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Spatial and temporal drivers of soil respiration in a tundra environment

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Tiivistelmä/Referat – Abstract

Arktisten alueiden maaperään on varastoitunut merkittäviä määriä hiiltä, joka on peräisin kasvillisuudesta. Hiiltä vapautuu maaperästä respiraatiossa kasvien juurten ja maaperän mikrobien hajotustoiminnan seurauksena. Pohjoisen pallonpuoliskon tundra-alueilla ekosysteemiin fotosynteesin kautta sitoutunut hiilen määrä on ollut suurempi kuin respiraatiossa ilmakehään vapautuvan hiilen määrä. Kylmien ja kosteiden olosuhteiden ansiosta arktiset maaperät ovat olleet merkittävä hiilen nielu. Lämpötilojen globaali nousu ja muutokset hydrologiassa ovat kuitenkin aiheuttaneet muutoksia hiilen kierrossa maaperän ja ilmakehän välillä. Arktiset alueet ovat erityisen herkkiä muutoksille, ja ne saattavat synnyttää voimakkaita takaisinkytkentöjä ilmaston lämpenemiseen. Tekijät, jotka säätelevät maaperän respiraatiovuota, tunnetaan heikosti, erityisesti niiden keskinäiset suhteet erilaisissa ympäristöissä ja niiden ajallinen dynamiikka. Maaperän respiraation ymmärtäminen prosessina on erittäin tärkeää, jotta voitaisiin paremmin ymmärtää ja ennustaa tulevia muutoksissa hiilen kierrossa globaalisti.

Tämän tutkimuksen tavoitteena oli tunnistaa maaperän respiraatiota sääteleviä ympäristötekijöitä tundralla maisemamittakaavalla ja niiden merkitystä kasvukauden eri vaiheissa. Tutkimusalue oli kahden tunturin välinen laakso Kilpisjärvellä, käsivarren Lapissa. Maaperän respiraatiota mitattiin käyttäen kammiomenetelmää sadalla tutkimuspisteellä 3 x 2 km alueella kolmesti kesän 2018 aikana. Alueelta kerättiin myös ympäristöaineistoa maaperän mikroilmastosta ja kasvillisuuden ominaisuuksista. Ympäristötekijöiden vaikutusta respiraatioon tarkasteltiin yleistetyillä lineaarisilla malleilla käyttäen erilaisia selittävien muuttujien yhdistelmiä. Tulokset osoittivat, että runsas kasvillisuus indikoi korkeaa respiraatiota, koska kasvien karike ja juuristo tuottavat maaperän mikrobeille hajotettavaa ainesta ja muita resursseja, kuten ravinteita. Suurin respiraatio mitattiin kasvukauden huippuna, jolloin korkea lämpötila aiheutti respiraation kasvua tutkimuspisteillä, jotka sijaitsivat tundraniityillä. Kasvillisuus ja maaperän laatu säätelevät siis myös respiraation lämpötilavastetta. Respiraatiovuo kasvoi lämpimässä vain paikoilla, joilla oletetaan olevan riittävästi ravinteita ja hajotettavaa aineista, jotta korkeampi respiraatio on mahdollinen. Tämän tutkimuksen mukaan maisemamittakaavalla kasvillisuuden tarjoamat resurssit ovat respiraatiolle tärkeämpiä kuin ilmastolliset tekijät sekä alueellisesti että ajallisesti. Jatkossa respiraatiotutkimus vaatii lisää empiiristä aineistoa, jotta tulevaisuuden muutoksia voidaan tarkemmin mallintaa. Etenkin respiraation valtavaan alueelliseen ja ajalliseen vaihteluun tulee kiinnittää huomiota arktisten alueiden tutkimuksessa.

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Tiivistelmä/Referat – Abstract

Arctic soils store significant amounts of carbon deposited by plants and litter. Carbon is released from the soil in respiration due to plant roots and decomposition by microbes. In the northern hemisphere, carbon inputs from photosynthesis have exceeded releases of carbon to atmosphere via respiration. Arctic soils have been a globally remarkable carbon sink due to cold and waterlogged conditions. However, rising global temperatures and changes in hydrology have caused the carbon fluxes in soil-atmosphere interface to alter. Arctic areas are considered especially vulnerable to climate change and alterations in the arctic soil carbon pools could create powerful feedbacks to warming. Furthermore, drivers controlling soil respiration flux remain poorly known, especially their contributions in different environments and their dynamics in time. Thus, understanding soil respiration as a process is vital in understanding future changes in the global carbon cycle.

The aim of this study was to identify environmental drivers of soil respiration in tundra at landscape-scale and their relative importance in different stages of growing season. The study area was a valley between two fells at Kilpisjärvi, Finland. Soil respiration was measured using the chamber method in 100 study sites on the 3 x 2 km landscape three times during the summer of 2018. Environmental data on soil microclimate and vegetation properties was gathered from the area as well. The impact of environmental conditions to respiration flux was studied using multiple generalized linear models with different explanatory variable combinations.

Results suggest that abundant vegetation causes high respiration by providing resources for belowground microbes and creating extensive root network. Highest respiration was measured in peak growing season, when elevated temperatures stimulated respiration exclusively in tundra meadows. It seems that vegetation and soil parameters also define the temperature response of respiration. The flux increased with elevated temperatures only on soils that are assumed to have adequate nutrient and carbon composition to support higher respiration. This study suggests that on landscape-scale, the resources provided by vegetation are of bigger importance to respiration than climatic changes both spatially and temporally. Moving forward, more empirical data is needed in order to accurately model future changes in respiration. Intense sampling efforts from the Arctic tundra areas that cover the large spatial and temporal variability of respiration are necessary.

Avainsanat – Nyckelord – Keywords
Soil respiration, carbon cycle, tundra, GLM, chamber method

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1. Introduction

A carbon flux is the amount of carbon exchanged between the Earth's carbon pools: atmosphere, hydrosphere, land areas and biosphere. Soil respiration flux is defined as carbon emitted from soil to the atmosphere from plant roots and decomposition by micro-organisms. Approximately 70-90% of the total carbon flux from ecosystems is derived from the soil as carbon dioxide (CO_2) (Segal & Sullivan, 2014; Zamolodchikov, 2015), forming the second largest carbon flux in the terrestrial cycle after primary production (Raich & Schlesinger, 1992; Davidson et al., 2002). Yet, soil respiration is one of the less known components of the ecosystem-atmosphere carbon budget, which is why understanding soil respiration flux is a key factor in comprehending the global carbon cycle and its interactions (Longdoz et al., 2000; Heinemeyer, A. et al., 2011; Phillips et al., 2017).

Arctic soils contain approximately twice as much carbon as there is present in the atmosphere (Tarnocai et al., 2009), which is nearly half of the carbon stored in soils globally (Hugelius et al., 2014). Tundra soils have been a carbon sink because of cold and waterlogged conditions and therefore slow decomposition rates, forming a globally important hotspot area of high soil organic carbon (Knowles et al. 2015; Sierra et al. 2015). Arctic soils have the potential of releasing growing amounts of stored carbon into the atmosphere due to changes in temperature, permafrost, snow cover, hydrology and vegetation that affect albedo (Nobrega & Grogan, 2008; Schadel et al., 2016; Zhang et al., 2019).

Increases in decomposition and soil respiration rates have already been observed and the changes are predicted to be most severe and abrupt in the arctic region (Longdoz et al. 2000; Knowles et al. 2015). These ecosystems are also considered the most sensitive to changes in the climate, because major parts of the flora and fauna on arctic regions are already existing on the edge of their environmental tolerance (McGuire et al., 2012; Knowles et al. 2015). Even slight changes in the soil respiration flux may create major alterations in the carbon cycle, trigger feedback impacts to climate, and alter the global temperatures (Davidson et al., 2002; Heinemeyer et al., 2011; Geng et al., 2012). It has been suggested that tundra ecosystems are shifting from being a carbon sink to a carbon source due to significantly changed environmental conditions, which have triggered respiration of long-term stored carbon (Schuur et al., 2009). Especially the balance between primary production and respiration, both stimulated by increasing temperatures, will determine the tundra carbon exchange in the future (McGuire et al., 2012; Euskirchen et al. 2017; Zhang et al., 2019). In order to predict future changes in the carbon cycle it is vital to identify processes affecting soil respiration, and their individual responses to environmental parameters in space and time (Eckhardt et al., 2019).

Even though the key role of arctic soils in global carbon cycle and as possible contributor to climate change is recognized, the underlying complex feedbacks and processes remain partly unclear (Raich & Schlesinger, 1992; Heinemeyer et al. 2011; Phillips et al., 2017). There is a clear mandate to more profoundly measure soil respiration as its role in the global carbon cycle is essential and the models predicting the future of terrestrial and atmospheric carbon pools rely on current knowledge (Longdoz et al., 2000; Nobrega & Grogan, 2008; Heinemeyer et al., 2011; Virkkala et al., 2018). Especially in the pursuit of predicting changes in global to regional level systems, the lack of understanding of the relative contributions of soil and aboveground vegetation to total ecosystem respiration is a major source of uncertainty in the models. Quantifying the balance between releasing carbon in respiration and carbon uptake via primary production is not enough on its own as these processes have differing responses to environmental change. Additionally, the contribution of factors within an ecosystem and between systems are not identical (Geng et al., 2012). Therefore, a more profound understanding of the processes affecting soil respiration in space and time is needed (Vargas et al., 2011; Phillips et al., 2017; Cannone et al., 2019; Eckhardt et al., 2019). When constructing estimates of future carbon cycling, it is necessary to investigate dynamics of individual growing seasons in addition to long timescale studies to unveil effects working on smaller timeframes (Lund et al., 2010). Observational studies in particular reveal spatio-temporal connections between soil, vegetation and atmosphere in profoundly heterogeneous tundra environments (Williams et al. 2006).

Recent CO_2 flux studies have focused on growing season (McGuire et al., 2012; Zhang et al., 2019) with relatively small data sets (Virkkala et al., 2018). In arctic regions, remote areas and harsh climatic conditions set limitations on field measurement intensity and amount of data gathered (Coffer & Hestir, 2019; Zhang et al., 2019). However, it is argued, that the CO_2 exchange varies greatly between ecosystems at landscape-scale and this kind of heterogeneity is often hidden in overly simple study designs. Many times, the variability between sampling points close to each other is as great as ones far from each other or even the ones that are experimentally manipulated (Phillips et al., 2017). However, it remains partly unclear what the drivers of these differences are and how they vary during and between seasons (Nobrega & Grogan, 2008; Zhang et al., 2019).

The scope of interest in this study lies in the landscape-scale dynamics of carbon dioxide respiration during one growing season. The aim is to answer following questions:

1. How does soil respiration vary in a tundra environment spatially and temporally during one growing season?
2. Which environmental drivers explain this spatio-temporal variation?

In terms of environmental drivers, this thesis focuses on the effect of vegetation, microclimate, and soil characteristics. These tightly linked main factors are usually considered to be important controlling respiration directly and indirectly (Burke et al., 2003; Virkkala et al., 2018). To capture the heterogeneous nature of tundra landscape, manual chamber measurements are deployed to describe and model the seasonal patterns on this spatial scale (McGuire et al., 2012; Pavelka et al., 2018; Vargas et al., 2011).

2. Theoretical framework

2.1 Soil respiration process

In soil respiration, carbon (C) is released from the soil due to respiration of belowground organisms or parts of them (Fig. 1). Soil respiration is most often divided to autotrophic respiration by plant roots and heterotrophic respiration by soil micro-organisms (Bond-Lamberty et al. 2018). Heterotrophic respiration consists of decomposition of recently dead plant tissue and older organic material (Schuur et al., 2009; Heinemeyer et al., 2011). Most of the respiration is fueled by energy from recently deposited organic material. Only a small portion of decomposition is derived from older carbon compounds (Ryan & Law, 2005). Majority of the soil organic carbon being decomposed is originated from vegetation through litter and root exudates (Susiluoto et al., 2008). There has been a serious effort to partition microbial and root-derived fluxes and their diverse environmental responses, which remain unclear (Heinemeyer et al., 2011; Segal & Sullivan, 2014; Phillips et al., 2017). In the tundra, majority of the flux is estimated to be of heterotrophic origin (Elberling & Brandt, 2003). In some environments, also carbonate weathering and other geochemical processes play a critical role in the soil-atmosphere carbon flux, but they are neglected in most of the relevant research (Vargas et al., 2011).

Soil respiration is the biggest CO_2 flux in the global carbon cycle after photosynthesis and 60-90% of ecosystem respiration origins from the soil (Raich & Schlesinger, 1992; Longdoz et al., 2000; Cahoon et al. 2006). Soil respiration strongly controls the balance between gross primary production

(GPP) and ecosystem respiration, being the main component of the carbon flux to the atmosphere from terrestrial ecosystems (Ryan & Law, 2005). Some of the soil carbon is also released in respiration as other compounds beside CO_2, such as methane. However, carbon dioxide is by magnitude the most significant gas being released in soil respiration and the scope of this study only involves carbon released as CO_2.

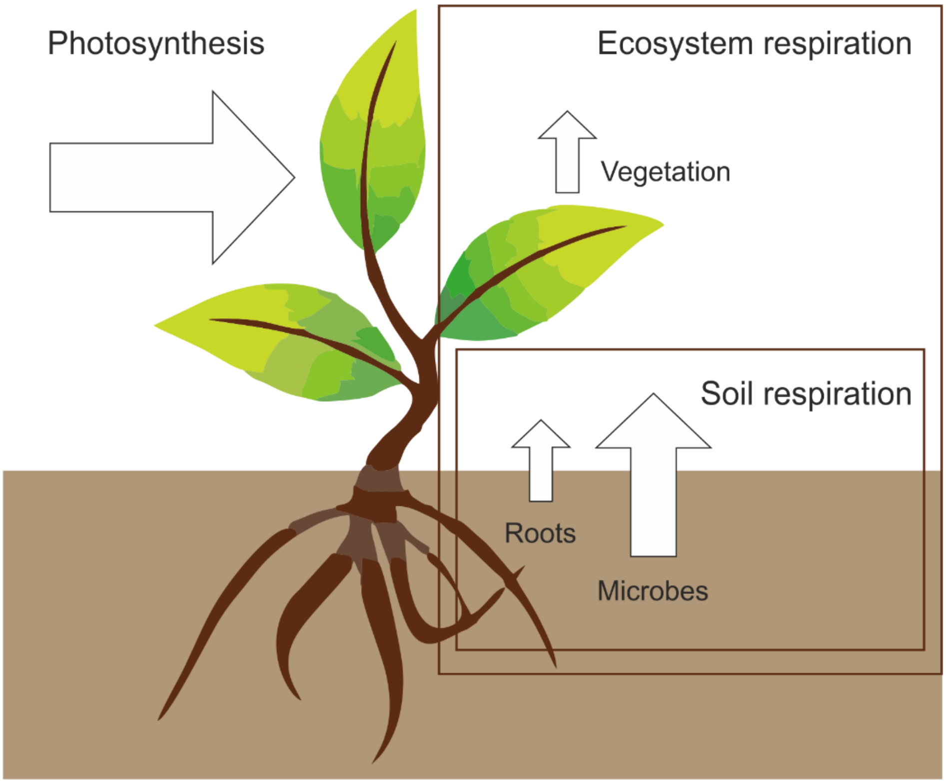

Figure 1. Main fluxes of carbon in the ecosystem-atmosphere interface. Arrows represent carbon dioxide input and output fluxes and their relative magnitudes (following Raich & Schlesinger, 1992). Soil respiration is usually considered as the total flux of carbon emitting belowground via autotrophs and heterotrophs, mainly plant roots and microbes respectively (Cahoon et al., 2016). Belowground respiration sources combined with the aboveground plant parts form ecosystem respiration, which describes the total carbon output from the plant-soil system to atmosphere. Most of the respiration flux is of heterotrophic origin (Reich & Schlesinger, 1992; Elberling & Brandt, 2003). However, the relative contributions of aboveground vegetation, roots and soil microbes to the ecosystem respiration flux are not completely described in different environments (Segal & Sullivan, 2014). The input carbon flux is gross primary production, which describes the amount of carbon engaged into the system via photosynthesis.

2.2 Environmental drivers

Respiration flux is a combination of biological and physical processes which are both highly variable in space and time in multiple scales. (Le Dantec et al., 1999; Longdoz et al., 2000; Vargas et al., 2011). As well as other biogeochemical cycles, it is controlled by a range of factors. Geng et al. (2012) define five independent controls: climate, parent material (soil), topography, biota, and time, following Jenny's soil forming factors (Jenny, 1941). These factors have differing contributions depending on the spatial and temporal scale on which the respiration and environment is measured and described. The nature of these environmental controls poses a challenge to estimating and predicting the flux. Many factors are interconnected, some overlapping and all of them highly dynamic and alternating in space and time (Vargas et al., 2011). The realized flux is an embodiment of all the processes present in the system and their interconnections. Ultimately, the magnitude of soil respiration depends on the activity of belowground fauna and plant roots. Prevailing environmental conditions determine available resources, such as moisture and availability of organic material, that enable respiration. Temperature, vegetation, and microbe biota regulate decomposition and thus, the CO_2 flux. Additionally, composition of soil microbe communities (Sørensen et al. 2006), landscape age (Whittinghill & Hobbie, 2011, 2012) and disturbance, for example herbivores (Moriyama et al., 2013), have been proven to influence soil carbon fluxes.

2.2.1 Climate

Climate has the most profound effect on soil respiration. It is mostly studied through soil temperature and moisture, that define majority of variation in soil respiration across arctic tundra (Illeris et al., 2004; Sierra et al., 2015). Temperature alone has been found to explain more than half of seasonal variation in soil respiration in tundra regions (Elberling, 2003; Biasi et al., 2014). In the tundra, respiration rates are generally low due to reduced decomposition and plant root activity in the cold. Also, a slight increase in temperature may cause profound changes in respiration, because the microbial and root activity is restricted by temperature in the tundra (Dorrepaal et al., 2009). Response could be quite rapid and usually exponential (Elberling, 2003; Hartley et al. 2008; Lee et al. 2010). Soil temperature generally correlates well with measured fluxes, if other factors, such as drought, do not limit below ground activities. (Longdoz et al., 2000; Dorrepaal et al., 2009; Heinemeyer et al., 2011). In the arctic tundra, highest respiration flux occurs during the peak growing season, when also increased photosynthesis causes high inputs of carbon into the soil (Lee et al., 2010; Baldocchi 2018; Zhang et al., 2019). However, cumulative wintertime respiration has been suggested to contribute to the annual respiration total more significantly (Elberling et al., 2008; Morgner et al. 2010; Trucco et al., 2012).

In addition to temperature, soil moisture has been argued to be a main driver of soil respiration in different tundra ecosystems and together they may explain significant amount of seasonal variation (Elberling, 2003; Nobrega & Grogan, 2008; Sommerkorn, 2008; Dagg & Lafleur, 2011). Soil moisture conditions on tundra landscape are implications of hydrological schemes determined by for example meso-topography, precipitation events and snow accumulation (Knowles et al., 2015). Soil parameters, such as porosity, density, and texture, determine the dynamics of water in the soil (Moyano et al., 2012; Sierra et al., 2015). Water in the soil acts both as a medium for diffusion of material, such as substrates and dissolved carbon, but also as a barrier for oxygen supply from the atmosphere. Most of the soil decomposers require both water and oxygen in order to function properly. High soil moisture has a limiting effect on the oxygen supply and the volume of soil pore space filled with water is often used as an indicator for oxygen availability (Brummell et al., 2012). Porosity of the soil greatly controls the penetration of air into the soil. Large pores favor respiration allowing gases to distribute effectively (Bouma & Bryla, 2000). When soil pores are filled with water, the dispersion of oxygen from the atmosphere to the soil disrupts, which hinders microbial activity. On the other hand, drought limits the decomposition activity and dispersal of organic matter and microbes in the soil, which also decreases respiration. Soil moisture content thus defines the contribution of aerobic respiration and slower, less effective anaerobic decomposition to the carbon dioxide flux. (Elberling, 2003; Davidson & Janssens, 2006; Moriyama et al., 2013). Also vegetation, especially plant roots, contribute to the soil oxygen levels, which might enable aerobic respiration also in waterlogged conditions (Sommerkorn, 2008).

