions in both permafrost (Kim and Tanaka, 2003) and nonpermafrost areas (Burke et al., 1997; Kulmala et al., 2014). Kim and Tanaka (2003) suggested that CH_4 emissions shortly after fire were due to permafrost thawing. However, there was no statistical indication of the relationship between CH_4 fluxes and variation in the active layer depth.

In studies in which CH_4 uptake increased postfire, the increase was often related to increase in soil temperature and decrease in soil moisture. Due to both CH_4 uptake and production increasing with temperature (Morishita et al., 2014; Schaufler et al., 2010), the CH_4 uptake tends to correlate more strongly with soil moisture in modelling the response of CH_4 uptake to soil moisture and temperature (Hashimoto et al., 2011; Morishita et al., 2014; Schaufler et al., 2010). However, when both factors are significant to CH_4 uptake, the highest

CH₄ uptake seemingly occurs at the highest soil temperatures (Whalen and Reeburgh, 1996). Increase in CH₄ uptake with increase in soil moisture is not unheard of in upland forest soils (Castro et al., 2000). The reason is that the moisture content necessary for enabling CH₄ emission is not easily reached in typically well-aerated and well-drained soils (Castro et al., 2000). Usually CH₄ uptake occurs between 20% and 60% water-holding capacity, with the strongest uptake occurring under drier conditions (Schaufler et al., 2010).

Estimates from the Community Land Model, which is a fully coupled global model that predicts various climate states (Lawrence et al., 2019) suggest that large-scale thawing of permafrost may lead to soil drying as water drains deeper in the soil column (Lawrence et al., 2015). Even though soil drying tends to favour CH₄ uptake, due to the heterogeneity of changes in the active layer depth and soil moisture, the response of CH₄ fluxes to permafrost thawing remains highly uncertain (Lawrence et al., 2015). Permafrost thawing is known to increase CH₄ emissions through increased methanogenic microbial activity (Dean et al., 2018). The expected increase in warming may also boost methanogenesis, due to microbial response to temperature (Morin, 2019). Conversely, research has shown that the microbial methanotrophic community, despite displaying higher activity at low temperatures, shifted towards a higher temperature-oriented community, increasing its population during permafrost thawing (Dean et al., 2018). The future CH₄ exchange in boreal forests as a result of warmer climate and permafrost thawing will also interact with the anticipated changes in fire regimes. For example, increased high-severity fires and concomitant reduction in the upper soil of the active layer may ultimately limit methanogenesis. On the other hand, low-severity fires may lead to increased CH₄ uptake by facilitating soil diffusivity at the soil surface.

Since the factors governing postfire CH₄ fluxes are still highly uncertain, further studies regarding the role of the soil C stock, microbial biomass (Köster et al., 2015a), mineral N (Jaatinen et al., 2004; Kulmala et al., 2014) and thickness of the forest humus layer (Jaatinen et al., 2004) would be worthwhile. Moreover, due to the recent discovery of CH₄ emissions from cryptogams (Lenhart et al., 2015), events that disrupt lichens and bryophytes (such as fires) may favour CH₄ uptake (Köster et al., 2017). Other observed drivers in CH₄ fluxes after fire in permafrost areas include soil pH, biomass of trees and ground vegetation (Köster et al., 2018).

3.2.4. Temperature sensitivity

The Q_{10} levels of GHGs other than CO_2 have not been studied as comprehensibly and even less for boreal forest soils. This may be partly because boreal forest soils are often a sink for CH₄, with uptake suggested to increase after fire (Kulmala et al., 2014; Morishita et al., 2014; Tas et al., 2014). In addition, studies have found that CH₄ uptake is only weakly linked to temperature (Borken and Beese, 2006; Castaldi and Fierro, 2005; Dörr et al., 1993), with soil moisture playing a greater role (Grant, 1999). Park et al., 2005 reported Q_{10} values of CH₄ oxidation varying from 2.57 to 2.69. Another study determined the CH₄ emissions with chamber measurements, finding Q_{10} values from 3.39 to 3.89 (Wang et al., 2015). However, most studies that have measured CH₄ production in incubation experiments have reported CH₄ emissions with Q_{10} values between 1.1 and 28 (Lupascu et al., 2018; Rath et al., 2002; Updegraff et al., 1995; van Hulzen et al., 1999). The noticeably wide variation in Q_{10} values related to CH₄ production has been associated with different phases of CH₄ production (Dalal and Allen, 2008). These include the initiation of anaerobiosis, the quantities of alternative electron acceptors and the quality and quantity of available substrates (Dalal and Allen, 2008). The possible effects of forest fires on CH₄ Q_{10} values could be linked to these phases, because fires alter the soil C quality and quantity, as well as soil microbial biomass.

