Soil CO_2 Efflux in Response to Forest Disturbances and its Spatial Variation in a Boreal Mixedwood Forest

by

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Abstract

Soil CO_2 efflux is a key component of the terrestrial carbon cycle as it is the second largest carbon flux between the atmosphere and terrestrial ecosystems after photosynthesis. The spatial and temporal variation of soil CO_2 efflux can be altered by various disturbancess, which in turn alter forest processes, structure, and biogeochemistry. In the first part of this thesis, I conducted a meta-analysis to assess the effects of disturbances on forest soil CO_2 efflux in boreal, temperate and tropical forests by collecting data on soil CO_2 efflux and disturbance regimes published between 1900 and June 2018. Boreal forest soil CO_2 efflux was increased by elevated CO_2 + warming and windthrow but decreased by fire. Temperate forest soil CO_2 efflux was increased by elevated CO_2, water addition, and warming. Tropical forest soil CO_2 efflux was increased by litter addition, thinning, water addition, and elevated CO_2 but reduced by litter removal. This study showed that forest management practices may be used to minimize climate change effects on soil CO_2 efflux but should not take the place of global warming mitigation strategies. This chapter also revealed the importance of partitioning soil CO_2 efflux to better understand the effects of disturbances on soil CO_2 efflux.

Following the literature review of disturbance effects on forest soil CO_2 efflux, I concentrated the second and third chapters of my thesis on quantifying spatial and temporal variation of soil CO_2 efflux and its components in a Canadian boreal mixedwood forest. Canada's boreal forest is dominated in the south by mixedwood forests so a better understanding of soil CO_2 efflux within this area will improve our ability to predict the response of the boreal carbon cycle to climate warming. The second chapter was conducted in a 1-ha boreal mixedwood forest located in Alberta, Canada to determine the fine-scale spatial and temporal variation of soil CO_2 efflux during three consecutive growing seasons. This site exhibited a moderate degree of spatial variation, mainly influenced by soil temperature, pH and dissolved organic nitrogen while the temporal variation was explained by soil temperature and moisture. Shrub-dominated patches had significantly higher soil CO_2 efflux than deciduous-dominated patches within the plot. In the third chapter, I examined the spatial and temporal variation of heterotrophic and autotrophic soil CO_2 efflux within the 1-ha plot using a root-exclusion trenching method. The results showed that because heterotrophic soil CO_2 efflux dominated total soil CO_2 efflux, changes in heterotrophic soil CO_2 efflux may lead to significant variations in total soil CO_2 efflux. Soil temperature, stand structure and pH influenced the spatial variation of heterotrophic soil CO_2 efflux while heterotrophic soil CO_2 efflux increased with warmer temperatures and higher water availability. The spatial variation of autotrophic soil CO_2 efflux was regulated by stand structure while its temporal variation could not be explained by any of the variables in this study. Autotrophic soil CO_2 efflux did not significantly differ among patches within our study but shrub-dominant patches exhibited significantly higher heterotrophic soil CO_2 efflux than deciduous-dominated patches.

Overall, this research reveals that disturbance effects on soil CO_2 efflux and its components need to be studied further to generate better models of carbon cycle response to global warming. It also clarifies the effect of species composition on soil CO_2 efflux and provides a recommendation for finer scale sampling protocol within a 1-ha boreal mixedwood forest. This thesis emphasizes that partitioning soil CO_2 efflux enhances our understanding of how disturbances may affect total soil CO_2 efflux.

Preface

This thesis is the original work of Oluwabunmi J. Akande.

A version of Chapter 2 will be submitted as: Quantifying disturbance effects on soil CO_2 efflux across forest biomes. This chapter was conceptualized by O.J. Akande with guidance from Fangliang He. O.J. Akande carried out data compilation and statistical analysis under the supervision of Fangliang He. The manuscript was written by O.J. Akande and revised by Fangliang He and Scott Chang.

A version of Chapter 3 will be submitted as: Spatial and temporal variation of soil CO_2 efflux in a Canadian boreal mixedwood forest.

A version of Chapter 4 will be submitted as: Spatial and temporal variation of heterotrophic and autotrophic soil CO_2 efflux in a Canadian boreal mixedwood forest.

These chapters were conceptualized by O.J. Akande under the supervision of Fangliang He. O.J. Akande and Fangliang He developed the sampling methodology while Scott Chang advised on the experimental design. All fieldwork was conducted and organized by OJ Akande from 2012 to 2014 and field equipment was provided by Fangliang He and Scott Chang. Data collection was carried by O. J. Akande with the assistance of several members of Fangliang He's lab. Laboratory analyses were carried out by O.J. Akande with the provision of the equipment by Scott Chang and training by Scott Chang's lab managers: Shujie Ren and Jin Hyeob-Kwak. All statistical analyses were carried out by O. J. Akande with some assistance by Dingliang Xing and Fangliang He. The manuscripts of both chapters were written by O.J. Akande and edited by Fangliang He.

Dedication

This is dedicated to my wonderful and supportive parents, Engr. Abayomi & Dr. Mrs. Elizabeth Akande, who sacrificed everything for me

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I would like to thank my supervisor, Dr. Fangliang He, for the opportunity to be a member in his lab and mentoring me through this program. He always gives me good advice, support and uses his expertise to enable me think outside the box. Thank you for everything. I can honestly say I am a better scientist and writer today than when I walked into our first meeting.

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Chapter 1: Introduction

1.1 Research Background

Atmospheric carbon dioxide (CO_2) concentration has increased from 390.5 ppm in 2011 to 405 ppm in 2018 (IPCC 2013; Blunden et al. 2018), mostly through the contribution of anthropogenic sources, i.e., burning fossil fuels and land use change. This means that despite global efforts to reduce or stabilize CO_2 emissions to the atmosphere, atmospheric CO_2 has steadily increased at a rate of 2.07 ppm per year between 2011 and 2018. In comparison, IPCC (2013) estimated that atmospheric CO_2 rose at the rate of 1.7 ppm per year between 1980 and 2011, showing that the carbon dioxide emissions are currently growing at a faster pace than previous decades. Increased concentrations of greenhouse gases, such as CO_2, trap heat in the atmosphere, causing global warming and other environmental consequences. These consequences include increased temperature, precipitation changes, increase in extreme events and possible changes to the terrestrial carbon cycle (IPCC 2013). Atmospheric CO_2 is absorbed by forest vegetation through photosynthesis, which allows plants to utilize CO_2 and store between 450 and 650 Gt of carbon (Figure 1-1). The CO_2 trapped in forest vegetation can be transferred to the soil and released to the atmosphere by soil CO_2 efflux. While the terrestrial carbon cycle could absorb a quarter of anthropogenic carbon emissions (Running 2008), if altered by climate change, it could potentially release more CO_2 to the atmosphere through soil CO_2 efflux, creating a positive feedback with global warming. It is, therefore, important to quantify forest CO_2 emissions so as to develop adequate mitigation plans and accurate climate models.

Soils contain 1500 - 2400 Gt of carbon, which is three times higher than the CO_2 in the atmosphere and two times higher than the CO_2 stored in forest vegetation (Khomik et al. 2006; Hossain et al. 2007; Smith 2012). Through soil CO_2 efflux, forests have been found to release between 40 and 98 Gt of carbon per year to the atmosphere, which is approximately 10 times the carbon emission from burning fossil fuels (Heinemeyer et al. 2007; Ferréa et al. 2012; Liang et al. 2016), making it a significant process in the terrestrial carbon cycle. The amount of CO_2 emitted from the soil is dependent on the rates of litter decomposition, root CO_2 efflux, and microbial activity. Since small changes in the terrestrial carbon cycle could trigger the release of more soil CO_2 in the form of soil CO_2 efflux, it is necessary to understand the role of forest soil CO_2 efflux in the global carbon cycle.

Soil CO_2 efflux is also used to calculate the forest carbon budget and measure productivity. Carbon is sequestrated by photosynthesis, which is also defined as gross primary productivity (GPP) and when autotrophic soil CO_2 efflux (AF_{CO_2}) is subtracted from GPP, the difference is net primary productivity (NPP), which is defined as the annual growth of carbon absorbed by forest biomass (Goulden et al. 2011). Heterotrophic soil CO_2 efflux (HF_{CO_2}) is subtracted from NPP to estimate the net ecosystem productivity (NEP) (Gower 2003). Therefore, the partitioning of total soil CO_2 efflux (F_{CO_2}) into HF_{CO_2} and AF_{CO_2} is necessary for the estimation of the forest carbon budget and the prediction of the soil CO_2 efflux response to climate change. There are various methods by which soil CO_2 efflux can be partitioned including component integration, root exclusion, isotopic and regression methods. However, all methods have been found to have their advantages and disadvantages, so no one method is universally accepted (Hanson et al. 2000; Kuzyakov 2006; Baggs 2006).

1.1.1. Disturbances and forest soil CO_2 efflux

Disturbances may alter forest processes and are an integral part of the ecosystem carbon dynamics. They can be grouped into different categories such as climate change, land-use change, and forest management practices, which may reduce forest biomass and interact with each other to modify forest dynamics. For example, forest fires change the forest structure, species composition and modify soil fertility (Ward et al. 2014). Fire is also known as a stand-replacing disturbance that is necessary for the regulation of the boreal carbon cycle and is expected to increase under climate change scenarios (Williamson et al. 2009). When fires reduce forest biomass, they immediately release CO_2 into the atmosphere during the fire and from the initial decomposition of residue but after some time (Burke et al. 1997; Czimczik et al. 2006), CO_2 may be sequestered in both the vegetation and soil under new stand growth (Lynch and Wu 2000). However, the rapid increase of forest fires under global warming may not give forests enough time to recover and sequester CO_2, thereby causing an increase in CO_2 emissions through soil CO_2 efflux. While the effects of fire are well-studied in boreal soil CO_2 efflux literature (Amiro et al. 2003; Czimczik et al. 2006; Singh et al. 2008; Yue et al. 2013), they are not as well-studied in temperate and tropical forests and may affect them differently. Other disturbances may also have varying effects on soil CO_2 efflux across different forests and to accurately predict the response of soil CO_2 efflux to disturbances, we need to account the spatial differences at the ecosystem-level.

1.1.2 Soil CO_2 efflux in Canadian boreal forests

35% of Canada's land area is occupied by forests, approximately 347 million hectares in total, most of which is occupied by boreal forests (Weber and Stocks 1998; Ullah et al. 2009;

Natural Resources Canada 2018). Boreal forests are characterized by short, warm summers and cold, long winters. They provide essential ecosystem services such as climate regulation and provision of raw materials. It has also been found that boreal soils generally store more carbon than its vegetation (Malhi et al. 1999) and as such, our knowledge of boreal carbon cycle could be used in mitigation plans to potentially sequester more carbon. Canadian boreal forest soils have been identified as a substantial part of the terrestrial carbon sink because in addition to its vast area (Houghton et al. 2009; Brandt et al. 2013), they have the ability to store a large amount of organic carbon (Martin et al. 2005; Kurz et al. 2013). Understanding the role of Canadian boreal forests in the terrestrial carbon cycle is instrumental in managing additional, unexpected CO_2 release through soil CO_2 efflux within the area.

Canadian boreal forests are defined as a mosaic of different-aged stands consisting of coniferous and deciduous tree species (Hansson 1992; Abele et al. 2014), often creating spatially heterogeneous stands within the forest. For this study, I used the accepted definition of mixedwood forests proposed by Martin et al. (2005) as forests that contain a mixture of between 25 and 75% of coniferous and deciduous tree species. Mixedwood forests have great ecological and economic value to Canada because they have high biodiversity and are used to accomplish harvesting needs (Park et al. 2005; Martin and Gower 2006). Due to the combination of different coniferous and deciduous species in boreal mixedwood stands, individual species may exhibit different phenology and forest processes in the mixedwood stands than pure-species stands. Despite the unique nature of boreal mixedwood forests, most of the carbon cycle literature is focused on pure stands (Martin et al. 2005; McCaughey et al. 2006). Considering that mixedwood forests are dominant in the southern part of Canada and also store large amounts of carbon (McCaughey et al. 2006), it is essential to improve our current knowledge of how species composition in boreal mixedwood forests influences the contribution of soil CO_2 efflux in the boreal carbon cycle.

Numerous environmental factors influence the spatial and temporal variation of F_{CO_2} HF_{CO_2}, and AF_{CO_2} in general. Majority of the temporal variation of F_{CO_2} in the boreal forest has been found to be primarily controlled by soil temperature (Rayment and Jarvis 2000; Griffis et al. 2004; Khomik et al. 2006) and soil moisture (Drewitt et al. 2002; Gaumont-Guay et al. 2008). Because some studies have found that soil moisture may confound the effects of temperature on soil CO_2 efflux (Davidson et al. 1998), there is need to research how both factors interact to affect F_{CO_2} and its components in boreal forests. The spatial variation of F_{CO_2} may be controlled by other variables such as DBH (Søe et al. 2004), soil nutrient availability (Xu and Qi 2001), and soil organic matter. The patchiness of different species in a boreal mixedwood stand could increase spatial variation of F_{CO_2} by influencing soil CO_2 efflux components (HF_{CO_2} and AF_{CO_2}) separately. Environmental factors that affect microbial activity and decomposition may determine the spatial variation of HF_{CO_2}, while fine root biomass and activity may be responsible for the spatial variation of AF_{CO_2} because it is closely linked to photosynthesis. By separating the effects of environmental factors on soil CO_2 efflux components in boreal mixedwood forests, we can better understand how these factors affect total soil CO_2 efflux and the boreal carbon budget.

1.2 Research objectives

Disturbances are expected to change the spatial patterns of aboveground and belowground processes (Turner 2010; Goulden et al. 2011), which are strongly linked to forest soil CO_2 efflux. My research goal for the first part of my thesis is to understand how forest soil CO_2 efflux in boreal, temperate and tropical regions respond to different disturbances and detect if there is a spatial trend in the response of forest soil CO_2 efflux. The research synthesizes current knowledge of the disturbance effects that have been studied in forest soil CO_2 efflux literature according to different types, leading to the recommendation of future research needs and suggestions for more accurate carbon cycle models in this subject area. By also studying disturbance effects on soil CO_2 efflux components, the underlying mechanism by which disturbances affect total soil CO_2 efflux may be better understood. While it is expected that there will be differences in disturbance effects across boreal, temperate, and tropical forests, this research will be able to distinguish the effect size of disturbances on soil CO_2 efflux across forest types. Therefore, the first research objective of this thesis is to quantify the spatial variation of disturbance effects on F_{CO_2}, HF_{CO_2} and AF_{CO_2} across global forests using data from published studies (Chapter 2).

The vast area of Canada's boreal forest is dominated in the south by mixedwood forests (McCaughey et al. 2006) and as such, increased understanding of carbon cycle within this area will improve our ability to calculate boreal carbon budgets and predict the response of the boreal carbon cycle to climate warming. One way of enhancing our current knowledge of the carbon cycle within Canada's boreal forest is by studying the spatial and temporal variability of soil CO_2 efflux in this region because it is a key component of terrestrial carbon cycling. Because the spatial variation of soil CO_2 efflux has been attributed to micro-topography variation (Rayment and Jarvis 2000), fine-scale variability of soil CO_2 efflux may be instrumental in developing accurate carbon cycle models. My second research goal is to determine the drivers of spatial and temporal variation of soil CO_2 efflux (F_{CO_2}) and recommend the number of sampling points needed to capture the variability within a Canadian boreal mixedwood forest accurately. However, our understanding of soil CO_2 efflux response to environmental disturbances may be improved by also studying and quantifying the contribution of its components (HF_{CO_2} and AF_{CO_2}). When total soil CO_2 efflux is partitioned, researchers may be able to determine how each component responds to changes in the environment and therefore, estimate changes in total soil CO_2 efflux more accurately. Therefore, the research objectives of the second part of the thesis are to (1) quantify the spatial and temporal variation of F_{CO_2} and its components (HF_{CO_2} and AF_{CO_2}) in a Canadian boreal mixedwood forest, (2) explore the relationship between environmental factors and soil CO_2 efflux (F_{CO_2}, HF_{CO_2}, and AF_{CO_2}) at spatial and temporal scales, (3) quantify the contribution of HF_{CO_2} and AF_{CO_2} to F_{CO_2} in a boreal mixedwood forest using a trenching root-exclusion method, and (4) determine the effects of species composition on F_{CO_2}, HF_{CO_2}, and AF_{CO_2}.

1.3 Thesis Structure

Chapter 1 (this chapter) provides a context and introduces the background of this thesis research by examining the different ways by which disturbances could influence spatial variation in global forest soil CO_2 efflux. It also explains the importance of boreal mixedwood soil CO_2 efflux in the global carbon cycle and introduces the general structure of the thesis.

Chapter 2 explores the first research objective of quantifying the spatial variation of disturbance effects on soil CO_2 efflux across boreal, temperate and tropical forests. I carried out an extensive meta-analysis and systematic review of disturbance effects on boreal, temperate and tropical forest soil CO_2 efflux and its components. I categorized the disturbances into five broad categories (climate change, land-use change, forest management, natural disturbances, and litter perturbations) and quantified its effects on soil CO_2 efflux across the forests.

Chapter 3 examines the spatial and temporal variation of F_{CO_2} in a 1-ha boreal mixedwood forest in Alberta and the relationship with several environmental factors and species composition. In this chapter, I also calculated the minimum number of sampling points required to estimate the mean F_{CO_2} within 10% and 20% error limit in the 1-ha plot and laid a foundation for the next chapter, which assesses the contribution of soil CO_2 efflux components to the total soil CO_2 efflux within the boreal mixedwood forest.

Chapter 4 partitions F_{CO_2} into heterotrophic (HF_{CO_2}) and autotrophic (AF_{CO_2}) soil CO_2 efflux using a trenching and root-exclusion method in the 1-ha boreal mixedwood forest. In this chapter, I was able to identify the drivers of autotrophic and heterotrophic soil CO_2 efflux, contributing to our knowledge of how disturbances may change total soil CO_2 efflux within this boreal mixedwood forest. Chapter 5 concludes this dissertation by summarizing the key findings of this thesis research and provides recommendations for further research needs.

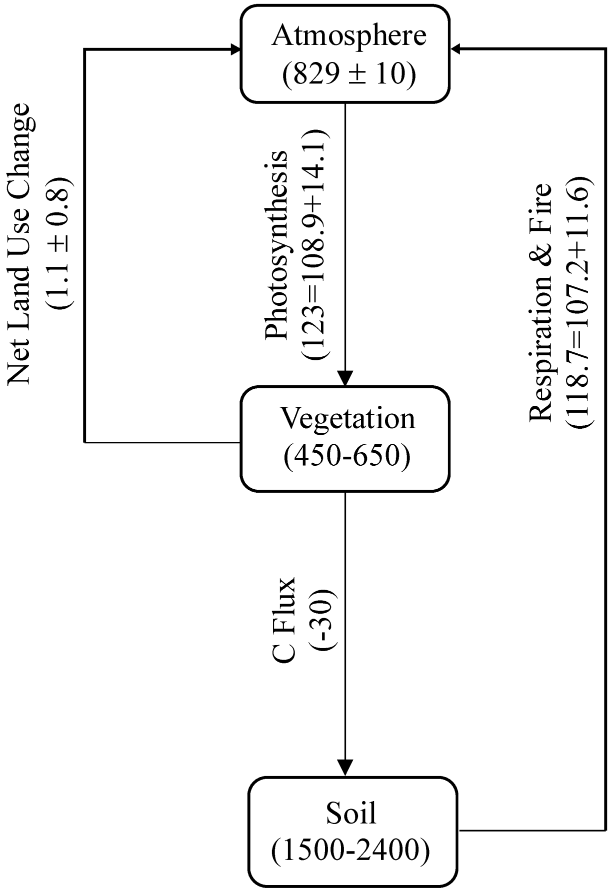

Figure 1-1. Simplified terrestrial carbon cycle showing cumulative carbon stocks and fluxes adapted from IPCC (2013). All numbers are in GtC (1GtC = 10^{15}gC) with the exception of net land use change flux, which is in GtC/yr. Carbon stocks are in boxes while carbon fluxes are represented by arrows. Using CMIP5 models, estimated change in terrestrial fluxes of photosynthesis and respiration with values of 14.1 and 11.6 GtC over a 10-year period respectively, were added to the global estimates.

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Chapter 2: Quantifying disturbance effects on soil CO_2 efflux across forest biomes

2.1 Summary

Forest soil CO_2 efflux is a crucial process in the terrestrial carbon (C) cycle that can be altered by disturbances. Previous analyses have focused on the effects of warming or elevated precipitation on biome soil CO_2 efflux and its components, but there is still little consensus on how forest soil CO_2 efflux responds to different disturbance s. Here, I carried out a global meta-analysis to quantify several disturbance effects on soil CO_2 efflux and its components across boreal, temperate and tropical forests based on 832 observations from 279 studies. Global forest soil CO_2 efflux was stimulated by climate change effects such as FACE (free air carbon enrichment), warming, and increased precipitation (19 to 40%) but was not altered by drought or land-use change while fire and litter perturbations significantly affected global forest soil CO_2 efflux. Boreal forest soil CO_2 efflux was stimulated by FACE + warming and windthrow while FACE, warming, increased precipitation, afforestation, site preparation, thinning, and litter addition stimulated temperate forest soil CO_2 efflux. Tropical forest soil CO_2 efflux was increased by added precipitation, elevated C, forest-to-grassland conversion, and litter addition. By partitioning soil CO_2 efflux into autotrophic and heterotrophic portions, I was able to identify several mechanisms by which some disturbances could influence total forest soil CO_2 efflux. This study highlights a need for more studies of disturbance effects on forest soil CO_2 efflux in certain regions such as Africa and Asia, as well as studies partitioning total soil CO_2 efflux for better representation and knowledge of its underlying mechanisms. This meta-analysis also shows the importance of accounting for differences between forest ecosystems when

incorporating disturbance effects on soil CO_2 efflux in the development of global C cycle models and projecting feedback between climate and the terrestrial carbon cycle.

2.2 Introduction

Humans have increased atmospheric carbon (C) levels by burning fossil fuels, deforestation, and other activities, thereby causing the acceleration of global warming (IPCC 2013). Soil CO_2 efflux (F_{CO_2}), the process by which soils emit carbon dioxide (CO_2) to the atmosphere, is the second largest flux in the terrestrial C cycle (Raich and Schlesinger 1992; Bahn et al. 2008). It consists of autotrophic (root) and heterotrophic (microbial) soil CO_2 efflux, emitting 68-90 GtC yr^{-1} and is responsible for the majority of ecosystem respiration in forests (Iqbal et al. 2008; Liang et al. 2016). Minor changes in the environment can alter F_{CO_2}, which may have a significant impact on the feedbacks between global climate change and terrestrial C balance (Raich et al. 2002; Houghton 2007). Therefore, understanding the response of F_{CO_2} to environmental changes is important for accurate modeling of climate change effects on the global C cycle.

Forests cover approximately 30% of the global land surface and sequester 40% of the belowground terrestrial C (Pregitzer and Euskirchen 2004; FAO 2010). Disturbances regulate forest dynamics by altering environmental conditions, biogeochemical processes, species composition, and forest structure (Zhang and Liang 2014). They can, therefore, influence autotrophic soil CO_2 efflux by changing aboveground and root biomass, fine root turnover, and root exudates or alter heterotrophic soil CO_2 efflux by affecting substrate availability for microbial decomposition (Kuzyakov and Larionova 2005; Houghton et al. 2009; Zhang and Liang 2014). However, there have been discrepancies in the differential response of soil CO_2

efflux components to forest disturbances across various studies. For example, Fei et al. (2015) found that warming increased heterotrophic soil CO_2 efflux but not autotrophic soil CO_2 efflux while Liu et al. (2016b) found that warming increased both heterotrophic and autotrophic soil CO_2 efflux. In addition, the differences in the response of soil CO_2 efflux to disturbances may cause additional uncertainties in the terrestrial C cycle. Quantifying the effect of forest disturbances on soil CO_2 efflux and its components enable researchers to identify the source of variations in the response of forest C cycle to environmental and climate changes.

For this meta-analysis, four broad categories of forest disturbances were identified. Warming, increased precipitation, drought, and increased atmospheric C concentration were grouped as global warming consequences that could significantly affect forest C dynamics (Harper et al. 2005; Selsted et al. 2012; Noh et al. 2016; Lu et al. 2017). In addition to climate change, human-induced disturbances such as land-use change and forest management practices also affect the forest C cycle by causing changes to forest biomass. Land-use change is the second largest source of anthropogenic emissions and directly releases about 1.6 GtC per year to the atmosphere (Houghton 1995; Foley et al. 2005; Peng et al. 2008; Lv et al. 2016). Land-use change was described as afforestation, land degradation, and conversion of natural forests to plantations, croplands, or grasslands. Forest management practices such as harvesting and site preparation are also used to provide ecosystem services such as the provision of food and various economic needs but they alter litter quality, species composition, biomass, and microbial activity of the forest (Peng et al. 2008; Luo et al. 2016; Smith et al. 2016), which could also cause significant changes in the forest C cycle via soil CO_2 efflux. Litter perturbations and natural disturbances such as fire and windthrow were also included in this meta-analysis. From previous studies, there is a considerable degree of uncertainty as to how forest C cycles change with climate change, land-use change, forest management practices, natural disturbances, and litter perturbations (Houghton 2003; Bonan 2008; Chertov et al. 2009; Zhang et al. 2015). Therefore, by taking the effects of different disturbances on soil CO_2 efflux into account, researchers may be able to accurately determine how the forest C cycle adapts to changing environmental conditions.

In this study, I aim to quantify and compare the effects of climate change, land-use change, forest management practices, natural disturbances, and litter perturbations on soil CO_2 efflux across boreal, temperate and tropical forests, which contain 33%, 25% and 42% of the world forest area, respectively (IPCC 2013). Boreal forest soils contain the second largest soil organic C pool in the world, storing about 20% of global C (Rayment and Jarvis 2000; Kane et al. 2006; McCaughey et al. 2006; Allison and Treseder 2011). They are often considered as C sinks because of their large areas and their ability to sequester soil C in the form of organic matter (Malhi et al. 1999). Fires (Czimczik et al. 2006; Yue et al. 2013; Köster et al. 2017), harvest (Moroni et al. 2007; Bergeron et al. 2008; Strukelj et al. 2015) and warming (Allison and Treseder 2008; Martins et al. 2017) are some of the disturbances that have been researched in boreal soil CO_2 efflux studies. Temperate forests contain less C than boreal and tropical forests, but more than 60% of the ecosystem C pool is concentrated within the soil (Dixon et al. 1994; Malhi et al. 1999; Thiffault et al. 2011). Elevated CO_2 (Suwa et al. 2004; Xie et al. 2005), warming (Lellei-Kovács et al. 2008; Noh et al. 2016) and land-use change (Euskirchen et al. 2003; Gong et al. 2014) are examples of disturbances that have been studied extensively in temperate forest soil CO_2 efflux literature. Tropical forests cover the largest forest area with high plant biodiversity and C storage but also has the potential to release additional CO_2 after disturbances as it constitutes the highest atmospheric C exchange of all terrestrial systems

(Wright 2010; Cavaleri et al. 2017). Soil CO_2 efflux in this forest is more influenced by soil moisture than temperature (Malhi et al. 1999; Bréchet et al. 2009) because of larger variations in soil moisture. The main disturbances studied in tropical ecosystem include litter manipulation (Fanin et al. 2011; Liu et al. 2017a), land-use change (Don et al. 2011; Wu et al. 2016), and drought (Cleveland et al. 2010; van Straaten et al. 2011). In general, disturbances could increase the spatial variation of soil CO_2 efflux rates across different biomes by causing changes to forest processes and environmental conditions (Akburak and Makineci 2013; Crowther et al. 2014). Because these three biomes jointly dominate the terrestrial C cycle, understanding disturbance effects on soil CO_2 efflux across boreal, temperate and tropical forests is expected to improve our understanding of the spatial variation in global forest soil CO_2 efflux.