Soil temperature and moisture are also most often linked to one another in ways that vary across environments and seasons, many times unlinearly (Sierra et al., 2015). For example, waterlogged conditions tend to decrease soil temperatures, which might cause temperature limitation to respiration (Eckhardt et al., 2019). The volumetric soil moisture optimum for heterotrophic respiration is estimated to be 35-37 % (Knowles et al., 2015; Menyailo et al., 2015). The optimum is dependent on soil type and soil organic carbon properties and respiration has been found to increase with soil moisture from 10 to 80 % of soil water holding capacity (Moriyama et al., 2013). Soil moisture and temperature are results of multiple feedbacks and effects. For example snow cover (Elberling, 2007; Aanderud et al. 2013; Sullivan, 2010), soil freezing and thawing cycles (Mikan et al. 2002; Elberling, 2003; Lee et al., 2010) and permafrost (Dorrepaal et al., 2009; Hicks Pries et al., 2013; Biasi et al., 2014) have their own impact on soil conditions especially in the arctic areas. Freezing not only limits the movement of micro-organisms but also removes water from liquid phase, making it unavailable for decomposers (Sierra et al., 2015). On the other hand, snow cover insulates the soil and enables respiration also during winter. Recognizing opposing factors controlling soil climatic conditions is vital, especially when looking into the annual patterns of respiration (Zhang et al., 2019).

2.2.2 Vegetation and soil

Soil respiration magnitude is controlled by quantity and quality of soil organic carbon (SOC) (Burke et al., 2003). Vegetation is the primary source of carbon in the soil via litterfall and root exudates (Phillips et al., 2019) and thus, belowground heterotroph activity is strongly linked to plant metabolism, photosynthesis, and carbon inputs to the soil (Ryan & Law, 2005; Semenchuk et al., 2016; Zhang et al., 2019). Vegetation parameters, such as aboveground biomass, height and cover indicate the magnitude of primary production and plant growth and thus the amount of carbon engaged in the plant-soil system (Geng et al., 2012; Virkkala et al., 2018). Primary production together with litter production explain variation in respiration relatively well in the tundra. In low productivity ecosystems, especially autotrophic respiration is low, when carbon inputs into the soil are not constant or sufficient (Ryan & Law, 2005).

Soil physical, chemical, and biological properties have fundamental roles in soil respiration processes (Virkkala et al., 2018). Soil type, structure, texture, and organic layer depth define overall soil quality and are connected to soil microclimate and vegetation. Soil heterotrophs and their community structures, driven by soil conditions, form a main component of the respiration and mediate also nutrient turnover (Biasi et al., 2008; Virkkala et al., 2018). Chemical composition of the soil controls the activity of decomposers. In addition to carbon, essential substances to plants and belowground microbes are e.g. nitrogen (N) and phosphorus (P) that are tightly linked to global carbon cycle. Plants are both providers and utilizers of nitrogen, which is why nitrogen cycle is closely related to vegetation patterns (Grogan & Jonasson, 2005; Biasi et al., 2008). Microbes use nitrogen in making enzymes needed for decomposition, as well as in biomass growth. N limitations can hinder respiration via both of these processes (Sistla et al., 2012). Spatial variability of vital nutrients is strongly based on plant and microbe community structures and hydrological schemes. In the arctic tundra, ecosystem functions are typically limited by nutrient availability and additional litter inputs usually stimulate decomposition and respiration (Williams et al., 2006; Sistla et al., 2012; Schadel et al., 2016; Phillips & Wurzburger, 2019). Low nutrient availability in the tundra is likely caused by waterlogged conditions and low temperatures (Eckhardt et al., 2019). Additionally, microbial respiration has been found to decrease with pH in tundra soils, due to the organic matter being least soluble at pH 4-5 and not available for decomposers (Schadel et al., 2016). Microbial communities also have different structures in soils with different pH and chemical composition. More acidic soils have greater proportion of fungi compared to bacteria, which usually results in lower respiration (Sundqvist et al., 2011; Whittinghill & Hobbie, 2012).

Vegetation regulates also soil abiotic conditions via affecting snow cover depth and thaw, soil surface albedo and radiation and affecting permafrost thaw during the growing season (Phillips &

Wurzburger, 2019). The duration and depth of snow cover have major impacts on vegetation processes by altering growing season length, soil nutrient availability and plant phenology (Zhang et al., 2019). Phenology and seasonal activity of plants contribute strongly to the soil organic matter quantity and quality in addition to direct respiration by roots (Ryan & Law, 2005; Elberling, 2007). Radiation has an indirect effect on soil respiration through plants because arctic tundra vegetation functions are limited by light availability for most of the year (Kuzyakov & Larionova, 2005). Also direct microbial stimulation by exposure to sunlight has been detected in the tundra (Cory et al., 2013).

Soil respiration is conceptually linked to multiple individual processes that have their own environmental responses and variance in space and time. Complex nature of the phenomenon poses a great challenge to quantifying and modelling it (Phillips et al., 2017). Environmental factors controlling soil respiration are very often tightly linked and form a network of impacts, where each component is an embodiment of others (Fig. 2). Virkkala et al. (2018) suggest dividing drivers into four categories: biota, where the carbon processes occur, resources required by the biota and regulators, which affect the processes. Fourth category is disturbance that disrupts processes and destroys biota. Disturbance includes geomorphological processes (thaw, cryoturbation), herbivory and disease (Virkkala et al., 2018).

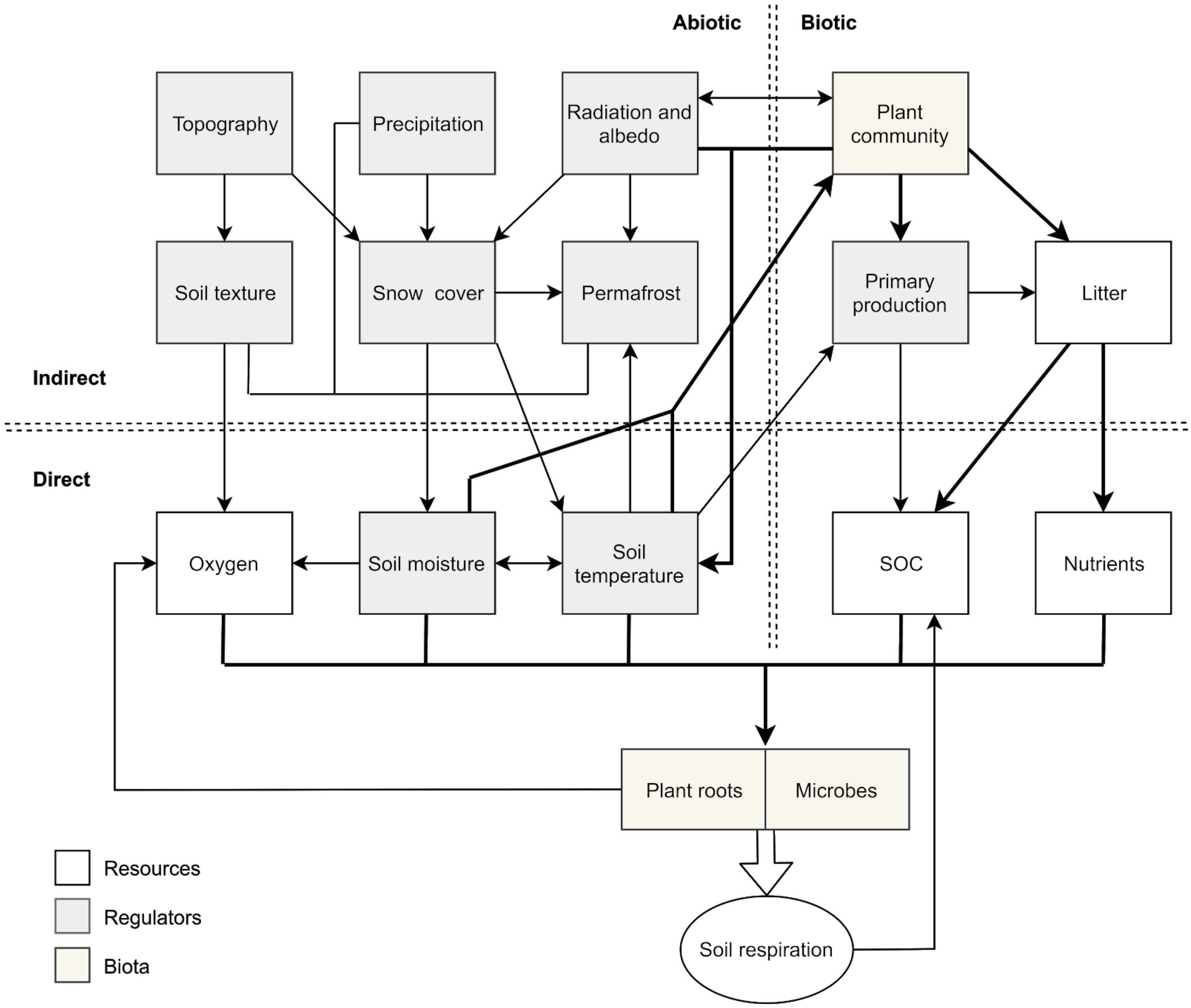

Figure 2. Conceptual model of the environmental factors controlling respiration and the most important relationships between factors (following Kuzyakov 2006; Geng et al. 2012; Virkkala et al. 2018). Arrows represent direction of effect and their width the strength of effect. Resources (white) are required by plant roots and microbes and thus essential for respiration processes. Most essential resources for decomposers are soil organic carbon (SOC), nutrients, oxygen, and water. Thus, soil moisture can be considered both limiting factor for oxygen availability as well as a resource supplying water for decomposers. Regulators (gray) mediate the magnitude of respiration or availability of resources. Biota (beige) are components through which the carbon fluxes occur.

3. Materials and methods

3.1 Study area

The study area is located in Kilpisjärvi, northwestern Finland (69°03´N 20°51E´) (Fig. 3). Size of the study area is approximately 600 hectares (3 x 2 km). Location in the valley between two mountain massifs, Mount Saana and Mount Jehkas, provides large environmental gradients related to topography, climate and vegetation. Relative height in the study area is approx. 250 m. Mean annual temperature in the region is -2°C and mean temperature in July is 11.2°C measured at Kilpisjärvi meteorological station, 1.5 km from the study area. (Pirinen et al., 2012). Mean annual rainfall is 492 mm. The climate in the area is strongly affected by its high-latitude location in proximity of the Arctic sea and the Scandes mountain range. Hydrological conditions in the area are variable in time. Stream discharge is regulated by snowmelt and precipitation events, as well as the moisture conditions on hill slopes. Partial snow cover persists on the area until June (Aalto, le Roux, & Luoto, 2013). Some of the streams and ridges are dried out during the warm growing season. Vegetation forms a gradient from the fell tops down to the valley adapting to change in moisture, temperature, radiation, and soil qualities. Majority of the area is above the tree line except for some locations in the river valley. Different habitats occur in patches and environmental conditions may have large variation at a small distance due to topography, hydrology, and disturbance. Dominant vegetation type is tundra heath that stretches across the landscape forming a mosaic with more moist meadows and drier patches with less abundant vegetation. Typical plants are low shrubs, such as dwarf birch (*Betula nana*) and crowberry (*Empetrum nigrum*). River valley meadows that have higher soil moisture and nutrient availability harbor species such as juniper (*Juniperus communis)* and wide variety of sedges. Wetlands with deep organic layers and high water table are formed in the mesotopographical depressions in the valley and mountain slopes as well as abundantly in the low-lying eastern parts of the area. Vegetation is lower and mostly consisting of herbaceous species such as *Eriophorum* and *Carex.* Higher on the mountain slopes, vegetation forms a mosaic of habitats of low shrubs, snowmelt-maintained meadows, and non-vegetated rocky patches. Geologically the area is part of the Scandes mountain range (Kemppinen et al., 2018).

The study design consists of 100 measurement sites. The size of a site is 5 x 5 m and the center and sides of it in four cardinal points were marked in the field with wooden sticks. The aim of the design is to represent all the most important spatial environmental gradients present on landscape-scale (fig. 3). Sites were selected based on previous observations on soil moisture and temperature, vegetation and topography provided by BioGeoClimate Modelling Lab research group at University of Helsinki.

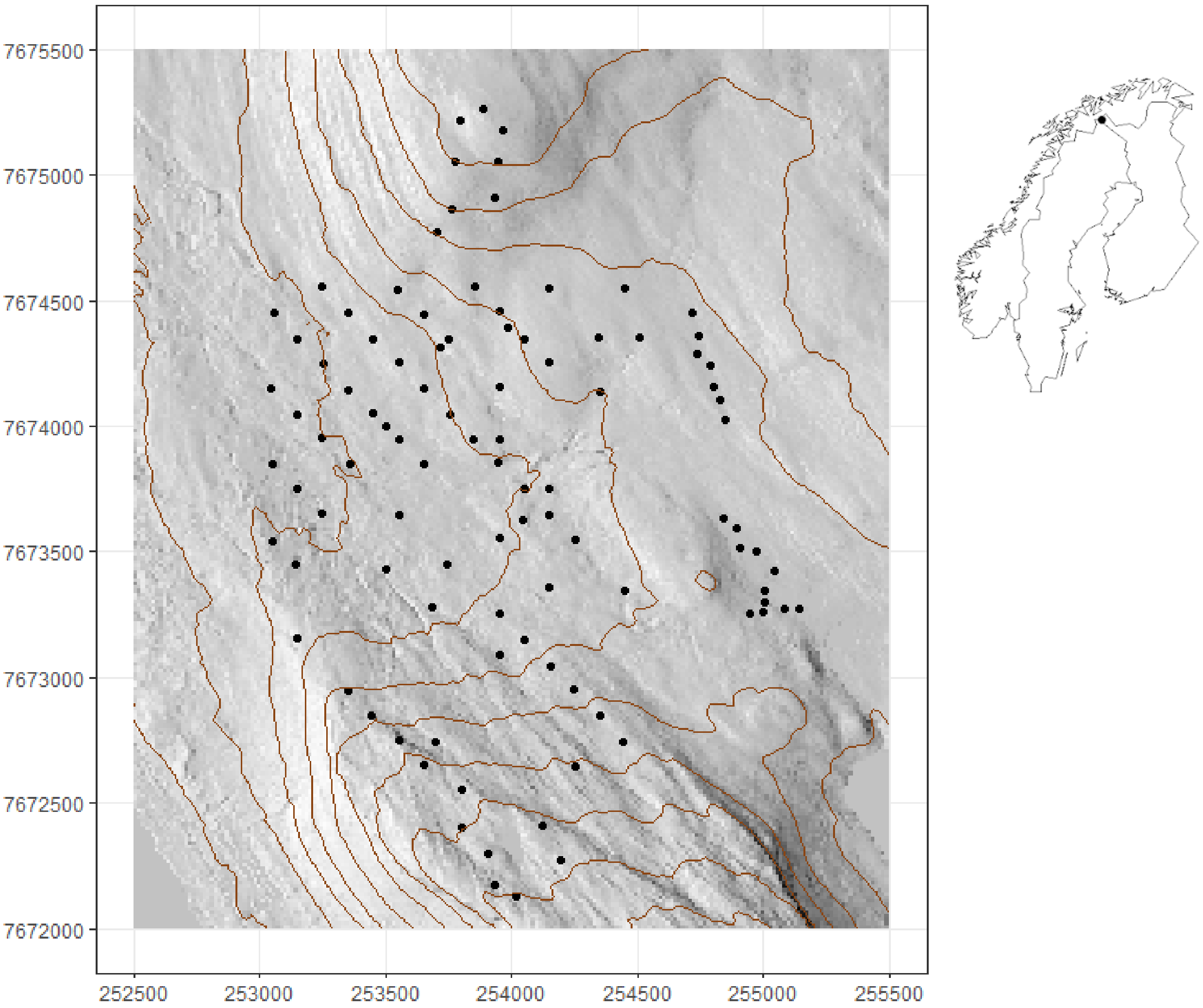

Figure 3. Kilpisjärvi area is located in northwestern Finland, close to the Swedish and Norwegian borders. Proximity to the Arctic Sea in the north affects the climate in the area. The study area is located between two mountains, Jehkas in the north and Saana in the south, visualized on the map with hillshade and 40m contour curves. On the axes are coordinates, distance in meters from the 0-latitude and –longitude (WGS84). The study sites (n=100) are marked with black dots. The mountain tops represent the driest sites in the design with shallow and rocky soils and sparse vegetation. In the valley, mesotopographic patterns create differing hydrological and microclimatic conditions that vary also on small spatial scale. The clustered sites on the eastern edge of the study area are located on a wetland and were included to incorporate as wide moisture gradient as possible.

3.2 Respiration flux data

3.2.1 Field measurements

Soil respiration data was collected during the summer of 2018 with chamber measurements. The dataset consists of three identical measurement campaigns that were conducted in early growing season (June), peak growing season (July) and in the end of the growing season (August), during the last week of each month. Campaigns lasted for 5 to 8 days depending on weather conditions (see appendix A for realized schedule). The closed static chamber system was chosen as a methodological approach because it is widely used in low productivity systems such as high latitude environments (Heinemeyer & McNamara, 2011). The chamber method is the most used method in studies that concentrate on spatial heterogeneity on local and landscape-scale, because the environmental conditions on the study site can be recorded on extremely fine scale (Williams et al., 2006; Pavelka et al., 2018; Virkkala et al., 2018).

At least two days prior to a measurement, a metal collar (height 8 cm, diameter 21 cm) was installed to the ground in a spot representing the vegetation cover and mesotopography in the middle of the site with visual estimation. Each collar was located at 1 to 7 meters distance from site center and positioned with a high accuracy GPS device (Trimble Geo 7X Handheld, Trimble Navigation, Sunnyvale, U.S.A). The collar was installed as deep as possible (1 to 3 cm) in the rocky and shallow soil with first precutting with a knife to target depth and airproofed with quartz sand when necessary (Hutchinson & Livingston, 2001). After installing the collar, aboveground vegetation, including the green moss, was clipped as carefully as possible with scissors (Grogan & Chapin Iii, 2000). Living plant roots were not interfered with in any way to minimize disturbance (Knowles et al., 2015), and thus the measured respiration flux can be considered as the sum of heterotrophic, autotrophic and litter respiration ignoring possible dissolved carbon loss according to the Total Belowground Carbon Flux (TBCF) approach (Phillips et al., 2017). At least 36-hour buffer time was left between the clipping and measurements in order to minimize the disturbance to soil and root processes from installing the collar and clipping the vegetation (Grogan & Chapin Iii, 2000).

Soil respiration was measured using a portable closed static chamber (V=7.28 liters) equipped with internal probes (Fig. 4). CO_2 concentration was measured with an infrared gas analyzer (GMP343, Vaisala, Vantaa, Finland), with five ppm resolution from an opening on top of the chamber. The chamber was also equipped with relative humidity and temperature probe (HMP75B, Vaisala, Vantaa, Finland). An integrated fan ensured even diffusion of CO_2 inside the chamber. The chamber was covered with reflecting material (aluminum foil) to eliminate heating effect from radiation (Heinemeyer & McNamara, 2011; Pavelka et al., 2018). In order to prevent leakage between the collar and the chamber, a heavy ventilator battery was placed on top of the chamber during the measurements (Fig. 4).