3.3. Nitrous oxide

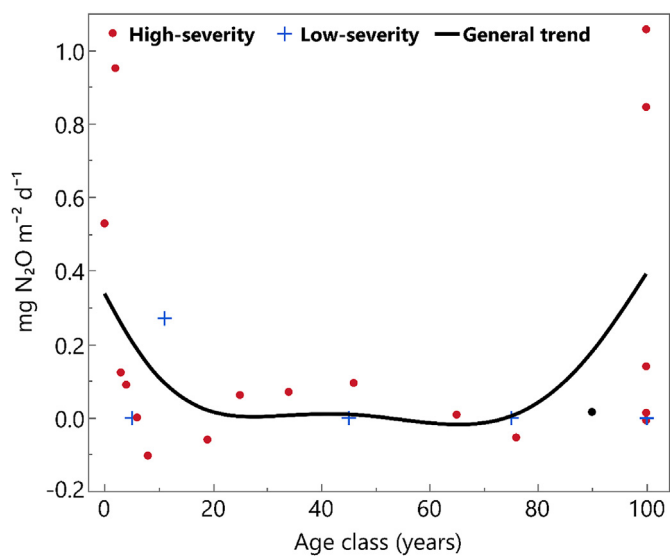The production of N_2O derives from both nitrification and

Fig. 5. Distribution of nitrous oxide flux (mg N_2O m^{-2} d^{-1}) over time. The dots represent the mean N_2O fluxes after high-severity fires, the crosses the fluxes after low-severity fires.

denitrification processes (Oertel et al., 2016). The mean denitrification rate in forest soils is about 1.9 kg N ha^{-1} yr^{-1} (Groffman et al., 2009), and in boreal forests this number is about 1.5–2 kg N ha^{-1} yr^{-1} (Cleveland et al., 1999), of which a small percentage derives from lichen and bryophyte species (Porada et al., 2017).

3.3.1. Fire severity

Due to the limited number of studies quantifying soil N_2O fluxes after fire, we could not identify a trend for each severity level separately (Fig. 5). Of the two studies that examined the effects of fire severity on N_2O fluxes (Morishita et al., 2015; Sawamoto et al., 2001), only one found significant differences between severity levels. Despite higher N_2O emissions after low-severity fires, Morishita et al. (2015) showed that these areas also resulted in higher flux variation, which could have been due to the formation of denitrification hotspots. As noted by Groffman et al. (2009), hotspots may account for a high percentage of denitrification, but are difficult to quantify. Moreover, fertilization with biochar reduces N_2O emissions (Case et al., 2015); thus, high-severity fires are more likely to suppress N_2O emissions, since they yield more charred materials than low-severity fires. Despite the overall need for more quantitative data on N_2O fluxes postfire, incorporating the analysis of the Q_{10} of denitrification and spatial variation of N_2O in postfire systems will be of great value towards an understanding of how fire severity affects these fluxes (Morishita et al., 2015).

3.3.2. Time after fire

An increase in soil N_2O emissions after fire was previously associated with the increase in ammonium (NH_4^+), the substrate for nitrification, and the decrease in nitrate (NO_3^-), the substrate for denitrification (Levine, 1994; Ullah et al., 2009). However, most studies done on the subject revealed that there is a slight decrease or no significant change in postfire N_2O fluxes (Figure S3) (Kim and Tanaka, 2003; Köster et al., 2017; Takakai et al., 2008). Currently, the prediction of N_2O fluxes is mainly limited by the uncertain interactive effects of a multitude of processes (e.g. soil moisture and temperature, availability of organic C, vegetation and enzymatic activity) together with their spatiotemporal variability (Butterbach-Bahl et al., 2013; Kim and Tanaka, 2003; Lenhart et al., 2015; Levine et al., 1988). For example, since cryptogams have become known as sources of N_2O (Lenhart et al., 2015), quick recovery of N-binding lichen or mosses may explain some of the lack of variation in N_2O emissions in the first years after fire

(Köster et al., 2015a).