Given that different environmental disturbances may cause unprecedented changes to the C cycle by altering the rate of soil CO_2 efflux, it is crucial to quantify the effects of different disturbances that may change the spatial variation of F_{CO_2}. With this knowledge, researchers can better predict the response of soil CO_2 efflux to evolving disturbances under future climate change scenarios. Previous meta-analyses have studied direct effects of some disturbances on biomes such as climate warming (Rustad et al. 2001; Lu et al. 2013; Wang et al. 2014), precipitation (Wu et al. 2011; Vicca et al. 2014; Liu et al. 2016b), nitrogen addition (Janssens et al. 2010; Zhou et al. 2014; Chen et al. 2015), global warming interactions (Zhou et al. 2016) and fire (Wang et al. 2012a) across different biomes. According to the IPCC (2013), it is also predicted that climate change will change the frequency and intensity of other forest disturbances. By synthesizing and comparing the effects of climate change, land-use change, forest management, natural disturbances, and litter perturbations, we can compare the strength and direction of various disturbance effects on soil CO_2 efflux in boreal, temperate and tropical forests. In order to quantify the response of soil CO_2 efflux and its components to different disturbances, data was compiled from published soil CO_2 efflux studies and was used to assess climate change, land-use change, forest management, natural disturbances, and litter perturbations effects on boreal, temperate and tropical forest soil CO_2 efflux and its components.

2.3 Materials and Methods

2.3.1 Data compilation

Peer-reviewed journal articles from 1900 to June 2018 were searched using the ISI Web of Science database. The search terms included keywords such as soil respiration, soil CO_2, belowground respiration and a wide range of disturbance types including changes in climate and land-use change (Tables A1, A2). For purposes of this study, this search was narrowed down to disturbance effects on boreal, temperate and tropical forest soil CO_2 efflux and excluded grasslands, deserts, agricultural lands, and other ecosystems. To determine if the study was in the boreal, temperate or tropical forest, the description given by the authors and the ecoregion classification by the World Wildlife Fund (Olson and Dinerstein 2002) were used. In addition to the initial search results, studies from the soil CO_2 efflux database developed by Bond-Lamberty and Thomson (2010) and data from previous meta-analyses on soil respiration (Wang et al. 2014; Liu et al. 2016b; Zhou et al. 2016) that fit the criteria were included. The disturbance categories were assessed in each forest biome to identify the spatial variation of its effects across boreal, temperate and tropical forest soil CO_2 efflux. This search generated thousands of publications, which were screened by reading abstracts and titles, yielding 832 observations from 279 studies that met the selection criteria with 16 disturbances and were analyzed in this meta-analysis (Fig. 2-1, Table A3).

Several criteria had to be fulfilled for studies to be included in this meta-analysis. Searches were limited to field experiments and excluded laboratory incubation to represent disturbance effects on soil CO_2 efflux under natural conditions. Studies lasting less than one growing season were also excluded. Each observation had at least one pair of total (F_{CO_2}), autotrophic (AF_{CO_2}) or heterotrophic (HF_{CO_2}) soil CO_2 efflux rates measured simultaneously in both control and disturbed treatments. If studies reported more than one disturbance level, each level was recorded and listed as a separate observation. In disturbance chronosequences, the sites described as "mature", "old" or "control" were treated as the control site. Studies in which the means, sample sizes and standard deviations could not be derived were excluded because these parameters are needed to conduct the meta-analysis. For studies that reported standard errors (SE), the standard deviations (SD) was computed as:

$$SD = SE * \sqrt{n} \tag{1}$$

where n is the sample size. When data were presented in figures, I extracted the data using WebPlotDigitizer (www.arohatgi.info/WebPlotDigitizer).

The studies included in this meta-analysis ranged from latitude 38.6°S to 67.8°N. MAT and MAP ranged from -10 to 38°C and 98 to 5000 mm respectively across all three forests (Fig. 2-2). Across the forests, soil CO_2 efflux was mostly measured using the IRGA method, followed by gas chromatography and soda-lime absorption. When necessary, soil CO_2 efflux values were converted from annual, monthly and daily units to μmol C m^{-2} s^{-1} for statistical comparison across different studies. Other variables extracted include country where the study was conducted, study area, latitude, longitude, disturbance type, mean annual temperature (MAT), mean annual precipitation (MAP), soil temperature (ST), soil volumetric water content

(VWC), the method of soil CO_2 efflux measurement and length of the study. For studies that did not record MAT or MAP, values were obtained using Bioclim data in WorldClim v. 1.4 (Hijmans et al. 2005).

2.3.2 Analysis

Meta-analysis is a statistical method of summarizing the results of various studies (Hedges et al. 1999). It was used here to assess the response of soil CO_2 efflux to disturbances in the boreal, temperate and tropical forests. I quantified the effect sizes of the responses of soil CO_2 efflux to disturbances by using log-transformed response ratios (LRR) for the overall dataset and in each forest group. Log response ratios were calculated as:

$$LRR = \ln\left(\frac{\bar{X}_t}{\bar{X}_c}\right) \qquad (2)$$

where $\bar{X}_t$ and $\bar{X}_c$ are the means of the treatment group (i.e. the soil CO_2 efflux rates after the disturbance) and control soil CO_2 efflux values respectively. The variance (v) for response ratio was calculated as:

$$v = \frac{s_t^2}{n_t\bar{x}_t^2} + \frac{s_c^2}{n_c\bar{x}_c^2} \qquad (3)$$

where n_t, $\mathrm{s_t}$, n_c, and s_t represent sample sizes and standard deviations of the treatment and control groups respectively. The weighting factor (w) was calculated using inverse pooled variance ($1/v$) for each study (Hedges et al. 1999; Luo et al. 2006). Weights of studies that provided multiple observations by the number of observations (n) per study were adjusted to generate the mean effect size (RR_{++}) and its standard error by using Eqns. 4 & 5:

$$RR_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}RR_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}} \tag{4}$$

$$s(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}}} \tag{5}$$

where m is the number of groups (e.g. forest types), and k is the number of comparisons in the i^{th} group. If RR_{++} was calculated using more than 20 data points, the 95% confidence interval was as $RR_{++} \pm 1.96 \times s(RR_{++})$. Comparisons of mean effect sizes were performed out using a Tukey HSD test.

Random effects models are commonly used in ecology to account for the differences of true effect size among studies (Gurevitch and Hedges 1999; Duguid and Ashton 2013). If the 95% CI overlaps with zero, the disturbance effects are considered non-significant. Positive effect sizes indicated that the disturbance increased soil CO_2 efflux while negative effect sizes indicated that the disturbance decreased soil CO_2 efflux. I calculated the percentage change of soil CO_2 efflux after disturbance by back-transforming the LRR using:

$$(e^{LRR} - 1) * 100\% \tag{6}$$

Random effect models were used to test for the differences among disturbance types within the forest biomes. I checked for publication bias by performing the Egger's regression test (Viechtbauer 2010) for asymmetry and funnel plots. Egger's regression test for asymmetry showed that there was no evidence of publication bias. Using meta-regression, the heterogeneity (Q_B) between studies, soil CO_2 efflux methods, and disturbance levels was calculated.

All meta-analyses were carried out using the 'rma' function of the metafor package in R (Viechtbauer 2010) and used to investigate relationships between the response ratio of soil CO_2

efflux components and other parameters such as latitude, time since disturbance, soil temperature and soil moisture content. All analyses were done in R using R Studio (version 0.99.902: developed by R Studio Team 2015).

2.4 Results

2.4.1 Overview of the data structure

The search generated 207 observations from boreal forests, 438 observations from temperate forests, and 187 observations from tropical forests (Fig. 2-1). There was moderate spatial variation in soil CO_2 efflux before disturbance or perturbation in boreal (CV=58%), temperate (CV=49%), and tropical (CV=44%) forests. Most of the temperate and boreal studies were carried out during growing seasons while most of the tropical forest studies were carried over the whole year. Soil temperature and moisture did not significantly differ between control and treatment sites across all disturbances.

In partitioning studies, 40 observations from 20 studies represented autotrophic soil CO_2 efflux while heterotrophic soil CO_2 efflux was represented by 67 observations from 34 studies. In control sites, autotrophic soil CO_2 efflux was lowest in temperate forests, followed by boreal and tropical forests, which ranged between 0.88 - 3.01 μmol C m^{-2} s^{-1} across the biomes. Heterotrophic soil CO_2 efflux in control sites was also lowest in temperate forests followed by tropical and boreal forests, ranging between 1.70 - 2.84 μmol C m^{-2} s^{-1}.

In general, climate change impacts such as elevated atmospheric CO_2, warming, and water addition significantly increased global forest soil CO_2 efflux by 28%, 18%, 40%, and 19%, respectively (Table 2-1). There was also significant heterogeneity between studies in the effects of elevated atmospheric CO_2 concentration and warming on soil CO_2 efflux. Land-use change showed no significant effects on global forest soil CO_2 efflux but exhibited significant study heterogeneity in soil CO_2 efflux response to afforestation, forest-to-cropland and forest-to-grassland conversion (Table 2-2). The forest management practices significantly affected global forest soil CO_2 efflux with harvesting and site preparation decreasing soil CO_2 efflux by 8% and 24%, respectively while thinning increased soil CO_2 efflux across all global forests (Table 2-3). There was significant study heterogeneity in soil CO_2 efflux response to harvest and thinning. Fire and litter removal decreased global forest soil CO_2 efflux while litter addition increased global forest soil CO_2 efflux (Table 2-3). There was significant study heterogeneity in fire, windthrow, litter removal, and litter addition effects on global forest soil CO_2 efflux.

Afforestation and forest-to-grassland conversion significantly decreased global forest soil heterotrophic CO_2 efflux (Table 2-4). Fire decreased both global forest soil autotrophic and heterotrophic soil CO_2 efflux while forest-to-plantation conversion, thinning, and warming significantly increased soil CO_2 efflux by 23%, 32%, and 17%, respectively (Table 2-4). There were no significant effects of some disturbances on global forest soil CO_2 efflux components because of limited sample size (Table 2-4). Due to the small sample sizes in some of the categories, I was unable to detect true disturbance effects on soil CO_2 efflux, possibly increasing the chances of committing type II errors. On the other hand, by involving a large number of published studies, I was able to minimize the type II errors in other categories and detect the true effect size of disturbances on boreal, temperate, and tropical soil CO_2 efflux.

2.4.2 Effects of climate change impacts on forest soil CO_2 efflux

Elevated atmospheric CO_2 concentration significantly increased temperate and tropical soil CO_2 efflux by 25.18% and 28.44% respectively but not boreal soil CO_2 efflux (Fig. 2-2a).

However, there was no significant difference in the response of soil CO_2 efflux to elevated atmospheric CO_2 concentration among boreal, temperate and tropical forests. Drought did not significantly affect temperate and tropical soil CO_2 efflux (Fig. 2-2a). Warming significantly increased temperate soil CO_2 efflux by 22.37% but not boreal and tropical soil CO_2 efflux. Water addition increased temperate and tropical soil CO_2 efflux by 20.14% and 17.85% respectively but not boreal soil CO_2 efflux. Elevated CO_2 + warming uniformly increased boreal and temperate soil CO_2 efflux by 55.88% and 32.75% respectively while warming + water addition and warming + drought did not affect temperate soil CO_2 efflux (Fig. 2-2a).

Warming increased the heterotrophic portion of temperate soil CO_2 efflux but had no effect on autotrophic soil CO_2 efflux (Fig. 2-4a). Drought did not have a significant effect on temperate autotrophic and heterotrophic soil CO_2 efflux, but limited sample sizes in tropical soil CO_2 efflux prevented a lack of noticeable effect.

2.4.3 Effects of land-use change and forest management practices on soil CO_2 efflux

Afforestation decreased boreal and tropical soil CO_2 efflux by 38.38 and 27.35% respectively but increased temperate soil CO_2 efflux by 33.88% (Fig. 2-2b). Across all forests, forest-to-cropland conversion did not significantly affect soil CO_2 efflux, but forest-to-grassland conversion only decreased boreal soil CO_2 efflux by 40.76%. Land degradation decreased boreal forest soil CO_2 efflux by 33.16% but had no effect on tropical soil CO_2 efflux. On the other hand, forest-to-plantation conversion decreased tropical forest soil CO_2 efflux by 12.79% but not temperate CO_2 efflux (Fig. 2-2b). The effect of land-use change was evident on temperate heterotrophic soil

CO_2 efflux but not boreal and tropical heterotrophic soil CO_2 efflux. However, there was no significant effect on autotrophic soil CO_2 efflux on boreal and temperate forests.

Site preparation and thinning increased temperate soil CO_2 efflux by 22.57% and 35.42% respectively (Fig. 2-3a). Clear-cut harvesting decreased boreal soil CO_2 efflux by 5.07% while partial-cut harvesting reduced tropical soil CO_2 efflux by 22.11%.

2.4.4 Effects of natural and litter perturbations on forest soil CO_2 efflux

Windthrow significantly increased boreal soil CO_2 efflux by 26.24% but not temperate soil CO_2 efflux (Fig. 2-3b). On the other hand, fire significantly decreased boreal and temperate soil CO_2 efflux by 25.08% and 12.77% respectively but not tropical soil CO_2 efflux. Litter removal reduced boreal, temperate, and tropical soil CO_2 efflux by 25.52%, 19.73%, and 39.39% while litter addition increased temperate and tropical soil CO_2 efflux by 7.77% and 67.38% respectively (Fig. 2-3b). Fire significantly decreased temperate autotrophic soil CO_2 efflux but not boreal autotrophic soil CO_2 efflux.

2.5 Discussion

Forest soil CO_2 efflux response to climate change effects

Humans have contributed to accelerated global warming, leading to atmospheric carbon dioxide levels exceeding 400 ppm. Direct consequences of climate change such as warming, water addition, and elevated atmospheric C concentration (FACE) were found to increase global forest soil CO_2 efflux while drought had no effect in this meta-analysis (Table 2-1). Warming increases soil temperature, which subsequently stimulates microbial activity, leaf litter decomposition and induce changes in plant phenology due to longer growing seasons (Chung et al. 2013) as was seen in temperate forests in this study. However, the non-significant response of boreal soil CO_2 efflux to warming may be attributed to the reduction of boreal root biomass (Bergner et al. 2004; Bronson et al. 2008) which may counter increased microbial activity. Another reason why warming may not significantly affect boreal soil CO_2 efflux is from lack of a significant effect on microbial activity due to water loss from increased transpiration as seen in some forests (Rustad et al. 2001; Allison et al. 2010; Xu et al. 2013). Tropical soil CO_2 efflux did not respond to warming because as Kirschbaum (2004) found, microbial activity may adapt to changes in air and soil temperature, causing no change in soil CO_2 efflux. The meta-analysis shows that warming did not affect autotrophic soil CO_2 efflux but stimulated heterotrophic soil CO_2 efflux (Table 2-4, Fig. 2-4) supporting the findings that warming regulates total soil CO_2 efflux by influencing the heterotrophic portion of soil CO_2 efflux. This observation is also supported by Aguilos et al. (2011), who found that warming significantly increased the heterotrophic portion of soil CO_2 efflux.

Water addition stimulated temperate and tropical soil CO_2 efflux but not boreal soil CO_2 efflux (Fig. 2-2a). This difference in forest soil CO_2 efflux response is supported by Deng et al. (2012), who found that variations in the soil condition and aboveground vegetation determines the effect of increased precipitation within various forests. An increase in water availability can stimulate microbial (Koide et al. 2010; Deng et al. 2012) and root (Yan et al. 2011) activity, which in turn increases heterotrophic and autotrophic components of temperate and tropical soil CO_2 efflux. Yan et al. (2011) found that soil moisture is essential for root development and microbial activity in areas where soil moisture is a limiting factor. There are several reasons for the non-significant effect of increased precipitation on boreal soil CO_2 efflux. First, this result suggests that soil moisture is not a limiting factor in this forest biome. Second, the confounding effect of soil temperature and moisture reported by Davidson et al. (1998), may cause changes in precipitation level to show no direct effect on boreal soil CO_2 efflux. Lastly, the explanation for the lack of non-significant effect of increased precipitation on boreal forests may be attributed to precipitation-induced changes in soil temperature having little impact on soil CO_2 efflux (Liu et al. 2016b). Drought was found to have no effect on either temperate and tropical forest soil CO_2 efflux, which is in agreement with Barba et al. (2016). They found that both heterotrophic and autotrophic soil CO_2 efflux did not respond to drought stress and suggested that this may be as a result of the drier environmental conditions reducing microbial biomass and metabolic activity (Barba et al. 2016). Specifically, Davidson et al. (2004) found that drought-induced stress causes the reduction of root CO_2 efflux while fine root mortality increases microbial CO_2 efflux, resulting in no net effect by subsequently reducing autotrophic soil CO_2 efflux and stimulating heterotrophic soil CO_2 efflux. This finding is in contrast with the observed result as there was a non-significant effect of drought on autotrophic or heterotrophic portions of soil CO_2 efflux due to its small sample size. This study suggests that the underlying mechanisms by which increased precipitation and drought influence forest soil CO_2 efflux differs between boreal, temperate, and tropical forest soil CO_2 efflux components.

Elevated atmospheric C concentration significantly increased temperate and tropical soil CO_2 efflux but not boreal soil CO_2 efflux (Fig. 2-2a). The increased soil CO_2 efflux after this impact is by stimulating microbial soil CO_2 efflux (Kou et al. 2007) or increasing root CO_2 efflux (Wang et al. 2012b) through various mechanisms. First, the stimulation of soil CO_2 efflux in response to elevated CO_2 can be as a result of increased fine root growth biomass (Matamala and Schlesinger 2000; Pregitzer et al. 2006) and litter production in forests (Lagomarsino et al. 2013). Second, elevated atmospheric CO_2 concentration has also been found to induce stem growth in some forests, leading to an increase in soil CO_2 efflux (Tingey et al. 2006). Third, there might be higher fine root turnover and increased microbial respiration from the higher decomposition of fine roots (Keidel et al. 2015), stimulating both autotrophic and heterotrophic portions of total soil CO_2 efflux. While these mechanisms may be responsible for increasing the autotrophic and heterotrophic components of forest soil CO_2 efflux, there was no evidence that elevated C increased either autotrophic and heterotrophic soil CO_2 efflux (Table 2-4) due to small sample size. On the other hand, the non-significant effect of FACE experiments on boreal forest soil CO_2 efflux is probably also due to the small sample size as the results in Fig. 2-2a showed that there was no statistical difference between the effects of elevated CO_2 on boreal, temperate, and tropical forests.

Of all the studies that incorporated more than one climate change factor, FACE + warming significantly increased global forest soil CO_2 efflux while the others had no effect on forest soil CO_2 efflux (Table 2-1). This finding suggests that when elevated C interacts with warming, it may generate an additive effect on soil CO_2 efflux while warming +water addition and warming + drought could cancel each other out, causing a net-zero effect on forest soil CO_2 efflux. Li et al. (2017) and Liu et al. (2017b) found that drought increased transpiration rates and could offset the positive effects of soil warming on fine root biomass and decomposition, supporting the overall finding of its effect on total soil CO_2 flux.

Forest soil CO_2 efflux response to land-use change

Land-use change showed non-significant effects on global forest soil CO_2 efflux but varying effects on boreal, temperate, and tropical forests (Table 2-2, Fig. 2-2b). Afforestation decreased tropical and boreal soil CO_2 efflux but increased temperate soil CO_2 efflux. Because afforestation involves the establishment of forests, the reduced soil CO_2 efflux could be as a result of increased forest carbon accumulation during the new growth in boreal and tropical forests. However, the partitioning results showed that boreal heterotrophic soil CO_2 efflux was reduced after afforestation (Table 2-4), probably because of reduced microbial biomass and activity. On the other hand, afforestation in temperate forests increased total CO_2 efflux by stimulating heterotrophic soil CO_2 efflux while tropical heterotrophic soil CO_2 efflux was not affected by afforestation. This suggests that the mechanism by which afforestation affects boreal and temperate soil CO_2 efflux is by influencing the heterotrophic portion of soil CO_2 efflux while afforestation affects tropical soil CO_2 efflux by other mechanisms.

Conversion of forests to grasslands reduced boreal soil CO_2 efflux, increased tropical soil CO_2 efflux, and had no effect on temperate soil CO_2 efflux. This finding may be attributed to changes in the soil organic carbon (SOC) pool, vegetation, and metabolic activity in both boreal and tropical forests (Smith and Johnson 2004; Navarrete et al. 2016). Land degradation did not significantly alter boreal or tropical soil CO_2 efflux, which may be explained by Rey et al. (2011), who observed that degraded lands had similar temperature and precipitation to natural forests but changed the vegetation cover and other climatic conditions, leading to no immediate effect on soil CO_2 efflux in boreal and tropical forests. Conversion of forests to plantation reduced tropical soil CO_2 efflux but had no effect on temperate soil CO_2 efflux while conversion of forests to croplands had no effect on boreal, temperate, and tropical soil CO_2 efflux. These observations could also be as a result of differences in vegetative cover and a combination of other factors as described by different studies (Kellman et al. 2007; Shi et al. 2009; Wang et al. 2013).

The results revealed that land-use change mostly affected the heterotrophic portion of soil CO_2 efflux (Table 2-4), suggesting that microbial activity and biomass is affected by land-use change because of differences in environmental conditions. Due to sample size limitation, I could not make definitive conclusions about the effects of land-use changes on autotrophic soil CO_2 efflux.

Forest soil CO_2 efflux response to forest management practices

Global forest soil CO_2 efflux was reduced by harvesting and site preparation but increased by thinning (Table 2-3). The direct mechanism by which harvesting reduces global forest soil CO_2 efflux could be through decreased aboveground biomass reducing root CO_2 efflux and microbial activity but not necessarily microbial composition as species composition does not usually change. Clear-cut harvesting did not change soil CO_2 efflux in temperate and tropical forests but decreased boreal soil CO_2 efflux while partial-cut harvesting only reduced tropical soil CO_2 efflux (Fig. 2-3a). This finding is in agreement with some studies that found that harvesting causes little or no change in soil CO_2 efflux due to stabilization of soil organic matter levels (Carter et al. 2002; Strömgren et al. 2012). The inconsistencies of the effects of harvesting on forest soil CO_2 efflux could also be as a result of differences in the underlying mechanisms of boreal, temperate, and tropical forests, which cannot necessarily be accounted for by partitioning soil CO_2 efflux as there was no evidence of its effect on autotrophic or heterotrophic soil CO_2 efflux. Site preparation treatment increased temperate soil CO_2 efflux but decreased boreal soil CO_2 efflux (Fig. 2-3a). During site preparation, litter and slash may be left behind causing increased microbial activity in temperate forests (Lundmark-thelin 1997), thereby increasing heterotrophic soil CO_2 efflux while reduced soil CO_2 efflux in boreal forests may be caused by reduced heterotrophic soil CO_2 efflux from reduction in microbial biomass and activity as found in other boreal studies (Persson et al. 2017; Strömgren et al. 2017).

On the other hand, thinning had a significant effect on global forest soil CO_2 efflux (Fig. 2-3a). Increased substrate from the added litter and increased soil temperature from canopy gaps created by thinning (Concilio et al. 2005; Asaye and Zewdie 2013; Bai et al. 2017), explains the significant effect of thinning on autotrophic and heterotrophic soil CO_2 efflux (Table 2-3). Thinning has also been found to cause root mortality, also leading to an increase of heterotrophic soil CO_2 efflux from root decomposition. These findings explain the underlying mechanism by which thinning increases soil CO_2 efflux in temperate forests.

Forest soil CO_2 efflux response to natural disturbances and litter perturbations

Fire and litter removal reduced global forest soil CO_2 efflux while litter addition increased global forest soil CO_2 efflux (Table 2-3). Fires occur naturally in boreal forests and are described as stand-replacing ecosystem processes that regulate C cycle processes (Weber and Stocks 1998; Wüthrich et al. 2002; Ward et al. 2014). Although fire may cause immediate C loss during combustion (Kim and Tanaka 2003; Yue et al. 2013), this study found that it reduced boreal and temperate soil CO_2 efflux (Fig. 2-3b). Fire decreased heterotrophic and autotrophic soil CO_2 efflux (Table 2-4), suggesting that there was lower root activity, microbial activity, and biomass. This is consistent with other studies that have found decreased soil CO_2 efflux after fire due to the reduction of microbial activity in boreal forests (Parks et al. 2016; Holden et al. 2016; Hu et al. 2017). The reduced autotrophic soil CO_2 efflux could be attributed to the decreased aboveground biomass after fires in temperate and boreal forests. On the other hand, it has been found that the low severity of short-term prescribed burning may result in no changes of soil CO_2 efflux (Plaza-Álvarez et al. 2017), as observed in tropical soil CO_2 efflux. Also, differences in recovery time may generate a zero-net effect on the effect of fires on soil CO_2 efflux in this region as stand replacement occurs.

Windthrow had no effect on global and temperate forest soil CO_2 efflux but increased boreal forest soil CO_2 efflux (Fig. 2-3b). The residue from windthrow may increase the heterotrophic soil CO_2 efflux by reducing soil organic carbon stock and increasing substrate availability, stimulating microbial biomass and activity (Mayer et al. 2017) in boreal forests. However, the increased microbial activity may also be canceled out by a reduction in root biomass and activity, causing no effect on temperate soil CO_2 efflux. Litter removal and addition could be directly linked to substrate availability, which altered boreal, temperate, tropical and global forest soil CO_2 efflux (Table 2-3, Fig. 2-3b). Litter removal also leads to a reduction of soil moisture, which reduces microbial biomass and activity, thereby decreasing heterotrophic soil CO_2 efflux (Han et al. 2015). Litter addition increases carbon turnover and nutrient availability to soil microbes, increasing the heterotrophic portion of total soil CO_2 efflux (Prévost-Bouré et al. 2010; Han et al. 2015).

2.6 Implications for future studies and terrestrial carbon cycle models

Forests are productive ecosystems and can be used for climate change mitigation plans and ecosystem services, but they are highly vulnerable to climate change effects (IPCC 2013). These results provide insight into the response of soil CO_2 efflux to different disturbances at biome and global forest scales and can aid in providing recommendations for future studies and improving terrestrial C cycle models.