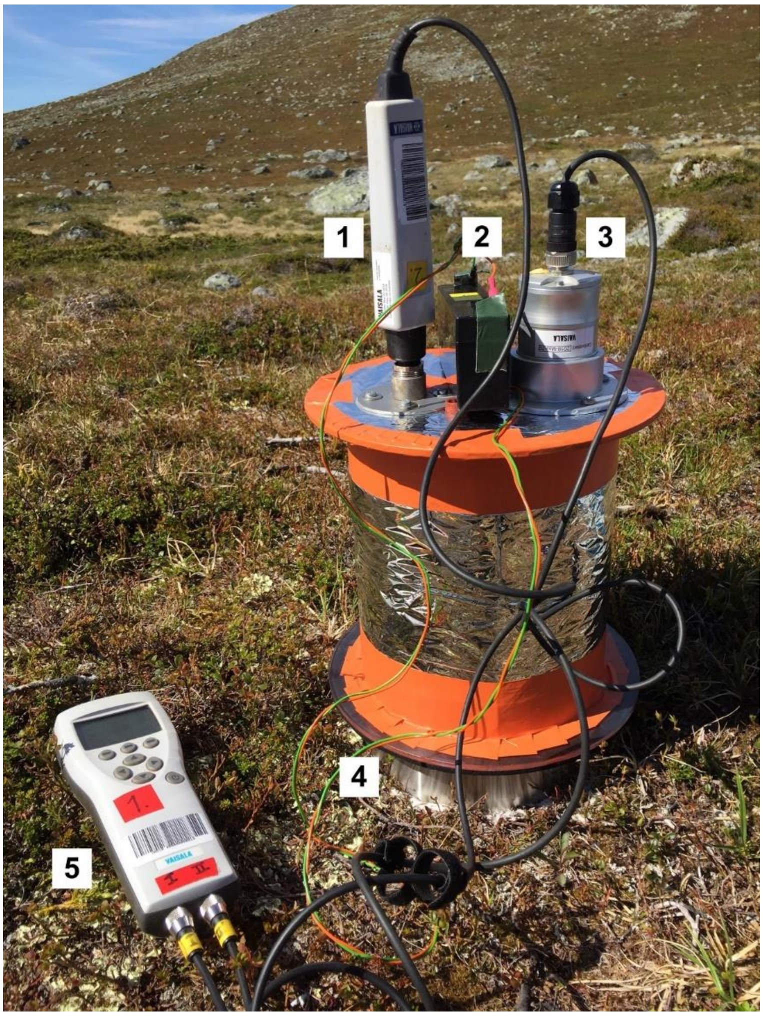

Figure 4. Chamber system used in the measurements. The chamber was placed carefully on top of the pre-installed collar (4) and the weight of the ventilator battery (2) was used to add pressure and prevent leakage between the chamber and the collar edge. Probes for CO_2 (3) and temperature and relative humidity (1) were installed through openings on the chamber top (see Pavelka et al., 2018). Probes were connected with wires to the data reader (5) through which the system was operated. The campaigns were conducted using two identical chamber systems.

Each measurement lasted 90 seconds (Knowles et al., 2015) and CO_2 concentration was recorded every five seconds with a data reader (MI70, Vaisala, Vantaa, Finland). To avoid logging noise, measurement was launched 20-30 seconds after the chamber was put into place. The flux is found to be altered in the beginning of the closure time due to pressure fluctuations caused by placing the chamber (Davidson et al., 2002; Pavelka et al., 2018). Measurement duration was somewhat shorter than in most of similar studies in order to limit errors due to changes in the concentration gradient between the soil and the chamber headspace while still logging adequate increasing trend of CO_2 (Davidson et al., 2002; ; Heinemeyer & McNamara, 2011; Eckhardt et al., 2019; Pavelka et al., 2018). Three replicate measurements were conducted in each site with adequate time in between for the CO_2 concentration to restore to ambient concentration (Le Dantec et al.,1999; Grogan & Chapin Iii, 2000). The quality of each measurement was controlled by a visual inspection from the concentration increase graph provided by the data reader. Linear trend was identified from every measurement (Davidson et al., 2002; Arndal et al., 2009) and there was no need to discard data due to nonlinearity caused by e.g. leakage.

3.2.2 Calculations

The data uploaded from the chamber data reader represented the CO_2 concentration (ppm) at a certain point in time after the launch of the recording. The data was converted to represent the respiration flux from soil area at certain speed and some modifications were made to remove noise from the data (fig 5.).

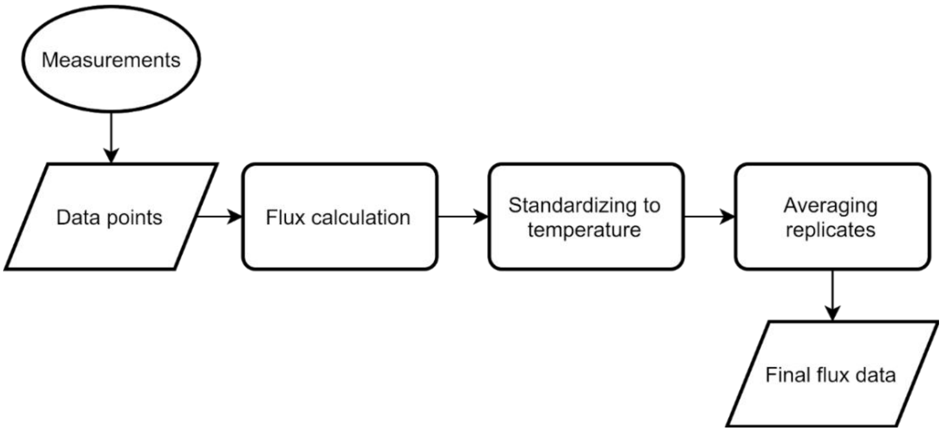

Figure 5. Workflow for creating the final carbon dioxide flux data set. The data was converted to µmol/m²/s, to represent the flux. To ensure the comparability of the different field campaigns, the flux values were standardized to temperature in order to minimize the effect of prevailing weather conditions on the analysis. Replicate measurements conducted on a site on the same day were averaged to remove noise.

The carbon dioxide flux per unit of time (*t*) on surface area (*A*) was calculated based on the change in CO_2 concentration inside the chamber (see Kulmala et al. 2004). In contrast to the formula used by Kulmala et al., recorded values were corrected by temperature, relative humidity, oxygen level and air pressure with the used probe in situ, thus these variables are not included in the calculations. For air pressure, the value from the meteorological station located 1.5 km from the area was used.

Correction functions are available from the manufacturer. Respiration flux (*F*) was calculated using the following equation:

$$F = \frac{\Delta C}{\Delta t} \times \frac{M}{Vmol} \times \frac{Vc}{A}$$

where *M* is the molecular mass of carbon dioxide (44.01 g/mol), *Vmol* is the molar volume (22,414 l/mol), ΔC is the change in CO_2 concentration and Δt change in time. Concentration change in time was defined by fitting a linear model, as suggested by Davidson et al. (2002) for measurements with low noise and nearly continuous data point logging (see also Eckhardt et al., 2019). The volume of the chamber (*Vc*) was determined by adding the site-specific collar volume to chamber volume (7.28 l). All flux values were converted from milligram/m^2/s to micromole/m^2/s, which is more widely used (Pavelka et al., 2018). The conversion was based on Ideal Gas Law that describes the relationship of gas mass and volume. The amount of CO_2 in micromoles is calculated by dividing the gas' mass in milligrams with the molar mass of carbon dioxide (44.01 g/mol).

Because the season proceeded, and weather changed during the two-month measurement period and measuring campaign the flux values needed to be standardized to temperature. The most significant driver for soil respiration is the temperature inside the chamber during measurement that varies strongly with weather. In order to unveil the true relationship between respiration and other environmental drivers on desired scale, and to maximize comparability between measured values, it is crucial to minimize the straight effect of temperature (Segal & Sullivan, 2014). This was done by fitting a model to describe the relationship between chamber temperature and respiration and then standardizing the flux to 16°C. The temperature value was chosen, because it represents the average temperature during the measurement period as suggested by Segal & Sullivan (2014). The mean of the average temperatures recorded inside the chamber was 16.19°C and median 16.01°C. The average temperature of July in the area was 15.1°C (FMI 2018). Different models were fitted to describe the relationship between the flux and the temperature inside the chamber. The best model fit was determined by AIC-value from the pool of most used functions (see Richardson et al., 2006). It was found that a simple linear model described the relationship best, with R^2 of 0.24. (Fig. 6). However, temperature responses of different measurement campaigns were not equal to the whole data. The final standardization was done by determining the model residuals for each observation and adding them to predicted value by the model at 16°C. The final values represent a prediction of the respiration value on each site at 16°C based on the linear model.

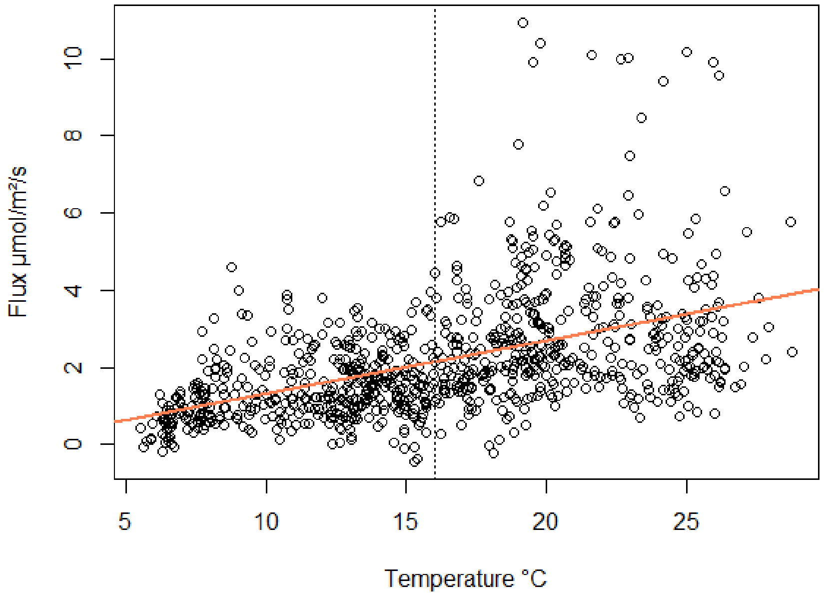

Figure 6. All 900 recorded respiration valued plotted against mean air temperature inside the chamber during the measurement. The relationship between the respiration flux and the temperature inside the chamber was best described with linear regression ($R^2 = 0.24$) and it was used as a base for the standardization. The final values for the further analysis were determined based on the idea of respiration flux that would have been recorded on the site at 16 °C (dashed line), assuming linear relationship between temperature and the flux.

To remove noise, the mean for the three replicate measurements was calculated for each site (n=100) and campaign (n=3). Thus, the number of flux values used in the final analysis was 300. On average, the range of replicate flux values measured on the site during same day was 0.47 µmol/m²/s. Measurements in one campaign ranged 5.96 µmol/m²/s on average. It can be argued, that replicate measurements are dependent on each other and can be averaged without losing information (see Williams et al., 2006).

3.3 Environmental data

Environmental data of vegetation, climate and soil parameters from the study sites was also gathered during the summer of 2018. Soil moisture and -temperature were recorded in situ during each CO_2 measurement using handheld probes (Field Scout TDR 3000, Spectrum Technologies, Inc., Brindgend, Wales, UK. Thermometer TD type T, VWR International, Radnor, Pennsylvania, USA, respectively) as suggested by Pavelka et al. (2018). Average value of three measurements in proximity of the collar was used in the analysis.

Aboveground biomass collected from the collars was dried in 65°C for two days and weighed, vascular plants and mosses separately (Dagg & Lafleur, 2011; Geng et al., 2012). Lichen biomass was negligible possibly due to grazing pressure (Susiluoto et al., 2008). The percentage of herbaceous and woody vascular vegetation was estimated visually pre-drying. Regrowth of vegetation occurred during the measurement period of two months in half of the sites. All fresh vegetation was clipped before measuring in the second and third campaign, but not included in the biomass sampling. Majority of the rapidly growing vegetation was herbaceous and the amount of vegetation regrown varied between none and almost identical to before taking the biomass samples in June. Biomass regrowth occurred mainly at meadow and wetland sites.

Vegetation and soil properties data set was provided by BioGeoClimate Modelling Lab research group. Data sets were gathered during the growing seasons of 2016-2018. Mineral and organic soil layer depths were measured in the site center. Soil samples were gathered from organic and mineral horizons in the site center separately and they were used to measure pH. Data for mineral layer pH was available from only half of the sites, which is why it was excluded from the data set. Vegetation properties were recorded once during the measurement period. Vegetation height and vascular plant cover variables represent the conditions in one m² area in the middle of the 5 x 5-meter study site. See appendix D for full list of variables and gathering methods.

Vegetation type classification was done based on photographs of collars taken prior to clipping. The goal was to coarsely characterize the dominant vegetation type inside the collar and its near surroundings (Table 1). Classification was based on the Circumpolar Arctic Vegetation Map introduced by Walker et al. (2005). Criteria focuses on abundance of plant functional types taking plant growth form, size, and taxonomical status into consideration. The study area has large gradient in elevation and hydrological conditions, which results in mosaic of soil patches with varying fertility and water resource. Generally, fennoscandian tundra consists of two dominant vegetation types: heath and meadow (Sundqvist et al., 2011). Less fertile patches host heath with woody shrubs, where vegetation thickness varies with soil moisture. Meadows are dominated by graminoid plants on more fertile, mesic soils (Dagg & Lafleur, 2011). Heath vegetation was further divided into two classes based on shrub growth form. Woody plants with height less than 5 cm were classified as prostrate shrubs and taller than 5 cm as erect shrubs. Additionally, barren soils with sparse vegetation and wetlands with high water table were classified separately.

Table 1. Vegetation type classes and their descriptions (following Walker et al., 2005).

ID	**Class**	**Description**
1	Barren	Very sparse and low-growing or nonexistent vegetation cover. Exposed soil, mosses, lichens.
2	Prostrate-shrub dominated heath	Dominated by prostrate shrubs < 5 cm tall, e.g. *Cassiope*.
3	Erect-shrub dominated heath	Dominated by erect dwarf shrubs > 5 cm tall, e.g. *Betula nana, Empetrum.*
4	Tundra meadow	Dominated by graminoid plants: sedges, forbs, grasses.
5	Wetland	High water table, moist elevated tussocks. Sedges, grasses, mosses, and forbs.

3.4 Analysis and modelling

The relative importance of each environmental driver was estimated by fitting models to describe the relationship between the variables and respiration flux. Statistical models provide means to mathematically examine, whether the environmental predictors explain variation in the response variable and what is the relative contribution of each predictor (Guisan et al., 2002). The modelling consisted of inspection of the data, creating models, and validating them (Fig. 7). The data was described with descriptive statistics, frequency histograms, scatterplots, and correlations. The seasonal differences of measured fluxes, soil temperatures and moisture were examined by analysis of variance (ANOVA) as well as the differences in environmental conditions between vegetation types. One-way ANOVA compares the amount of variation between groups (here, months and vegetation types) with the variation within a group. Significance of differences in variance were determined with Tukey's test, which compares each pair of mean of different classes and identifies if the difference between means is greater than expected standard error (Arndal et al., 2009; Dagg & Lafleur, 2011). The variance of observations was expected to be great due to the environmentally heterogeneous nature of the study area. All calculations and modelling were conducted using RStudio software (R Core Team, 2018). See list of R-packages used in this study in appendix E.

The approach to identify most important environmental variables was multivariable modelling and generalized linear models (GLM), that have been used in carbon flux modelling (Bolstad et al., 2004;

Geng et al., 2012). They are applicable for discovering cause and effect relationships in empirical data, along with addressing a conceptual model based on a theoretical framework. GLM's are extensions of linear models, that allow non-linearity by including polynomials. In this study, a gaussian relationship was assumed in the models, due to relatively normally distributed response variable that included negative values (see Guisan et al., 2002). The selection of variables for the models was based on their statistical characteristics as well as their conceptual significance. For the optimal modelling result, multicollinear variables were removed, while also considering their role in the conceptual model. Multicollinear variables, with correlation greater than |0.7| may cause bias in models, because they might have similar response to the dependent variable. Explanatory power of the model does not increase when adding multiple closely related variables (Guisan et al., 2002; Geng et al., 2012). Correlations were calculated using the Pearson method and significance levels were based on the p-value, where *** < 0.001, ** < 0.01, * < 0.05.

In total, 16 generalized linear models with first and second order polynomial terms (with *poly* -function in R) were created (Fig. 7). Environmental predictors were divided into three thematic groups: soil climate (C), soil properties (S) and vegetation (V). The soil properties models were created with subset of data (n=90) that did not include NA's of the explanatory variables. The effect of each group of variables was modelled for four data sets. Monthly data sets consisted of data gathered in each measurement campaign (June, July, August) and pooled data set combined of all the observations to represent the growing season as a whole. In addition to the thematic models, also full model with all the variables was created for each data set. In the full models, the variables were chosen with backwards (step down) selection, were all of the variables are included in the first draft of model. The variable with highest p-value is removed until all variables reach targeted significance. Variables were accepted in the full model if their p-value was < 0.05 (*). The elimination of variables from full models was based on a principle of parsimony, that prefers simple models over more complicated ones. The smaller number of variables weakens the model's ability to predict responses accurately, but has lower variance in errors (Guisan et al., 2002). Stepwise selection is a widely used traditional approach for identifying and ranking environmental drivers in flux studies (Geng et al., 2012).

The goodness of the models was evaluated by their predictive performance and ability to explain deviance in respiration. Multiple validation parameters were calculated to describe the model performance and enable comparing of models. Deviance explained (D^2) measures the explanatory power of the model. The parameter indicates, how much of the deviance of the dependent variable in the data is explained by the explanatory variables. Predictive performance of a model indicates how well it describes conditions outside the data used to create the model and if it can be used outside the original spatial framework. Predictive performance was evaluated with leave-one-out cross-validation method (LOOCV), where one observation is left out of the data used to fit the model and the value of said observation is predicted using a model based on the remaining observations. Prediction was repeated 100 times with the seasonal models and 300 times with the pooled models to create estimates for each observation. Cross-validation is particularly useful for validating models created for small data sets (Hawkins et al., 2003). LOOCV-predicted values were compared to observed values with Spearman correlation method, where higher value indicates better predictive accuracy in the model. The root mean square error (RMSE) was calculated based on the LOOCV - values to estimate magnitude of errors as indicator for model accuracy.

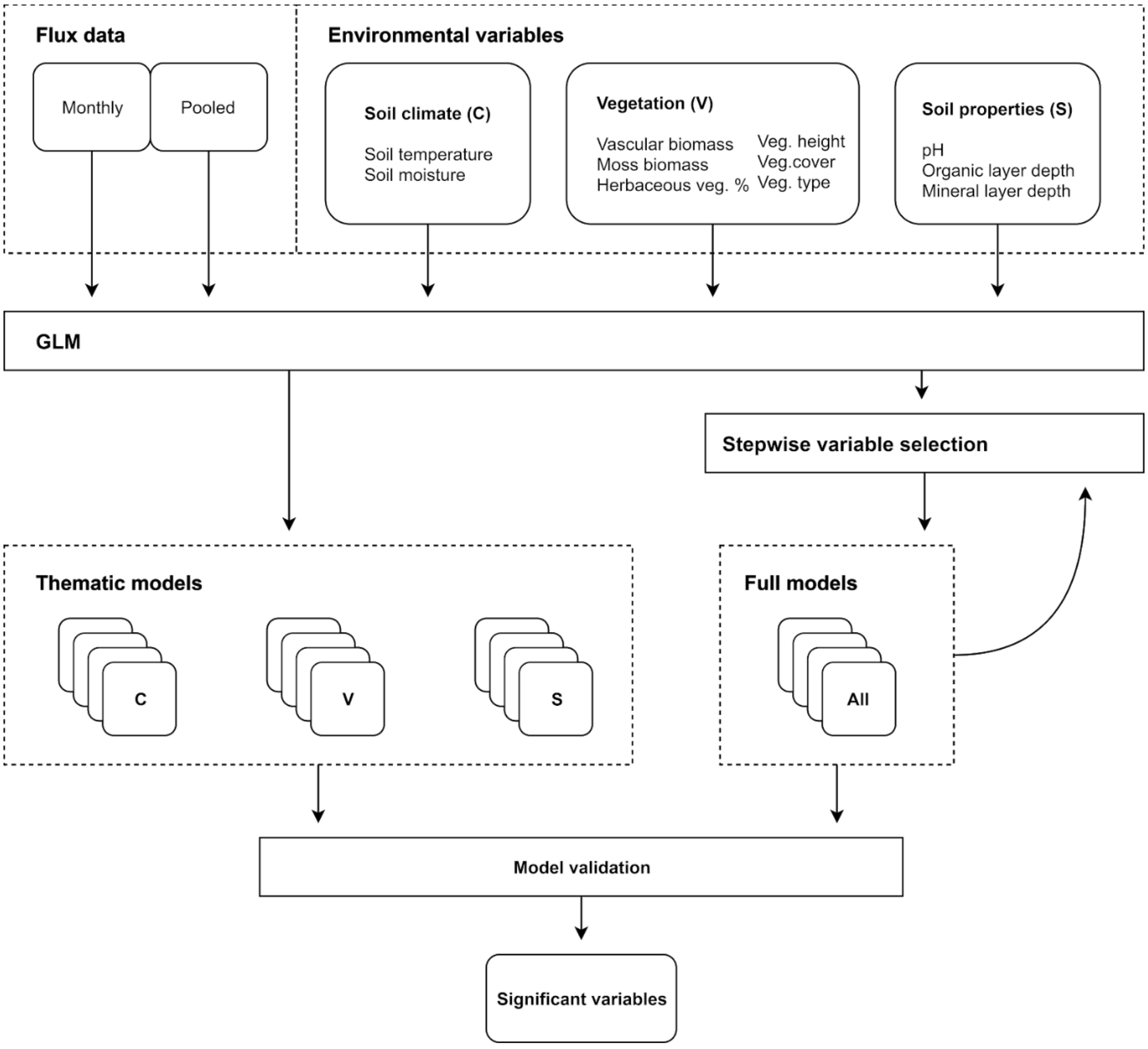

Figure 7. Workflow for the modelling consisted of variable selection part, modelling part, validation part and results. Environmental variables were divided into three groups (C, V and S), to create thematic models. Full models included all the variables, but their number was reduced via repeated stepwise selection procedure. All the models were executed for monthly data, gathered in June, July, and August separately, as well as for pooled data of all observations. As a result, the models provide information on which model is most fit to describe the most influential variables controlling soil respiration on the area.