3.3.3. Environmental conditions in permafrost and nonpermafrost areas

Most of the studies selected that measured N_2O fluxes after fire were performed in areas underlain by permafrost (Table S1). Regardless of permafrost presence, soil temperature was the main driver for N_2O emissions (Kim and Tanaka, 2003; Köster et al., 2015a, 2017; Ribeiro-Kumara et al., 2019). Additionally, Köster et al. (2017) showed that the interaction between soil temperature and depth of the active layer also affected N_2O emissions. The production of N_2O generally increases with soil moisture up to 60–70% of the water-filled porous space and with soil temperature up to 37 °C (Dalal and Allen, 2008). However, these factors may also interact with other soil properties that affect the N_2O fluxes. For instance, the activity of the enzyme N-acetyl-β-glycosami-nidase is sensitive to temperature changes, increasing at lower temperatures and thereby regulating the use of different substrates for the denitrification process (Koch et al., 2007). This chain of intertwined processes may potentially mask and weaken the power for N_2O flux prediction of the most commonly measured GHG drivers — soil moisture and temperature. Furthermore, with the thawing of permafrost and resulting drier soil conditions, current forest soils that are sources of N_2O may turn into transient sinks, as Goldberg and Gebauer (2009) observed in an artificial drought experiment.

3.3.4. Temperature sensitivity

The Q_{10} related to N_2O fluxes has rarely been measured, and even less after forest fires. Values recorded from different soils vary between 2.5 and 6.2 (Abdalla et al., 2009; Ambus, 1993; Maag and Vinther, 1999), but values as high as 8 have been reported when NO_3^+ and soil moisture were not limiting factors (Dobbie et al., 1999). Since N_2O fluxes originate from nitrification and denitrification (Abdalla et al., 2009), the Q_{10} of these processes governs the Q_{10} of the N_2O fluxes. For example, the Q_{10} of denitrification is sensitive to soil moisture, but even more sensitive to increasing temperatures (Abdalla et al., 2009). This is because the N cycle is a chain of multiple temperature-sensitive microbial processes (Butterbach-Bahl et al., 2013). The effects of warming on soil N_2O emissions may be greater than on CO_2, since simulations have shown that the Q_{10} of denitrification exceeds that of CO_2 (Schaufler et al., 2010; Schindler et al., 2009). Since forest fires, especially those of high severity, tend to increase soil temperatures, they may further reinforce this. Yet, fires also alter the soil moisture content, in which case the effect is dependent on whether the new moisture conditions are in the optimal range for N_2O production.

4. Conclusions

This review has focused on four different standpoints to explore the effects of fire on GHG fluxes in boreal forests: fire severity, time after fire, physical environment, and Q_{10}. The effect of fire severity on R_s is well established within the literature reviewed: High-severity fires have stronger effects on both respiration components than low-severity fire. However, these effects are not as defined for each respiration component separately. R_s generally increases as a function of time after fire, with the re-establishment of vegetation cover governing the recovery of soil CO_2 emissions. Fire effects on soil CO_2 emissions in permafrost areas are tightly linked to fire-induced changes in SOM throughout the soil profile. The fire-severity effects on CH_4 and N_2O fluxes are still uncertain, since very few studies have been conducted after low-severity fires. Upland boreal forests in permafrost and nonpermafrost areas seem to act as CH_4 sinks during the fire succession, although a strong trend has not yet been identified. The fire effects on CH_4 fluxes may be associated with soil moisture and diffusivity conditions at the time of fire and active layer depth after fire. The direction of the N_2O fluxes across a fire succession is still uncertain, while soil temperature is the most studied driver for N_2O emissions. It remains uncertain how expected climate warming will affect GHGs after fire, although existing

warming and drying experiments for CO_2 already provide conflicting results. As reviewed, the discrepancies in measurement methods and experimental design pose the main restrictions to generalizing findings and thus should be considered carefully.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envres.2020.109328. All the data are available online at http://dx.doi.org/10.17632/v7gxtvv9z3.1. Scripts for the analyses are available at https://github.com/c-riku/datainbrief-repo.

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