First, this analysis revealed that the effects of disturbances on global forest soil CO_2 efflux and soil CO_2 efflux in individual forest biomes were different. For example, elevated atmospheric CO_2 (FACE) and FACE + warming uniformly increased soil CO_2 efflux while drought uniformly had no effect on soil CO_2 efflux in temperate and tropical forests. Warming and water addition, however, had varying effects on boreal, temperate, and tropical forest soil CO_2 efflux. While land-use change appeared to have non-significant effects on global forest soil CO_2 efflux, different land-use changes had different effects on boreal, temperate, and tropical soil CO_2 efflux. Other disturbances that reduced forest soil CO_2 efflux included harvesting, site preparation, fire, and litter removal while thinning and litter addition increased forest soil CO_2 efflux. This knowledge can be used to develop mitigation plans for ecosystem-based climate change effects on soil CO_2 efflux. Second, this study shows that climate change effects are not always additive because while FACE + warming increased soil CO_2 efflux, warming + drought and warming + water addition showed no effect on soil CO_2 efflux. Therefore, including the interaction between elevated C and other disturbances in the prediction of terrestrial C cycle response to global warming will help researchers develop more accurate C cycle models. Third, studies that partitioned total soil CO_2 efflux into autotrophic and heterotrophic soil portions showed different responses to various disturbances as found in other meta-analyses (Wang et al. 2014; Liu et al. 2016a). Therefore, partitioning soil CO_2 efflux into autotrophic and heterotrophic soil CO_2 efflux is important as it allows researchers to better understand underlying mechanisms of the C cycle response to sudden changes in the environment (Heinemeyer et al. 2012; ArchMiller and Samuelson 2016; Jiang et al. 2017). However, this meta-analysis was limited by small sample sizes of autotrophic and heterotrophic soil CO_2 efflux. This study shows that more soil CO_2 efflux partitioning studies are needed to enhance our knowledge of mechanisms involved in the effects of disturbance on soil CO_2 efflux. Fourth, some studies had significant heterogeneity in soil CO_2 efflux measurement methods used suggesting that the development of standardized protocols for soil CO_2 efflux measurements across all disturbances will reduce variability between different studies. Finally, this study showed gaps in our current knowledge of disturbance effects on soil CO_2 efflux as there were some disturbances that are poorly represented in forest soil CO_2 efflux literature. For example, more studies on climate change effects in boreal and tropical forests are necessary to better understand the effects of climate change on global forests. Also, disturbance effects on tropical forest soil CO_2 efflux need to be better researched in Africa, Australia, and parts of Asia to increase the representation of soil CO_2 efflux studies in those areas and reduce uncertainty in tropical forest C cycle models.

Table 2-1 Pooled effect sizes (%), 95% confidence intervals (CIs), and study heterogeneity (Q_B) of soil CO_2 efflux to climate change across forests. Positive and negative values indicate increased and decreased soil CO_2 efflux after disturbance. The significance of effect sizes and study heterogeneity are denoted by asterisks (*** *P* < 0.001, ** *P* < 0.01, * *P* < 0.05).

Disturbance Type	**RR (%)**	**95% CI**	**Q_B (Study)**
Elevated C (51)	**27.6*****	(18.0, 28.2)	**83.7*****
Warming (46)	**18.0*****	(9.9, 22.5)	**72.4*****
Elevated C + Warming (7)	**39.5*****	(19.4, 63.5)	3.3
Drought (38)	-9.9	(-12.9, 4.9)	36.3
Water Add. (28)	**18.5*****	(12.4, 25.8)	18.9
Warming + Water Add. (3)	4.1	(-18.8, 55.5)	4.8
Warming + Drought (5)	-1.3	(-16.1, 15.4)	4.8

Table 2-2 Pooled effect sizes (%), 95% confidence intervals (CIs), and study heterogeneity (Q_B) of soil CO_2 efflux to land-use change across forests. Positive and negative values indicate increased and decreased soil CO_2 efflux after disturbance. The significance of effect sizes and study heterogeneity are denoted by asterisks (*** *P* < 0.001, ** *P* < 0.01, * *P* < 0.05).

Disturbance Type	**RR (%)**	**95% CI**	**Q_B (Study)**
Afforestation (27)	0.11	(-22.9, 13.8)	**36.5*****
Forest to Cropland (63)	-9.4	(-8.5, 17.0)	**143.8*****
Forest to Grassland (33)	-1.3	(-8.1, 23.8)	**44.2*****
Land Degradation (8)	-29.2	(-38.2, 8.7)	8.2
Forest to Plantation (19)	1.2	(-18.8, 11.6)	18.1

Table 2-3 Pooled effect sizes (%), 95% confidence intervals (CIs), and forest heterogeneity (Q_B) of soil CO_2 efflux to forest management practices, natural disturbances, and litter perturbations across forests. Positive and negative values indicate increased and decreased soil CO_2 efflux after disturbance. The significance of effect sizes and study heterogeneity are denoted by asterisks (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

Disturbance Type	**RR (%)**	**95% CI**	**Q_B (Study)**
Forest Management			
Harvest (146)	**-7.7***	(-25.4, -6.5)	**137.2*****
Site preparation (31)	**-23.7***	(-39.5, -6.3)	6.9
Thinning (27)	**22.6***	(3.0, 45.8)	**102.2*****
Natural Disturbances and Litter Perturbations			
Fire (102)	**-19.4*****	(-24.4, -11.1)	**147.2*****
Windthrow (15)	0.61	(-17.8, 16.9)	**12.1***
No Litter (45)	**-36.8*****	(-38.2, -27.5)	**39.5***
Litter Addition (31)	**31.8*****	(14.5, 37.3)	**74.8*****

Table 2-4 Pooled effect sizes (%), 95% confidence intervals (CIs), and forest heterogeneity (Q_B) of autotrophic and heterotrophic soil CO_2 efflux (F_{CO_2}) to forest disturbances. Positive and negative values indicate increased and decreased soil CO_2 efflux after disturbance respectively. The significance of effect sizes and study heterogeneity are denoted by asterisks (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).

	Autotrophic F_{CO_2}			**Heterotrophic F_{CO_2}**		
Disturbance Type	**RR (%)**	**95% CI**	**n**	**RR (%)**	**95% CI**	**n**
Afforestation	-7.5	(-43.8, 4.4)	5	**-21.9**	(-43.5, -2.8)	5
Drought	9.8	(-14.1, 40.4)	3	17.2	(-3.9, 42.1)	3
Elevated C	14.8	-	1	31.6	(-13.6, 100.6)	4
Elevated C + Warming				50.2	(-18.6, 79.2)	2
Fire	**-76.7**	(-92.0, -31.4)	5	**-20.8**	(-30.7, -9.7)	6
Harvest	14.6	(-80.6, 57.0)	6	18.1	(-6.8, 19.7)	14
Forest-to-Cropland	-40.2	-	1	6.9	(-19.2, 32.6)	3
Forest-to-Grassland	-3.1	-	1	**-46.8**	(-72.5, -6.0)	3
Forest-to-Plantation	7.4	(-5.5, 20.3)	5	**22.9**	(18.0, 28.0)	6
No Litter				-29.6	-	1
Thinning	21.0	(12.9, 31.2)	5	**32.1**	(7.6, 43.2)	7
Warming	0.1	(-15.6, 18.7)	6	**17.3**	(10.7, 24.5)	9
Warming + Drought	-1.2	-	1	28.6	-	1
Warming + Water Add.	25.1	-	1			
Water Addition	23.7	-	1			
Windthrow	-43.5	-	1	5.2	(-18.8, 106)	3

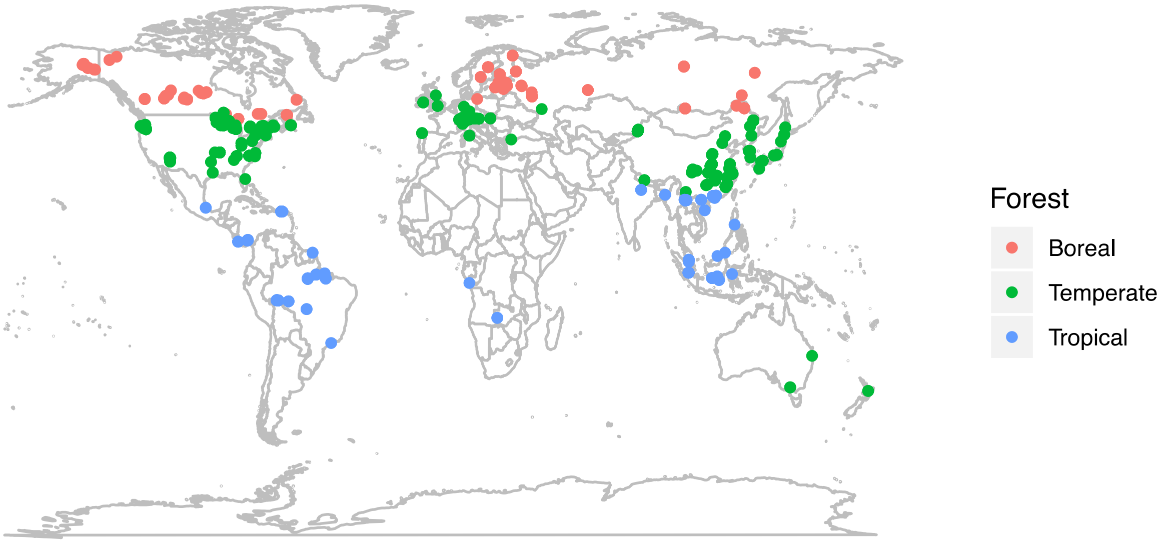

Figure 2-1 Global distribution of studies of forest disturbances on boreal, temperate, tropical and subtropical soil CO_2 efflux included in this meta-analysis.

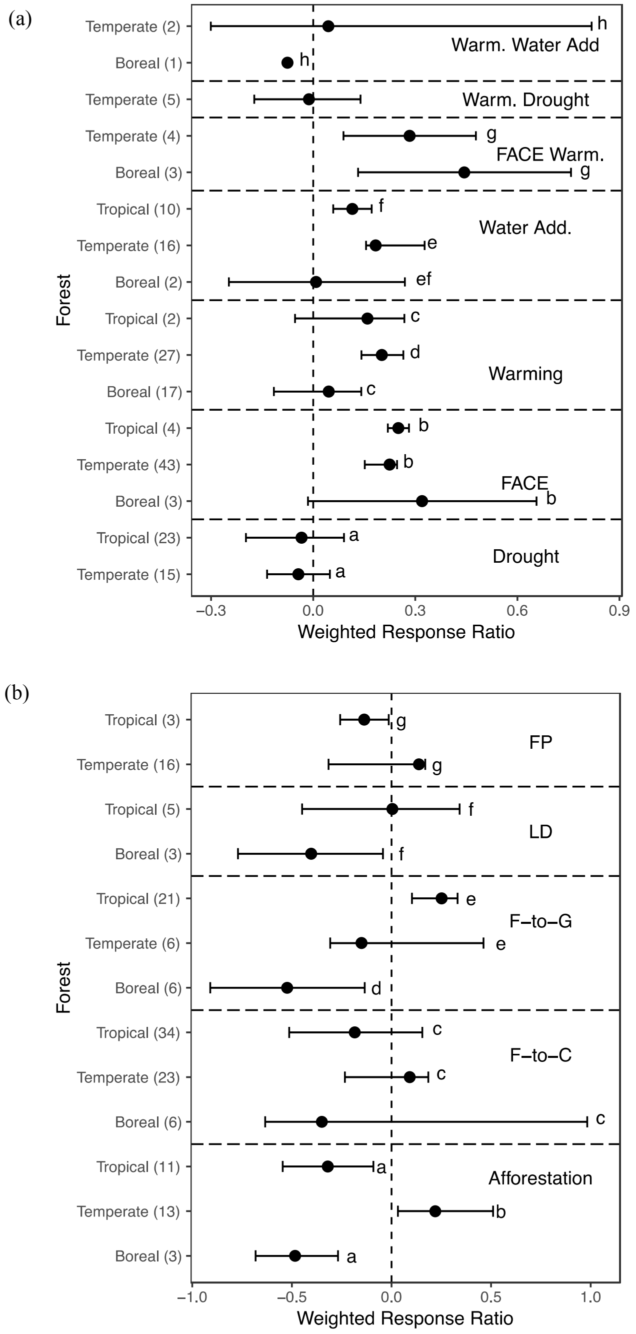

Figure 2-2 Weighted response ratio (RR_{++}) of climate change* (*a*) and land-use change* (*b*) on boreal, temperate, and tropical soil CO_2 efflux. Error bars represent 95% bootstrapped confidence intervals (CIs). The number of observations is in parentheses beside the categorical variables. Disturbance effects are considered significant if 95% CI do not overlap zero (the vertical dashed line).

*where Warm Water Add., warming + water addition; Warm Drought, warming + drought; FACE Warm., elevated CO_2 + warming; Water Add., water addition; FACE, elevated CO_2; FP, forest-to-plantation; LD, land degradation; F-to-G, forest-to-grassland; F-to-C, forest-to-cropland.

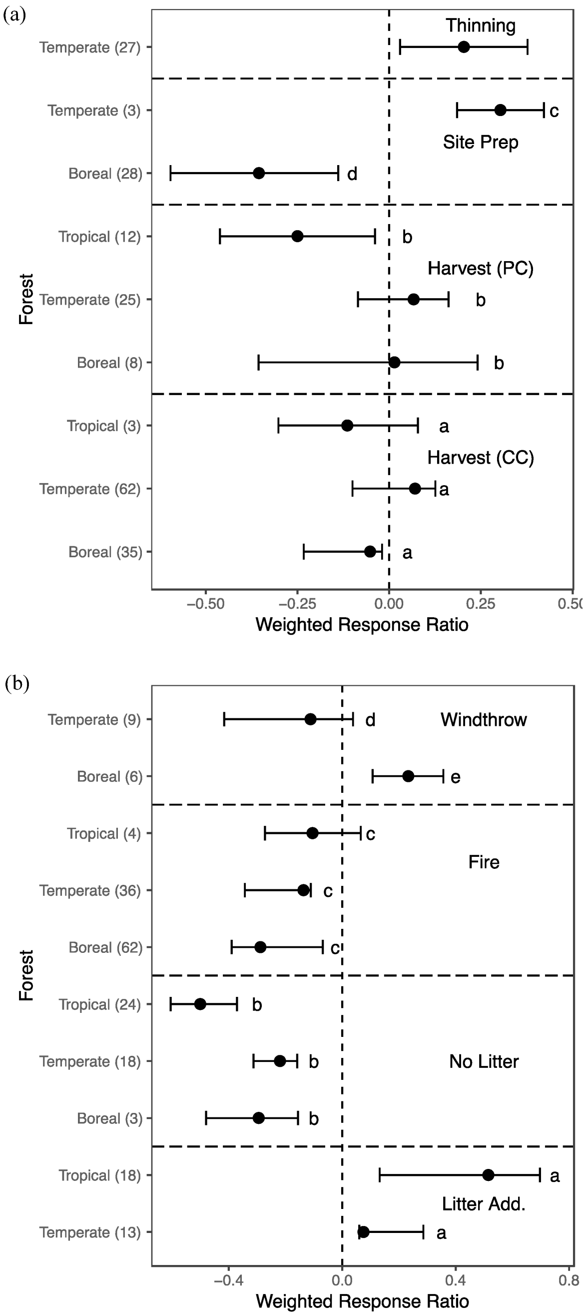

Figure 2-3 Weighted response ratio (RR_{++}) of forest management practices* (*a*) natural disturbances and litter perturbations* (*b*) on boreal, temperate, and tropical soil CO_2 efflux. Error bars represent 95% bootstrapped confidence intervals (CIs). The number of observations is in parentheses beside the categorical variables. Disturbance effects are considered significant if 95% CI do not overlap zero (the vertical dashed line).

*CC, clear-cut; PC, partial cut.

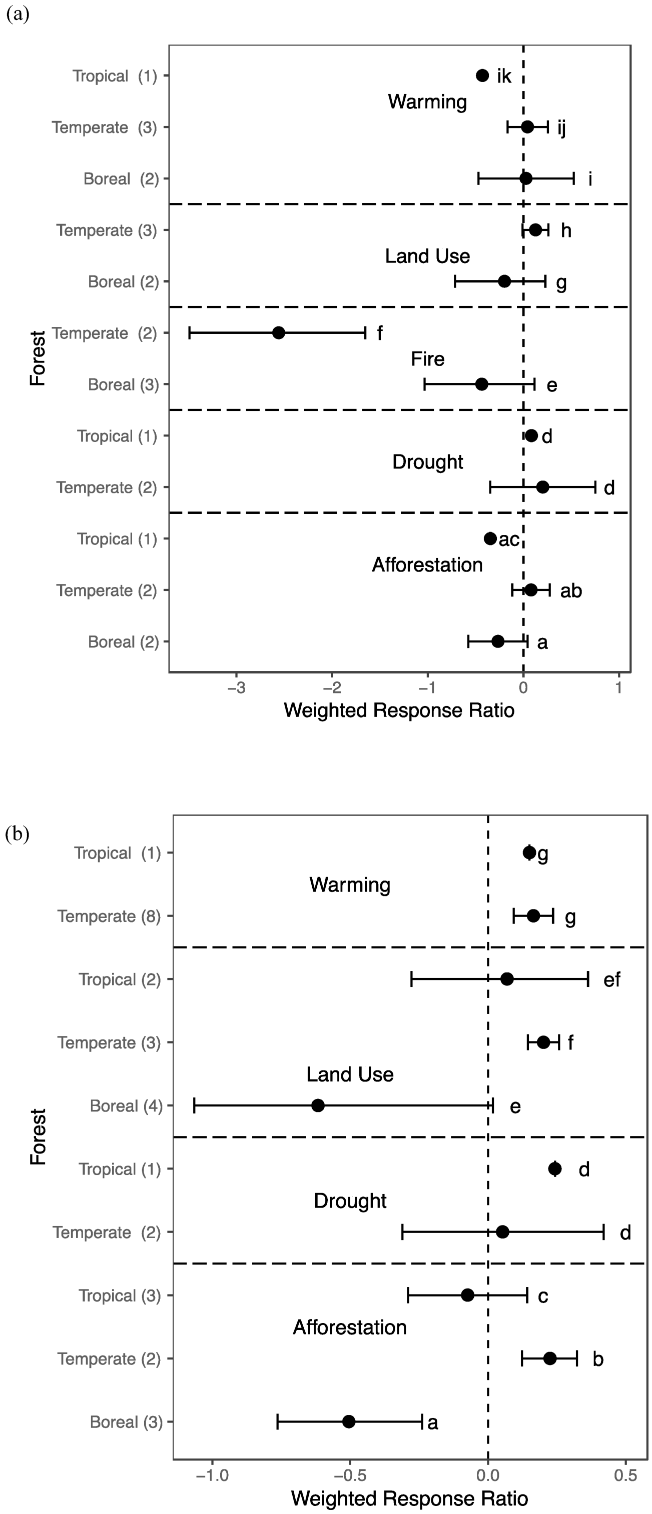

Fig.2-4 Weighted response ratio (RR_{++}) of autotrophic (*a*) and heterotrophic (*b*) soil CO_2 efflux of boreal, temperate, and tropical forests. Error bars represent 95% bootstrapped confidence intervals (CIs). The number of observations is in parentheses beside the categorical variables. Disturbance effects are considered significant if 95% CI do not overlap zero (the vertical dashed line).confidence intervals (CIs).

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2.8 Supporting Information

Appendix A1. Search Terms used in the meta-analysis for locating disturbance experiments in the Web of Science database from 1900 to June 2016

Appendix A2. Classification of Disturbance Types in the meta-analysis

Appendix A3. Site Details of the data used in our meta-analysis

Chapter 3: Spatial and temporal variation of soil CO2 efflux in a Canadian boreal mixedwood forest

3.1 Summary

Boreal mixedwood forests are productive, store large amounts of carbon in the soil, and are ecologically and economically important. They may display significant spatial and temporal variation depending on the species composition within the stand. The spatial and temporal variation of soil CO_2 efflux and other environmental variables was examined within a 1-ha boreal mixedwood forest in Alberta, Canada over three consecutive growing seasons. For the spatial analysis, soil CO_2 efflux ranged from 2.9 to 11.7 μmol CO_2 m^{-2} s^{-1} across subplots within the stand and exhibited a moderate degree of spatial variation with a spatial CV of 30%. Semi-variograms showed moderate spatial dependence of soil CO_2 efflux with a range of 8.23 m. Structural equation modelling found that soil CO_2 efflux was directly influenced by soil temperature, pH and dissolved organic nitrogen (DON) but indirectly influenced by soil moisture, basal area, distance to nearest tree, and dissolved organic carbon (DOC). Temporal variation of soil CO_2 efflux was primarily explained by an exponential relationship with soil temperature (R^2=50%) and soil moisture (R^2=19%) with a Q_{10} of 2.64. Soil CO_2 efflux was significantly higher in shrub-dominated patches than deciduous-dominated patches while coniferous and mixed patches did not significantly differ from the other patches. This study suggests that the fine-scale variation and species composition is important in determining the soil CO_2 efflux in boreal mixedwood forests.

3.2 Introduction

The boreal forest is one of the largest biomes and contributes about 4 Gt C yr^{-1} to the terrestrial carbon cycle (Allison and Treseder 2011; Moore et al. 2011; Seedre et al. 2011). Globally, the carbon storage of boreal soils is one of the largest in the world, storing between 230 and 460 Gt of carbon (Bergner et al. 2004). One of the ways by which soils emit this accumulated carbon is in the form of carbon dioxide (CO_2) through the process of soil CO_2 efflux (Raich and Schlesinger 1992). Boreal forest soil CO_2 efflux is particularly important because of its ability to release the large amount of stored carbon under global warming scenarios (Allison and Treseder 2008; Bergeron and Fenton 2012).

Canada has the second highest area of boreal forests after Russia, with over 50% of the country falling within the boreal region (Bergeron and Fenton 2012). The amount of carbon sequestered in Canadian boreal soils has been estimated to be between 65 and 104 Gt of carbon (Pypker and Fredeen 2003). Climate change may increase the rate of Canadian boreal soil CO_2 efflux by altering the frequency and intensity of extreme events (Williamson et al. 2009) and further increasing the concentration of atmospheric CO_2, thereby causing more global warming. Fires typically occur in Canadian boreal forests, causing an immediate increase in carbon emission rates and generating postfire stands that may be dominated by a single species (Amiro et al. 2009). Therefore, most boreal soil CO_2 efflux studies have been carried out in these pure stands such as aspen and black spruce forests (Swanson and Flanagan 2001; Bergeron et al. 2007; Das Gupta and Mackenzie 2016). Mixedwood forests, which are forests that have a combination of single species within the forest, also occupy a large percentage of the Canadian boreal area but are not extensively represented in soil CO_2 efflux literature (Khomik et al. 2006; Strukelj et al. 2015). The mixture of deciduous and coniferous species in boreal forests has been found to increase fine root productivity, causing a possible increase in autotrophic soil CO_2 efflux

(Brassard et al. 2011; Laganière et al. 2012). It has been suggested that mixedwood forests have higher productivity and larger amounts of soil organic matter than either deciduous or coniferous-dominated forests (McCaughey et al. 2006; Laganière et al. 2012). Therefore, a better understanding of the effects of tree species composition on boreal mixedwood soil CO_2 efflux would improve the ability of researchers to develop more accurate models of the boreal carbon cycle.

Several environmental factors contribute to the high spatial and temporal variation of soil CO_2 efflux observed in literature (Søe and Buchmann 2005; Saigusa et al. 2008; Qi et al. 2010; Dore et al. 2014; Das Gupta and Mackenzie 2016). The primary controls of variation in forest soil CO_2 efflux have been identified as soil temperature and moisture. Warmer temperatures cause increased soil CO_2 efflux during summer while colder temperatures reduce soil CO_2 efflux in the extreme winters of boreal forests (Du et al. 2013). Because the rate at which soils warm is slower than air, air temperature is not as influential as soil temperature on soil CO_2 efflux (Czimczik et al. 2006). It has also been found that boreal soil CO_2 efflux is more affected by soil temperature than soil moisture as the forests are not moisture-limited (Khomik et al. 2006; Li et al. 2008; Laganière et al. 2012). When soil moisture does not directly affect soil CO_2 efflux, it could confound the effect of soil temperature on soil CO_2 efflux (Davidson et al. 1998; Khomik et al. 2006, 2010). Therefore, the effect of soil temperature and moisture on the spatial and temporal variation of boreal mixedwood soil CO_2 efflux can be used to determine the response of F_{CO_2} to changing climatic conditions.

Other environmental factors such as dissolved organic carbon (DOC) and nitrogen (DON) also drive soil CO_2 efflux and sites with high C/N ratio are associated with lower soil CO_2 efflux (Qi et al. 2010; Shi and Jin 2016). Stand structure and species distribution may also contribute to the spatial variation of soil CO_2 efflux because they affect the forest floor, leaf litter and phenology, which could also cause changes in the heterotrophic (microbial) and autotrophic (root) components of soil CO_2 efflux (Russell and Voroney 1998; Maestre and Cortina 2003; Singh et al. 2008; Bréchet et al. 2009; Shi and Jin 2016). When different species occur together in forests, they may add a layer of complexity to the existing spatial variation of soil CO_2 efflux because species influence the microenvironment around them. The underlying mechanisms of mixedwood soil CO_2 efflux may be complicated by different growth and photosynthetic rates of deciduous and coniferous tree species. Therefore, understanding the relationship between environmental factors and the fine-scale spatial variation of mixedwood soil CO_2 efflux can give better estimations of the regional carbon budget.

Previous mixedwood soil CO_2 efflux studies are primarily focused in eastern Canada (Khomik et al. 2006; McCaughey et al. 2006; Laganière et al. 2012) but this study attempts to quantify the spatial and temporal variability of boreal mixedwood soil CO_2 efflux in western Canada. The overall objectives of this study were to: (1) assess the spatial variation of soil CO_2 efflux in a 1-ha boreal mixedwood forest, (2) analyze the effects of environmental factors and tree species composition on the spatial variation of boreal mixedwood soil CO_2 efflux, (3) determine the influence of soil temperature and moisture on the seasonal variability of soil CO_2 efflux, and (4) estimate the sampling intensity required to provide a reliable prediction of soil CO_2 efflux at a local scale.

3.3 Materials and Methods

3.3.1 Study site

The study site is a one-hectare boreal mixedwood plot located within the George Lake Research Site (53°57'N, 114°06'W), approximately one-hour northwest of

Edmonton, Alberta in Canada. This site is located in the dry mixedwood sub-region of the Boreal Forest natural region and is characterized by a short, warm summer and a cold, long winter (Downing and Pettapiece 2006). The climate is boreal with a 30-year average minimum temperature in January of -15.5°C and maximum daily temperature in July of 22.8°C. Mean annual precipitation was 492 mm with 338.2 mm falling as rain during the growing season (May to September). The soil in this study area is well-drained Orthic Gray Luvisol, moderately fine textured, ranging from sand clay loam to silt clay loam. The site contains 11 tree species and is mainly dominated by a mixture of White Spruce (*Picea glauca*), Aspen (*Populus tremuloides*), Birch (*Betula sp.*), Balsam Poplar (*Populus balsamifera*) and Beaked Willow (*Salix bebbiana*) representing about 98.7% of the total basal area. Trees with at least 1 cm DBH were inventoried and mapped within the plot, and the total stand density is 4317 trees ha^{-1}.