4. Results

4.1 Environmental conditions

The weather in Kilpisjärvi in peak growing season during measurements in 2018 was slightly warmer and drier than usual. Air temperature in July was 3.9 °C higher than monthly average (observations 1981-2010) and received precipitation 51% of average (Pirinen et al., 2012). Soil temperature had 15°C range during the measurement period with median of 8.15°C. Based on ANOVA, the measured soil temperatures were significantly warmer in July than other two months ($p<0.001$) (appendix H). Median soil temperature values in July were 6.1°C higher than in June and 6.9°C higher than in August. June and August were similar to each other, although temperature range among sites was larger in August (Fig. 8). Also, single remarkably high soil temperature values (39.5°C) were recorded, likely due to measurement errors. These values that clearly do not represent true conditions, were deleted and replaced with estimates. Measured soil moisture ranged from 3.8% to 85% with median of 18.4%. Soil moisture did not vary significantly during the season.

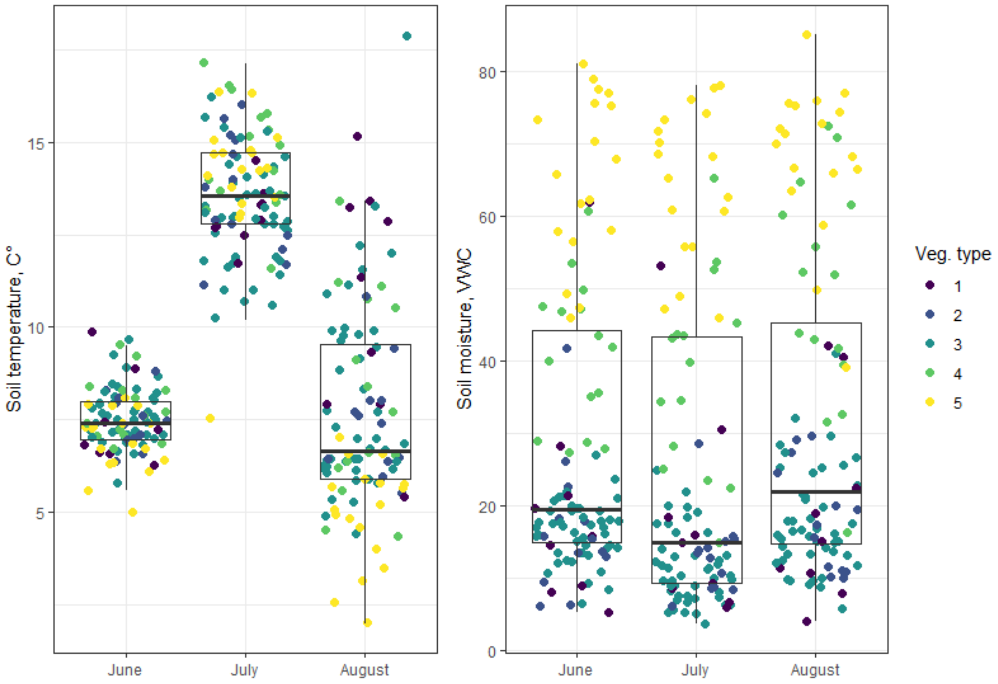

Figure 8. Soil temperature and soil moisture values measured in situ in three measuring occasions. The point colors represent vegetation types. Soil temperature peaked in July and did not follow vegetation patterns. Soil moisture conditions were relatively stable during the study period and no significant temporal differences were detected ($p > 0.1$). Soil moisture followed vegetation patterns with the highest values in the wetland and meadow sites (classes 5 and 4). Below median soil moisture values were recorded most often in barren and heath sites (classes 1, 2 & 3).

All the soils in the area were acidic with maximum pH of 6.5, with the most acidic ones associated with heath vegetation and alkaline associated with meadows and wetlands (Fig. 9). These two types had also significantly larger portions of herbaceous vegetation, based on ANOVA. All the vegetation variables had a minimum value of 0, which means that some measurements were conducted on very sparsely or non-vegetated sites. Most of the vegetation in the area was woody, and low in biomass. Tundra heath sites with a lot of shrubs had the highest biomass, vegetation cover and height. Most of the study sites were classified as erect shrub vegetation type (3) (n=46). The distribution of other types was more even (frequencies 1=9, 2=11, 4=15, 5=18). Meadow type had significantly deeper mineral soil layer than other types and wetland had by far the deepest organic layers. In terms of moisture, wetland and meadow sites were significantly different from each other and types 1-3 (p<0.001). Wetlands had the wettest soils and barren sites together with heath sites the driest (Fig. 9). Soil temperature did not follow vegetation patterns in the area.

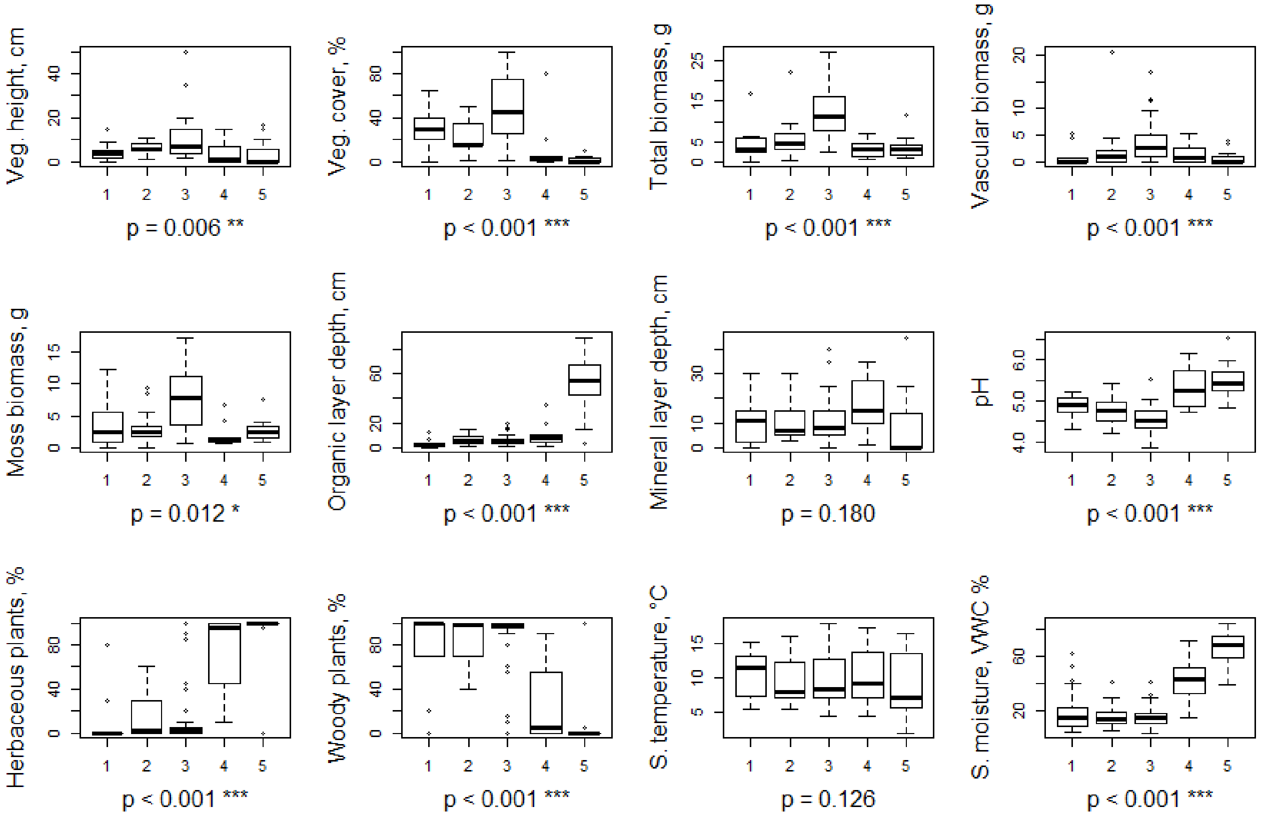

Figure 9. The variation of environmental variables in vegetation type classes (1=barren, 2=prostrate shrubs, 3=erect shrubs, 4=graminoid, 5=wetland). Statistical significances of vegetation type explaining the environmental variable are based on the p-value. Vegetation type is a significant predictor for all the variables except soil temperature and mineral layer depth. See appendixes F and G for descriptive statistics and histograms of environmental variables.

4.2 Respiration flux

Most of the measured respiration flux values were relatively small, with mean of 2.15 µmol/m²/s and median of 1.92 µmol/m²/s. Maximum respiration flux of 9.95 µmol/m²/s was recorded in July. However, 95% of the observations were below 4.4 µmol/m²/s. Also negative flux values were recorded in all the campaigns (n=14), which was possibly due to very low or nonexistent respiration or it being overpowered by other processes in the soil and chamber airspace. Temporal differences were detected during the peak growing season. The flux measured in July was significantly higher than other two months ($p < 0.001$) (appendix H). Minimum flux was recorded in June, but the average fluxes of June and August were not significantly different from each other. Standard deviation of the flux was 0.92, 1.80 and 0.96 in June, July, and August respectively. Spatially, the flux follows vegetation patterns (Fig. 11). Based on ANOVA, the flux measured on meadow sites (class 4) was significantly higher ($p < 0.05$) than on other vegetation types (Fig. 10).

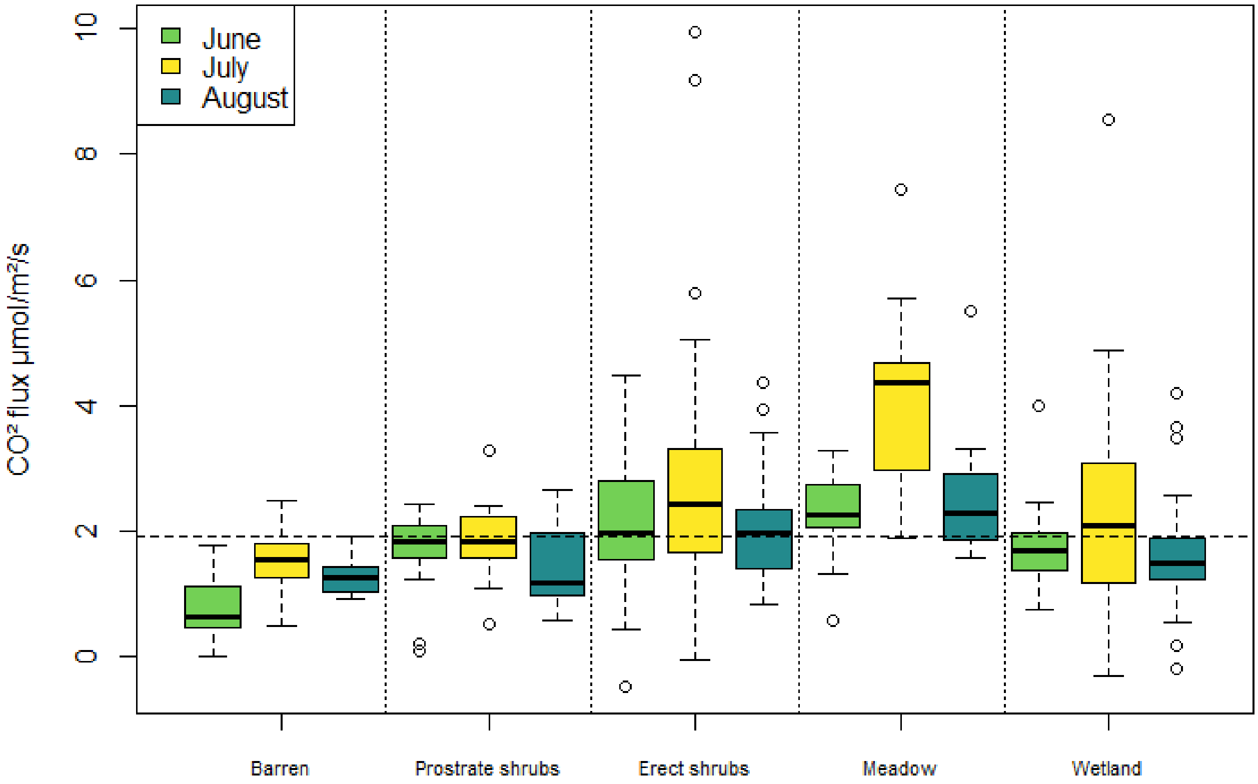

Figure 10. Recorded soil respiration flux on three measurement occasions in different vegetation types. Box edges represent the 25th and 75th percentile of the data with median value in the middle. The dashed horizontal line represents the median value of all the observations (1.92 µmol/m²/s). On average, the flux is lowest on the barren sites (1.27 µmol/m²/s) and highest on graminoid dominated sites (2.97 µmol/m²/s). The flux peaked in July in all the vegetation types. Temporal difference between measuring campaigns was detected exclusively on meadow type.

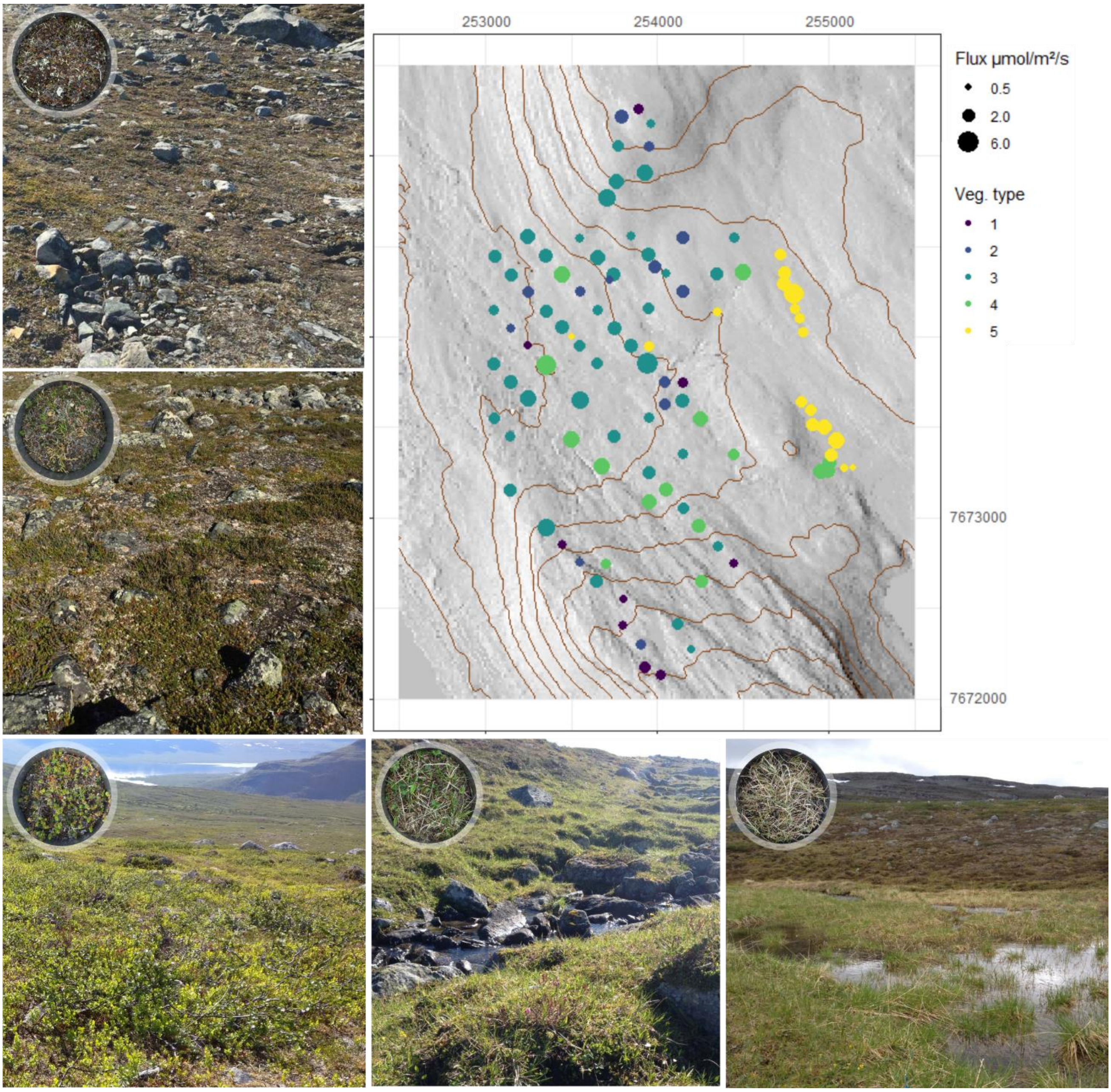

Figure 11. Recorded mean flux values on each site and site vegetation types (colors) with hillshade of elevation model. Photographs are examples of vegetation types (1-5, up-down, left-to-right) on the area. Top left corners represent examples of the vegetation inside the chamber collars. Highest respiration values were recorded in the meadows (4) of the valley and erect shrub heath sites (3) on the slope of Jehkas. On barren sites (1) at felltops fluxes were generally low, as well as on prostrate shrub sites (2). The variance in flux of wetland sites (5) was large.

4.3 Multicollinearity of the variables

The correlations between variables were described using Pearson's correlation method. Statistical significance levels are based on the p-value. Correlations were calculated using the pooled data. The respiration flux was most strongly correlated with vegetation height (0.25***) (Fig. 12). It was also correlated with soil temperature (0.19**) and the percentage of herbaceous (0.14*) and woody (-0.12*) vegetation on the plot. Some of the environmental variables were found to be multicollinear, with correlation higher than |0.7|. The herbaceous and woody vegetation shares were highly correlated (-0.97***), because they are portions of one biomass sample and always add up to 100%. Soil moisture was correlated with organic layer depth (0.76***) and the portions of herbaceous and woody vegetation (0.76*** and -0.74***). This was probably because of strong contribution of soil moisture in formation of deep organic soil layers in wetlands and the abundance of herbaceous vegetation. Vascular plant biomass and total biomass were highly correlated (0.81***), because the total biomass is mostly the result of vascular plant mass and the contribution of mosses is smaller. Due to multicollinearity, total biomass and woody vegetation variable were not used in the modelling. Organic layer depth and herbaceous vegetation variable were not used in the full models together with variables they are multicollinear with. Based on the correlation matrix, the environmental variables are dependent on each other. On sites that have high soil moisture, there is also low vegetation cover and biomass, deep organic layer, high pH, and herbaceous vegetation share. On sites with shallower, drier, and more acidic soil the vegetation is more woody and has greater cover, height, and mass. Strongest relationships, that were not considered multicollinear in this study (|<0.7|), were found between soil moisture and organic layer pH (0.65***) and vegetation cover and vascular plant mass (0.60***). See appendix I for full correlation matrix.