3.3.2 Data collection

The 1-ha site was divided into 25 subplots measuring 20×20 m each. Within each subplot, a random point was chosen as the original starting point (O) and two other points were located at 2 m and 5 m away from the original point in a straight line. In total, 75 points were located within the hectare (Fig. 3-1). Soil flux measurements were taken at each point twice per month from July to September in 2012 and June to September of 2013 and 2014 between the hours of 9.00 a.m. and 4.00 p.m. PVC soil CO_2 efflux collars with a height of 7cm were inserted 3 cm into the soil one week before measurement to avoid unstable CO_2 fluxes and minimize disturbance during readings. The soil CO_2 efflux was measured using the LI-8100A automated soil CO_2 flux system with 20-cm survey chamber attachments (LI-COR Inc., Lincoln, NE, USA). However, to avoid agitation of the soil layer and because they have been found not to impact soil CO_2 efflux within mixedwood stands significantly (Laganière et al. 2012), mosses were not cleared within the soil collars. Every soil CO_2 efflux measurement was taken for 90 seconds on days without rain to minimize measurement error with a dead band of 30 seconds. Three measurements were taken at each point and CO_2 efflux was determined using exponential functions.

Soil temperature and soil volumetric water content was measured near the soil CO_2 efflux collar at 10 cm depth using the Omega soil temperature probe and the auxiliary ECH2O model EC-10 soil moisture probe (Decagon Devices, Inc., Pullman, WA) respectively. The distance and DBH of trees within 5 m of the soil collar were recorded during the measurement period. Soil samples were collected from the top layer (0-15 cm soil depth) from each point in 2013 and 2014 and transported to the laboratory. The samples were air-dried and passed through a 2-mm sieve. Soil pH was measured with a 1:10 soil-water ratio. The solution was shaken for 30 minutes and pH was measured with an Orion benchtop pH meter (Thermo Orion, Beverly, MA). Dissolved organic N (DON) and C (DOC) were measured using a Shimadzu TOC-V/TN analyzer (Shimadzu Corp. Kyoto, Japan).

3.3.3 Statistical analyses

Soil CO_2 efflux, soil temperature, and soil moisture data were averaged by time and subplot for statistical analysis. Data were tested for normality using the Shapiro-Wilk's test and were log-transformed when necessary before statistical analyses. Geostatistical analyses were used to analyze spatial variation and to identify the scale of spatial autocorrelation in soil CO_2 efflux, temperature, and moisture (Song et al. 2013; Wu et al. 2015). Semivariance ($\gamma(h)$) was calculated using Eq. (1):

$$\gamma(h) = \frac{1}{2N} \sum_{i=1}^{N(h)} [y(i) - y(i+h)]^2 \quad (1)$$

where $y(i)$ is the value of y at point i, $y(i+h)$ is the value at a distance of h away from point i and $N(h)$ is the number of pairs of observations separated by distance h (Rochette et al. 1991). Semivariance grows with distance and explains the relationship between different points as points closer to each other are more related than points further apart (Søe and Buchmann 2005). The empirical variogram was fitted using linear, spherical, Gaussian, and exponential models and the best model was determined using the R^2 value which was then used in the kriging interpolation. The nugget (C_0), the sill (C_0+C) and the range (a) of a variogram were calculated to characterize the spatial heterogeneity of the variables in this dataset. The degree of spatial dependence is calculated by the proportion of the structural variance (C) to the sill (C_0+C). Weak spatial dependence is represented by values less than 0.25, moderate spatial dependence values fall within 0.25 and 0.75, while values greater than 0.75 show strong spatial dependence. Outliers were removed before analysis and ordinary block kriging was used to produce kriged maps.

I constructed a structural equation model (SEM) to quantify the direct and indirect effects of environmental factors on the spatial variation of soil CO_2 efflux using correlations. The number of sampling points (n) required for estimating mean soil CO_2 efflux within 10% and 20% of the actual value at the 95% probability level was calculated using Eq. (2) (Yim et al. 2003; Ohashi and Gyokusen 2007):

$$n = {t_\alpha^2 s^2}/{E^2} \quad (2)$$

where t_α is Student's t-value with the degrees of freedom at the probability level of α, s is the standard deviation and E is the error limit.

To assess the temporal variability in soil CO_2 efflux, temperature, and moisture during the growing season (months and years), I conducted repeated-measures ANOVA with Tukey multiple comparisons (HSD) test and coefficient of variation (CV). CV values above 100% signify high variability, values between 10% and 100% signify moderate variability and values below 10% signify low variability (Hu et al. 2016). The relationship between soil CO_2 efflux and soil temperature was fitted using the exponential Eq. (3) (Tang et al. 2006; Deng et al. 2013).

$$F_{CO_2} = ae^{b(T-10)} \quad (3)$$

where F_{CO_2} is the soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}), T (°C) is the soil temperature at 5-cm depth and a (also F_{CO_2} at 10°C), b, c, and d are the fitted parameters in the regression equation. Using b from Eq. (2), Q_{10} (temperature sensitivity of soil CO_2 efflux) was calculated for each year with the equation: $Q_{10} = e^{10b}$, where Q_{10} is the temperature sensitivity. All statistical analyses were conducted using the R program (R Core Team 2018) and 'gstat' package (Graeler et al. 2016) was used for geostatistical analyses.

3.4 Results

3.4.1 Spatial variation of F_{CO_2}

The mean growing season F_{CO_2} averaged between 5.00 and 5.75 μmol CO_2 m^{-2} s^{-1} over the three growing seasons in this study (Table 3-1). Soil CO_2 efflux showed significant spatial autocorrelation across the different years with an average range of 8.23 m and CV value of 30% (Table 3-2). Soil CO_2 efflux exhibited moderate spatial variability with CVs ranging from a minimum of 31.0% in August 2012 to a maximum of 49.3% in September 2013 (data not shown). The spatial dependence of soil CO_2 efflux, as determined by the variograms, ranged from moderate to strong spatial dependence in the three growing seasons (Table 3-2). The range of autocorrelation in soil CO_2 efflux, as found by spherical and exponential models, varied from 6.41 to 12.15m in the growing seasons. Kriged results also revealed how the patterns of F_{CO_2} changed from 2012 to 2014 (Fig. 3-2) showing both spatial and temporal variation in this study.

3.4.2 Factors affecting spatial variability of F_{CO_2}

Small CV values of soil temperature (5.63 to 5.89%) in the three growing seasons indicated that soil temperature exhibited low spatial variability while soil moisture exhibited moderate spatial variability with CV values between 27.6 and 38.5% (Table 3-2). Overall, soil temperature showed weak spatial dependence with a range of 16m and correlated with the spatial variation of soil CO_2 efflux (R^2=0.079, p=0.015). Soil moisture also showed weak spatial dependence and no correlation with the spatial variation of soil CO_2 efflux. Therefore, the effects of individual environmental variables on spatial variation in soil CO_2 efflux were explored and I found pH, dissolved organic nitrogen (DON) and CN ratio also significantly affected the spatial variation in F_{CO_2} (Table 3-3).

The results of SEM analysis indicated that pH, soil temperature, and DON directly controlled soil CO_2 efflux (Fig. 3-3). Soil moisture indirectly affected soil CO_2 efflux via soil temperature, which basal area (BA), DOC, and distance to nearest tree (DT) indirectly influenced soil CO_2 efflux via DON. Type 1 errors were minimized by using an alpha level of 0.05 to determine which variables significantly affected soil CO_2 efflux, both directly and indirectly. Estimated number of soil CO_2 efflux sampling points at 10% error limit at 95% probability were 36, 43 and 56 and with 20% error margin at 95% probability, the sampling points were 9, 11 and 14 in 2012, 2013 and 2014 respectively (Table 3-1). These findings, therefore, show that by sampling 75 points within the hectare, I was able to minimize type II error in the analysis.

3.4.3 Factors controlling temporal variation of soil CO_2 efflux

Using subplots as a random factor, linear mixed-model with repeated-measures ANOVA showed that soil CO_2 efflux varied significantly among months and individual measurement points (F=47.75, $P<0.001$) but not among the different years. Soil CO_2 efflux peaked in July 2012, July 2013 and August 2014 with average values ranging from 6.25 to 6.78 μmol CO_2 m^{-2} s^{-1}. The lowest average monthly soil CO_2 efflux was in September 2012, September 2013 and June 2014 with values between 3.93 and 4.75 μmol CO_2 m^{-2} s^{-1}. The highest temporal CV value of soil CO_2 efflux of 27.1% occurred in 2014 and the lowest temporal CV value of 21.2% was in 2013.

Soil CO_2 efflux had a significant exponential relationship with soil temperature (R^2 =0.53, $P<0.001$) (Fig. 3-2). Q_{10} values derived from Eq. (2) ranged from 2.16 to 2.90 over the three growing seasons (Table 3-2). Linear regression results showed that soil moisture explained a small yet significant part of the temporal variation in the overall soil CO_2 efflux (R^2=0.19, P=0.002), but the effect of soil moisture on soil CO_2 efflux for individual years were either non-significant (2012 and 2014) or marginally significant (2013, R^2=0.22, P=0.04). The multiple linear regression of soil temperature and moisture explained 62.5% of the temporal variation of the overall soil CO_2 efflux ($P<0.001$).

3.4.4 Tree species composition and soil CO_2 efflux

The study plot was composed of patches (i.e., the 20×20 m subplots) dominated by coniferous, deciduous, shrubs and mixed coniferous and deciduous tree species. I found that species composition had no significant relationship with soil moisture but had significant associations with soil CO_2 efflux and temperature (Fig. 3-5). Shrub-dominated stands exhibited significantly higher soil CO_2 efflux than deciduous-dominated patches and soil temperature was significantly higher in shrub-dominated patches than coniferous- and deciduous-dominated patches. Soil moisture did not significantly differ among different patches within the study site.

3.5 Discussion

Spatial variation of soil CO_2 efflux

The average soil CO_2 efflux of 5.37 μmol CO_2 m^{-2} s^{-1} reported in this study (Table 3-1) is similar to the average F_{CO_2} rate of 5.29 μmol CO_2 m^{-2} s^{-1} reported by Laganière et al. (2012) and falls within the ranges of other Canadian boreal mixedwood forest soil CO_2 efflux reported in literature (Mallik and Hu 1997; Khomik et al. 2006). I detected moderate spatial variability and significant autocorrelation with ranges of 8.23m in total soil CO_2 efflux (Table 3-2). The spatial variability observed in this study was expected as moderate spatial variation in boreal soil CO_2 efflux has been attributed to the relationship between F_{CO_2} and environmental factors, (Russell and Voroney 1998; Das Gupta and Mackenzie 2016). Khomik et al. (2006) found that the degree of spatial variation in soil CO_2 efflux varied over temporal scales and increased gradually during the growing season because of changes in microbial activity. This study corroborates this finding as spatial variation peaked in the middle of the growing season and dropped at the end of the sampling period probably due to smaller differences in photosynthetic rates with cooler temperatures. This pattern of spatial variation can also be explained by the effects of species composition on soil CO_2 efflux. Individual tree species such as spruce and aspen have been found to affect soil CO_2 efflux components differentially by influencing the soil temperature, light penetrating the canopy, understory vegetation, nutrient availability, and organic matter (Khomik et al. 2006; Laganière et al. 2012). Therefore, the spatial variation of total soil CO_2 efflux in this study may be dependent on the distribution of tree species with the boreal mixedwood forest due to the changes in aboveground processes.

Overall, soil temperature and moisture showed little spatial variation and weak spatial dependence, initially suggesting that other factors may be responsible for the moderate spatial dependence found in soil CO_2 efflux (Table 3-2). In contrast, results of the structural equation modeling (SEM) showed that soil temperature significantly affected the spatial variation of soil CO_2 efflux and soil moisture indirectly influenced soil CO_2 efflux via soil temperature. This confounding relationship between soil temperature and soil moisture was documented in a study by Davidson et al. (1998) where they found that soil moisture and temperature covaried and had a confounding effect on the spatial variability of Q_{10} within a temperate mixed hardwood forest. This study, therefore, suggests that soil moisture indirectly influences soil CO_2 efflux via soil temperature on the spatial variation of F_{CO_2} in this boreal mixedwood forest.

The interaction of soil temperature and moisture with other environmental factors influenced F_{CO_2} as was seen in the SEM diagram (Fig. 3-3), which could better explain the source of spatial variation. pH and DON were found to directly influence soil CO_2 efflux factors, suggesting that environmental chemistry also determined the spatial variation of F_{CO_2}. DOC, basal area and distance to nearest tree indirectly affected soil CO_2 efflux through DON. These results are supported by previous studies, which found that forest floor characteristics and understory vegetation could be determinants of the spatial heterogeneity in boreal soil CO_2 efflux (Lavoie and Mack 2012; Das Gupta and Mackenzie 2016). Luo & Zhou (2006) also found that when pH is less than 7, soil CO_2 efflux increases with increasing pH, as found in this study. The significant effect of DON on soil CO_2 efflux found in this study was supported by Janssens et al. (2010), who identified boreal forests as severely nitrogen-limited environments, and as such, nitrogen addition increases microbial activity and leaf photosynthesis. The environmental drivers of F_{CO_2} indicate that soil chemistry influences the spatial variation of soil CO_2 efflux by interacting with microbial activity in the soil and associations with root CO_2 efflux, and therefore, heterotrophic soil CO_2 efflux in this boreal mixedwood forest.

Temporal variation in soil CO_2 efflux

The lowest soil CO_2 efflux occurred in September and June when soil temperatures dropped and peaked in July and August, reflecting changes in the temporal patterns of soil temperature. This temporal pattern is consistent with observations in Albertan boreal forests because most studies have observed that the highest soil CO_2 efflux occurred between July and August (Saurette et al. 2006; Arevalo et al. 2010; Chang et al. 2016). These results suggest that boreal soil CO_2 efflux might be affected by the phenology of tree species and other forest processes. For example, photosynthesis has been found to reach optimum conditions at air temperatures between 15 and 30°C (Högberg et al. 2001; Khomik et al. 2006), which occurs in the middle of the growing season in boreal forests, and could potentially increase total soil CO_2 efflux. The increased temperature during the warmer season may also increase soil CO_2 efflux by stimulating microbial activity. These changes in plant and microbial activity may increase the rates of soil CO_2 efflux by increasing heterotrophic and autotrophic soil CO_2 efflux.

Previous soil CO_2 efflux studies have found that temperature significantly affects the temporal variation of boreal soil CO_2 efflux (Rustad and Fernandez 1998; Scott-Denton et al. 2003; Griffis et al. 2004; Khomik et al. 2006; Saurette et al. 2006; Wang et al. 2011a) and this study reinforced these findings by showing that a large portion of the temporal variation (Fig. 3-4a) in soil CO_2 efflux can be explained by soil temperature. The exponential relationship between soil temperature and F_{CO_2} (Table 3-4) is also consistent with other boreal studies (Mallik and Hu 1997; Khomik et al. 2006; Saurette et al. 2006; Laganière et al. 2012). The Q_{10} values of this study varied between 2.16 and 2.90 (Table 3-4) which is similar to the average accepted global value of 2.5 reported in the literature (Saurette et al. 2006; Kellman et al. 2007) and some boreal studies (Rayment and Jarvis 2000; Laganière et al. 2012). In comparison to other single species boreal studies (Russell and Voroney 1998; Morén and Lindroth 2000; Griffis et al. 2004; Khomik et al. 2006) and the boreal mixedwood forest study by Khomik et al. (2006), the Q_{10} in this study is lower suggesting that the site may be more resilient to temperature changes than the other study sites. However, Khomik et al. (2006) found that differences in Q_{10} values across boreal forests could be as a result of factors such as measurement period (growing season vs. annual). Curiel Yuste et al. (2004)found that while seasonal Q_{10} is mainly temperature dependent, the values may be confounded by differences in phenology, which could cause changes in Q_{10} values across different boreal forests. Therefore, increased soil CO_2 efflux studies in boreal mixedwood forests during growing seasons could enable more accurate estimations of the temperature sensitivity of boreal soil CO_2 efflux under global warming scenarios.

Soil moisture has been identified as another primary control of temporal variation in soil CO_2 efflux (Lloyd and Taylor 1994; Davidson et al. 2004; Søe and Buchmann 2005; Li et al. 2008). In this study, soil moisture also explained part of the temporal variation in soil CO_2 efflux over the sampling period (Fig. 3-4b) and these results are consistent with the findings of Moroni et al. (2009) and Kelsey et al. (2012), who found that soil moisture plays a minor role in determining the temporal pattern of boreal soil CO_2 efflux. When combined with soil temperature, soil moisture helped to explain the majority of the temporal variation of soil CO_2 efflux, leading to the conclusion that these are the main drivers of temporal patterns in F_{CO_2} within the boreal mixedwood study area.

The number of sample points required to estimate soil CO_2 efflux in this study ranged from 35 to 56 sample points within the 10% error limit at the 95% probability level (Table 3-1). Davidson et al. (2002) estimated the number of measurement points in a temperate mixed hardwood forest was 41 while Adachi et al. (2005) reported values between 67 and 85 measurement points in tropical forests at the same error limit and confidence level. These findings suggest that the estimated number of sampling points in the boreal mixedwood forest is similar to temperate mixed hardwood forests and the sampling effort of this study was adequate in estimating within 10% of the mean soil CO_2 efflux. This result demonstrates that researchers need to assess fine-scale spatial variation to give reliable estimates of boreal mixedwood carbon emissions from the soil.

Effects of tree species composition and soil CO_2 efflux

Previous studies (Bauhus et al. 1998; Stoyan et al. 2000; Wang et al. 2011b; Prescott and Vesterdal 2013) have observed that species composition influences microbial activity, root biomass and stand structure, which in turn affects soil CO_2 efflux components. Consistent with these findings, Laganière et al. (2012) carried out a direct comparison of black spruce, aspen and mixedwood forests in Quebec to determine the effects of forest composition on soil CO_2 efflux and found that mixedwood stands emit more CO_2 than pure stands via the heterotrophic component. Their finding suggests that the combination of species within a single forest has higher F_{CO_2} in comparison to stands dominated by single-species in the boreal forest. However, this study focused on the effects of species composition on the variation of soil CO_2 efflux within the mixedwood forest stand, and found that certain species combination increased the soil CO_2 efflux in some patches, creating hotspots in the study area (Fig. 3-2). The results indicated that there was no significant difference between patches dominated by single species, either coniferous or deciduous stands, and mixed patches. This finding is in contrast to the findings of Laganière et al. (2012), suggesting that while boreal trees have been found to affect the understory plant community and the associated microenvironment, there is no distinct difference in soil CO_2 efflux in deciduous, coniferous, and mixed patches within this mixedwood forest. However, patches dominated by shrubs significantly emitted more CO_2 than deciduous-dominated patches but not coniferous or mixed patches. Shrubs have been found to immobilize large amounts of nutrients in boreal mixedwood forests during the growing season (Chávez and Macdonald 2010). Nutrient availability can increase microbial activity and heterotrophic soil CO_2 efflux, suggesting that this is the underlying mechanism for the differences in soil CO_2 efflux between shrubs and deciduous-dominated patches. These results show that understanding the soil CO_2 efflux according to species composition within mixedwood forests is important in understanding fine-scale spatial variation of boreal soil CO_2 efflux.

3.6 Conclusion

Soil CO_2 efflux is important in boreal mixedwood forests because they have high productivity and large soil carbon storage, making this forest vulnerable to changes in environmental conditions as a result of global warming. The goal of this study was to quantify the spatial and temporal variation of soil CO_2 efflux in a boreal mixedwood forest over three growing seasons. There was significant moderate spatial variability of soil CO_2 efflux with spatial autocorrelation ranges up to 12.15m. Kriging results showed that the spatial variation of soil CO_2 efflux varied between 2012 and 2014 growing seasons. Through SEM, I found that soil temperature, pH and DON directly affected the spatial variation of soil CO_2 efflux while soil moisture, basal area, DOC, and distance to nearest tree indirectly influenced soil CO_2 efflux via soil temperature and DON. The temporal variation of soil CO_2 efflux was primarily regulated by soil temperature and peaked between July and August. The Q_{10} value was 2.64 and is slightly below the average values reported in the boreal literature and the Q_{10} values reported in pure stands, showing that the boreal mixedwood stand in this study may be more resilient to sudden changes in temperature. Soil moisture partly influenced the temporal variation of soil CO_2 efflux, and when combined with soil temperature, it explained more of the temporal variation in this study. I was able to determine that the number of sampling points required to estimate the mean soil CO_2 efflux within 10% error limit ranged between 36-56 in a typical boreal mixedwood stand. Shrub-dominated patches emitted more CO_2 than deciduous-dominated patches, also showing that understanding the effects species composition on soil CO_2 efflux is important in explaining spatial variation within boreal mixedwood forests. This study highlights the importance of studying boreal mixedwood forests at fine scales to improve our current knowledge of the boreal carbon cycle and its sensitivity to changing temperatures. This study also showed that accounting for the composition of tree species within stands may be instrumental in modeling the soil CO_2 efflux of boreal mixedwood forests.

Table 3-1 Growing season mean and relative standard error (RSE) of soil CO_2 efflux (F_{CO_2}, μmol CO_2 $m^{-2}s^{-1}$), soil temperature (ST, °C), soil moisture (SM, m^3m^{-3}) and required sample size for estimating soil CO_2 efflux at 95% probability level within ±10% and ±20% of the sample mean.

Year	Mean F_{CO_2} (±RSE)	ST (±SE)	VWC (±SE)	Required sample size to estimate soil CO_2 efflux	
				±10%	±20%
2012	5.42 (2.40)	12.45 (0.11)	0.253 (0.006)	36	9
2013	5.75 (2.09)	12.47 (0.09)	0.319 (0.006)	55	14
2014	5.00 (2.00)	11.83 (0.10)	0.203 (0.004)	56	14
Overall	5.37 (1.30)	12.21 (0.06)	0.256 (0.003)	35	9

Table 3-2 Fitted semivariogram parameters for 2012, 2013, 2014 and overall soil CO_2 efflux (F_{CO_2}), soil temperature (ST) and soil moisture (SM).

Year	Var.	Model	Nugget (C_o)	Sill (C_o+C)	Spatial Dep.	Range (m)	CV (%)	R^2
2012	R_s	Spherical	0.017	0.042	0.40	6.41	30.03	0.171
	ST	Spherical	0.00088	0.0022	0.40	28.00	5.69	0.834
	SM	Spherical	0.027	0.077	0.35	10.83	28.50	0.834
2013	R_s	Exponential	0.049	0.065	0.75	12.15	32.82	0.162
	ST	Gaussian	0.00036	0.0032	0.11	12.17	5.63	0.930
	SM	Spherical	0.017	0.046	0.37	13.00	27.56	0.818
2014	R_s	Spherical	0.044	0.070	0.63	7.80	37.46	0.560
	ST	Gaussian	0.00066	0.0028	0.24	12.01	5.98	0.973
	SM	Spherical	0.015	0.094	0.16	17.30	38.48	0.878
Overall	R_s	Spherical	0.015	0.061	0.25	8.23	29.67	0.604
	ST	Gaussian	0.00043	0.0025	0.17	15.92	4.91	0.894
	SM	Spherical	0.011	0.054	0.20	11.26	28.48	0.728

Table 3-3 Descriptive statistics and regression coefficient (R^2) between soil parameters and soil CO_2 efflux (F_{CO_2}). Boldfaces indicate significance at the $\alpha = 0.05$ level.

Variable[a]	Mean	Range	R^2	P
Soil chemical and physical properties				
pH	4.71	3.40-7.29	**0.071**	0.012
DON	0.49	0.09–1.03	**0.077**	0.016
DOC	1.32	0.08–12.22	0.010	0.393
CNR	2.93	0.61–14.29	**0.052**	0.049
Subplot Structure				
BA (cm^2)	3289.13	37.8 – 14695.9	0.016	0.281
NNeigh	30.72	3 - 94	0.001	0.532
DT (m)	1.49	0.25 – 4.18	0.000	0.964
Mean DBH	9.39	2.64 – 35.97	0.003	0.625
Max DBH	31.00	6 - 55	0.039	0.088

[a] DOC, dissolved organic carbon; DON, dissolved organic nitrogen; BA, basal area of within 5m radius; NNeigh, number of nearest neighbors within 5m radius; DT, distance of nearest tree; Mean DBH, mean diameter at breast height; Max DBH, maximum diameter at breast height; CNR, dissolved carbon-to-nitrogen ratio.

Table 3-4 Equation parameters of the exponential model $F_{CO_2} = ae^{b(T-10)}$, where R is the soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}), a is the soil CO_2 efflux rate at 10°C, *b* is the change of R with one-unit change of T, which is the soil temperature (°C). The regression coefficient (R^2) and Q_{10} (temperature sensitivity) calculated from Eqn. 1. All models were significant at $P < 0.05$.

Year	*a*	*b*	R^2	Q_{10}
2012	4.08 ± 0.37	0.1040 ± 0.0248	0.52	2.83
2013	4.65 ± 0.36	0.0771 ± 0.0236	0.37	2.16
2014	3.95 ± 0.23	0.1064 ± 0.0170	0.75	2.90
Overall	4.22 ± 0.18	0.0972 ± 0.0125	0.53	2.64

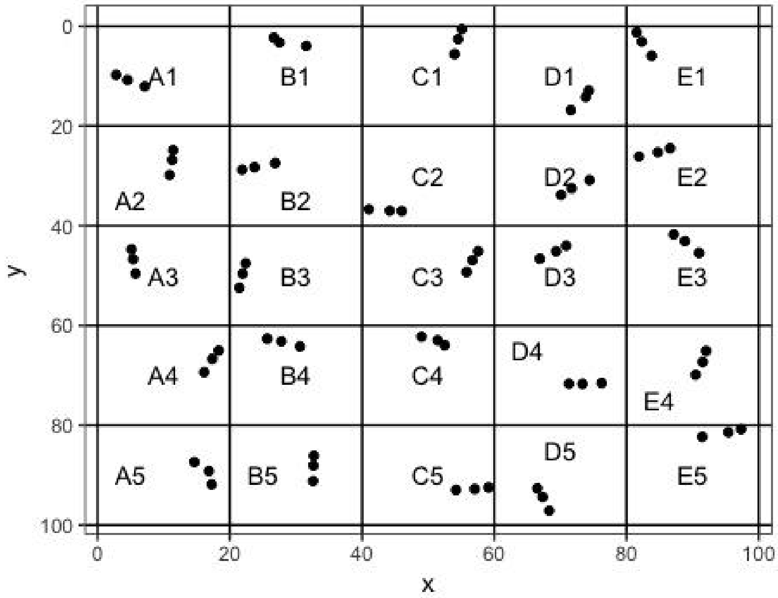


Figure 3-1 Sampling distribution of points and subplots within the 1-ha George Lake boreal mixedwood plot.