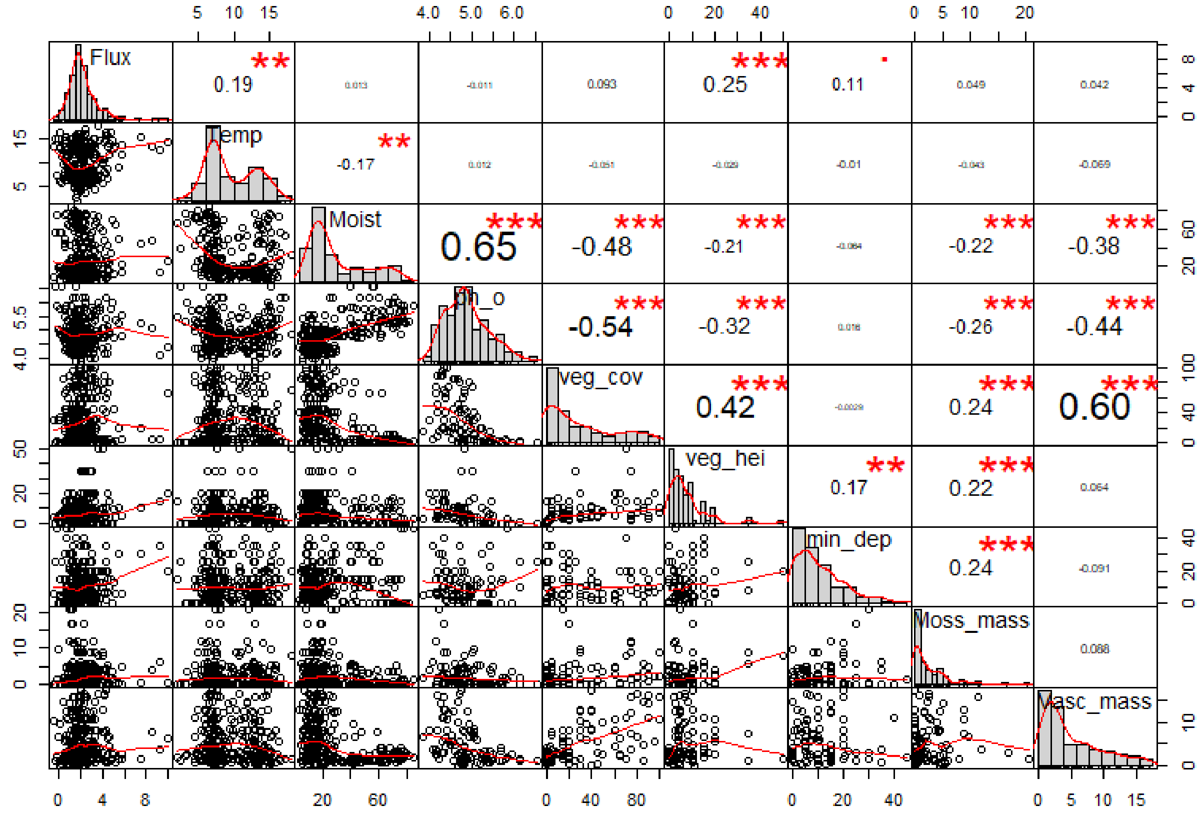

Figure 12. The scatterplots, frequency histograms and correlation values of flux and environmental variables. Only correlations below multicollinearity threshold (< |0.7|) are included. Stars represent statistical significance based on the p-value, where *** < 0.001, ** < 0.01, * < 0.05. *Observations of vegetation cover (veg_cov) and height (veg_hei), moss and vascular plant biomass (Moss_mass and Vasc_mass), and soil mineral layer depth (min_dep) were gamma distributed. Recorded respiration flux (Flux), soil temperature (Temp), moisture (Moist) and organic layer pH (ph_o) were normally distributed. Histograms of each variable frequency are provided in appendix F. Soil layer depths, pH and vegetation height were not available from every site (n ≤ 5).*

4.4 Modelling results

The models had big differences in explanatory power and predictive performance. Vegetation models and full models with all the variables had the highest deviance explained values and strongest correlation between observed and predicted flux values (Table 2). The full models predicted by far most accurately. Soil microclimate and soil properties were not as powerful predictors and the model performance was overall poorer in these thematic models. Some data sets were easier to model than others. Models fit for June and August had highest D^2 and smallest RMSE. July was the hardest month to model with every variable set. In the July data, there were quite a lot of respiration flux observations that stood outside the 95% fractile (n=13) and the models were not able to predict the values close to the maximum (Fig. 13). In general, pooled models did not have the best explanatory power but their confidence intervals were smaller than in monthly models and they were relatively good in predicting.

Table 2. Model validation parameters for all the models. Data-column (1-4) indicates the data set used in the fit (June, July, August, pooled, respectively). D^2 is deviance explained as portions of 1. Correlation between LOOCV-predicted values and observed values (r_s) represents model's predictive accuracy. Significance levels are based on the p-value. RMSE is the mean square error of the predictions in µmol/m^2/s.

Model	**Soil climate**				**Vegetation**			
Data	1	2	3	4	1	2	3	4
D^2	0.15	0.08	0.10	0.08	0.30	0.22	0.28	0.20
r_s	0.31**	0.14	0.17*	0.17**	0.36***	0.35***	0.45***	0.44***
RMSE	0.89	1.79	0.95	1.31	0.82	1.64	0.86	1.18
Model	**Soil properties**				**Full**			
Data	1	2	3	4	1	2	3	4
D^2	0.15	0.06	0.12	0.07	0.35	0.21	0.30	0.23
r_s	0.24*	-0.08	0.07	0.17**	0.44***	0.41**	0.48***	0.43***
RMSE	0.86	1.88	0.97	1.28	0.79	1.57	0.77	1.10

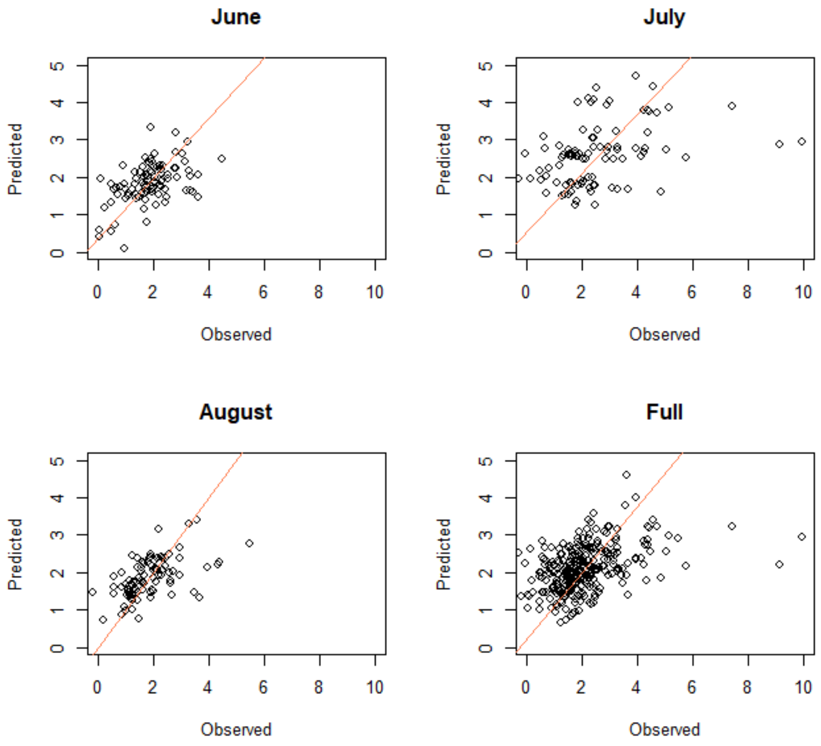

Figure 13. Observed flux values against LOOCV -predicted values by full models. The predicted values were consistently lower than observed values in all the data sets, except for the lowest observations. The models were not able to predict maximum values recorded in July very accurately. The model for July data also had a wider range of predictions for similar observed values.

According to the models, vegetation variables predict the respiration pattern most accurately. The vegetation models performed best of the thematic models and the importance of vegetation variables was highlighted in the full models. The models indicate that respiration increases with abundance of vegetation. Vegetation type variable was significant in all the full models with p<0.001*** except August, where p=0.002**. Especially erect shrub and meadow types indicated high respiration (Fig. 11). Vegetation height was significant in June and total growing season model (p<0.001***). Interestingly, even though vegetation cover was not significant in vegetation models, it was significant in August model (p=0.049*). Respiration increased with higher plants and vegetation cover (Fig. 14). Biomass variables (vascular plants, mosses and total mass) were not significant in neither vegetation nor full models.

Although soil climate and properties models did not explain respiration very well on their own, some of the variables were significant in the full models. Soil temperature was significant in June (p=0.002**) and pooled (p=0.001**) full models. However, the relationship with respiration altered during the growing season. In June and July, the trend was negative and in August and total growing season it was positive (Fig. 14). Soil moisture was not significant in the full models. Of the soil properties variables, pH and mineral layer depth showed significance in the full models. A unimodal relationship with pH and respiration was detected in August (p=0.02*), where the optimal pH was 5.5. There was also an optimum mineral layer depth of 20-25 cm in the pooled full model (p=0.04*) that indicated peak respiration (Fig. 14).

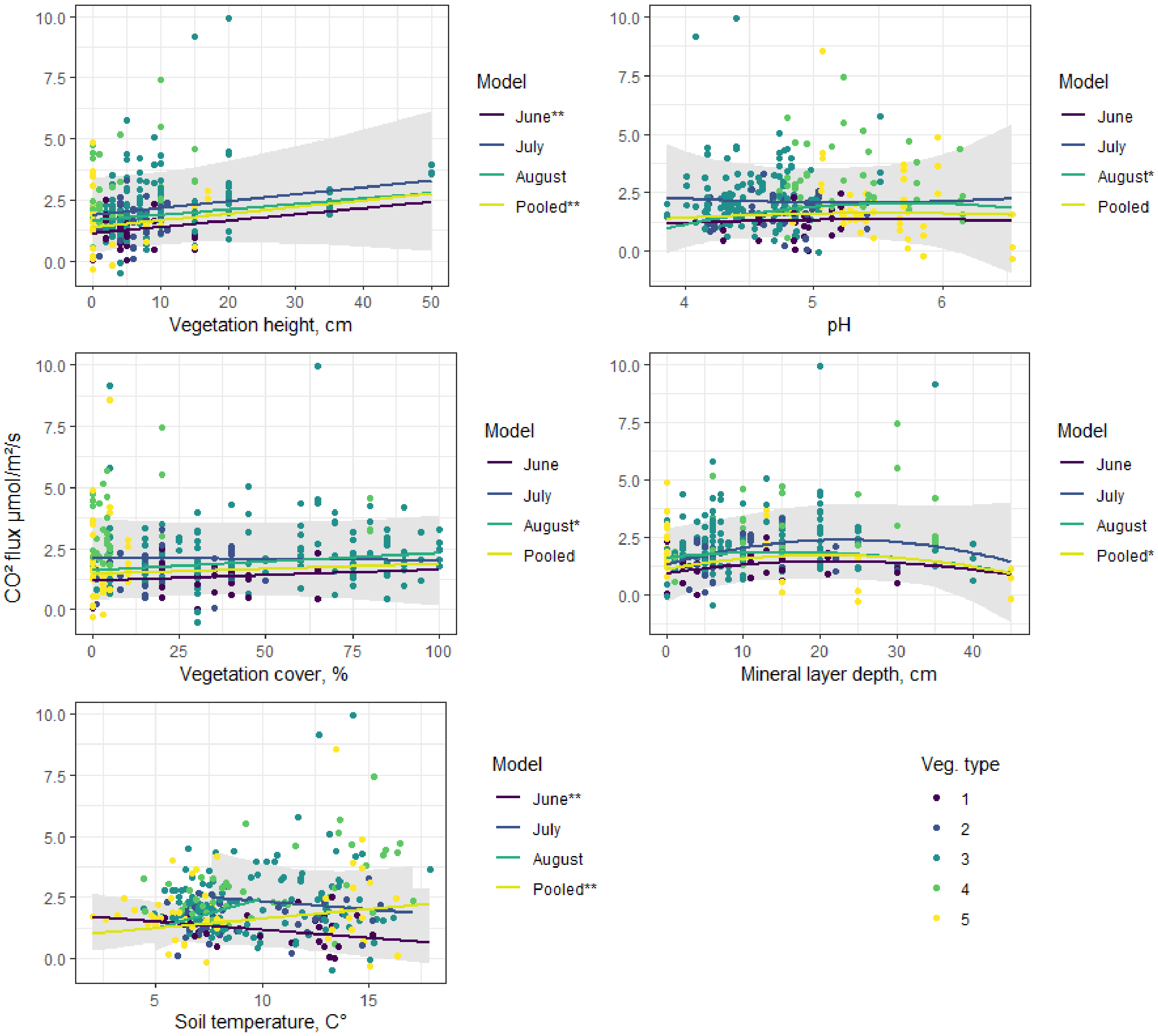

Figure 14. Full model responses of respiration flux to significant variables of full models, when all other variables in the data are set as their means. Confidence interval represents, where 95% of the model predictions should land. No variable was significant in all of the models. Respiration had an increasing relationship with vegetation height and cover and unimodal relationship with mineral layer depth and pH. Soil temperature was significant in June and pooled models, but directions of response were opposing.

5. Discussion

Soil respiration values measured in this study are comparable with other growing season chamber measurements in tundra (Table 3). Mean values are of the same magnitude than previously reported, however naturally greater than those of high arctic, for example Greenland, where mean air and soil temperatures are significantly lower. The range of fluxes is quite large in this study, pushing the limits of tundra growing season respiration flux estimates. Maximum values exceed other studies in almost every vegetation type. Contrary to other studies, in this data there were also flux values of equal or below zero, as no detection limit was applied in the measurements and negative values were included in the data.

Table 3. Reported soil respiration flux mean, maximum and minimum values at tundra environments (µmol/m²/s). Not all related research reports exact fluxes or does not partition ecosystem respiration fluxes to belowground and aboveground components. All flux values on this table are unstandardized.

Authors	**Year**	**Region**	**Environment**	**Mean**	**Min**	**Max**
This study	2018	Kilpisjärvi, Finland	Barren	1.22	0.32	2.21
			Heath, prostrate shrubs	1.90	0.52	5.17
			Heath, erect shrubs	2.39	0.56	10.42
			Meadow	2.89	0.58	8.46
			Wetland	1.75	< 0	9.89
Knowles et al.	2015	Niwot Ridge, Colorado, USA	Dry tundra	1.72	0.76	4.24
			Mesic tundra	2.26	1.48	3.07
			Wet tundra	2.03	1.18	3.45
Sommerkorn et al.	2007	Lake Labaz, Siberia	Wet sedge	0.33	0.22	0.44
Elberling & Brandt	2003	Zackenberg, Greenland	Heath	0.7	0.2	1.1

5.1 Environmental drivers for soil respiration

5.1.2 Temporal drivers

According to the results, the respiration flux was relatively low in the early growing season (mean=1.87 µmol/m²/s), peaked in July (mean=2.70 µmol/m²/s) and returned to prevailing level in the late season (mean=1.90 µmol/m²/s). A great amount of the temporal variation in respiration during the measurement period was caused by radical increase in respiration in July on graminoid dominated meadow sites. Also soil temperatures were at height during the time, which agrees well with previous research that suggest that most of the temporal variation in respiration is explained by changes in soil temperature (Elberling & Brandt, 2003; Nobrega & Grogan, 2008). Primary production reaches its peak usually in the middle of the growing season and thus increases carbon inputs into the soil which may also cause respiration to peak at the same time, most often observed in July in arctic tundra (McGuire et al., 2012; Moriyama et al., 2013; Coffer & Hestir, 2019).

Other vegetation types apart from meadows did not have a strong response to soil temperature increase in July. Similar pattern has been detected in previous studies in tundra systems, where soil temperature has an increasing effect on respiration only on sites with high soil carbon and nutrient content as well as moderate soil moisture (Dagg & Lafleur, 2011; Moriyama et al., 2013). Low overall temperature sensitivity among vegetation types also agrees well with previous research, where flux has been found to remain quite stable during growing season (Grogan & Jonasson, 2005; Nobrega & Grogan, 2008; Cahoon et al., 2016). Warmer soil temperature does not drive increased respiration, if the belowground biota suffers from other limitations, such as of nutrients, oxygen, or water. Microbial communities on other vegetation types may be also be acclimated to lower temperatures and thus do not respond to the increasing temperature as strongly (Moriyama et al., 2013). It has been suggested before, that soil conditions not only determine the dominant vegetation, microbial community, and nutrient cycling, but also the response of these factors to changes in climate (Mikan et al., 2002; Sundqvist et al., 2011).

Positive relationship between soil respiration and soil temperature has been identified multitude of times (Burke et al., 2003; Knowles et al., 2015; Baldocchi et al., 2018). However, in this study, the temperature response was different between the measuring occasions. Respiration seemed to decline with increasing soil temperature in June and July, when the trend was increasing in August and during the growing season as a whole. Similar response has been shown before (see Geng et al., 2012; Knowles et al., 2015). It seems that respiration increases with temperature when comparing measurements on local scale within the same environment, vegetation type or single study site. However, this finding is not enough to be generalized across the landscape, where different factors, such as soil organic matter quality driven by vegetation, are of bigger importance (Elberling & Brandt, 2003; Nobrega & Grogan, 2008; Dagg & Lafleur, 2011). It can be stated that soil temperature could also be used to describe larger temporal patterns, such as between seasons or years, as it does not describe the differences between sites very accurately. Furthermore, large data sets with multiple flux measurements in diverging soil temperature conditions may provide a more robust temperature relationship. In this study, the limited range of soil temperatures may have caused the effect to be weaker.

Warm growing season may also have caused the decomposing not to be limited by temperature in the area at all. Microbes have been found to be active year-round and are not necessarily responsive to spring temperature increase (Nobrega & Grogan, 2008), but rather experience high temperatures as stress caused by higher evaporation and decomposers being acclimated to cold conditions (Moriyama et al., 2013; Sierra et al., 2015; Baldocchi et al., 2018). It is noteworthy, that similar patterns of declining respiration with temperature in the tundra have been found in higher soil temperatures than in this data (> 25°C). Grogan and Chapin (2000) suggested that the positive relationship between respiration and increasing temperatures detected in multiple experimental studies is a result of microbial biota acclimating to altered conditions rather than the elevated temperature stimulating decomposing activity directly. However, there is no consensus whether soil respiration continues to increase also on the upper end of the arctic temperature range or if it saturates or declines (Hartley et al., 2008; Sierra et al., 2015).

Respiration was possibly limited by other resources rather than temperature during the early and peak growing season. In the August and pooled models, the role of soil quality was highlighted more than in the other two data sets, possibly suggesting, that litter inputs originating from the growth during the summer provide enough carbon for respiration, which was not necessarily true in the early season. Also root mortality due to biomass clipping may influence the temperature response. It remains unclear, what the relative contributions of stimulated microbial activity, root respiration and increased carbon inputs via primary production are to the respiration increases during growing season (Sullivan et al., 2008). If the autotrophs are mostly responsible for the respiration temperature response, it may be that microbial activity does not significantly increase in warmer temperatures, especially when acclimated to cold.

The flux standardization process may have distorted the soil temperature responses of respiration. The soil temperature in June had a significant positive relationship with the unstandardized respiration flux ($p<0.001$), and correlated with the air temperature inside the chamber used for standardization (0.65***). Standardization may have altered the direction of respiration temperature response in June. Similar significant relationships were not found in July or August. Thus, soil respiration was possibly limited by temperature in the early growing season.