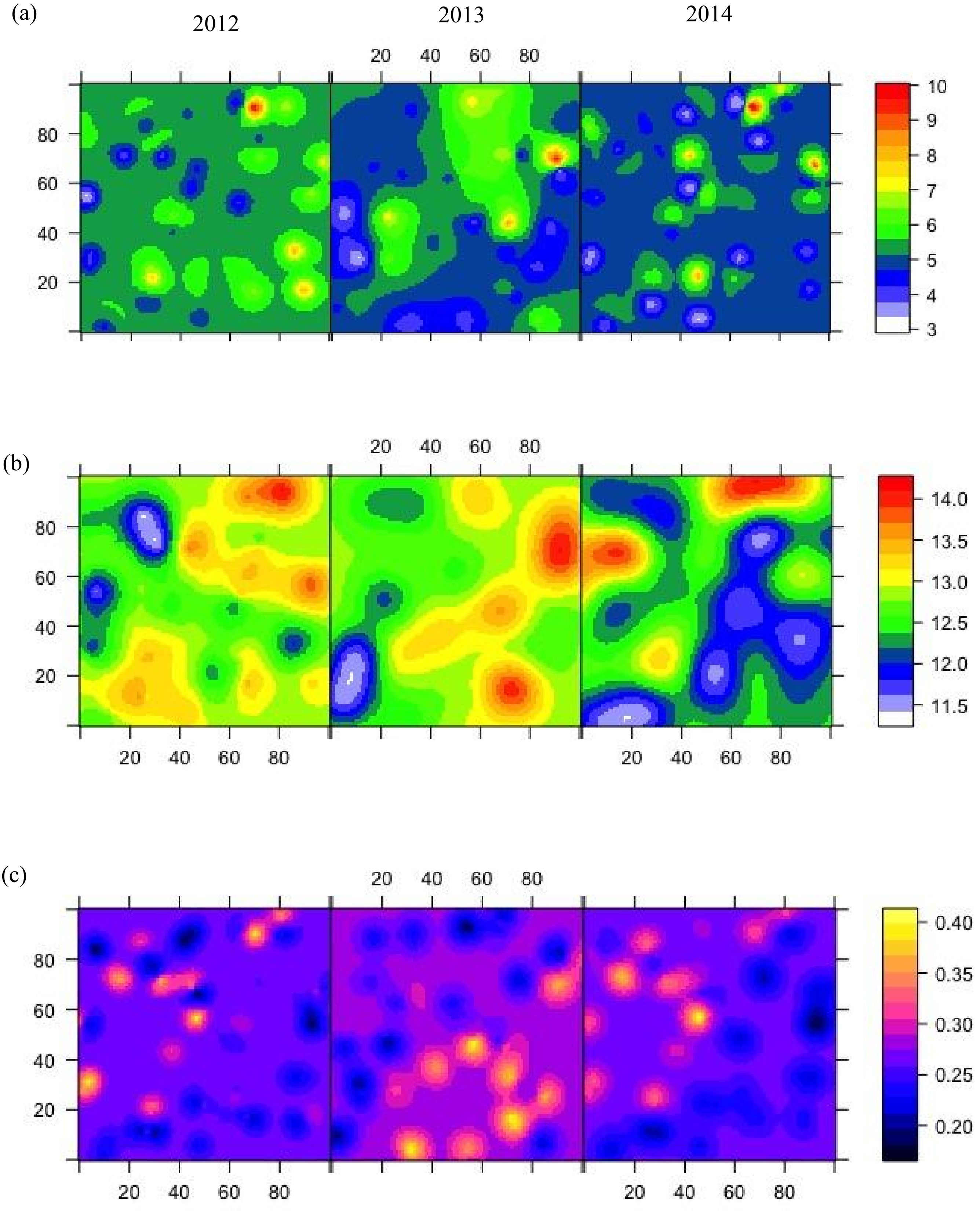


Figure 3-2 Kriged maps of (a) soil CO_2 efflux (F_{CO_2} in µmol CO_2 $m^{-2}s^{-1}$), (b) soil temperature (ST in °C) and (c) soil moisture (SM in m^3m^{-3}) in 2012, 2013, and 2014.

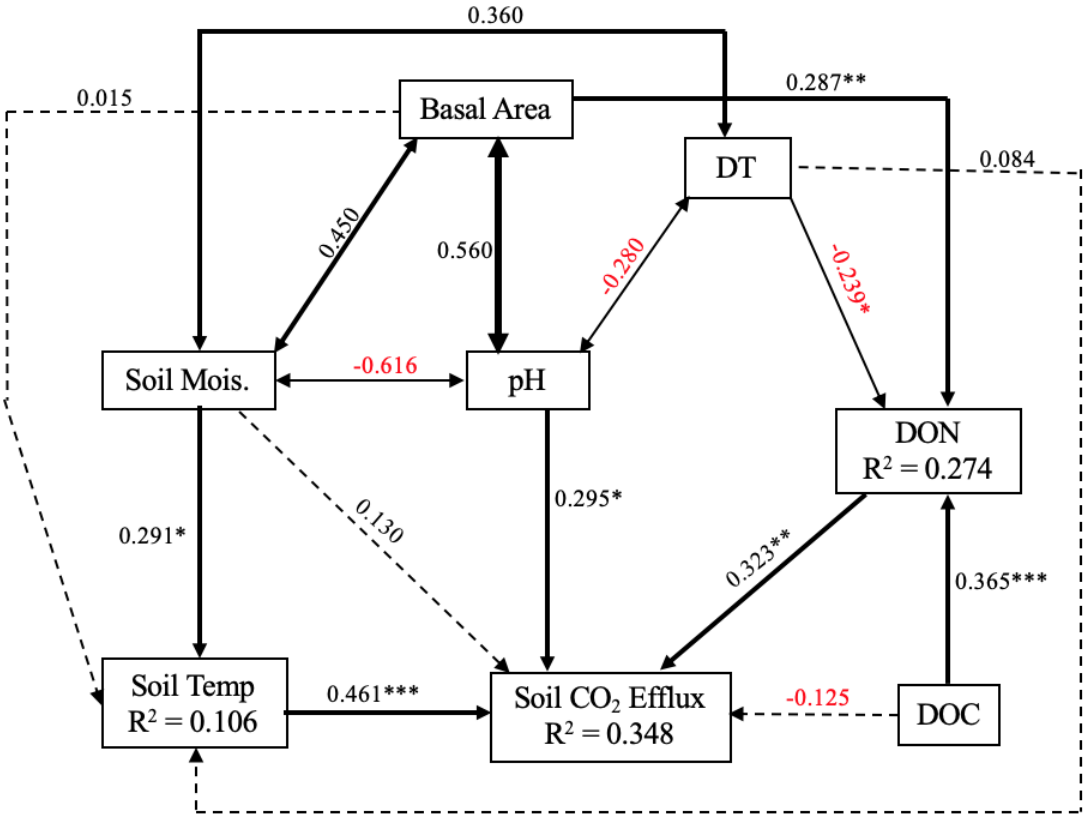


Figure 3-3 Structural equation model showing relationships between soil CO_2 efflux, soil moisture, soil temperature and other environmental factors (χ^2=2.619, df=7, *P*=0.918; CFI=1.000; TLI=1.227, RMSEA *P*-value = 0.949). Causal relationships are shown with single-headed arrows and covariances are represented by double-headed arrows. Red values indicate negative relationships and dashed lines represent non-significant relationships (P ≥ 0.05). The significance of the path coefficients are as follows: * P<0.05, ** P<0.01, *** P<0.001. Thickness of arrows is representative of the strength of the relationship between the variables. F_{CO_2}, soil CO_2 efflux; ST, soil temperature; SM, soil moisture; DON, dissolved organic nitrogen; DT, distance to nearest trees; BA, basal area within 5m of the sampling point.

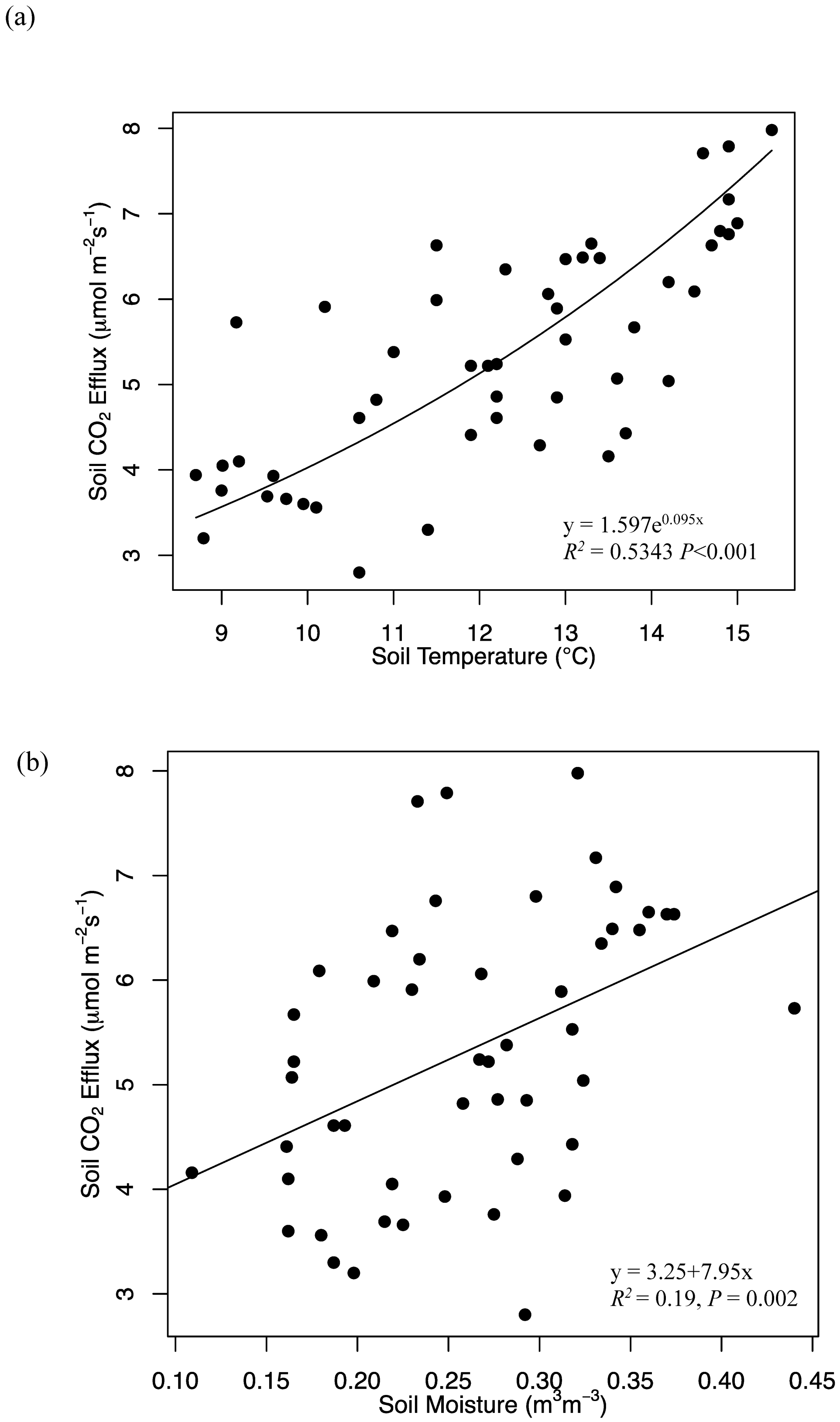
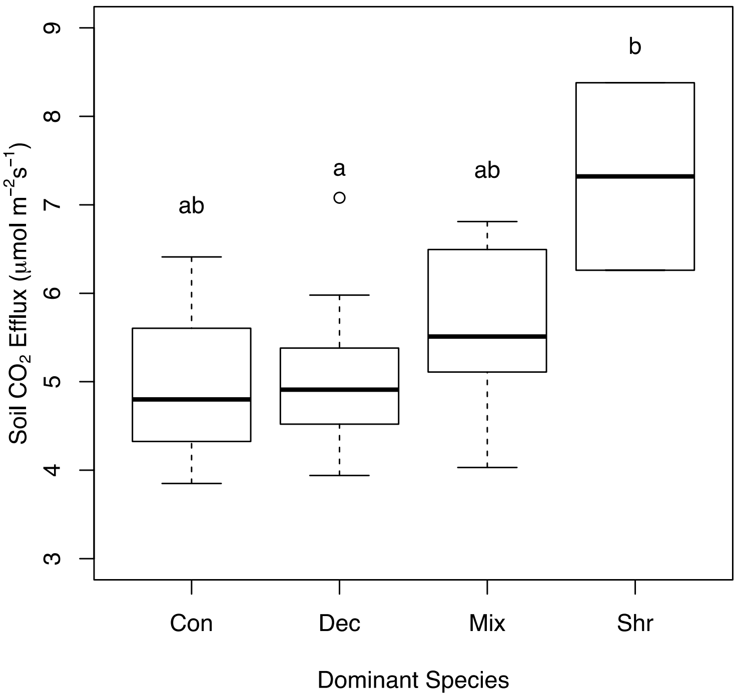


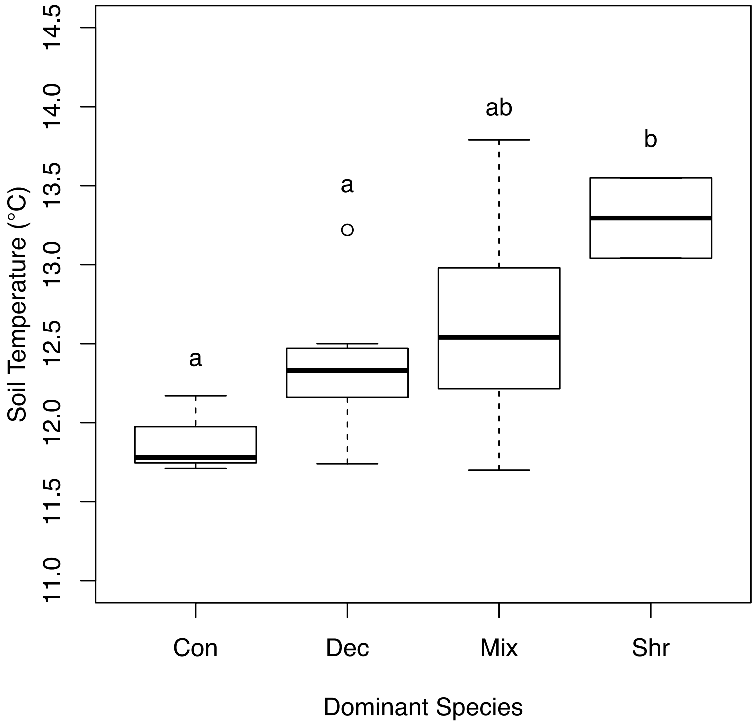
Figure 3-4 Relationship between soil CO_2 efflux (μmol CO_2 $m^{-2}s^{-1}$) and *(a)* soil temperature (°C) *(b)* soil moisture (m^3m^{-3}) over the sampling period.

(a)



Soil CO$_2$ Efflux (µmol m^{-2}s^{-1})
3
4
5
6
7
8
9
ab
a
ab
b
Con
Dec
Mix
Shr
Dominant Species

(b)



Soil Temperature (°C)
11.0
11.5
12.0
12.5
13.0
13.5
14.0
14.5
a
a
ab
b
Con
Dec
Mix
Shr
Dominant Species

(c)

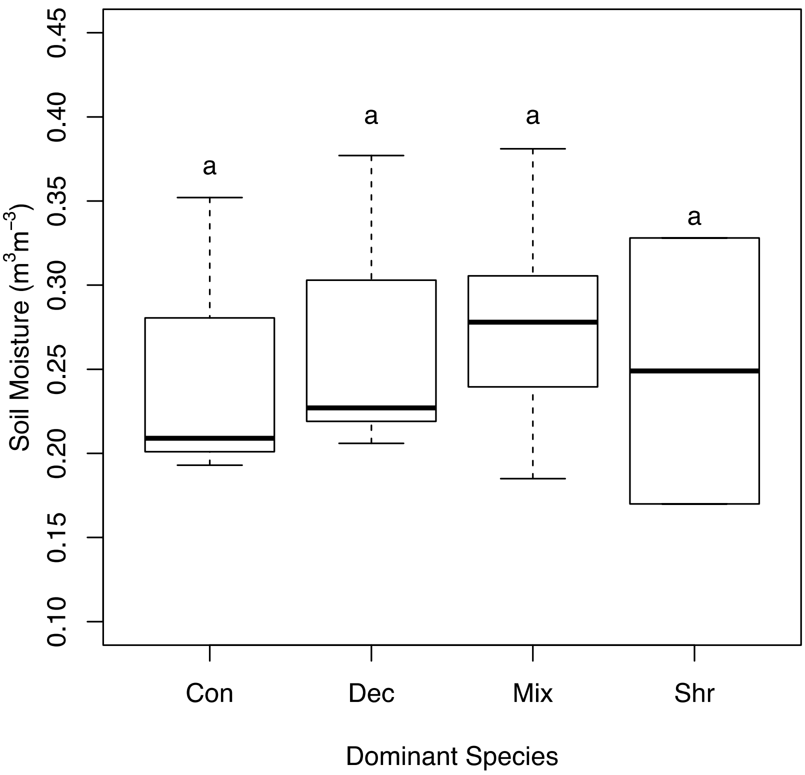


Figure 3-5 Effects of tree biodiversity on (a) soil CO_2 efflux, (b) soil temperature, and (c) soil moisture. Letters indicate significant differences at the $\alpha = 0.05$ level.

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Chapter 4: Spatial and temporal variation of heterotrophic and autotrophic soil CO_2 efflux in a boreal mixedwood forest

4.1 Summary

Quantifying heterotrophic and autotrophic soil CO_2 efflux is necessary to understand the spatial and temporal variation of boreal soil CO_2 efflux and improve our current knowledge of its contribution to the global carbon cycle. I examined the spatial and temporal variation of heterotrophic (HF_{CO_2}) and autotrophic (AF_{CO_2}) soil CO_2 efflux within a Canadian boreal mixedwood forest. The mean heterotrophic and autotrophic soil CO_2 efflux was 4.07 μmol CO_2 m^{-2} s^{-1} and 1.32 μmol CO_2 m^{-2} s^{-1} which is 75% and 25% of total soil CO_2 efflux. The temporal variation of HF_{CO_2} was explained by soil temperature, moisture and other climatic variables with a Q_{10} value of 3.93 while none of the measured variables explained the temporal variation of AF_{CO_2}. Soil temperature primarily controlled the spatial variation of heterotrophic soil CO_2 efflux along with maximum DBH, basal area, and pH while the spatial variation of AF_{CO_2} was controlled by mean DBH and dissolved organic nitrogen (DON). AF_{CO_2} did not significantly differ with patch composition, but shrub-dominant patches exhibited significantly higher HF_{CO_2} than deciduous-dominated patches. This study highlights the need to determine the environmental drivers and effects of species composition on soil CO_2 efflux components in boreal mixedwood to model the response of boreal carbon cycle to climate change.

4.2 Introduction

Higher atmospheric concentrations of greenhouse gases such as carbon dioxide (CO_2) has led to warmer temperatures of 0.74°C above average and is expected to increase by an additional 0.2°C every decade under current global warming scenarios (IPCC 2014).

Increased atmospheric CO_2 could also lead to changes in the global carbon cycle by creating a positive feedback between soil CO_2 efflux and global warming. Soil CO_2 efflux is a significant component of the terrestrial carbon cycle and it is the process by which CO_2 is transferred from the soil to the atmosphere, accounting for a majority of forest ecosystem respiration (Schlesinger and Andrews 2000; Davidson et al. 2006). Total soil CO_2 efflux (F_{CO_2}) is composed of microbial and root soil CO_2 efflux, which are referred to as heterotrophic (HF_{CO_2}) and autotrophic (AF_{CO_2}) soil CO_2 efflux respectively. Heterotrophic soil CO_2 efflux (HF_{CO_2}) largely comes from the decomposition of organic matter and litter by the soil organisms while autotrophic soil CO_2 efflux (AF_{CO_2}) is derived directly from the roots and associated microbial populations (Ekblad and Högberg 2001; Lalonde and Prescott 2007). Quantifying soil CO_2 efflux components will lead to better predictions of climate change effects on total soil CO_2 efflux.

Soil CO_2 efflux can be partitioned into the two soil CO_2 efflux components by several methods including root exclusion, component integration, regression analysis and isotopic labeling (Kuzyakov 2006; Baggs 2006). Because of the heterogeneity in methods for partitioning soil CO_2 efflux and large discrepancies in reported values, root CO_2 efflux has been found to vary from 10% to 90% in forest ecosystems (Hanson et al. 2000). The different partitioning methods have been found to oversimplify sources of CO_2 and no one method is devoid of limitations (Hanson et al. 2000; Jinyan and Chuankuan 2006), but they provide a range of estimated percentage contributions of HF_{CO_2} and AF_{CO_2} to total soil CO_2 efflux. In particular, trenching in combination with root exclusion has been described as a practical approach for separating soil CO_2 efflux into its different components (Yi et al. 2007). Trenching methods are low-cost and simple but one of their disadvantages is that disturbances to the soil profile may cause an immediate surge of soil CO_2 efflux from microbial respiration from decomposing roots and increased loss of carbon from root exudates, thereby overestimating heterotrophic soil CO_2 efflux (Bond-Lamberty et al. 2011). These problems may be mitigated by installing deeper soil collars weeks before soil CO_2 efflux measurements. Other disadvantages of this partitioning method include increased soil moisture, increased soil temperature, and decreased dissolved organic matter content within the collar (Baggs 2006; Ngao et al. 2007; ArchMiller and Samuelson 2016). While there is no standard method to quantify autotrophic and heterotrophic soil CO_2 efflux in forest ecosystems (Jinyan and Chuankuan 2006), the trenching method is an inexpensive way to estimate the contribution of soil CO_2 efflux components to total soil CO_2 efflux in forests.

The spatial and temporal variation of total soil CO_2 efflux is dependent on the effects of environmental and climatic factors on HF_{CO_2} and AF_{CO_2}. Soil moisture (Suseela et al. 2012; Moyano et al. 2013), temperature (Kutsch et al. 2010) and soil organic matter (Gaumont-Guay et al. 2009) have been found to influence heterotrophic soil CO_2 efflux by affecting environmental conditions for microbial decomposition. On the other hand, AF_{CO_2} is affected by phenology and photosynthesis (Bond-Lamberty et al. 2004; Ryan and Law 2005; Tang et al. 2006; Savage et al. 2013), as root activity is dependent on plant physiology. The relationship between environmental factors and soil CO_2 efflux components may be complicated by some factors that affect both HF_{CO_2} and AF_{CO_2}. For example, photosynthesis also influences the rate of HF_{CO_2} (Bond-Lamberty et al. 2004) and soil temperature could affect the release of CO_2 from roots (Olsson et al. 2005; Wei et al. 2010). Soil CO_2 efflux components have also been found to respond differently to environmental disturbances such as drought, warming, and nitrogen addition (Eliasson et al. 2005; Drake et al. 2012; Risk et al. 2012; Fei et al. 2015; Hinko-Najera et al. 2015). Therefore, understanding the relationship between environmental drivers and soil CO_2 efflux components can explain the underlying mechanisms driving the spatial and temporal variation of total soil CO_2 efflux and help in developing better models of the boreal carbon cycle.

In boreal forests, root CO_2 efflux has been found to contribute between 4% and 65% to total soil CO_2 efflux (Chen et al. 2002; Subke et al. 2006; Laganière et al. 2012). However, most of these studies have been on pure stands such as aspen or spruce with little emphasis on boreal mixedwood forests. Therefore, the objectives of this study were to: (1) quantify the contribution of heterotrophic (HF_{CO_2}) and autotrophic (AF_{CO_2}) soil CO_2 efflux components to total soil CO_2 efflux (F_{CO_2}), (2) examine the effect of environmental factors on the spatial and temporal variation of HF_{CO_2} and AF_{CO_2}, and (3) identify the impact of species composition on AF_{CO_2} and HF_{CO_2}in a boreal mixedwood forest.

4.3 Materials and Methods

4.3.1 Study site

The one-hectare plot is located within the George Lake Research Site (53°57'N, 114°06'W), northwest of Edmonton, Alberta. This boreal mixedwood site is located in the dry mixedwood sub-region of the Boreal Forest natural region and is considered to be a moist, rich site with species like balsam poplar, aspen and white spruce dominating mixed stands (Downing and Pettapiece 2006). The 30-year average daily temperature varied between -15.5°C in January and 22.8°C in July. Mean annual precipitation was 492 mm with a majority of the precipitation falling as rain during the growing season (May to September). The well-drained Orthic Gray Luvisol in this area was moderately fine textured, ranging from sand clay loam to silt clay loam. 11 tree species including White Spruce (*Picea glauca*), Aspen (*Populus tremuloides*), Birch (*Betula sp.*), Balsam Poplar (*Populus balsamifera*) and Beaked willow (*Salix bebbiana*) were present in the plot. The trees with at least 1 cm DBH were inventoried and mapped within the plot, and the total stand density was approximately 4300 trees ha^{-1}.

4.3.2 Data collection

The study site was divided into 25 subplots of 20×20 m each. A random point was chosen within each subplot as the original starting point (O) and two other points were located at 2 m and 5 m away from the original point in a straight line resulting in a total of 75 points. Soil flux measurements were taken at each of these points every two weeks from July to September in 2012 and June to September of 2013 and 2014 between the hours of 9.00 a.m. and 4.00 p.m. At each point, two PVC CO_2 efflux collars with different heights were inserted to measure total and heterotrophic soil CO_2 efflux rates. The first collar with a height of 7cm was inserted 3 cm into the soil to measure total soil CO_2 efflux and aboveground litter was removed to avoid unstable CO_2 fluxes. The deeper collar with a height of 40 cm was inserted about 36cm into the soil to sever roots around the collar and measure heterotrophic soil CO_2 efflux. Roots were manually removed from the deeper collar by clipping without disturbing the soil profile to minimize disturbances. Autotrophic CO_2 efflux was estimated by subtracting the flux in the deeper collar from the flux in the shallow collar. The LI-8100A automated soil CO_2 flux system with 20-cm survey chamber attachments (LI-COR Inc., Lincoln, NE, USA) was used to measure soil CO_2 efflux. Mosses were not removed within the soil collars to avoid agitation of the soil layer and because they have been found not to impact soil CO_2 efflux within mixedwood stands significantly (Laganière et al. 2012). The soil CO_2 efflux measurement was taken for 90 seconds with a dead band of 30 seconds on days without rain to minimize measurement error.

Omega soil temperature probe and the auxiliary ECH2O model EC-10 soil moisture probe (Decagon Devices, Inc., Pullman, WA) were used to measure soil temperature and volumetric water content respectively. The distance and DBH of trees within 5m of the soil collar were recorded over the course of the growing season. Soil samples were collected from the top layer (0-15 cm soil depth) at each point in 2013 and 2014 and transported to the laboratory for further analysis. The samples were air-dried and passed through a 2-mm sieve to determine the soil pH was measured using a 1:10 soil-water ratio. The solution was shaken for 30 minutes and pH was measured with an Orion benchtop pH meter (Thermo Orion, Beverly, MA). Dissolved organic N (DON) and C (DOC) were measured using a Shimadzu TOC-V/TN analyzer (Shimadzu Corp. Kyoto, Japan).