It has also been suggested that soil temperature may be overridden by soil moisture in the models, when moisture is significant predictor also for temperature (Hibbard et al., 2005). In this data, soil temperature and moisture had a negative relationship with correlation -0.11 (**). Models have been prone to problems detecting temperature and moisture responses of respiration, when both variables are simultaneously changing and experiencing both highs and lows during the same season (Rustad et al., 2001; Knowles et al., 2015). In addition to temperature, the environmental responses were not changing drastically during the growing season. Vegetation parameters remained important throughout the growing season and the abundance of leafy vegetation predicted respiration in all the models.

5.1.2 Spatial drivers

The most important spatial drivers for soil respiration based on the models are vegetation parameters: type, height and (in August) cover. Sites with high plant leaf cover and overall abundant vegetation most likely stimulate decomposers with great organic compound inputs via litter and root exudates (Bowman et al., 2004; Phillips & Wurzburger, 2019). The result is consistent with previous research in similar environments, where vegetation cover, leaf area and gross primary production explained respiration well (Nobrega & Grogan, 2008; Susiluoto et al., 2008; Lund et al., 2010). The chemical composition and diversity of litter have been found to strongly predict respiration especially on landscape-scale by altering the quantity and quality of SOM (Hicks Pries et al., 2013; Knowles et al., 2015).

Highest respiration values were recorded on meadow sites, where fertile soils host adequate resources for decomposers including moisture, oxygen, nutrients, and organic carbon. Meadows have been found to significantly differ from tundra heath by their soil microbial community and soil fertility that seem to be especially suitable for effective decomposing (Sundqvist et al., 2011). Additionally, the litter of graminoids and forbs is known to have high decay rates (Lund et al., 2010). Also erect shrub heath with abundant leafy vegetation indicated high respiration according to the models resulting most likely from large root biomass and high SOM content (Grogan & Chapin Iii, 2000). Even though quantities of substrates, such as nitrogen and phosphorous, were not available for modelling in this study, it can be assumed that aboveground vegetation abundance and type indicate belowground biomass and soil organic matter content at least to some degree in a tundra environment with nutrient limitation (Grogan & Jonasson, 2005; Geng et al., 2012). Sites higher on the fell slopes that had shallower soils and moisture limitation, had the lowest respiration rates. Thin snow cover on topographically exposed sites results in harsh winter conditions, which limit productivity, and reduces quality of soil organic matter (Elberling, 2007; Dagg & Lafleur, 2011). Different plant species compositions and plant functional groups have effects on soil microbes, nutrient cycling, and even temperature response of respiration. (Bowman et al., 2004; Sundqvist et al., 2011; Knowles et al., 2015). They most likely influence the response of respiration flux to vegetation types.

In August, in addition to vegetation height and type parameters, also vegetation cover and pH showed significance. According to the results, optimum pH for high respiration in the area is around 5, which is associated with meadow sites. Respiration experiences a slight decline with increasing or decreasing pH from there. It has been suggested that slightly acidic tundra is strongly related to plant species richness and diversity (Sundqvist et al., 2011), as well as high quality SOM (White et al. 2004), which results to efficient decomposition. Soil organic matter quality is a result of litter chemical composition affected by plant species and growth form (Hobbie et al., 2000). Additionally, mineral layer depth was found significant in the total growing season full model. Soil depth in this area may indicate the availability of soil nutrients and fertile growth environment for plants and microbes (Grogan & Chapin Iii, 2000). Deepest mineral soils were found in the valley that hosted high respiration rates in comparison to shallow and rocky soils at the fell tops.

The relationship between soil moisture and respiration was found to be unimodal, with optimum volumetric water content of 40%. This agrees well with previous research (see Nobrega & Grogan, 2008; Moyano et al., 2013; Eckhardt et al., 2019). Similarly, Knowles et al. (2015) estimated the balance point between moisture and oxygen limitation to be 30-45% on mountain tundra. Surprisingly, soil moisture was not significant in the full models and did not explain the spatial or temporal patterns of respiration very well. Usually it has been found to control respiration strongly in tundra (Elberling, 2003, Biasi et al., 2014). However, vegetation types were found to follow soil moisture patterns in the area, which may have overridden the effect of soil moisture in the models. Ultimately, vegetation communities are formed as a response to long-term soil moisture conditions driven by topography (Dagg & Lafleur, 2011), and thus soil moisture effect is present also in this area.

Although moisture is widely considered an important landscape-scale driver, also contradicting results have been reported from various tundra environments, where soil moisture was not very important for respiration (see Grogan & Jonasson, 2005; Susiluoto et al., 2008; Hagedorn et al., 2010). This implies that respiration activity was not limited by soil moisture conditions in the area but conflicts with the idea presented earlier about elevated temperatures causing drought stress. The problem may also again be that of scale, because soil respiration has been found to follow moisture patterns on a seasonal level, but not in relation to individual precipitation events. It has been suggested that on a larger spatial scale with more variation in moisture, the effect on soil respiration would be greater (Hicks Pries et al., 2013). In the relationship between respiration, moisture and temperature, hysteresis (the dependence of the state of a system on its history) has been suggested as a reason for the response to be inconsistent. Drought periods before or in between measurements may be capable of stressing autotrophs and/or heterotrophs and decreasing their abilities to respond to moisture (Knowles et al., 2015).

5.2 Quality assessment of the methods

5.2.1 Field methods

Respiration flux is known to be highly variable in time between days and even during one day. In a study concentrating on environmental responses, it would be ideal to minimize the small temporal variation in the flux by conducting measurements in similar circumstances every time. This was not possible conducting 900 measurements on the course of two months, but some steps were taken in order to limit the error. The weather effect, that is differences in conditions caused by radiation, air temperature and rain, is important control of gas fluxes, especially when they are only observed for short time periods. In this study, fluxes recorded in different conditions were standardized to temperature, in order to minimize these effects. Precipitation may affect diffusion of CO_2 in the soil pores by displacing gases or lowering diffusion. Effects may persist for several days. Some of the measurements were conducted on windy days, which may cause alterations in the respiration flux especially in coarse soils (Davidson et al., 2002; Ryan & Law, 2005). However, weather conditions during measurement campaigns were relatively stable, and the differences in weather conditions between days were considered negligible.

Differences may occur in measurements conducted at different points during the day, due to alterations in radiation induced temperature and rain episodes. Diurnal variation in the flux has been found to be significant, but similar between ecosystems (Geng et al., 2012). Using a daily mean of multiple measurements from different times during the day could minimize the effect of diurnal variation in the data. However, only one measuring occasion per site per campaign could be conducted, due to the labor-intensive nature of the measurements. The measurements were conducted approximately between 10:00 and 20:00 during the day and thus, non-desired diurnal variation is probably present in the data. However, the time of measurement on each site is random (see Moriyama et al., 2013), that is, time of measurement at different environments and sites on different campaigns is not the same at each measurement occasion, as determined by individual schedules of each field assistant. It is assumed that no intense enough biased patterns caused by diurnal variation were created to disturb the results.

Multiple approaches could be used to calculate carbon dioxide fluxes from measurement data (Kandel et al., 2016). Using the slope of linear regression in the flux calculation process has been shown to cause underestimation of fluxes in soils with certain porosities. Usually non-steady-state chambers of equivalent size to ones used here, underestimation ranges from 15 % to negligible (Davidson et al., 2002). However, it has been suggested that in short chamber closure times of only a few minutes, linear regression produces most stable results (Kandel et al., 2016). It can also be argued that identical measurement protocol and calculations are enough to compare fluxes spatially and temporally within this specific data set. The comparability of these measurements to other studies remains unclear and needs to be assessed further.

Although chamber method is widely used in measuring soil carbon fluxes, there are several factors that may distort the measured flux from the original. Setting the chamber in place always alters the gas exchange in the soil-atmosphere interface to some extent. The chamber system used was not equipped with a vent, that may have led to unstable pressure inside the chamber, when gas concentrations and temperature alter during measurements. Decreased or increased pressure in the headspace compared to ambient air, may result to under- or overestimation of the flux, due to changes in the concentration gradient between the soil and the headspace. However, in short measurements, these errors should be small (Longdoz et al., 2000). The chamber system used was equipped with a fan, that should ensure the homogenous concentration of gases in the chamber headspace. However, there are some conflicting opinions on if the fan causes major disturbance to concentration gradient or not (Ryan & Law, 2005).

Inserting the collars is a major source for disturbance measuring the soil carbon flux. Especially the autotrophic component of soil respiration may be severely underestimated due to disturbance in fine roots (Heinemeyer et al., 2011). Disturbance may cause both increases and decreases in the carbon dioxide flux. Invaded roots are no longer able to produce CO_2, but on the other hand, heterotrophs may profit from alleviated competition and increased soil moisture no longer affected by the roots (Menyailo et al., 2015). The collars were kept in place during the whole measurement period to minimize disturbance and time consumed in collar installations. However, they were sometimes moved out of their place due to herbivore activity on the area. The collars were secured carefully before every measurement. Uneven sealing of the collars between sites may have altered the fluxes and leading to over- and underestimations of the respiration flux. Installing collars deep enough to rocky soils without damaging plant roots and shoots was a challenge, which may have led to differences in collar stability and possibilities for spatially uneven lateral CO_2 flow (Davidson et al., 2002; Virkkala et al., 2018). On sites where soil moisture is high, the sealing tends to be more secured, which may lead to overestimation of fluxes on those sites (Heinemeyer & McNamara, 2011).

Clipping the aboveground vegetation prior to measurements is considered less invasive than most methods, but it alters the movements of carbon between plant parts and the soil. Clipping prevents photosynthesis and thus the transport of new organic compounds to plant roots, which may cause increased root mortality. Increased respiration levels have been reported after aboveground biomass removal and it is possibly result of root decomposition (Kuzyakov, Y., 2006; Nobrega & Grogan, 2008; Susiluoto et al., 2008; Eckhardt et al., 2019). It is possible that the respiration observed in this study was entirely heterotrophic or the contribution of autotrophic and heterotrophic respiration was different in the measurements conducted in the first campaign and in later measurements.

On the other hand, also previously assimilated carbon may be used by both autotrophs and microbes for respiration in the rhizosphere. Many plants also store and utilize carbon reserves for regrowth after clipping (Kuzyakov, Y., 2006). It can be argued that the major effect from removing the vegetation occurs during the first hours after the treatment and does not influence flux measurements conducted. It has been found in previous studies, where similar procedure was conducted, that majority of the root biomass is unharmed after the clipping and microbial biomass remains completely unaltered. The carbon, water and nutrient allocation patterns remain quite stable shortly after the treatment and no confirmation of bias in the heterotrophic flux due to clipping procedure has been presented (Nobrega & Grogan, 2008; Eckhardt et al., 2019). Observed regrowth in half of the study sites suggests that neither in this study were roots destroyed by the clipping. It remains unclear, how the belowground conditions in the soil altered during the study period of two months and if the comparability of the campaigns is questionable.

5.2.2 Modelling

Modelling soil respiration and the controlling factors is a methodological challenge. The vast number of study sites and large variation and measurement caused the models not to detect many straightforward relationships with high reliability. Multivariate modelling enables incorporating multiple environmental variables that change simultaneously. Effects are usually sufficiently reduced to proportion when controlled by other factors, compared to single-factor studies, which often result in overestimations of effects. However, limitations include complex responses and non-straightforward results. Effects are not necessarily additive or predictable by other variables. (Dieleman et al., 2012; Sierra et al., 2015). Responses of variables may be covered with others and cause-effect relationships are difficult to detect. Especially when conducting field examinations on naturally occurring gradients, the complexity of the studied processes may confound the difference between actual and apparent controlling factors (Geng et al., 2012). Furthermore, the methodological approach using chambers provides good spatial preciseness, but lacks the possibilities to track fine scale temporal variability. Three measurement campaigns may be enough to capture variance during the growing season as a whole, but hides any episodic effects in between (Vargas et al., 2011; McGuire et al., 2012; Grant et al., 2015). Increasing the temporal sampling intensity would provide information on variability of the flux but also add noise and possibly make modelling efforts increasingly complex. With limited amount of data that accurately grasps the high variability of the flux, any upscaling from single or few measurements to larger areas or time frames must be done with extreme care (Arndal et al., 2009). The question of quantifying high temporal and spatial variation is in the core of soil carbon flux research and poses a major challenge for all modelling efforts (Phillips et al., 2017; McGuire et al., 2012).

Unveiling the temporal patterns in respiration was strongly relying on soil climate variables that were the only explanatory variables recorded as time series. It has been found that excessive use of abiotic factors in respiration modelling will result in weaker models, due to high variance in respiration in climatically similar environments (Knowles et al., 2015). It is likely, that on landscape-scale, spatial variability of resources and limitation set by soil and vegetation are of greater importance to soil respiration patterns, than temporal changes in soil climate. To further investigate the temporal aspect of soil respiration response to environmental change, more time series of variables should be included in the modeling. Plant phenology is crucial to temporal patterns of respiration (Ryan & Law, 2005; Zhang et al., 2019) and in this study, vegetation parameters were recorded only once. For example, changes in leaf area and litter quantity could have improved the models, if incorporated in this study. It has been suggested that the relationship between respiration and moisture is highly dependent on soil type and properties (Moyano et al., 2012; Moriyama et al., 2013), which were not described in the models very profoundly. Brummell et al. (2012) highlights the importance of soil gas diffusivity, that controls respiration even more than biological activities. The diffusivity of carbon dioxide and ambient air in the soil has a very straightforward effect on respiration measured with chambers. In efforts to characterize the moisture response of respiration in varying environments, it is important to take soil properties more carefully into consideration, as there is no total agreement on the effect of soil characteristics to respiration moisture response (Moriyama et al., 2013). In this study, for example soil porosity index and bulk density could have been incorporated to increase the explanatory power of soil properties models and the importance of soil characteristics in the respirations spatial pattern description.

Biomass was used as indicator for primary production and amount of carbon inputs to the soil via vegetation. The biomass variables were not adding much value to the models as they were non-significant in all the models. Especially moss mass was not important and eliminated from the full models either first or second of the variables. Mosses have been found to contribute significantly to the ecosystem primary production especially in the late growing season (Arndal et al., 2009). However, in this study, they were clipped in the early growing season, when biomass was not in its peak. The moss biomass clipping was found to be especially challenging without creating disturbance to the surface soil and plant roots. Furthermore, the sites with highest moss biomass were also the ones with less other resources, such as nutrients and moisture, which may have caused the effect to be covered by other, more robust responses. Aboveground vascular biomass is not necessarily the best indicator for soil respiration either, because the aboveground vegetation in the collar does not always represent the situation in the soil. Plant roots are key factor in soil respiration and their sphere of influence extends further than what could be expected. On some sites the collar was installed on less vegetated part of the site due to practical reasons (see Bowman et al., 2004; Arens et al., 2008; Heinemeyer et al., 2011). In the study design, biomass was relatively low in all the sites and spatial differences were not great enough to be shown in the respiration as the study design did not include birch forests. If it did, the biomass could have more accurately indicated the amount of organic matter available for decomposers and thus be of greater significance in predicting respiration activity. On the other hand, plant species have different functionalities in terms of biomass' relationship to photosynthesis, growth, and carbon exchange (Susiluoto et al., 2008). Additionally, woody shrub vegetation has higher biomass but is decomposed slower than lighter herbaceous vegetation (Hobbie et al., 2000).

Instead of total plant biomass, the mass of green leaves could have been used. It has been suggested to be significant in respiration prediction models (Zamolodchikov, 2015). Also leaf area index (LAI) could describe the photosynthesis and carbon use patterns similarly (Williams et al., 2006; Lund et al., 2010; Virkkala et al., 2018). Belowground biomass has a direct effect to the soil respiration via autotrophic respiration and is strongly linked to the activity of heterotrophs, which is why belowground biomass is most likely more important predictor of soil respiration than total aboveground biomass (Geng et al., 2012).

Quantity of soil organic matter or soil nutrient composition was not included in this study, which leads to relying on assumptions of the relationship of vegetation type and soil chemical composition. Vegetation type or size does not necessarily indicate the amount of root respiration or litter suitability for decomposing, even though sometimes used as proxies. The nutrient limitations are difficult to detect without laboratory measurements and their possibly differing occurrence in vegetation types is poorly known (Sundqvist et al., 2011; Sistla et al., 2012). Including variables of soil carbon and nitrogen contents in the models would assure that the temporal differences in respiration between vegetation types is based on nutrient limitation on other sites rather than some other factors driving increased respiration in the tundra meadows. On the other hand, it can be assumed that pH and organic layer depth indicate these parameters at least to some degree. Additionally, vegetation type classification, that appeared to be of immense importance in predicting respiration, was done based of photographs. This results in growing amount of uncertainty and subjectivity. Especially classifying types including same plant species, for example shrub types and barren class, is most likely prone to error. More objective classification could have been done based on quantitative plant species ground data, by visual estimation in situ, or using vegetation indices derived from remotely sensed data.

6. Conclusions

The aim of this study was to identify the spatial and temporal patterns of soil respiration and the environmental factors controlling the flux on landscape-scale during the growing season. The variability of respiration was captured with 100 sample sites and three measurement campaigns. Modelling respiration with this data set was challenging due to limited environmental variables and the complex nature of the soil respiration process. Models could not grasp the spatial and temporal variation of respiration in the area very accurately.

The models suggest that spatially, respiration follows vegetation patterns and abundant vegetation predicts high respiration rates given adequate abiotic resources. Meadow and heath sites with mesic moisture conditions and great productivity had the highest respiration. The most influential variables in the models were vegetation size parameters and vegetation type. Belowground respiration was most likely stimulated by high quality soil organic matter with great pools of carbon and vital nutrients provided by plant litter and roots. Respiration flux did not show very robust temporal patterns. Respiration peaked in July due to strong temperature response in meadow sites. The relative importance of the most important environmental variables remained throughout the season.

These results imply that not only is soil organic matter quality and quantity the main spatial control on landscape-scale, carbon and nutrient inputs from plants also seem to affect the respiration response to increases in temperature. Tundra landscape respiration seems to be most strongly limited by soil organic matter quality rather than climatic conditions. Soil temperature and moisture are long-term landscape-scale controls that define the distribution of vegetation and thus, soil chemical properties on annual or inter-annual scale (Fig. 15).

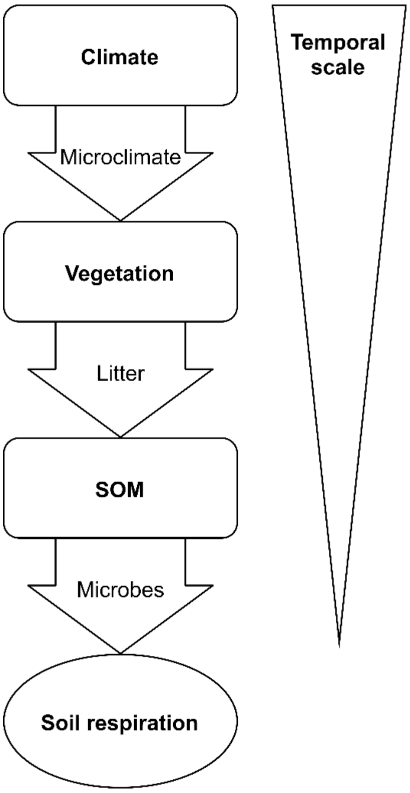

Figure 15. The most important processes for soil respiration on landscape-scale according to the models. Factors form a hierarchy, where climate controls the formation of vegetation patterns and plants provide organic matter inputs for microbes to decompose. The temporal scale on which the factors are important drivers of respiration, is represented on the right. The amount and chemical composition of litter provided by vegetation was most likely the primary control of respiration on the area during growing season. However, climate is most likely an important factor driving differences between growing seasons. The hierarchy also determines the respiration response to changes. Alterations in the microclimate do not appear in respiration flux if belowground resources are not adequate to support it.

The spatial and temporal heterogeneity of carbon fluxes remains the greatest challenge in soil respiration modelling. Soil respiration data still lacks coverage in describing the effect of episodic events and climatic extremes as well as spatial mosaic that often includes respiration hotspots. Available respiration data is currently in great part limited to collection of snapshots in terms of temporal and spatial variability. In order to accurately upscale information and produce reliable models on possible future changes in carbon fluxes soil-atmosphere interface, the entire gradient of environmental conditions needs to be taken into consideration more carefully. More intense field sampling efforts with carefully selected environmental variables are needed to further assess the role of environmental factors in controlling respiration flux in space and time.

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8. Appendixes

Appendix A: Field campaigns

Campaign	**Dates**	**Conducted by**
Installing the collars and collecting biomass	19.6.-29.6.2018	Anna-Maria Virkkala & Outi Seppälä
Measurement campaign 1	27.6.-5.7.2018	Aino-Maija Määttänen & Outi Seppälä
Measurement campaign 2	23.7.-27.7.2018	Elisa Hanhirova & Outi Seppälä
Measurement campaign 3	27.8.-31.8.2018	Aino-Maija Määttänen & Outi Seppälä

Appendix B: Field work form

Table B1. Field work form was filled out during the measurements in the field. Identification was done by site and campaign numbers. Each replicate measurements were distinguished by the time the measurement started logged on the data reader. In order to track possible sources for errors the field worker's name and numbers of equipment used (chamber, CO2- and RH-probes, data reader) were written down. Collar height was used to calculate the true velocity of the chamber. Weather conditions were controlled to determinate possible effect of prevailing weather (data not shown). Each measurement was classified based on the aspect of weather affecting the measurements the strongest (1=cloudy, 2=windy, 3=sunny, 4=rainy, 5=partly cloudy).

Site		Soil moisture	
Date		Soil temperature	
Name		Collar height	
Campaign n.		Weather	
Equipment		Other	
SR_1		Notes	
SR_2		Notes	
SR_3		Notes	

Appendix C: Data

Site	pH	Veg. cover	Veg- height	Org. depth	Min. depth	Veg. type	Moisutre_6	Temp._6	Moisutre_7	Temp._7	Moisture_8	Temp_8	Moss_mass	Vasc._mass	Total_mass	%_herbac.	%._woody	Flux_6	Flux_7	Flux_8
19	NA	75	2	1	20	3	15.5	6.1	12	14.1	19.7	7.5	11.42	15.95	27.37	0	100	2.31	1.28	1.43
25	4.45	75	5	3	15	3	28.4	6.4	10	12.6	17.4	8.5	1.5	12.21	13.71	2	98	2.85	1.74	2.33
31	4.33	70	15	4	40	3	21.6	7	10	11.6	21.1	7.8	0	11.15	11.15	0	100	2.23	0.61	1.57
37	4.35	100	7	5	10	3	26.7	6.7	14.1	12.8	20	8	2.38	15.75	18.13	0	100	2.50	1.77	2.41
91	4.31	90	15	5	10	3	17.9	4.4	12.3	11.4	16.4	7	2.51	10.98	13.49	2	98	2.02	2.39	1.60
97	4.35	20	10	2	25	3	18.3	6.5	9	13	19.4	8.1	16.69	3.09	19.78	2	98	2.30	1.18	1.12
103	4.76	25	35	15	25	3	41.1	6.2	12.5	12.6	27	8.3	5.92	1.04	6.96	85	15	2.80	2.42	2.95
109	4.23	15	5	10	30	2	29.7	7.4	8.4	12.1	26.2	8	20.62	1.64	22.26	0	100	1.23	1.09	0.98
115	5.02	75	35	8	8	3	17	6.3	9.7	11	19.3	7.4	8.88	7.25	16.13	0	100	1.91	2.25	2.17
181	4.82	70	50	20	20	3	32.2	17.9	16.4	10.6	23.7	7.5	8	1.53	9.53	100	0	3.62	3.96	3.57
187	4.3	20	15	7	30	1	18.9	7.9	9.4	13.6	19.7	9.9	0	3.07	3.07	0	100	1.11	0.49	0.94
193	4.99	5	5	7	7	2	29.2	7.6	14.3	13.8	22.6	8.1	1.06	1.66	2.72	30	70	1.93	1.83	1.97
199	4.51	15	7	5	15	3	14.2	6.7	6.3	13.3	13.6	7.1	0.96	4.79	5.75	5	95	3.33	2.92	2.62
247	5.51	5	5	6	6	3	10	9.5	13.3	11.7	22	7.5	4.94	2.74	7.68	90	10	3.33	5.78	2.97
265	5.23	20	10	20	30	4	55.8	5.6	45.2	15.3	49.8	9.2	0.61	1.34	1.95	70	30	3.03	7.44	5.50
271	4.32	95	20	7	7	3	29.7	7.7	8.4	13	15.6	6.6	2.28	5.35	7.63	0	100	3.16	2.03	1.22

595	589	577	523	517	511	505	481	439	433	427	421	403	388	355	349	325	277
4.57	4.77	4.37	4.79	4.17	4.4	4.15	4.98	4.54	4.2	3.86	4.08	4.77	5.85	4.95	4.33	4.85	4.6
30	40	60	0	65	40	75	20	5	8	15	5	1	3	80	30	0	85
3	10	15	0	20	5	3	3	8	4	3	15	1	3	15	10	0	10
3	4	5	1	7	2	3	5	8	5	5	5	2	20	5	5	0	6
4	20	5	1	7	2	15	5	8	5	5	35	3	45	10	10	0	20
3	3	3	4	3	3	3	3	3	2	3	3	2	5	4	3	1	3
14.4	17.9	21.3	43.8	16.6	14.9	27.4	15.1	13.5	27.5	22.9	9.8	10.2	85	43	25.2	4.1	17.6
6.1	7	6.2	13.4	8.8	6.1	5.3	7.8	9.9	5.5	6.9	6.2	11.4	6.6	4.4	4.9	13.2	5.8
8.1	7.4	7.3	34.5	9	3.8	13.1	16.4	10.4	13.9	5.6	13.1	15.4	77.6	14.9	5.4	8.6	5.1
13.7	14.7	12.9	15.2	13.5	14.6	11.8	11.9	15.3	11.7	12.9	12.7	12.8	14.8	11.6	10.2	12.9	12.8
18	18.5	20.8	35.1	21.3	10.7	19.7	19.3	14.6	17.9	17.2	9.3	6.2	75.3	35.6	13.6	5.4	17.9
7.7	7.7	7.4	9.5	8.1	9.3	6.6	7.1	8.3	6.4	6.9	7.2	8.3	7.4	7.1	5.8	8.9	8.2
1.51	0	4.75	0	0	0	11.8	3.59	0	1.76	1.87	6.3	0	1.53	0.22	8.79	0	5.75
12.71	17.39	4.47	0.54	2.43	12.91	3.59	8.06	6.87	3.38	6.61	3.55	0.21	1.89	6.66	12.85	0.93	4.74
14.22	17.39	9.22	0.54	2.43	12.91	15.39	11.65	6.87	5.14	8.48	9.85	0.21	3.42	6.88	21.64	0.93	10.49
2	0	5	100	40	0	5	2	0	0	2	2	20	100	10	0	30	0
98	100	95	0	60	100	95	98	100	100	98	98	80	0	90	100	70	100
2.52	1.94	1.79	0.57	2.31	1.76	1.71	1.34	0.95	2.30	2.03	1.93	0.22	1.10	3.24	1.83	0.05	2.81
3.16	4.29	2.44	1.87	4.40	1.58	3.16	3.49	0.66	1.41	1.60	9.17	1.61	0.70	4.58	3.97	1.73	2.66
1.63	1.96	2.02	1.65	2.69	1.38	1.00	2.19	1.23	0.84	1.49	1.22	1.25	-0.18	3.30	1.64	1.25	2.93

979	967	961	919	913	901	895	889	835	823	811	757	751	745	739	733	679	667
6.13	5.46	4.89	4.52	4.61	4.01	4.44	4.28	4.7	4.76	4.73	4.41	4.84	4.4	4.18	NA	4.86	4.18
2	1	5	20	20	30	15	90	1	15	5	100	5	65	40	60	30	90
1	1	3	8	5	20	3	3	2	10	10	10	10	20	4	20	5	5
2	10	10	10	15	3	1	10	7	1	35	10	4	1	1	5	2	7
25	10	15	10	15	6	1	15	10	15	35	20	4	20	20	6	10	7
4	4	4	2	2	3	3	3	3	2	4	3	3	3	3	3	3	3
60.1	51.9	52.2	17.4	11.2	12.6	13.8	5.9	13.4	19.5	61.5	16.2	13.3	25.4	25.6	11.8	15.1	24.6
6.6	10.8	10.5	7.7	8	5.4	11.1	9.2	8.3	6.5	11.1	5.9	5.9	6.5	6.4	9.6	9.9	6.4
25.2	53.6	43.6	15.9	12.8	5.4	20.1	11.2	7.6	13.6	43.7	7.6	6.8	24.9	11.5	17.6	6.4	11.8
16.4	13.4	14	11.1	15	13.6	13.9	11.9	14.1	15.6	13.2	11	14.6	14.3	15.7	12.8	15.4	14.4
27.5	53.5	47.2	15.8	9.5	15.1	17	12.1	14.2	18.3	47.5	12.3	14.3	17.1	14.6	16.2	17.6	16.1
8.3	7.7	7.1	7	8.8	7.1	7.9	6.6	7.6	6.6	7.7	7.6	8	8.7	7.7	7.2	8.4	7.6
2.03	3.28	3.35	1.43	0	4.23	2.59	5.08	0	4.57	0	8.8	1.21	0.47	0	2.71	1.58	0.78
1.19	1.16	1.49	5.62	3.37	8.02	8.09	14.46	2.72	2.27	0.61	10.88	7.73	6.19	8.07	10.61	1.61	16.38
3.22	4.44	4.84	7.05	3.37	12.25	10.68	19.54	2.72	6.84	0.61	19.68	8.94	6.66	8.07	13.32	3.19	17.16
40	95	40	5	2	2	0	0	0	0	100	5	0	5	0	0	10	0
60	5	60	95	98	98	100	100	100	100	0	95	100	95	100	100	90	100
2.14	2.25	2.30	1.70	1.58	2.80	1.46	1.01	0.80	1.82	2.30	2.77	1.59	4.49	2.05	0.88	0.64	1.81
4.36	2.91	3.02	1.93	3.28	3.21	1.79	1.87	2.03	2.22	2.51	3.30	2.42	9.95	1.54	2.55	1.62	4.17
2.13	2.29	1.83	2.66	1.15	1.97	1.06	2.27	0.84	1.18	2.58	2.05	1.65	4.37	1.13	3.06	0.85	1.97

11214	11213	11212	11211	11210	11209	11208	11207	11205	11204	11203	11202	11201	1159	1135	1123	1075	1045
5.04	5.14	5.04	4.69	4.79	4.73	4.69	NA	4.84	5.21	4.95	4.92	4.96	4.73	6.15	4.57	4.58	4.85
30	35	40	50	60	45	85	30	65	20	35	40	30	15	1	45	85	45
4	4	4	7	5	9	8	4	9	2	6	5	5	4	1	4	10	5
2	3	3	5	3	8	5	3	13	2	5	0	3	3	10	2	5	1
0	11	11	2	2	13	0	6	0	13	5	15	4	5	10	2	5	10
3	1	2	3	3	3	3	3	1	1	2	1	1	3	4	1	3	3
16.6	7.9	10	16.1	9.8	12.1	9.9	8.9	40.5	42.1	20	22.5	15.1	15.8	70.9	11.5	9.2	20.9
12	9.3	9.4	10	9.8	10.9	9.8	13.3	7.9	15.2	6	11.4	13.4	12.2	8.4	12.9	7.3	11.6
18.4	6.8	10.8	9.1	7.1	11.4	22	17.6	53.1	16.1	28.6	30.5	18.5	19.8	52.7	14.9	10.3	19.2
15.1	12.7	12.9	13	13	13.2	11.8	13.5	11.7	13.3	12.5	12.5	13.3	16.2	17.1	12.7	13.6	13.1
12.5	9	6.4	13.3	6.5	10.9	18.2	17.7	62	21.5	41.8	28.2	14.6	17.7	46.8	15.9	8.5	21.5
7.2	6.6	7.6	7	7.8	9.7	7	7.2	6.6	7.2	6.8	7	7.4	8.9	7.6	6.3	7.9	6.9
9.53	0	0	3.81	4.5	1.58	2.03	0	0	5.21	0	4.41	0	0	0	0.85	3.72	4.86
6.82	6.01	8.59	10.11	8.13	3.11	14.78	10.25	2.29	0.53	9.48	12.43	0	5.67	1.35	5.57	1.14	0.53
16.35	6.01	8.59	13.92	12.63	4.69	16.81	10.25	2.29	5.74	9.48	16.84	0	5.67	1.35	6.42	4.86	5.39
0	0	40	0	0	20	2	0	0	80	2	0	0	5	90	0	45	20
100	100	60	100	100	80	98	100	100	20	98	100	0	95	10	100	55	80
1.70	1.77	2.41	1.98	3.42	3.20	0.44	-0.49	0.47	0.96	0.10	0.62	0.01	0.98	1.32	0.49	1.53	0.69
-0.06	0.71	2.30	1.53	2.24	5.06	3.26	1.32	2.33	2.50	1.60	1.54	1.35	1.66	2.35	1.27	2.97	1.90
1.99	1.42	2.61	2.11	4.35	3.95	1.92	1.51	1.64	1.90	2.10	1.08	1.02	1.15	1.57	1.40	1.42	1.40

12211	12210	12209	12208	12207	12206	12205	12204	12203	12202	12201	11225	11224	11221	12220	11220	11216	11215
5.69	5.96	5.4	6.54	5.73	5.74	5.14	5.42	4.85	5.8	4.79	4.68	4.94	4.19	NA	NA	4.73	5.41
0	0	0	0	0	0	0	0	4	4	4	40	15	50	NA	20	80	15
0	0	0	0	0	0	0	0	NA	NA	NA	11	6	8	NA	2	7	6
45	55	65	40	3	8	35	3	NA	NA	4	6	5	2	NA	1	16	9
13	0	0	25	15	15	15	35	NA	NA	NA	4	6	6	NA	21	6	22
5	5	5	5	5	4	4	4	4	4	4	2	2	2	5	1	3	2
68.2	66.5	75.9	39.2	49.8	32.6	72.4	39.5	16.3	41.8	31.6	15.6	24.6	11	66.0	10.7	19.8	11.7
5.1	3.5	5.7	2.6	5.2	6.2	4.5	6.4	9.1	11.2	6.6	8	6.4	6.4	5.9	5.4	6.4	10.8
62.5	70.1	73.4	55.8	55.8	34.4	43.2	28.3	23.5	39.8	22.6	8.9	15.1	8.7	46.0	6.1	9.7	6.2
14.7	14.7	16.3	15.1	16.4	16.5	15.8	15.7	14.2	14.9	13.7	14	14.7	16	14.3	14.5	10.7	15.2
67.9	73.3	77	56.5	49.3	43.6	40	28	28.8	41.9	29	13.6	15.6	13.8	46.0	8.2	15.8	13
6.7	6.9	6.7	5.6	6.3	6.7	7.2	6.9	8.1	8.4	8.3	7.4	7.5	7.1	8.1	6.8	6.8	7
0.1	3.44	0	0	0	1.97	5.27	4.05	0	1.67	0	4.56	2.05	0	1.09	0	2.44	0
3.93	2.68	1.47	1	1.18	1.06	0.85	0.84	4.34	1.31	1.6	0	2.52	2.54	2.17	2.34	16.47	3.14
4.03	6.12	1.47	1	1.18	3.03	6.12	4.89	4.34	2.98	1.6	4.56	4.57	2.54	3.26	2.34	18.91	3.14
100	95	100	100	100	100	100	100	40	50	95	0	60	0	100	0	5	40
0	5	0	0	0	0	0	0	60	50	5	100	40	100	0	100	95	60
2.20	2.44	2.45	1.59	1.68	2.00	1.91	2.22	2.71	2.19	2.78	2.27	1.64	2.03	0.74	1.65	3.63	2.10
3.68	4.86	2.45	-0.31	0.12	4.72	4.45	4.23	4.65	3.78	5.69	2.39	0.52	2.03	3.91	1.79	4.22	1.57
3.48	3.64	1.28	0.18	0.54	1.82	2.15	2.43	2.87	2.93	3.13	1.29	0.58	1.18	1.49	0.92	2.33	0.98

12224	12223	12222	12221	12219	12218	12217	12216	12215	12214	12213	12212
5.46	5.66	5.38	5.32	5.06	5.07	5.23	5.36	4.83	5.28	5.22	5.7
1	3	3	0	10	5	10	5	0	0	0	0
15	NA	4	0	17	NA	10	8	0	0	0	0
15	NA	6	90	70	NA	55	45	55	80	65	75
15	NA	6	0	0	NA	0	0	0	0	0	0
5	5	4	5	5	5	5	5	5	5	5	5
66.7	63.5	64.7	72.7	69.9	58.8	71.4	74.3	75.2	76.9	72	75.5
2	7	7.7	6.6	5.8	5.8	4.9	4.6	5.7	3.2	4.8	4
68.6	74.1	65.3	60.9	49	47.2	68.3	65.2	60.6	78	71.7	76
7.6	14.2	13.6	13.8	14.3	13.5	13.3	13.1	14.1	13	14.7	15.1
75.5	58.1	60.6	62.2	57.8	47.3	65.8	70.4	61.7	81	78.9	77.6
6.3	7.3	7.4	7.9	7.3	7.9	7.3	7.4	7.9	5	6.4	6.1
0	0.32	0.55	0	1.04	4.04	0	0	0	0	0.23	1.03
1.87	0.93	0.69	3.43	3	7.63	2.69	1.58	4.11	2.19	2.78	3.25
1.87	1.25	1.24	3.43	4.04	11.67	2.69	1.58	4.11	2.19	3.01	4.28
100	100	100	100	95	100	0	100	100	100	100	100
0	0	0	0	5	0	100	0	0	0	0	0
1.70	0.90	3.27	1.36	1.89	4.00	1.64	1.40	1.38	1.75	1.75	1.97
2.15	1.17	5.15	2.02	2.88	8.56	1.17	0.80	1.67	2.44	1.67	3.09
0.57	1.43	1.90	1.63	2.57	4.19	1.46	1.55	1.23	1.38	1.60	1.89

Appendix D. Environmental variables

Variable	Method	Year
% of plants herbaceous / woody	Visual estimate	2018
Biomass (Vascular, moss)	Biomass sampling	2018
Mineral layer depth	In situ measurement	2016-2018
Organic layer depth	In situ measurement	2016-2018
pH	Soil sampling	2018
Soil moisture	In situ measurement	2018
Soil temperature	In situ measurement	2018
Vegetation cover	Visual estimate	2017-2018
Vegetation height	In situ measurement	2017-2018
Vegetation type	Visual estimate	2018

Appendix E: R-packages

Package	Reference	Used for
flux	Jurasinski et al. (2014)	flux standardisation
ggnewscale	Campitelli (2019)	graphs
ggplot2	Wickham (2016)	graphs
gridExtra	Auguie (2017)	graphs
hydroGOF	Zambrano-Bigiarini (2017)	RMSE calculation
jTools	Long (2019)	graphs
PerformanceAnalytics	Peterson & Carl (2019)	correlation matrix
raster	Hijmans (2019)	maps
rasterVis	Lamiguero & Hijmans (2019)	maps
rgdal	Bivand et al. (2019)	maps
tidyr	Wickham & Henry (2019)	data management
viridis	Garnier (2018)	graph colors

Appendix F: Variable frequencies

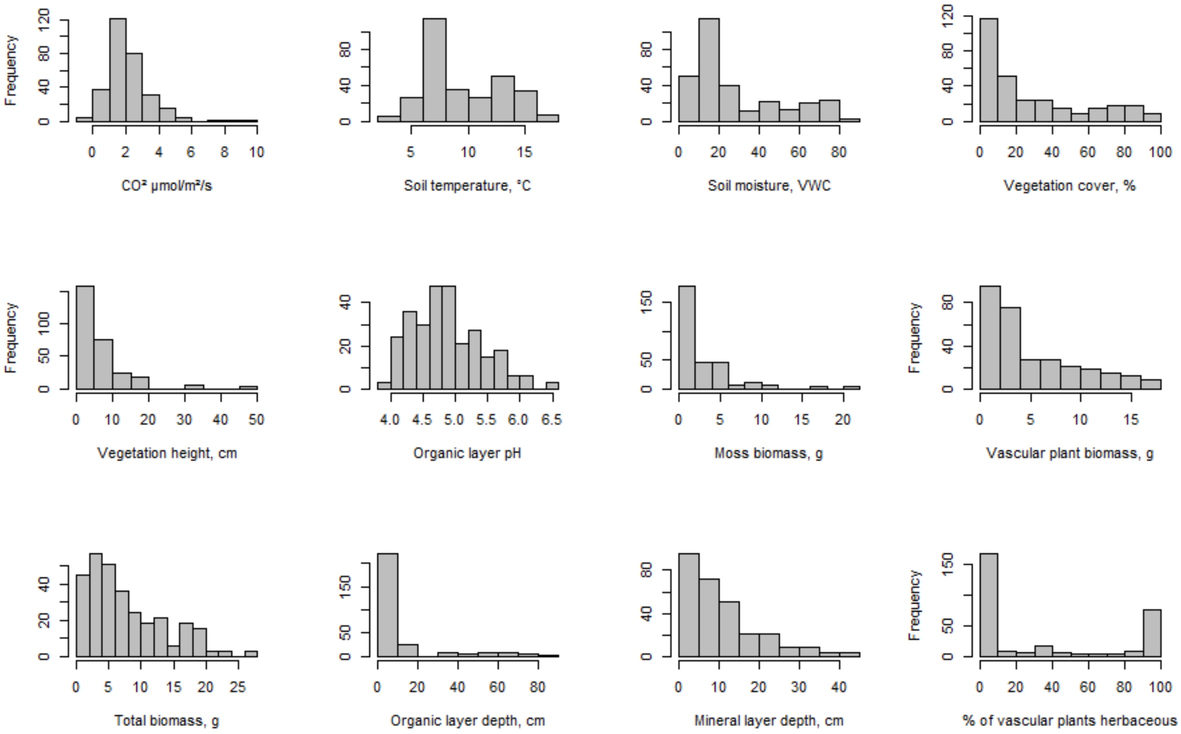

Figure F1. Frequency histograms of respiration flux and environmental variables in the data.