4.3.3 Statistical analyses

Soil CO_2 efflux, soil temperature, and soil moisture data were averaged by measurement period and subplot for statistical analysis. I tested the data for normality using the Shapiro-Wilk's test and non-normal data was log-transformed when necessary before statistical analyses. AF_{CO_2} was calculated by subtracting HF_{CO_2} in the deeper collar from R_s and the percentage contribution of AF_{CO_2} and HF_{CO_2} to F_{CO_2}. Spatial differences in autotrophic and heterotrophic soil CO_2 efflux was determined using one-way ANOVA. The classification and regression tree analysis (CART) was used to explain the effect of environmental factors on the spatial variation of soil CO_2 efflux in which the regression trees were pruned to avoid overfitting the data in the 'rpart' package (Therneau and Atkinson 2018). Geostatistical analyses were used to analyze the spatial variation of autotrophic and heterotrophic soil CO_2 efflux rates and construct kriging interpolations (Song et al. 2013; Wu et al. 2015). The semivariance ($\gamma(h)$) was calculated using Eq. (1):

$$\gamma(h) = \frac{1}{2N}\sum_{i=1}^{N(h)}[y(i) - y(i+h)]^2 \qquad (1)$$

where $y(i)$ is the value of y at point i, $y(i+h)$ is the value at a distance of h away from point i and $N(h)$ is the number of pairs of observations separated by distance h (Rochette et al. 1991). The nugget (C_0), the sill (C_0+C) and the range (a) of the semivariogram were used to characterize the spatial heterogeneity of the variables in the dataset. The degree of spatial dependence was calculated by the proportion of the structural variance (C) to the sill (C_0+C). Spatial dependence less than 0.25 was classified as weak, between 0.25 and 0.75 was classified as moderate, while values greater than 0.75 were identified as strong spatial dependence. Outliers were removed before analysis and ordinary block kriging was used to produce kriged maps.

Repeated-measures ANOVA and Tukey's HSD comparisons were conducted to assess the temporal variability of soil CO_2 efflux, temperature and moisture between months and years. Coefficient of variation (CV) values above 100% signify high variability, values between 10% and 100% signify moderate variability and values below 10% signify low variability (Hu et al. 2016). The relationship between soil CO_2 efflux components, soil moisture, and soil temperature were fitted using both linear regressions and the modified exponential Eq. (2), respectively:

$$HF_{CO_2} \text{ or } AF_{CO_2} = ae^{b(x)} \qquad (2)$$

where HF_{CO_2} or AF_{CO_2} are heterotrophic and autotrophic soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) respectively, x is soil temperature (°C) at 5-cm depth at 5-cm depth and a, b, c, and d are the fitted parameters in the regression equation. Using b from Eq. (2), the Q_{10} (temperature sensitivity of soil CO_2 efflux) was calculated for each year with Eq. (3):

$$Q_{10} = e^{10b} \qquad (3)$$

where Q_{10} is the temperature sensitivity. The effect of tree species composition on soil CO_2 efflux were also compared in the 1-ha plot.

All statistical analyses were conducted in the R Studio environment using the R program (R Core Team 2018) and 'gstat' package (Graeler et al. 2016) was used for geostatistical analyses.

4.4. Results

4.4.1 Spatial variation of heterotrophic and autotrophic soil CO_2 efflux

Over the three growing seasons, average heterotrophic soil CO_2 efflux (±SE) was 4.07 ± 0.12 μmol CO_2 m^{-2} s^{-1} and autotrophic soil CO_2 efflux was 1.32 ± 0.12 μmol CO_2 m^{-2} s^{-1} (Table 4-1). The contribution of heterotrophic (HF_{CO_2}) and autotrophic (AF_{CO_2}) components to total soil CO_2 efflux (F_{CO_2}) were 75% and 25% respectively (Fig. 4-1). In the individual years, the contribution of AF_{CO_2} to F_{CO_2} gradually increased from 17.8% to 33.7% and the contribution of HF_{CO_2} to F_{CO_2} gradually decreased. HF_{CO_2} had a lower spatial variation with moderate spatial variation and coefficient of variation values between 32% and 34% while AF_{CO_2} exhibited high spatial variation in 2012 and 2013 with values above 100% and moderate spatial variation in 2014 and overall data with values of 89% and 81% respectively (Table 4-1). The results of one-way ANOVA analysis found that HF_{CO_2} (F=6.42, P<0.001) had significant spatial variation while AF_{CO_2} (F=0.07, P=0.83) did not vary significantly across the patches within the 1-ha study site. Mean DBH and DON were significant predictors of the spatial variation in autotrophic soil CO_2 efflux (Fig. 4-2a). Soil temperature, maximum DBH, total basal area, pH and basal area of the nearest tree (SpBA) were significant predictors of spatial variation in heterotrophic soil CO_2 efflux

(Fig. 4-2b). Type I errors were minimized by setting the alpha-level at 0.05, which is how the significant predictors of soil CO_2 efflux were determined in the CART analysis.

The results of semivariogram analysis showed that the range of autocorrelation in heterotrophic soil CO_2 efflux, as found by spherical models, varied from 6.48 to 32.10 m (Table 4-2). There was also moderate spatial dependence in heterotrophic soil CO_2 efflux generating the resulting kriging interpolations within the 1-ha sampling site in Fig. 4-3a. Autotrophic soil CO_2 efflux, on the other hand, showed no spatial autocorrelation (Table 4-2). Therefore, I could not use ordinary kriging to produce the interpolation but I was able to use inverse distance weighting instead (Fig. 4-3b).

4.4.2 Temporal variation of heterotrophic and autotrophic soil CO_2 efflux

The temporal pattern of HF_{CO_2} followed the general pattern of F_{CO_2}, peaking between July and August of the individual years (Fig. 4-1). Results of repeated-measures ANOVA with subplots as random effects showed that there were significant differences in HF_{CO_2} (F=47.75, P<0.001) and AF_{CO_2} (F=10.06, P<0.001) between individual measurements and monthly. There were no significant differences between annual soil CO_2 efflux of autotrophic and heterotrophic CO_2 efflux. HF_{CO_2} exhibited an exponential relationship with soil temperature, which explained 54 % of the temporal variation with a Q_{10} value of 3.93 (Table 4-3) but AF_{CO_2} showed no relationship with soil temperature (Fig. 4-4a). There was a linear relationship between HF_{CO_2} and soil moisture, also explaining 23% of the temporal variation (Fig. 4-4b) but there was no relationship between AF_{CO_2} and soil moisture in this study. Results in Table 4-4 present linear regression results of temporal variation in soil CO_2 efflux components with climatic variables such as air temperature and precipitation. Air temperature was found to have significant effects on heterotrophic soil CO_2 efflux but none of the climatic factors in this study affected the temporal variation of autotrophic soil CO_2 efflux (Table 4-3).

4.4.3 Tree species composition and soil CO_2 efflux components

Autotrophic soil CO_2 efflux was not significantly different in patches dominated by deciduous species, coniferous species, mixed species or shrubs (Fig. 4-5a). Heterotrophic soil CO_2 efflux was significantly higher in patches dominated by shrubs than other deciduous-dominated patches (Fig. 4-5b). The patches dominated by coniferous and mixed species did not have significant differences in HF_{CO_2}.

4.5 Discussion

Contribution of AF_{CO_2} and HF_{CO_2} to F_{CO_2}

In this study, it was found that AF_{CO_2} contributed 25% to total soil CO_2 efflux (Table 4-1), which falls within the wide range of 10 to 90% contribution estimated in previous literature (Hanson et al. 2000). In comparison to other boreal forests, some studies have estimated AF_{CO_2} contribution to be about half of the total soil CO_2 efflux (Högberg et al. 2001; Bhupinderpal-Singh et al. 2003; Arevalo et al. 2010; Bond-Lamberty et al. 2011; Kukumägi et al. 2017), which is higher than the estimate derived in this study. This discrepancy in AF_{CO_2} contributions may be due to differences in measurement methods and species composition as partitioning in some of these studies were carried out by girdling and in stands dominated by single species like aspen, spruce, poplar and jack pine stands. These findings are closer to the estimates of Laganière et al. (2012) in a boreal mixedwood forest, who found that total soil CO_2 efflux was primarily dominated by heterotrophic soil CO_2 efflux with AF_{CO_2} to F_{CO_2} contribution of 4 -14%. O'Connell et al. (2003) and Schuur et al. (2006) found that heterotrophic soil CO_2 efflux dominates total summer soil CO_2 efflux rate in Canadian boreal forests consistent with HF_{CO_2} and AF_{CO_2} rates reported in this stand. The lower percentage contribution of AF_{CO_2} in this study could also be due to the limitation of the partitioning method used in this study because the trenching and root exclusion partitioning method may have overestimated HF_{CO_2} by increasing soil moisture through reduced transpiration losses (Hanson et al. 2000; Arevalo et al. 2010).

While the challenges of partitioning by trenching and root exclusion method have been discussed in previous literature such as transpiration losses and increased heterotrophic soil CO_2 efflux from the decay of collars (Kuzyakov 2006; Baggs 2006), these results show that trenching method of partitioning may take a longer time in boreal forests. Therefore, the actual autotrophic soil CO_2 efflux may take longer than 3 growing seasons to be determined from this partitioning method.

Spatial variation of AF_{CO_2} and HF_{CO_2}

Moderate spatial variation was observed in heterotrophic soil CO_2 efflux with a CV of about 26% (Table 4-1). The spatial variation of HF_{CO_2} may be related to the spatial variation of microbial biomass and activity, which is regulated by several environmental factors including soil temperature, soil organic matter decomposition and moisture (Subke et al. 2011; Wu et al. 2016). There were significant differences in HF_{CO_2} across the patches, suggesting that microbial composition associated with different species within the patches may have also varied across the study site. Autotrophic CO_2 efflux had higher spatial variation than heterotrophic CO_2 efflux in the mixedwood stand (Table 4-1) with high spatial variation and CV values averaging over 80%. The spatial variation of autotrophic soil CO_2 efflux may be driven by the aboveground tree diversity and root biomass (Gomez-Casanovas et al. 2012; Savage et al. 2013). Therefore, the differences of spatial variation in autotrophic and heterotrophic soil CO_2 efflux could be explained by the fact that environmental factors and microbial activity may not be as spatially heterogeneous as root biomass within a mixed-species stand. However, we also found that AF_{CO_2} did not significantly differ across individual patches within the study site, suggesting that the differences in autotrophic soil CO_2 efflux are not patch-dependent, but the large spatial variation may be caused by hot spots within the boreal mixedwood forest.

The spatial variation of HF_{CO_2} in the study site was primarily regulated by soil temperature, maximum DBH, basal area and pH (Fig. 4-2a), which indicates that these variables affect microbial activity in the boreal mixedwood forest while mean DBH and DON regulated AF_{CO_2}. This suggests that HF_{CO_2} and AF_{CO_2} in this mixedwood forest also exhibit differential responses to disturbances and environmental changes as seen in other ecosystems (Yan et al. 2010; Wang et al. 2014a; Liu et al. 2016a, 2016b). These results also show that microbial activity was regulated by soil temperature and pH. Hannam et al. (2006) supported the findings by observing higher microbial biomass and composition in soils with higher pH. The influence of basal area on heterotrophic soil CO_2 efflux could also be explained by the observation of Hannam et al. (2006) as they found that microbial biomass decreased with harvesting. This suggests that there may be higher microbial biomass and activity with increasing basal area and maximum DBH within the study site. It is, therefore, crucial to partition boreal mixedwood forest soil CO_2 efflux into different components to understand the underlying mechanisms of environmental changes on the boreal forest carbon cycle.

Temporal variation of AF_{CO_2} and HF_{CO_2}

The temporal pattern of HF_{CO_2} was similar to the temporal pattern of F_{CO_2} over the three growing seasons (data not shown) and this was a result of the high percentage contribution of HF_{CO_2} to F_{CO_2}. Soil temperature and moisture significantly explained most of the temporal variation in F_{CO_2} (Fig. 4-4). Warmer air temperature increases microbial activity and soil temperatures, which in turn stimulates HF_{CO_2} (Jinyan and Chuankuan 2006; Li et al. 2010), during the growing seasons in boreal forests. The relationship between HF_{CO_2} and soil moisture is also consistent with Allison & Treseder (2008), who observed that drying suppresses microbial activity in boreal soils. This means that microbial activity should increase with higher soil moisture leading to higher heterotrophic soil CO_2 efflux in this study. The results, therefore, suggest that the temporal variation of total soil CO_2 efflux is driven by the temporal variation of HF_{CO_2} in this study through the relationship with soil temperature and moisture.

Autotrophic soil CO_2 efflux was lowest at the beginning of the study, suggesting that CO_2 emissions from the severed roots could have been present in the trenched collars (Ngao et al. 2007; Arevalo et al. 2010; Luan et al. 2012). As a result, heterotrophic soil CO_2 efflux at the beginning of this study may have also included residual autotrophic soil CO_2 efflux. The contribution of AF_{CO_2} to F_{CO_2} changed throughout the experiment but showed no temporal relationship with soil moisture, soil temperature and other climatic factors (Table 4-3, Figs. 4-1 & 4-3). This pattern is in agreement with Subke et al. (2011), who found that AF_{CO_2} may not respond to temperature or moisture changes because it is potentially controlled by substrate supply and other aboveground processes. These processes include transpiration (Grossiord et al. 2012), root dynamics (Jinyan and Chuankuan 2006), and photosynthesis (Ruehr and Buchmann 2009; Wang et al. 2014b), which could have influenced the temporal variation of root CO_2 efflux in this study. The dependence of AF_{CO_2} on these processes could also explain why climatic conditions such as air temperature and humidity did not significantly influence the temporal variation.

Effects of species composition on soil CO_2 efflux components

Canadian boreal mixedwood has been described as a mosaic of different stands with complex understory interactions (Martin and Gower 2006; Chávez and Macdonald 2010), which also causes spatial heterogeneity of total soil CO_2 efflux. Heterotrophic soil CO_2 efflux was significantly higher in patches dominated by shrubs than deciduous-dominated patches (Fig. 4-5a), indicating that microbial activity is higher in patches dominated by shrubs than deciduous-dominated patches. This finding is supported by Chávez & Macdonald. (2010), who found that microbial activity has been increased by the nutrient availability associated with shrubs. Autotrophic soil CO_2 efflux in this study did not significantly differ between patches (Fig. 4-5b). This observation could be also be explained by the results of the CART analysis (Fig. 4-2b) where mean DBH rather than tree species-dependent effects influenced AF_{CO_2}.

4.6 Conclusion

In conclusion, HF_{CO_2} exhibited moderate spatial variation and was influenced by soil temperature, maximum DBH, pH and basal area, while AF_{CO_2} showed high spatial variation and was influenced by mean DBH and DON. Heterotrophic soil CO_2 efflux was 75% of the total soil CO_2 efflux and the temporal variation correlated with soil temperature, moisture, and air temperature. Heterotrophic soil CO_2 efflux followed a similar seasonal pattern to total soil CO_2 efflux, peaking between July and August. The temporal variation of autotrophic soil CO_2 efflux showed no relationship with the environmental and climatic factors measured in this study and contributed 25% to the total soil CO_2 efflux. Autotrophic soil CO_2 efflux peaked later than heterotrophic soil CO_2 efflux between August and September. The composition of tree species in the study site affected the HF_{CO_2} component but not AF_{CO_2}. Overall, this study highlights the need to partition soil CO_2 efflux in mixedwood forests for accurate predictions of climate change effects on the boreal soil carbon cycle. Also, the effects of tree composition and the underlying mechanisms on mixedwood forest soil CO_2 efflux should be considered when estimating the carbon budget in boreal ecosystems.

Table 4-1 Growing season mean and relative standard error of soil CO_2 efflux (±1RSE) (μmol CO_2 m^{-2} s^{-1}), percentage contribution to total soil CO_2 efflux and coefficient of variation (%) of heterotrophic and autotrophic soil CO_2 efflux.

	Heterotrophic F_{CO_2}			Autotrophic F_{CO_2}		
Year	Mean (RSE)	%TSR	CV (%)	Mean (RSE)	% TSR	CV (%)
2012	4.57 (3.94)	82.22	34.22	0.99 (14.14)	17.78	127.92
2013	4.31 (3.71)	76.90	33.17	1.32 (12.88)	23.12	109.85
2014	3.32 (3.61)	66.34	31.87	1.68 (10.12)	33.66	89.44
Overall	4.07 (2.95)	74.71	26.18	1.32 (9.09)	25.32	81.47

Table 4-2 Fitted semivariogram parameters for 2012, 2013, 2014, and overall heterotrophic and autotrophic soil CO_2 efflux

Year	Partition	Model	Nugget (C_o)	Sill (C_o+C)	Spatial Dep.	Range (m)	R^2
2012	Het.	Spherical	0.031	0.049	0.63	17.30	0.834
	Aut.	ND	-	-	-	-	-
2013	Het.	Spherical	0.027	0.043	0.63	32.10	0.876
	Aut.	ND	-	-	-	-	-
2014	Het.	Spherical	0.020	0.036	0.56	6.48	0.789
	Aut.	ND	-	-	-	-	-
Overall	Het.	Spherical	0.015	0.027	0.56	53.97	0.850
	Aut.	ND	-	-	-	-	-

Table 4-3 Parameters of the exponential model $HF_{CO_2h}=ae^{bT}$, where HF_{CO_2} is the heterotrophic soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}), *a* is the soil CO_2 efflux rate at 0°C, *b* is the change of R with one-unit change of *T*, which is the soil temperature (°C), the correlation coefficient (R^2) and Q_{10} (temperature sensitivity) calculated from Eqn. 2. All models were significant at $P < 0.05$.

Year	*a*	*b*	R^2	Q_{10}
2012	0.315 ± 0.124	0.203 ± 0.029	0.77	7.61
2013	1.529 ± 0.533	0.083 ± 0.027	0.28	2.30
2014	0.873 ± 0.173	0.109 ± 0.015	0.77	2.98
Overall	0.717 ± 0.165	0.137 ± 0.017	0.75	3.93

Table 4-4 Linear regression of climatic variables on temporal variation of HF$_{CO_2}$ and AF$_{CO_2}$ Boldfaces indicate significance at the $\alpha = 0.05$ level.

		Heterotrophic F$_{CO_2}$		Autotrophic F$_{CO_2}$	
Variable	Mean	R^2	P	R^2	P
Ppt (mm)	1.93	-	N.S.	-	N.S.
AirTemp (°C)	15.69	**0.35**	**<0.001**	-	N.S.
Max. Temp (°C)	22.18	**0.22**	**<0.001**	-	N.S.
Min. Temp (°C)	8.99	**0.41**	**<0.001**	-	N.S.
Humidity (%)	71.80	-	N.S.	-	N.S.

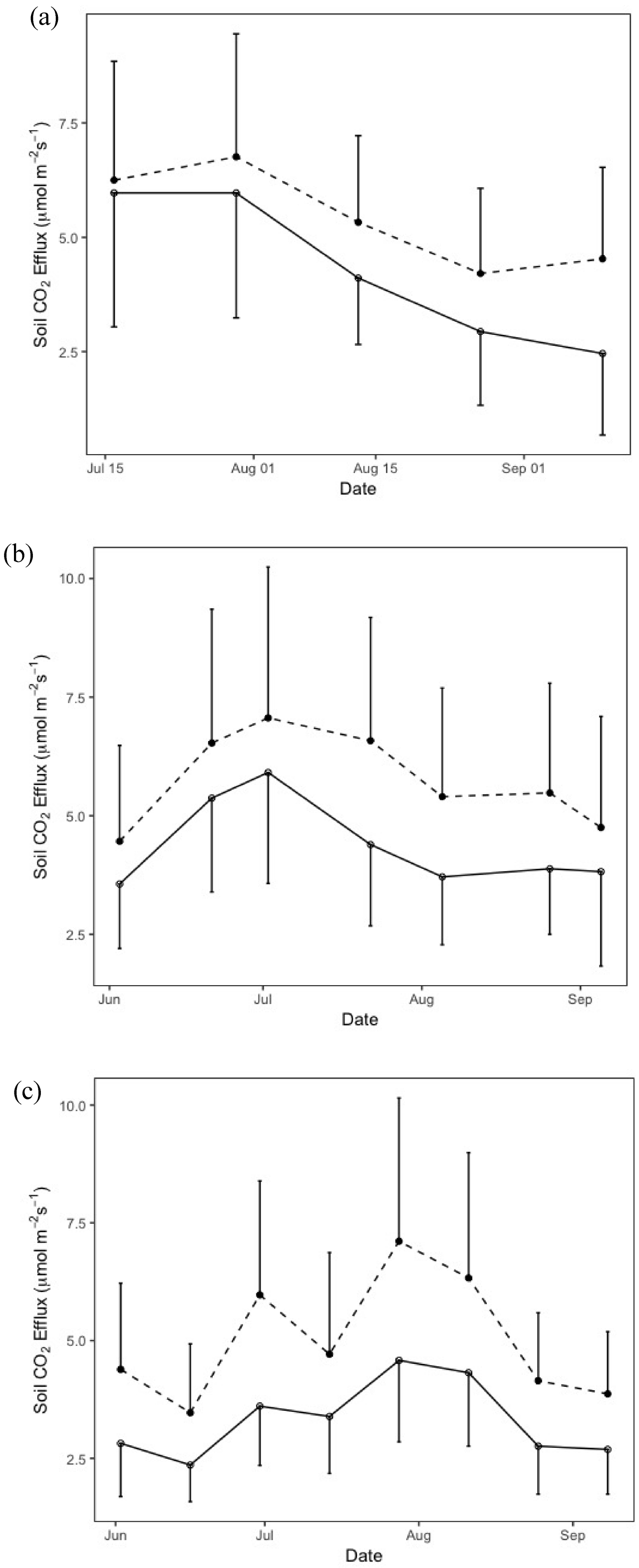


Figure 4-1 Monthly variation of (a) F_{CO_2}, total soil CO_2 efflux in μmol CO_2 m^{-2} s^{-1} (filled circle, dashed line) and (b) HF_{CO_2}, heterotrophic CO_2 efflux in μmol CO_2 m^{-2} s^{-1} (open circle, solid line) in (a) 2012 (b) 2013 and (c) 2014 growing season.

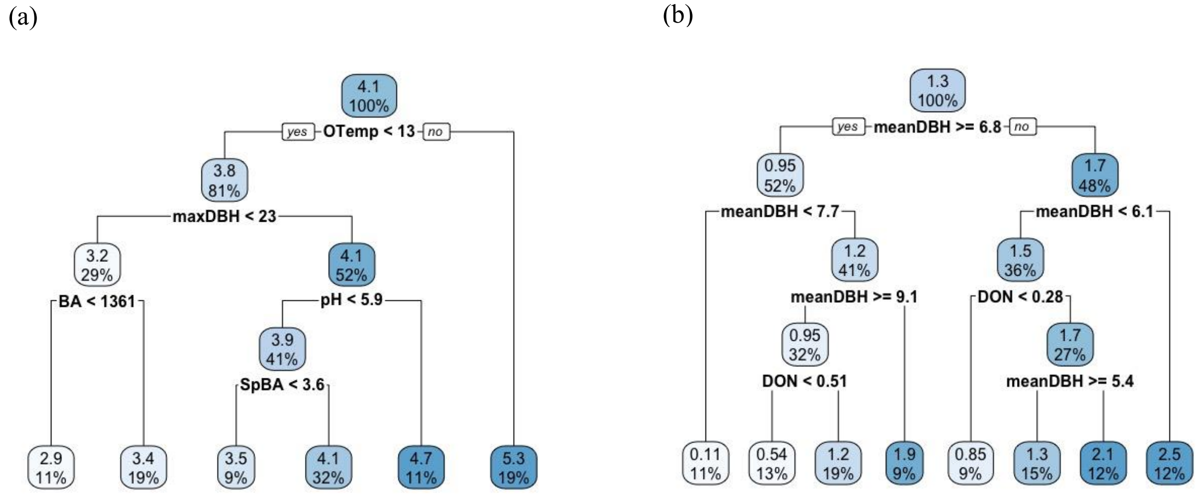


Figure 4-2 Regression tree of (a) heterotrophic and (b) autotrophic soil CO_2 efflux showing predicted values and percentages.

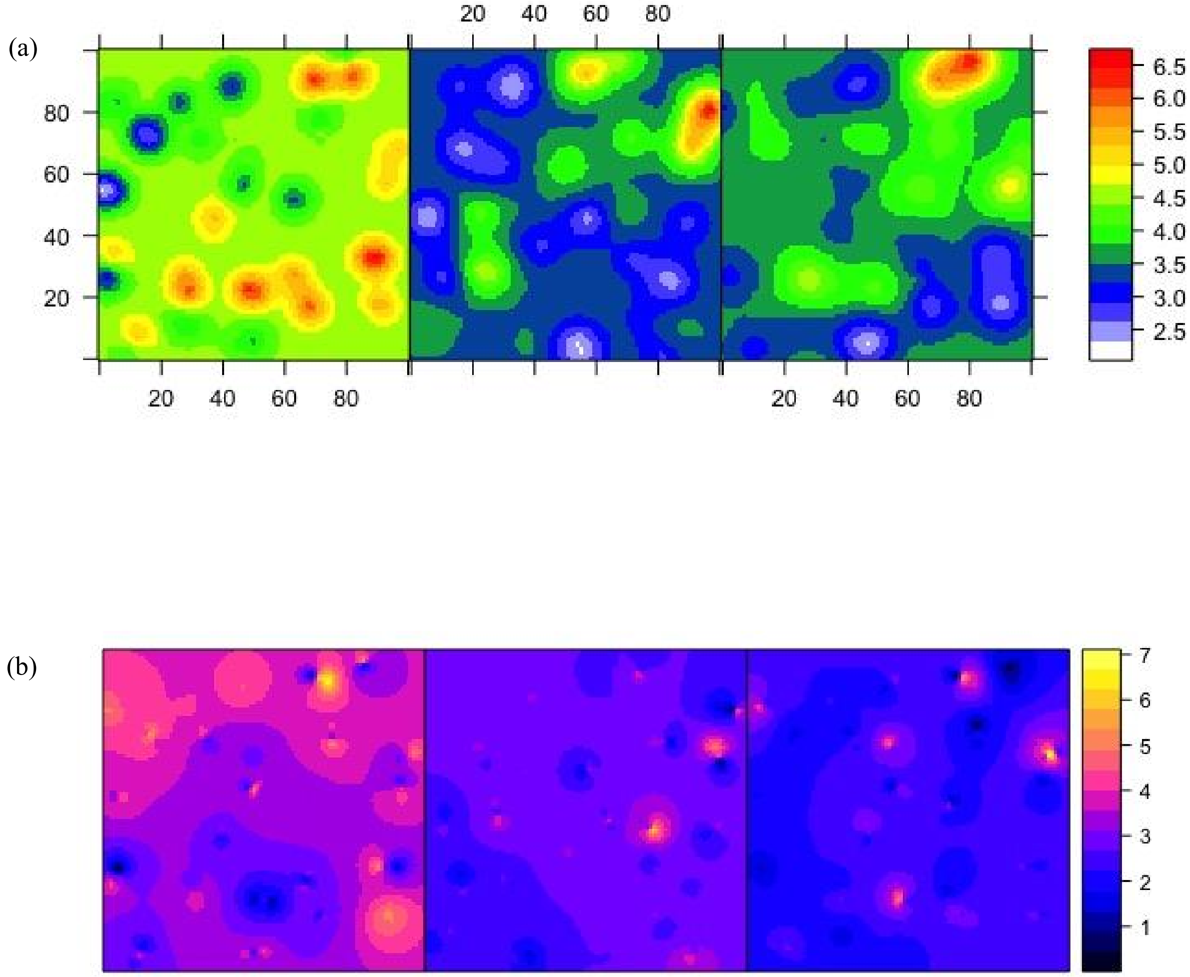


Figure 4-3 (a) Kriging interpolation for heterotrophic CO_2 efflux and (b) Inverse distance weighted interpolation for autotrophic CO_2 efflux.