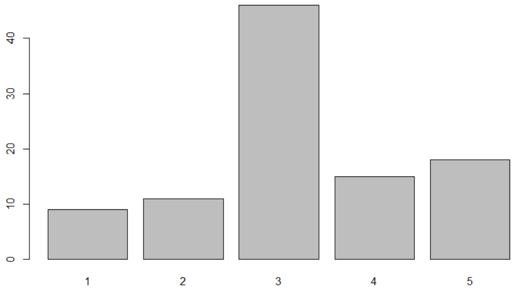

Figure F2. Frequencies of vegetation types in the data (1=barren, 2=prostrate shrubs, 3=erect shrubs, 4=graminoid, 5=wetland).

Appendix G. Descriptive statistics

Table G1. The key descriptive statistics of environmental parameters and measured respiration flux. NA's were introduced by four variables. Respiration flux, soil temperature and moisture statistics are calculated from the pooled data of all observations during the summer.

Variable	**Mean**	**Median**	**Min**	**Max**	**SD**	**95% fractile**	**NA's**
Respiration, µmol/m^2/s	2.15	1.92	-0.49	9.96	1.34	4.40	
S. temperature, °C	9.58	8.15	2.0	17.9	3.44	15.21	
S. moisture, VWC %	28.60	18.35	3.80	85.0	21.96	74.11	
Veg. height, cm	7.38	5.0	0	50.0	8.11	20.0	5
Veg. cover, %	29.76	20.0	0	100.0	30.32	90.0	
Total biomass, g	7.61	5.75	0	27.37	6.04	19.55	
Vascular biomass, g	5.10	3.20	0	17.39	4.55	14.83	
Moss biomass, g	3.51	1.32	0	20.62	3.60	8.91	
Org. layer depth, cm	13.33	5.0	0	90.0	19.99	65.0	4
Min. layer depth, cm	11.38	10.0	0	45.0	10.15	31.5	5
Herbaceous plants, %	34.92	5.0	0	100.0	42.65	100.0	
Woody plants, %	64.08	95.0	0	100.0	42.99	100.0	
pH		4.82	3.86	6.54		5.82	5

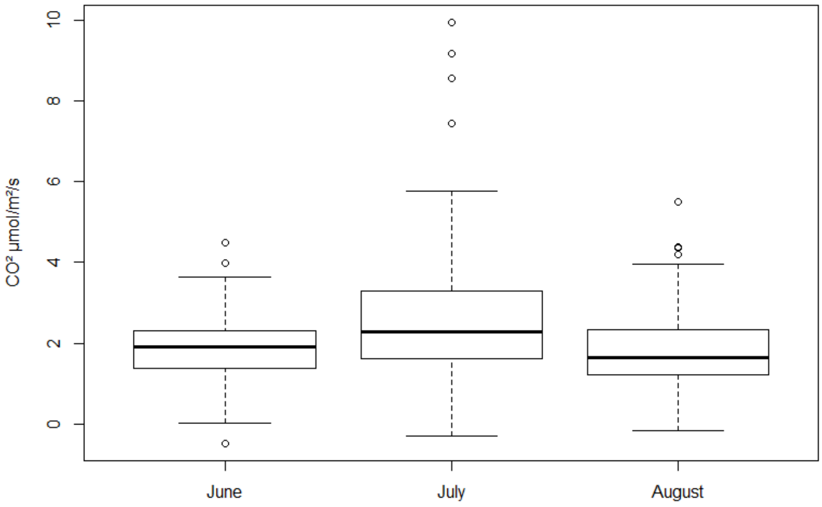

Figure G1. Respiration of carbon dioxide on three separate measuring occasions.

Appendix H. TukeyHSD

Table H1. TukeyHSD multiple comparisons of means of respiration flux and environmental variables in vegetation types (1=barren, 2=prostrate shrubs, 3=erect shrubs, 4=graminoid, 5=wetland). with 95% confidence level.

```
Respiration flux
          diff         lwr        upr     p adj
2-1  0.4385459 -0.43017049  1.3072622 0.6374070
3-1  1.1021753  0.37065064  1.8336999 0.0004421
4-1  1.7775281  0.93283624  2.6222200 0.0000002
5-1  0.7425819 -0.07528753  1.5604513 0.0951804
3-2  0.6636294  0.03282365  1.2944352 0.0336685
4-2  1.3389823  0.57984327  2.0981213 0.0000205
5-2  0.3040360 -0.42514023  1.0332123 0.7826963
4-3  0.6753529  0.07806549  1.2726402 0.0177620
5-3 -0.3595934 -0.91830458  0.1991178 0.3951740
5-4 -1.0349463 -1.73532778 -0.3345647 0.0006087
```

```
Soil moisture
          diff       lwr       upr     p adj
2-1 -3.1490028 -9.806147  3.508141 0.6924652
3-1 -4.0259259 -9.631743  1.579891 0.2827179
4-1 23.4185185 16.945479 29.891558 0.0000000
5-1 46.7833333 40.515840 53.050827 0.0000000
3-2 -0.8769231 -5.710911  3.957065 0.9875175
4-2 26.5675214 20.750090 32.384952 0.0000000
5-2 49.9323362 44.344516 55.520157 0.0000000
4-3 27.4444444 22.867314 32.021575 0.0000000
5-3 50.8092593 46.527746 55.090773 0.0000000
5-4 23.3648148 17.997654 28.731976 0.0000000
```

```
Soil temperature
           diff        lwr       upr     p adj
2-1 -0.77094017 -3.1158575 1.5739772 0.8958400
3-1 -0.81629630 -2.7908934 1.1583008 0.7880219
4-1 -0.16000000 -2.4400683 2.1200683 0.9996915
5-1 -1.75000000 -3.9576667 0.4576667 0.1918186
3-2 -0.04535613 -1.7480838 1.6573715 0.9999935
4-2  0.61094017 -1.4381961 2.6600764 0.9248647
5-2 -0.97905983 -2.9473179 0.9891983 0.6503815
4-3  0.65629630 -0.9559555 2.2685481 0.7973552
5-3 -0.93370370 -2.4418272 0.5744197 0.4359449
5-4 -1.59000000 -3.4805328 0.3005328 0.1450760
```

```
Vegetation height
          diff        lwr       upr     p adj
2-1  0.9658120  -4.218176  6.149800 0.9861750
3-1  5.4666667   1.101358  9.831975 0.0060320
4-1 -1.3611111  -6.632722  3.910500 0.9543444
5-1 -1.5777778  -6.618402  3.462846 0.9113361
3-2  4.5008547   0.736577  8.265132 0.0101187
4-2 -2.3269231  -7.112709  2.458863 0.6695493
5-2 -2.5435897  -7.073685  1.986505 0.5362254
4-3 -6.8277778 -10.711840 -2.943716 0.0000226
5-3 -7.0444444 -10.608704 -3.480185 0.0000012
5-4 -0.2166667  -4.846776  4.413442 0.9999383
```

```
Vegetation cover
          diff        lwr        upr     p adj
2-1  -9.094017 -25.056028   6.867994 0.5218576
3-1  19.133333   5.692117  32.574549 0.0010915
4-1 -21.955556 -37.476135  -6.434976 0.0011985
5-1 -28.379085 -43.553437 -13.204733 0.0000051
3-2  28.227350  16.636768  39.817933 0.0000000
4-2 -12.861538 -26.810148   1.087071 0.0866351
5-2 -19.285068 -32.847378  -5.722757 0.0011092
4-3 -41.088889 -52.063596 -30.114182 0.0000000
5-3 -47.512418 -57.991768 -37.033069 0.0000000
5-4  -6.423529 -19.463424   6.616365 0.6587360
```

```
Total biomass
          diff        lwr        upr     p adj
2-1  1.3411111  -1.849535  4.5317567 0.7776068
3-1  6.9186667   4.231903  9.6054307 0.0000000
4-1 -1.6468889  -4.749297  1.4555190 0.5912564
5-1 -1.4822222  -4.486116  1.5216713 0.6573460
3-2  5.5775556   3.260715  7.8943965 0.0000000
4-2 -2.9880000  -5.776187 -0.1998132 0.0288359
5-2 -2.8233333  -5.501472 -0.1451945 0.0330991
4-3 -8.5655556 -10.759289 -6.3718219 0.0000000
5-3 -8.4008889 -10.452939 -6.3488389 0.0000000
5-4  0.1646667  -2.407714  2.7370474 0.9997858
```

```
Moss biomass
          diff        lwr        upr     p adj
2-1  1.6097436 -0.7062714  3.9257586 0.3154675
3-1  2.6091111  0.6588519  4.5593703 0.0026294
4-1  0.3700000 -1.8819653  2.6219653 0.9914251
5-1 -0.4511111 -2.6315672  1.7293449 0.9795989
3-2  0.9993675 -0.6823731  2.6811082 0.4787416
4-2 -1.2397436 -3.2636232  0.7841360 0.4471089
5-2 -2.0608547 -4.0048530 -0.1168564 0.0316009
4-3 -2.2391111 -3.8314911 -0.6467312 0.0013084
5-3 -3.0602222 -4.5497573 -1.5706872 0.0000004
5-4 -0.8211111 -2.6883421  1.0461199 0.7473544
```

```
Vascular plant mass
          diff       lwr        upr     p adj
2-1 -0.2686325 -2.799785  2.2625200 0.9984220
3-1  4.3095556  2.178134  6.4409767 0.0000006
4-1 -2.0168889 -4.478042  0.4442643 0.1647411
5-1 -1.0311111 -3.414112  1.3518902 0.7585121
3-2  4.5781880  2.740228  6.4161477 0.0000000
4-2 -1.7482564 -3.960137  0.4636238 0.1942785
5-2 -0.7624786 -2.887057  1.3621001 0.8619257
4-3 -6.3264444 -8.066743 -4.5861464 0.0000000
5-3 -5.3406667 -6.968566 -3.7127669 0.0000000
5-4  0.9857778 -1.054903  3.0264582 0.6753046
```

```
Herbaceous percentage
         diff        lwr       upr     p adj
2-1  3.085470 -13.752197 19.923137 0.9870336
3-1 -1.933333 -16.111918 12.245251 0.9958102
4-1 63.111111  46.739092 79.483130 0.0000000
5-1 81.666667  65.814527 97.518806 0.0000000
3-2 -5.018803 -17.245231  7.207624 0.7923356
4-2 60.025641  45.311828 74.739454 0.0000000
5-2 78.581197  64.448129 92.714264 0.0000000
4-3 65.044444  53.467679 76.621210 0.0000000
5-3 83.600000  72.770927 94.429073 0.0000000
5-4 18.555556   4.980594 32.130517 0.0019616
```

```
pH
          diff          lwr          upr     p adj
2-1 -0.1341346 -0.393876992  0.125607761 0.6166481
3-1 -0.3087500 -0.531729633 -0.085770367 0.0016431
4-1  0.4479167  0.194856886  0.700976447 0.0000193
5-1  0.6430147  0.395186700  0.890842712 0.0000000
3-2 -0.1746154 -0.358072625  0.008841855 0.0706603
4-2  0.5820513  0.363017278  0.801085286 0.0000000
5-2  0.7771493  0.564181336  0.990117307 0.0000000
4-3  0.7566667  0.582799737  0.930533596 0.0000000
5-3  0.9517647  0.785604611  1.117924801 0.0000000
5-4  0.1950980 -0.009666492  0.399862570 0.0701750
```

```
Organic layer depth
         diff        lwr       upr     p adj
2-1  2.7094017 -4.7838717 10.202675 0.8584803
3-1  1.9111111 -4.3987897  8.221012 0.9206447
4-1  8.0170940  0.5238207 15.510367 0.0292564
5-1 48.4222222 41.1361763 55.708268 0.0000000
3-2 -0.7982906 -6.2394222  4.642841 0.9944334
4-2  5.3076923 -1.4702285 12.085613 0.2021134
5-2 45.7128205 39.1647269 52.260914 0.0000000
4-3  6.1059829  0.6648513 11.547115 0.0190970
5-3 46.5111111 41.3590986 51.663124 0.0000000
5-4 40.4051282 33.8570346 46.953222 0.0000000
```

```
Mineral layer depth
           diff         lwr        upr     p adj
2-1  0.02564103  -6.7433708  6.7946529 1.0000000
3-1  0.55555556  -5.1444625  6.2555736 0.9988683
4-1  6.58333333  -0.3000924 13.4667591 0.0684210
5-1 -3.13333333  -9.7151473  3.4484806 0.6869916
3-2  0.52991453  -4.3853051  5.4451341 0.9983185
4-2  6.55769231   0.3086341 12.8067505 0.0343839
5-2 -3.15897436  -9.0741626  2.7562139 0.5852058
4-3  6.02777778   0.9561495 11.0994060 0.0107830
5-3 -3.68888889  -8.3429341  0.9651564 0.1917451
5-4 -9.71666667 -15.7624488 -3.6708845 0.00014
```

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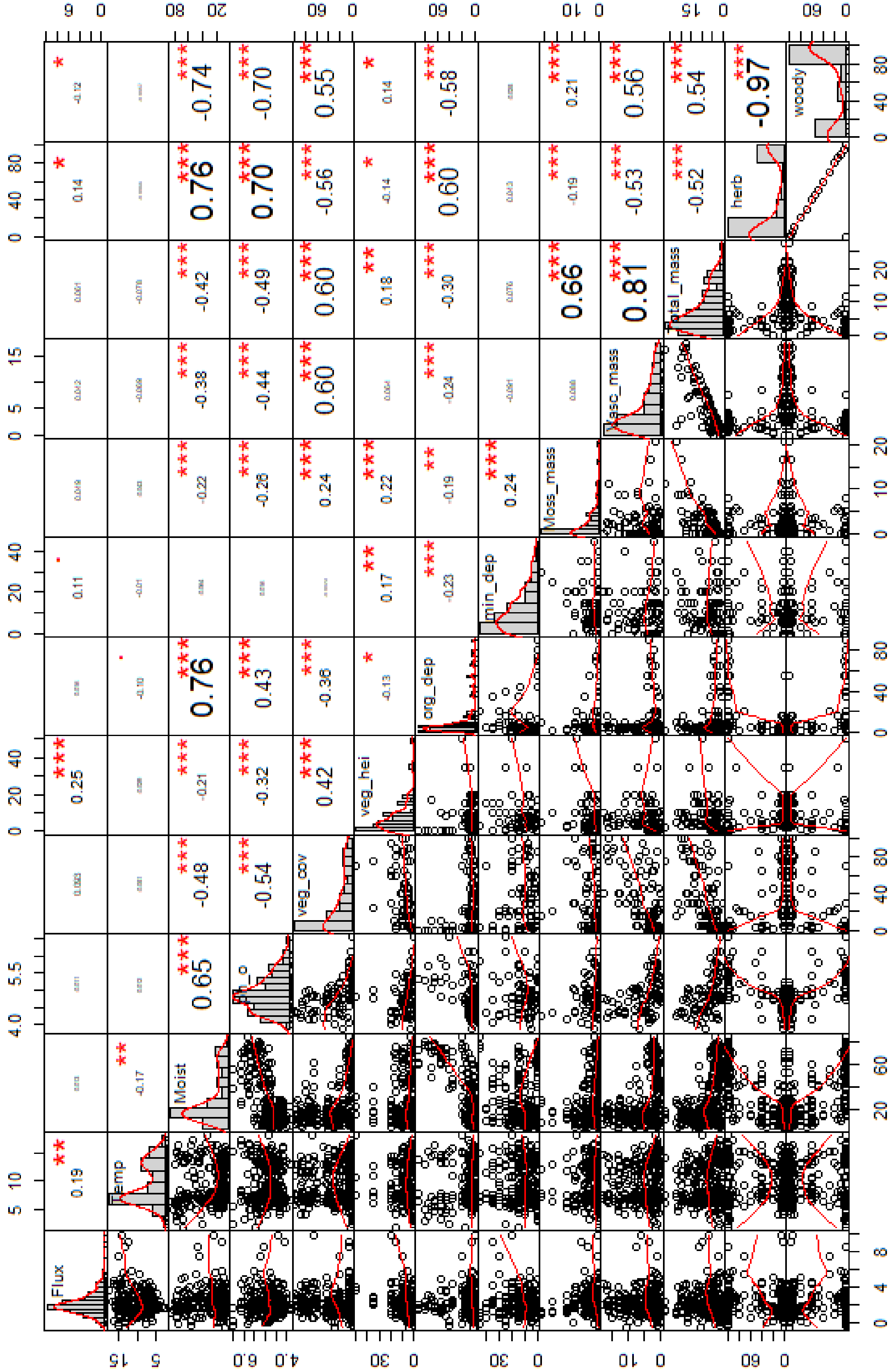
Table H2. TukeyHSD for respiration flux, soil temperature and soil moisture in different measuring campaigns (June, July, August).

```
Respiration flux
                             diff        lwr        upr     p adj
Mean_July-Mean_August  0.80614788  0.3747855  1.2375103 0.0000444
Mean_June-Mean_August -0.01785821 -0.4492206  0.4135042 0.9947709
Mean_June-Mean_July   -0.82400609 -1.2553685 -0.3926437 0.0000291

Soil temperature
                        diff        lwr        upr     p adj
Mean_July-Mean_August  6.104  5.4563691  6.7516309 0.0000000
Mean_June-Mean_August  0.221 -0.4266309  0.8686309 0.7009577
Mean_June-Mean_July   -5.883 -6.5306309 -5.2353691 0.0000000

Soil moisture
                        diff        lwr       upr     p adj
Mean_July-Mean_August -3.649 -10.958551  3.660551 0.4685018
Mean_June-Mean_August  2.355  -4.954551  9.664551 0.7284708
Mean_June-Mean_July    6.004  -1.305551 13.313551 0.1307530
```

Appendix I. Correlation matrix



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