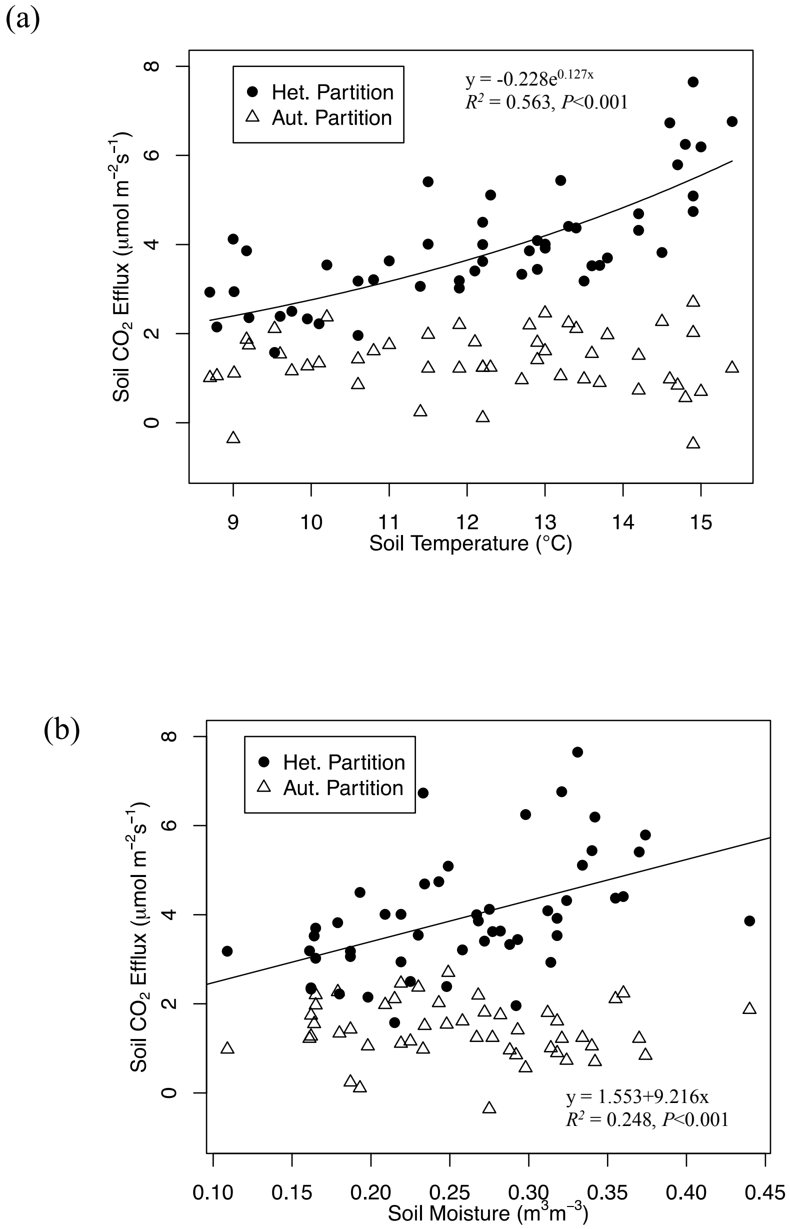
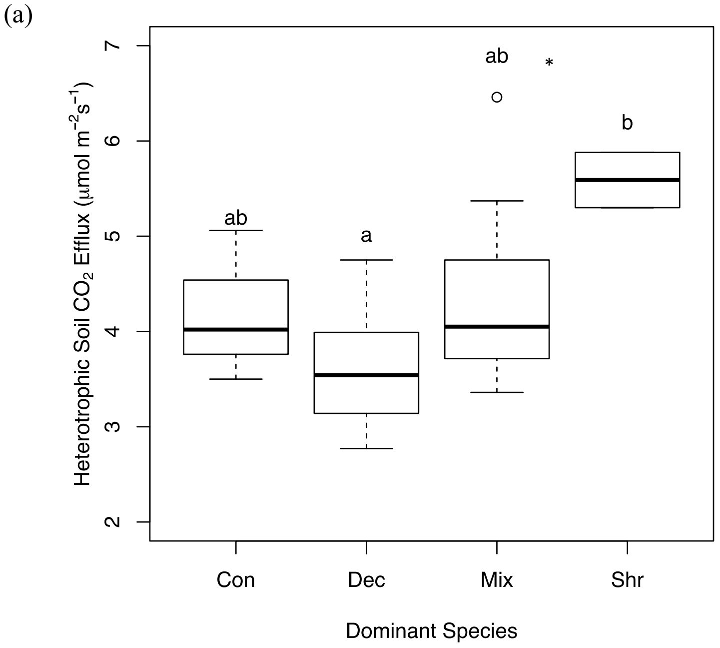


Figure 4-4 Relationship between soil CO$_2$ efflux components, i.e. heterotrophic (HFCO$_2$) and autotrophic (AFCO$_2$) soil CO$_2$ efflux (µmol CO$_2$ m^{-2} s^{-1}) with (a) soil temperature (^{o}C) and (b) soil moisture (m^{3}m^{-3}). Regression lines shown are for relationships with HFCO$_2$ as soil temperature and moisture showed no relationship with AFCO$_2$.



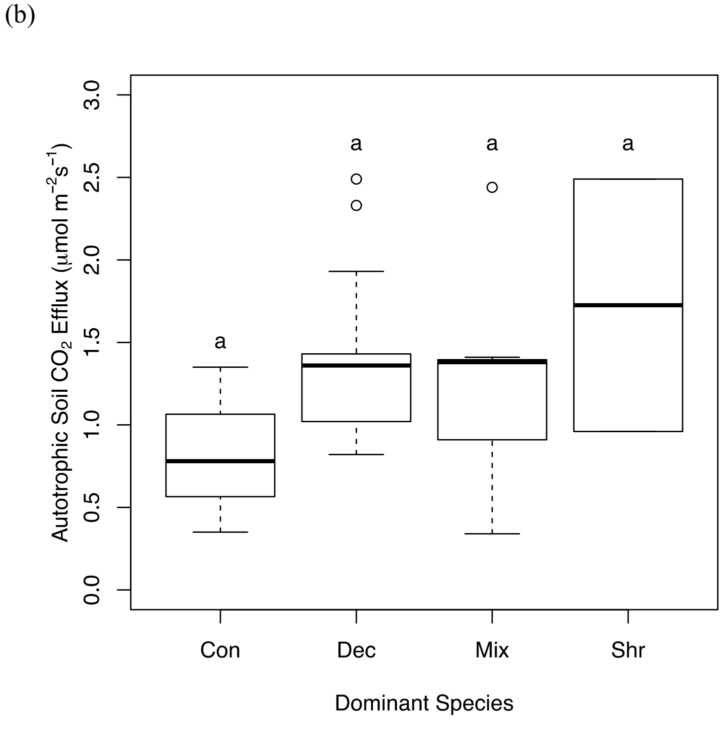


Figure 4-5 Effects of tree biodiversity on (a) heterotrophic and (b) autotrophic soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}).

4.7 Literature Cited

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Chapter 5: Conclusion

5.1 There is moderate spatial variation in global and fine-scale soil CO_2 efflux

In Chapters 2 & 3, I was able to determine that soil CO_2 efflux exhibits moderate spatial variation in boreal, temperate, and tropical forests. The coefficient of variation in meta-analysis before disturbances ranged from 44% to 58%, which is higher than the CV (27.6 to 38.5%) in the boreal mixedwood forest studied in Chapter 3. This higher CV at the global level can be explained for various reasons. First, the heterogeneity of measurement methods including IRGA, soda lime absorption and gas chromatography could contribute to the larger spatial variation seen in the meta-analysis. Through meta-regression, this finding is supported by the significant study heterogeneity being attributed to the differences in these methods. Second, the differences in species composition across boreal, temperate, or tropical forests may be responsible for the spatial variation in soil CO_2 efflux. This is supported by Laganière et al. (2012), and other studies (Stoyan et al. 2000; Johnson et al. 2008; Dias et al. 2010) who found that species composition influences soil CO_2 efflux. The results of Chapter 3 also support this finding as I found that shrub-dominated patches had higher soil CO_2 efflux than deciduous-dominated patches. Third, the effect of soil temperature, moisture and other environmental factors could determine the moderate fine-scale and global scale soil CO_2 efflux as was found in Chapters 2 and 3. For example, water addition influenced soil CO_2 efflux in tropical forests but not boreal forests because of the differences in environmental conditions. DON, pH, and basal area are environmental factors that can also affect the spatial variation of soil CO_2 efflux as was identified in Chapter 3.

Overall, this research shows that environmental factors at global and fine-scale could contribute to the spatial variation of soil CO_2 efflux. This conclusion is supported by Kelsey et al. (2012), who found significant spatial variation at both plot and landscape scale. They found that plot-scale variation and landscape-scale variation are similar probably because variation of soil CO_2 efflux at smaller scales may generate the spatial variation at larger scales. Therefore, we need to understand fine-scale spatial variation of soil CO_2 efflux to model larger scale spatial variation of soil CO_2 efflux.

5.2 The effects of climate change may be weaker on soil CO2 efflux in boreal forests than temperate and tropical forests

In Chapter 2, I found the effects of climate change on soil CO_2 efflux are not as straightforward as may be assumed because they vary between forest types. The effects of climate change like elevated CO_2, water addition, and warming significantly increased global forest soil CO_2 efflux while drought reduced forest soil CO_2 efflux. Elevated CO_2 has been found to increase soil CO_2 efflux, as was seen across temperate and tropical forests, by stimulating plant growth and microbial growth rates (Blagodatskaya et al. 2010; Deng et al. 2010; Smith et al. 2013). On the other hand, elevated CO_2 had no effect on boreal soil CO_2 efflux in this meta-analysis, probably due to small sample size. There was no statistical difference between the response of boreal, temperate, and tropical soil CO_2 efflux to elevated atmospheric CO_2, suggesting that with increased sample size, boreal soil CO_2 efflux may significantly increase with elevated atmospheric CO_2 concentration. When partitioned into heterotrophic and autotrophic soil CO_2 efflux, elevated CO_2 has been found to have contradicting effects on microbial activity (Blagodatskaya et al. 2010) but increase fine root biomass (Smith et al. 2013).

However, due to the small sample sizes of climate change effects on soil CO_2 efflux components in this meta-analysis, the underlying mechanism by which climate change affects soil CO_2 efflux through its components could not be confirmed.

Water addition also increased temperate and tropical forest soil CO_2 efflux but not boreal soil CO_2 efflux. Water addition has been found to increase total soil CO_2 efflux because microbial activity is primarily limited by moisture in temperate and tropical forests (Thomas et al. 2011). The lack of a significant effect on boreal soil CO_2 efflux may be because of the small sample size and the covariance between soil temperature and moisture, making the individual effects hard to separate (Davidson et al. 1998; Khomik et al. 2006). Drought, on the other hand, was found to have an effect on global forest soil CO_2 efflux but not temperate, tropical or components of soil CO_2 efflux. These findings could be explained by the inconsistent effects of drought on soil CO_2 efflux that has been found in previous studies (Ohashi et al. 2014; Liu et al. 2016), probably due to differences in the response of soil CO_2 efflux components.

This meta-analysis revealed that warming increases temperate soil CO_2 efflux by increasing microbial biomass and activity but has no effect on boreal and tropical soil CO_2 efflux. The underlying mechanism of the non-significant effect of warming on boreal soil CO_2 efflux is that drying suppresses soil CO_2 efflux in colder regions (Allison and Treseder 2008), but a small sample size and increased evapotranspiration could also be responsible for the lack of a significant effect of warming on tropical soil CO_2 efflux. The only significant effect of climate change on boreal soil CO_2 efflux was FACE + warming. However, with increased sampling, there is a possibility that other climate change effects may stimulate boreal soil CO_2 efflux.

5.3 Land-use change and harvesting have effects while natural disturbances and litter perturbations have similar effects on soil CO_2 efflux across biomes

This thesis showed that afforestation reduced soil CO_2 efflux in boreal and tropical forests but increased in temperate forests. Conversion of forest to grassland reduced boreal soil CO_2 efflux while there were no statistical differences in other land-use changes. The observations of land-use change could be explained by differences in vegetation types and as Hudgens & Yavitt (1997) observed, interactions of numerous factors can introduce some uncertainty in the response of soil CO_2 efflux to land-use change.

Clear-cut harvesting reduced boreal soil CO_2 efflux while partial-cut harvesting reduced tropical soil CO_2 efflux, by probably influencing aboveground biomass. Site preparation also decreased boreal soil CO_2 efflux but increased temperate soil CO_2 efflux. These differences in the effects of harvesting and site preparation on different biomes may be attributed to the differences in aboveground biomass, time since harvesting, and environmental conditions which may take time to change after harvesting (Peng et al. 2008). Thinning, on the other hand increased total soil CO_2 efflux by affecting soil CO_2 efflux components. The creation of gaps in the canopy increases sunlight, which leads to warmer temperatures for microbial activity (Vesala et al. 2005; Lei et al. 2018) as was seen in this study. Thinning has been found to reduce root biomass and thereby decrease autotrophic soil CO_2 efflux in some studies (Sullivan et al. 2008; Ryu et al. 2009; Olajuyigbe et al. 2012) but this is in contrast to the finding of increased autotrophic soil CO_2 efflux in this meta-analysis. However, increased temperature may also increase autotrophic soil CO_2 efflux after thinning (Cheng et al. 2015), which is in agreement with these findings.

Other disturbances like fire, litter removal, and litter addition had similar effects across the boreal, temperate, and tropical forests. Fire reduced boreal soil CO_2 efflux in this meta-analysis and this agrees with the findings of several studies in which fire reduces autotrophic soil CO_2 efflux (Tan et al. 2012; Sun et al. 2014). Fire could reduce boreal and temperate soil CO_2 efflux by decreasing substrate availability, thereby reducing microbial activity and biomass as was seen in this study. In tropical forests, fire is not a natural disturbance and is only used for forest management purposes and so its effects may not be as noticeable in those regions as seen in boreal forests. Litter perturbations influences soil CO_2 efflux by increasing soil CO_2 efflux with increased litter and decreasing soil CO_2 efflux by reduced litter, altering substrate availability for microbial decomposition, thereby affecting the heterotrophic portion of total soil CO_2 efflux. Windthrow, on the other hand, increased only boreal soil CO_2 efflux possibly by providing more substrate for increased microbial activity and heterotrophic soil CO_2 efflux.

In general, the second chapter reveals gaps in our current knowledge of disturbance effects on soil CO_2 efflux and its components across boreal, temperate, and tropical forests. It shows that climate change will mostly increase soil CO_2 efflux but with appropriate forest management practices, some of the rapid increases by climate change may be curbed. However, due to the fast rate of climate change, forest management practices alone cannot mitigate the unprecedented increase of forest soil CO_2 efflux.

5.4 Temporal variability in the boreal mixedwood forest is explained primarily by soil temperature and moisture

In Chapter 3, temporal variation was mostly controlled by soil moisture and soil temperature. This means that seasonality, as expected, controls the temporal variation because of warmer temperatures and increased water availability. The conclusion generated from this study is that soil temperature and soil moisture affect temporal variation but has less effect on its spatial variation because environmental chemistry and species composition also influenced spatial variation. The species composition of the boreal mixedwood forest also plays an important role in its spatial variation because soil CO_2 efflux was significantly higher in patches dominated by shrubs. This could be explained by higher microbial activity in shrub-dominated patches, which may increase total soil CO_2 efflux by stimulating the heterotrophic component. This study was also able to generate the number of sample points within a 1-ha boreal mixedwood forest needed to estimate the true soil CO_2 efflux mean, which can be used as a guide for future soil sampling protocols.

5.5 Partitioning soil CO_2 efflux may be an appropriate method to identify underlying mechanisms

In Chapter 2 & 4, partitioning of soil CO_2 efflux into autotrophic and heterotrophic soil CO_2 efflux was useful in identifying possible underlying mechanisms. The meta-analysis in Chapter 2 revealed that the mechanism by which some disturbances affect soil CO_2 efflux. For example, warming increased heterotrophic soil CO_2 efflux but not autotrophic soil CO_2 efflux, suggesting that warming increases microbial biomass and activity. This is supported by some studies (Hartley et al. 2007; Schindlbacher et al. 2012; Wu et al. 2016; Wang et al. 2017) that found the warming effect on soil CO_2 efflux is mostly by increasing heterotrophic soil CO_2 efflux. Afforestation also showed that the differences in the response of boreal and temperate soil CO_2 efflux could be explained by the heterotrophic portion of soil CO_2 efflux. Chapter 2 found that land-use change affected temperate autotrophic soil CO_2 efflux but not boreal autotrophic soil CO_2 efflux. However, due to small sample sizes, it was difficult to identify the disturbance effects on soil CO_2 efflux.

In Chapter 4, partitioning total soil CO_2 efflux into heterotrophic and autotrophic soil CO_2 efflux shed more light on the source of spatial and temporal variation found in Chapter 3. Autotrophic soil CO_2 efflux exhibited more spatial variation than heterotrophic soil CO_2 efflux and this may be as a result of the roots of the different tree species within the forest. The underlying mechanism by which soil temperature mediates the spatial variation in this boreal mixedwood forest soil CO_2 efflux is by stimulating microbial biomass and activity in conjunction with other environmental variables such as DBH, basal area and pH. The spatial variation in autotrophic soil CO_2 efflux is controlled by DBH and dissolved organic nitrogen, meaning that nitrogen addition could stimulate this component as seen in some other studies (Bowden et al. 2004; Deng et al. 2010). While nitrogen addition has been found to have no significant change in forest soil CO_2 efflux in some studies (Zhou et al. 2014), this study shows that nitrogen addition may be instrumental in stimulating the autotrophic component of this boreal mixedwood forest. There was no relationship between temporal variation of AF_{CO_2} and soil temperature or moisture but soil temperature and moisture influenced temporal variation of HF_{CO_2}. This probably is due to temporal variation of AF_{CO_2} being more influenced by phenology (Ruehr and Buchmann 2009; Bronson and Gower 2010) while changes in environmental conditions stimulate heterotrophic activity within the soil. The effect of species composition on total soil CO_2 efflux is generated by its effect on the heterotrophic soil CO_2 efflux within this forest. Therefore, this chapter shows that the underlying mechanism by which species composition influences HF_{CO_2} in the study site is by affecting microbial composition and activity.

5.6 Recommendations and future research needs

First, the results of the meta-analysis revealed significant gaps in our current knowledge of disturbance effects across different forests. Some disturbances are more studied in certain forests but there is a lack of representation in other forests. This should be addressed in future soil CO_2 efflux research. This study also shows that while partitioning is important for identifying the underlying mechanisms of soil CO_2 efflux, many studies have not incorporated partitioning into studying the effects of disturbances on soil CO_2 efflux. By partitioning soil CO_2 efflux response to disturbances, researchers can better understand how each component reacts to changes in the environment.

Second, further research needs to be carried out on the spatial and temporal variation of boreal mixedwood forests, especially in the western part of Canada. This study quantified soil CO_2 efflux in a 1-ha boreal mixedwood plot but more studies within the area are needed to help in accurate estimation of the regional carbon budget. The results also show that estimating mean soil CO_2 efflux within 10% error limit requires approximately 45 points within a 1-ha area and may be sufficient to quantify soil CO_2 efflux of the area. More studies of sample size requirement can help researchers establish guidelines of sampling effort within the boreal mixedwood region.

Third, there should be more partitioning studies in boreal mixedwood forests and across all forests as this study shows that the factors affecting the spatial and temporal variation of autotrophic and heterotrophic soil CO_2 efflux differ. This finding will help in identifying the underlying mechanisms of spatial and temporal variation of total soil CO_2 efflux across boreal mixedwood forests.

5.7 Literature Cited

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Appendix

Appendix A1 Search Terms used in the meta-analysis for locating disturbance experiments in the Web of Science database from 1900 to June 2018 (Thomas Reuters, New York, NY, USA). Number of publications generated by the search in parentheses

Disturbance Types	Search Terms
Climate Change (5,318)	TS=((soil respiration OR soil CO2 OR carbon dynamics OR soil carbon dioxide OR soil carbon efflux OR soil carbon flux* OR soil carbon emission OR root respiration OR autotrophic respiration OR heterotrophic respiration OR microb* respiration) AND (drought OR decreas* precipitation OR precipitation decreas* OR decreas* rain OR rain decrease* OR exclu* precipitation OR precipitation exclu* OR exclu* rain OR rain exclu* OR throughfall OR precipitation reduc* OR reduc* precipitation OR wet treat* OR increas* precipitation OR precipitation increas* OR add* water OR water add* OR irrigat* OR precipitation enhance* OR rain OR warm* OR temperature increas* OR temperature elevat* OR FACE OR Free-Air enrichment OR CO2 enrich*) AND (boreal OR temperate OR tropical) AND (forest))
Land Use (3,191)	TS=((soil respiration OR soil CO2 OR carbon dynamics OR soil carbon dioxide OR soil carbon efflux OR soil carbon flux* OR soil carbon emission OR root respiration OR autotrophic respiration OR heterotrophic respiration OR microb* respiration) AND (deforestation OR degrad* OR land use OR conver*) AND (boreal OR temperate OR tropical) AND (forest))
Forest Management (2,665)	TS=((soil CO2 OR soil carbon dioxide OR soil carbon efflux OR soil carbon emission OR root respiration OR autotrophic respiration OR microb* respiration OR belowground respiration OR heterotrophic respiration) AND (harvest* OR thinn* OR log* OR understory OR litter* OR input OR biochar OR manag* OR

	clear cut* OR clearcut* OR burn OR slash*) AND (boreal OR temperate OR tropical) AND (forest))
Natural Disturbances (1,289)	TS=((soil CO2 OR Soil carbon dioxide OR soil carbon efflux OR soil carbon emission OR root respiration OR autotrophic respiration OR microb* respiration OR belowground respiration OR heterotrophic respiration) AND (fire OR storm OR wind* OR insect OR hurricane OR typhoon OR acid* OR flood* OR herbivore OR omnivore OR beetle) AND (boreal OR temperate OR tropical) AND (forest))

Appendix A2 Classification of Disturbance Types into climate change, forest management, land-use change, natural disturbances, and litter perturbations

Climate Change	**Forest Management**	**Land-Use Change**	**Other Disturbances**
Warming	Harvesting	Afforestation	***Natural Disturbances***
Elevated CO_2	Thinning	Forest-to-Cropland	Fire
Added precipitation	Site Preparation	Land Degradation	Windthrow
Drought		Forest-to-Plantation	
		Forest-to-Grassland	***Litter Perturbations***
			Litter removal
			Litter addition

Appendix A3 Site Details of the data used in the meta-analysis. The country, site, latitude, longitude, type of disturbance, n (number of data units extracted from each paper) and the study from which they are obtained. The disturbance types in our meta-analysis include land use (LU), afforestation (Aff), drought (Dr), thinning (Thin), FACE (free-air carbon enrichment), windthrow (Win), harvest (Har), water addition (WA), warming (Warm), litter manipulation (LM), site preparation practices (SP), and forest management (FM).

Country	Site	Coordinates	Disturbance	n	References
Boreal Ecosystems					
Canada	Linaria, Alberta	54.20, -114.13	LU, Aff	12	Arevalo et al. (2010)
Canada	FRCN, Quebec	49.27, -74.34	Har	1	Bergeron et al. (2008)
Canada	BSAWE, Manitoba	55.88, -98.33	Warm	2	Bronson et al. (2008)
Sweden	Flakaliden	64.12, 19.45	Warm, FACE	3	Comstedt et al. (2006)
Canada	Goose Bay, Labrador	53.74, -59.57	Har, Fire	2	Hagemann et al. (2010)
Russia	Pushchino, Moscow	54.83, 37.58	LU	4	Larionova et al. (1998)
Canada	Eskwanonwatin Lake, Ontario	49.17, -88.65	Har, SP	3	Mallik & Hu (1997)
Finland	Mekrijarvi Res. Station	62.78, 30.97	Warm, FACE	3	Niinisto et al. (2004)
USA	Tetlin Junction, Alaska	63.31, -142.60	Fire	1	O'Neill et al. (2003; 2006)
USA	Hajdukovich, Alaska	63.86, -145.20	Fire	1	O'Neill et al. (2003; 2006)
USA	Tok Junction, Alaska	63.33, -142.95	Fire	1	O'Neill et al. (2003; 2006)
USA	Delta Junction, Alaska	63.92,-145.73	Fire	1	O'Neill et al. (2003; 2006)
Canada	Aleza Lake Res. For., B.C.	54.02,-122.12	Har	7	Pypker & Fredeen (2003)
Canada	BOREAS, Prince Albert, Sask.	53.92, -104.69	Har	1	Streigl & Wickland (1998)
Sweden	Fagelfors, South Sweden	57.22, 25.83	Har	4	Stromgren & Mjofors (2012)
Russia	Yakutsk, Siberia	62.32, 129.50	Fire, Har	2	Takakai et al. (2006)
Canada	Chapleau, Ontario	47.70, -83.60	Har, SP	8	Webster et al. (2016)
Finland	Southern Finland	61.80, 24.32	Har, SP	5	Pumpanen et al. (2004)
USA	Tok Junction, Alaska	63.33, -142.95	Fire	3	O'Neill et al. (2002)

China	Heilongjiang	51.09, 125.13	Fire	9	Tan et al. (2012)
Canada	BOREAS, Manitoba	56.15, -96.73	Fire	4	Burke et al. (1997)
Canada	BOREAS, Saskatechewan	53.85, -104.63	Har	4	Howard et al. (2004)
Canada	BOREAS, Manitoba	55.91, -98.23	Fire	4	Czimczik et al. (2006)
USA	CPCRW, Alaska	65.18, -147.27	Fire	5	Kim & Tanaka (2003)
Finland	Mekrijarvi Res. Stat.	62.78, 30.97	FACE, Warm	4	Pajari et al. (1995)
Finland	SMEAR II	61.87, 24.28	Fire, Har	2	Kulmala et al. (2014)
USA	Delta Junction, Alaska	63.92, -145.73	Warm	1	Allison & Treseder (2008)
USA	Delta Junction, Alaska	63.92, -145.73	Warm	1	Allison et al. (2010)
USA	Delta Junction, Alaska	63.92, -145.73	Warm, Fire	3	Bergner et al. (2004)
USA	Thompson, Manitoba	63.92, -145.73	Warm	2	Bronson & Gower (2010)
Canada	Al-Pac Mill, Alberta	54.98, -113.52	Aff	2	Chang et al. (2016)
Canada	Athabasca OSR, Alberta	56.72, -111.35	Fire	2	Das Gupta & Mackenzie (2016)
USA	Central Alaska	63.92, -145.73	Warm	1	German & Allison (2015)
USA	Fairbanks, Alaska	64.85, -147.72	LU	4	Grünzweig et al. (2003)
Estonia	Tudu	59.18, 26.87	Wind	4	Köster et al. (2011)
Estonia	Halliku	58.72, 26.92	Wind	1	Köster et al. (2011)
Estonia	Slitere National Park	57.62, 22.32	Wind	1	Köster et al. (2011)
Finland	Varrio SNR	67.77, 29.58	Fire	3	Köster et al. (2014)
Canada	Tshiigetchic, NWT	67.43,-133.75	Fire	1	Köster et al.(2017)
Canada	Eagle Plains, Yukon	66.37, -136.72	Fire	2	Köster et al.(2017)
Estonia	Jarvelsja	58.25, 27.27	Har	4	Kukumägi et al. (2017)
Russia	Evenkia, Siberia	64.23, 100.17	Fire	4	Masyagina et al. (2015)
Sweden	Central Sweden	60.98, 16.40	SP	3	Mjofors et al. (2015)
Russia	Odintsovo, Moscow	56.13, 37.43	Har	2	Molchanov et al. (2017)
USA	Fairbanks, Alaska	65.17, -147.47	Fire	3	Morishita et al. (2015)
Canada	Pasadena, Newfoundland	48.97, -63.63	Har	6	Moroni et al. (2009)

Mongolia	ILTER	51.02, 100.75	WA, Warm	6	Sharkhuu et al. (2016)
Canada	BERMS, Saskatchewan	54.08, -106.00	Fire, NL	5	Singh et al. (2008)
Russia	Yekaterinburg	56.85, 60.61	LU	3	Smorkalov & Vorobeichik (2015)
China	DaXing'anling Mountains	51.89, 121.91	Fire	2	Song et al. (2017)
Canada	BOREAS, Prince Albert, Saskatchewan	53.88, -104.65	Har	2	Streigl & Wickland (1998)
Sweden	Strada	54.00, 15.00	Har	1	Strömgren et al. (2012)
Sweden	Several sites	NA	Har, SP	7	Strömgren et al. (2017)
Canada	BOREAS, Manitoba	55.80, -97.87	Fire	6	Wang et al. (2003)
China	Daxing'an Mountains	51.09, 125.13	Fire	2	Hu et al. (2017)
Canada	Chibougamau, Quebec	49.27, -74.04	Har	2	Payeur-Poirer et al. (2012)
Russia	Valdai Upland	58.27, 33.23	LU	4	Lyuri et al. (2013)
Sweden	Flakaliden	64.12, 19.45	Warm	2	Strömgren et al. (2001)
Finland	Juupajoki	61.84, 24.29	SP	10	Pearson et al. (2012)
Estonia	Vihterpalu	59.18, 23.77	Fire	5	Köster et al. (2016)
Canada	Wandering River, Alberta	55.35, -112.52	Warm	2	Munir et al. (2015)
Temperate Ecosystems					
USA	Duke Forest	35.97, -79.08	FACE	1	Bernhardt et al. (2006)
USA	Central Maine	45.17, -68.67	Warm	1	Rustad & Fernandez (1998)
USA	Minnesota	46.5, -91.03	Har, Fire	3	Euskirchen et al. (2003)
Turkey	Istanbul	41.15, 28.99	Thin	1	Akburak & Makineci (2015)
USA	Coast Range, Oregon	45.46, -123.85	Har	3	Campbell & Law (2005)
USA	West Cascades, Oregon	44.73, -122.58	Har	3	Campbell & Law (2005)
USA	East Cascades, Oregon	44.48, -121.64	Har	3	Campbell & Law (2005)

USA	Tyler County, Texas	30.65, -94.08	CC, Har	2	Londo et al. (1999)
Ireland	Co. Laois, Irish midlands	52.95, -7.25	Thin	1	Olajuyigbe et al. (2012)
USA	Stone Valley, Pennsylvania	40.67, -77.90	Warm, WA	3	McDaniel et al. (2014)
USA	FACTS-II, Rhinelander, Wisconsin	45.68, -89.63	FACE	6	Pregitzer et al. (2008)
USA	Duke Forest, North Carolina	35.97, -79.08	FACE	1	Allen et al. (2000)
USA	Chesapeake Bay, MD	36.88, -76.55	FACE	3	Ball & Drake (1998)
UK	Northumberland, England	55.17, -2.05	Har	1	Zerva & Mencuccini (2005)
USA	Northern Arizona	35.09, -111.76	Aff, Thin	2	Sullivan et al. (2008)
USA	Arizona	34.16, -111.76	WA, Aff	3	Selmants et al. (2008)
China	Maoxian Mountain Ecosystem, Sichuan	31.62, 103.90	Thin	2	Pang et al. (2013)
USA	Prospect Hill, Harvard Forest, MA	42.53, -72.18	Dr	1	Borken et al. (2006)
USA	Duke Forest, NC	35.97, -79.08	FACE	2	Jackson et al. (2009)
USA	FACTS-II, Rhinelander, Wisconsin	49.68, -89.63	FACE	4	Pregitzer et al. (2006)
Switzerland	SCC FACE, Basel	47.47, 7.51	FACE	1	Bader et al. (2010)
Switzerland	Basel	47.55, 7.60	FACE	1	Mildner et al. (2015)
USA	Duke Forest, NC	35.97, -79.08	FACE	1	Taneva & Gonzalez-Meler (2011)
USA	Norfolk, Connecticut	42.88, -72.28	WA	1	Wu & Lee (2011)
USA	Duke Forest, NC	35.80, -76.67	Dr	1	Noormets et al. (2010)
Japan	Hokkaido University	42.67, 141.60	Warm	3	Noh et al. (2016)
Germany	*Coulissenhieb II*	50.13, 11.70	Dr	1	Muhr & Borken (2009)
Australia	Wombat State Forest, Victoria	-37.42, 144.09	Dr	1	Hinko-Najera et al. (2015)
China	BNR, Henan Province	33.33, 111.78	Warm, Dr	9	Liu et al. (2016)
New Zealand	Purukohukohu Expt. Catch.	-38.60, 176.22	Har	2	Tate et al. (2006)

USA	MOFEP, Missouri	37.10, -91.20	Har	2	Xu et al. (2011)
China	GFF, Heilongjiang Province	55.17, 124.12	Fire	2	Sun et al. (2014)
China	Baoying Ag. Farm, Jiangsu Province	33.37, 119.25	Thin	3	Fang et al. (2016)
Spain	Galicia	43.15, -7.75	Thin	2	Fernandez et al. (2012)
Spain	Spain	NA	LU	2	Merino et al. (2004)
China	BNR, Henan Province	33.33, 111.78	Aff	1	Luan et al. (2012)
Japan	Teshio Expt. For.	44.92, 142.02	Warm	1	Aguilos et al. (2011)
USA	Duke Forest, NC	35.97, -79.08	FACE	1	Andrews & Schlesinger (2001)
Germany	Solling	51.52, 9.57	Dr	1	Borken et al. (1999)
USA	Harvard Forest, Massachusetts	42.83, -72.30	Warm	1	Contosta et al. (2011)
USA	MOFEP, Missouri	37.10, -91.20	Har	11	Concilio et al. (2005)
USA	Flagstaff, Arizona	35.45, -111.77	Fire, Thin	4	Dore et al. (2010)
USA	Duke Forest, NC	35.97, -79.08	FACE	5	Drake et al. (2012)
China	BNR, Henan Province	30.33, 111.78	Dr	3	Lu et al. (2017)
Hungary	Sikfokut Expt. For.	47.92, 20.43	LM	3	Fekete et al. (2014)
Australia	FESA Victoria	-37.48, 144.08	Fire	2	Fest et al. (2015)
USA	Oak Ridge, Tennessee	35.90, -84.24	FACE, Warm	6	Garten et al. (2009)
USA	Duke Forest, NC	35.97, -79.08	FACE	1	George et al. (2003)
USA	Oak Ridge, Tennessee	35.90, -84.24	FACE, Warm	1	George et al. (2003)
China	Xinjiang	44.33, 81.387	Aff	2	Gong et al. (2012)
USA	UMBS, Michigan	45.58, -84.72	Har	8	Gough et al. (2007)
China	Heilongjiang LNNR	47.18, 128.89	Har, LU	9	Han et al. (2018)
USA	Duke Forest, NC	35.97, -79.08	FACE	1	Hamilton et al. (2002)
USA	Georgia	34.65, -85.35	Warm	1	Hubbard et al. (2004)
USA	Ithaca, NY	42.5, -76.5	LU	3	Hudgens & Yavitt(1997)
USA	Trumansburg, NY	42.5, -76.5	LU	3	Hudgens & Yavitt(1997)

USA	Michigan Tech U. FFC	46.64, -88.48	Warm, WA	3	Jarvi & Burton (2013)
USA	Gus Pearson Nat. Area, Flagstaff, AZ	35.27, -111.70	Fire	2	Kaye & Hart (1998)
Korea	Sambong Exp. For.	35.45, -127.64	Har	1	Kim (2008)
USA	WRCCRF, Washington	45.83, -121.90	Har	2	Klopatek (2002)
Canada	Lakevale, Nova Scotia	45.75, -61.95	Har	1	Lavoie et al. (2013)
Canada	Pomquet, Nova Scotia	45.66, -61.84	Har	1	Lavoie et al. (2013)
USA	Oregon	44.43, -121.57	Har	1	Law et al. (2001)
Korea	Seoul, South Korea	37.59, 127.03	Warm, Dr, WA	5	Li et al. (2017)
USA	Duke Forest, NC	35.97, -79.08	FACE	1	Matamala & Schlesinger (2000)
USA	VFEF, Ohio	39.18, -82.33	Fire, LM	4	McCarthy & Brown (2006)
USA	Harvard Forest, Massachusetts	42.83, -72.30	Warm	1	Melillo et al. (2002)
USA	Harvard Forest, Massachusetts	42.83, -72.30	Warm	1	Melillo et al. (2011)
Germany	Jena, Thuringia	50.8, 41.58	Fire	1	Näthe et al. (2018)
Japan	Yoshiwa	34.18, 132.13	Har	2	Nakane et al. (1996)
Japan	Takayama field Station	36.13, 137.42	Warm	2	Noh et al. (2017)
USA	Duke Forest, NC	35.97, -79.08	FACE	1	Oishi et al. (2014)
USA	LTSP, Missouri	37.02, -93.21	Har	2	Ponder Jr. (2005)
France	Barbeau Nat. Forest, Paris	45.58, -84.72	LM	2	Prevost-Boure et al. (2010)
USA	Arizona	35.30, -111.59	Fire, WA	9	Ross et al. (2012)
Ireland	Dooray Forest	52.9, -7.25	Aff	3	Saiz et al. (2006)
Austria	Archenkirch	47.58, 11.64	Warm, Dr	3	Schindlbacher et al. (2012)
Austria	Western Austria	47.58, 11.64	Warm	1	Schindlbacher et al. (2009)
Canada	Haliburton Forest	45.22, -78.58	Har	1	Peng & Thomas (2006)

Canada	Haliburton Forest	45.22, -78.58	Har	2	Shabaga et al. (2015)
China	LNR, Heilongjiang	47.18, 128.89	Har, LU	9	Shi et al. (2015)
Korea	Yangpyeong Expt. For.	37.55, 127.57	Thin	3	Son et al. (2004)
USA	Flambeau River State For. Wisconsin	45.62, -90.79	Har	2	Stoffel et al. (2010)
USA	Flagstaff, Arizona	35.45, -111.77	Thin, Fire	2	Sullivan et al. (2010)
China	Changbai FES, Chinese Acad. Of Sci	42.40, 128.08	FACE	1	Sun et al. (2017)
Japan	Teshio Expt. For.	45.05, 142.10	Har	1	Takagi et al. (2009)
USA	United States	NA	Thin	2	Templeton et al. (2015)
Japan	Hirosaki University	40.52, 140.22	Warm	1	Teramoto et al. (2018)
Japan	Kyushu	31.85, 131.30	Warm	1	Teramoto et al. (2016)
China	Hebei Province	42.17, 117.20	LU	4	Wang et al. (2013)
China	Laoshan Expt. Station	45.35, 127.58	Thin	2	Wang et al. (2013)
Japan	Takayama field station	36.13, 137.42	Har	2	Yashiro et al. (2012)
USA	Lower Michigan	44.50, -84.50	Fire	9	Yermakov & Rothstein (2006)
UK	Oxfordshire	51.78, -1.33	LM	2	Bréchet et al. (2018)
China	Jilin Province	42.40, 128.08	FACE	1	Zhou et al. (2010)
USA	Northern Minnesota	47.00, -92.40	Har	5	Kurth et al. (2014)
Canada	Ontario	47.05, -87.40	Har	3	Laporte et al. (2003)
USA	Maine	45.67, -69.17	CC	1	Lytle & Cronan (1998)
USA	CFC, Minnesota	46.68, -92.52	Warm, Dr	5	Martins et al. (2017)
USA	HWRC, Minnesota	47.95, -91.76	Warm, Dr	5	Martins et al. (2017)
China	Laoshan Station, MEFF	45.33, 127.57	Har	1	Zu et al. (2009)
Switzerland	South Switzerland	46.17, 9.00	Fire	2	Wüthrich et al. (2002)
Canada	Montreal	45.56, -73.18	Har	2	Ullah & Moore (2011)
Nepal	Mardi Watershed	28.25, 83.94	LU	3	Awasthi et al. (2005)
China	Hubei Province	29.03,113.52	LU	3	Iqbal et al. (2008)

China	TGRA, Zugui Area	30.63, 110.30	LU	6	Iqbal et al. (2010)
China	Sichuan Basin	31.27, 105.47	LU	2	Wang et al. (2008)
China	Huitong Nat. Res. Station	26.83, 109.83	LMan	2	Wang et al. (2013)
China	Jiangsu Province	31.98, 119.23	LU	1	Shi et al. (2009)
China	Yizhou State For. Cen., Fujian Province	26.12, 117.45	Har	4	Guo et al. (2010)
China	Hangzhou	30.23, 120.15	LU	4	Fan et al. (2015)
China	Dexing County, Jiangsu Province	29.13, 117.92	Har	1	Ma et al. (2013)
China	Guantangyi F.F., Hubei Province	29.71, 113.88	Har	3	Tang et al. (2016)
China	Xinkou Expt. For. Cen. Fujian	26.19, 117.43	LU	2	Yang et al. (2007)
China	Hunan Province	26.83, 109.75	Thin	1	Tian et al. (2009)
China	Yizhou State For. Cen. , Fujian Province	26.12, 117.45	Har, Fire	12	Guo et al. (2016)
China	Sanming, Fujian	25.18, 117.47	LU	2	Guo et al. (2016)
China	Shankou Township, Linan city	30.23, 119.70	LU	3	Hu et al. (2018)
China	Jiulingtou F. F., Hubei Province	30.98, 110.78	Thin	6	Lei et al. (2018)
USA	Meritt Island Nat. Wildlife Res. Miami	28.63, 117.47	FACE	1	Li et al. (2007)
China	FEGCRS, Fujian Province	26.16, 117.47	LM	4	Liu et al. (2017)
China	Zhejiang Province	30.37, 120.30	LU	2	Liu et al. (2011)
China	Jian’ou, Fujian province	27.02, 118.12	LU	5	Sheng et al. (2010)
China	CAS, Sichuan	30.73, 103.54	LM	2	Wang et al. (2015)
China	Zhejiang Province	30.25, 119.84	Har	3	Wang et al. (2018)
China	Huitong Nat. Res. Stat., Hunan	26.67, 109.43	LM	2	Wang et al. (2013)
China	Wulongchi Expt. Stat.	32.75, 111.22	LM	4	Wu et al. (2017)

China	Hunan Province	28.10, 113.03	LM	6	Yan et al. (2013)
China	Wulongchi Expt. Stat.	32.75, 111.22	LU	2	Zhang et al. (2018)
Australia	Tohey Forest, Brisbane	-27.50, 135.03	Fire	1	Zhao et al. (2015)
USA	Oregon	44.44, -121.61	CC	3	Law et al. (2003)
Japan	Nagano Prefecture	36.33, 138.55	Har	2	Matsushita et al. (2015)
Austria	Hollengebirge	47.79, 13.64	Win	4	Mayer et al. (2017)
USA	Anna & Archer Hun. W.F., NY	43.98, -74.23	Warm	3	McHale et al. (1998)
USA	Harvard Forest, Massachusetts	42.83, -72.30	Win	2	Millikin & Bowden (1996)
Korea	Korea University, Seoul	37.59, 127.03	Warm	2	Noh et al. (2016)
Canada	Halliburton Forest, Ontario	45.29, -78.64	Har	6	Shabaga et al. (2017)
USA	Morgan County, Ohio	39.99, -82.33	Aff, LU	4	Shrestha et al. (2009)
USA	Coconico Nat. For., Arizona	35.45, -111.77	Fire	1	Sullivan et al. (2011)
China	Nanjing city, Jiangsu Province	31.98, 118.85	LU	1	Sun et al. (2014)
Japan	Hiroshima University	34.40,132.73	FACE, Warm	10	Wang et al. (2012)
China	Jiufeng Nat. For. Park, Beijing	40.06, 116.10	LM	2	Xiao et al. (2015)
China	Maoxian MERS	31.62, 103.88	Warm	1	Xu et al. (2017)
China	Pingyuan Forestry Farm	43.75, 81.15	SP, WA	6	Yan et al. (2011)
China	Pingyuan Forestry Farm	43.75, 81.15	WA	6	Yan et al. (2014)
USA	Oklahoma	34.02,-94.82	Dr	2	Zhang et al. (2016)
Switzerland	Davos	46.80, 9.84	Warm	1	Hagedorn et al. (2010)
Switzerland	Davos	47.47, 7.50	FACE	1	Hagedorn et al. (2013)
Switzerland	Davos	46.80, 9.84	Warm	1	Streit et al. (2014)
Canada	Lakevale, Nova Scotia	45.75, -61.95	Har	1	Kellman et al. (2015)
Canada	Pomquet, Nova Scotia	45.75, -61.95	Har	1	Kellman et al. (2015)
Austria	Rax Mountain Area	47.73, 15.69	Win	2	Mayer et al. (2014)

Austria	Hollengebirge	47.73, 15.69	Win	2	Mayer et al. (2014)
China	Linkong Mountain Nature Reserve, Shanxi Province	36.52, 112.02	Thin	9	Cheng et al. (2015)
Germany	Swabian Jura	47.98, 8.75	Thin	3	Dannenmann et al. (2007)
USA	Manistee National Forest, Michigan	44.80, -85.80	Har	2	Toland & Zak (1994)
USA	Harvard Forest, Massachusetts	42.50, -72.17	Warm	1	Peterjohn et al. (1994)
USA	Maine	44.85, -70.53	Har	1	Fernandez et al. (1993)
USA	Eastern Cascades, Oregon	44.43, -121.57	Har	1	Irvine & Law (2002)
USA	Durham, NC	35.97, -79.08	FACE	1	King et al. (2004)
USA	Rhinelander, WI	45.67, -89.62	FACE	2	King et al. (2004)
USA	ORNL, TN	35.9, -84.33	FACE	1	King et al. (2004)
Italy	POPFACE, Tuscania	42.37, 11.8	FACE	3	King et al. (2004)
Austria	National Park Kalkalpen	47.84, 14.44	Win	3	Kobler et al. (2015)
USA	Oregon	44.44, -121.61	Har	3	Law et al. (2003)
Tropical Ecosystems					
China	DBR, Guangdong	23.17, 112.17	LMan	6	Han et al. (2015)
China	Ailaoshan Station, Jingdong, Yunnan	24.53, 101.02	LMan, Warm	2	Wu et al. (2016)
China	DBR, Guangdong	23.17, 112.17	LM	3	Fang et al. (2015)
China	Guanzhou, Guangdong	23.33, 113.50	FACE	1	Liu et al. (2010)
China	DBR, Guangdong	23.17, 112.17	Aff	4	Huang et al. (2016)
Phillipines	Laguna	14.15, 121.18	LU	1	Bae et al. (2013)
Mexico	Cofre de Perote Volcano	19.50, -96.99	LU	2	Adolfo (2006)
China	Guangdong Province	23.16, 112.23	WA	3	Deng et al. (2012)
China	Guangzhou	23.33, 113.5	FACE	1	Deng et al. (2013)
China	Guangdong	23.33, 113.5	FACE	1	Liu (2011)

Costa Rica	Gulfo Dulce For. Res.	8.72, -83.62	LM	2	Leff et al. (2012)
Zambia	Kataba Forest Reserve	-15.43, 23.25	Har	2	Merbold et al. (2011)
Puerto Rico	Luquillo Expt. Forest	18.3, -65.83	LU, LM	7	Li et al. (2005)
China	Guangdong Province	23.16, 112.23	Aff	2	Tang et al. (2006)
China	DBR, Guangdong Province	23.15, 112.52	LM	3	Yan et al. (2006)
China	DBR, Guangdong Province	23.16, 112.51	Aff	2	Yi et al. (2007)
Costa Rica	Gulfo Dulce For. Res.	8.72, -83.62	Dr	2	Cleveland et al. (2010)
Brazil	Fazenda Nova Vida	-10.17, -62.82	LU	3	Fernandes et al. (2002)
China	DBR, Guangdong Province	23.15, 112.52	LM	3	Yan et al. (2009)
Puerto Rico	Luquillo Expt. Forest	18.38, -65.72	LM, LU	5	Li et al. (2004)
Puerto Rico	Luquillo Expt. Forest	18.38, -65.72	LU	2	Li et al. (2006)
Indonesia	Sumatra	-1.05, 102.15	Fire, Har, LU	5	Ishizuka et al. (2002)
China	Guangzhou	23.33, 113.50	FACE	1	Deng et al. (2010)
China	Xishuangbanna	21.92, 101.27	Dr	1	Zhang et al. (2015)
Indonesia	Sulawesi	-1.49, 120.06	Dr	1	van Straaten et al. (2011)
China	DNR, Guangdong	23.16, 112.23	Dr, WA	6	Jiang et al. (2013)
Brazil	Tapajos Nat. For.	-2.90, -54.95	Dr	1	Davidson et al. (2008)
Malaysia	Paosh	2.97, 102.27	Har	1	Yashiro et al. (2008)
China	Yunnan Province	21.82, 100.83	LU	2	Wu et al. (2016)
Malaysia	Negeri Sembilan	3.01, 102.24	LU, Aff	3	Mande et al. (2014)
Brazil	Para State	-2.93, -47.52	Har, LU	3	Davidson et al. (2000)
Brazil	Para State	-2.90, -54.95	Dr	1	Brando et al. (2008)
Brazil	Mato Grosso	-12.69, -55.36	Fire	2	Brando et al. (2016)
Panama	Gigante Peninsula	9.1, -79.90	LM	2	Bréchet et al. (2018)
Brazil	Para State	-2.98, -47.52	Dr	1	Cattânio et al. (2002)
China	Guangzhou	23.33, 113.50	FACE	1	Chen et al. (2012)
Brazil	Para State	-1.72, -51.45	Dr	3	da Costa et al. (2014)

Brazil	Tapajos Nat. Forest	-2.90, -54.95	Dr	1	Davidson et al. (2004)
China	DBR, Guangdong	23.17, 112.17	Dr, WA, LMan	5	Deng et al. (2018)
Brazil	Santa Virginia	-23.41, -45.25	LU	1	do Carmo et al. (2012)
Congo	Pointe Noire	-4.35, 11.75	Aff	1	Epron et al. (2006)
China	Naban River Watershed	22.07, 100.53	LU	1	Goldberg et al. (2017)
Indonesia	Jambi Province	-1.05, 102.15	LU	6	Hassler et al. (2015)
China	Jianfengling, Hainan Island	18.73, 108.85	CC	2	Jiang et al. (2017)
Brazil	Tapajos Nat. Forest	-3.04, -54.95	Har	6	Keller et al. (2005)
French Guiana	Paracou	5.25, -52.92	Aff, Har	2	Janssens et al. (1998)
India	India	23.62, 92.53	Aff	2	Lalnunzira & Tripathi (2018)
China	Xishuangbanna	21.91, 101.27	LU	3	Lang et al. (2017)
Puerto Rico	Caribbean Nat. Forest	18.30, -65.33	LU	1	Liu & Zou (2002)
China	Heshan Hilly LIES, Guangdong	22.68, 112.90	LU, LM	2	Liu et al. (2008)
Malaysia	Dermakot Forest Reserve	5.23, 117.18	Har	1	Mori et al. (2017)
Brazil	Tapajos Nat. Forest	-2.90, 54.95	Dr	1	Nepstad et al. (2002)
Puerto Rico	Luquillo Expt. Forest	18.3, -65.83	Dr	3	O’Connell et al. (2018)
Malaysia	Lambir Hills Nat. Park	4.2, 114.03	Dr	1	Ohashi et al. (2014)
Brazil	Brazilian Amazon Basin	-9.88, -67.07	LU	11	Salimon et al. (2004)
Panama	BCI	9.15, -79.85	LU	1	Schwendenmann et al. (2007)
Panama	Sardinilla	9.32, -79.63	LU	1	Schwendenmann et al. (2007)
India	Uttar Pradesh	25.15, 82.58	LU	3	Singh et al. (2015)
Brazil	Para	-1.72, -51.46	Dr	1	Sotta et al. (2007)
Brazil	Castanhal	-1.32, -47.95	WA, LMan	2	Vasconcelos et al. (2004)

China	Chinese Academy of Forestry	22.08, 107.43	Warm	3	Wang et al. (2017)
China	Xishuangbanna	21.92, 101.27	Har, LU, WA	3	Werner et al. (2006)
Puerto Rico	Bisley Research Watershed	18.30, -65.83	Dr	3	Wood & Silver (2012)
China	Xishuangbanna	22.07, 100.53	LU	1	Zhao et al. (2018)
Indonesia	Central Kalimantan	-2.32, 114.02	Fire, LU	5	Arai et al. (2014)
Southeast Asia	Southeast Asia	NA	LU	6	Hergoualc'h & Verchot (2014)
Indonesia	Tanjung Putting Nat. Park	-2.79, 11.82	LU	4	Hergoualc'h et al. (2017)
Indonesia	Gambut, South Kalimantan	-3.43, 114.67	LU	2	Inubushi et al. (2003)
Panama	Sardinilla	9.32, -79.63	LU	1	Pendall et al. (2010)
Panama	BCI	9.15, -79.63	LU	1	Pendall et al. (2010)
Panama	BCI	9.15, -79.85	LM	2	Sayer et al. (2007)
China	DBR, Guangdong	23.17, 112.17	Warm	1	Li et al. (2017)