Carbon exchange in boreal ecosystems: upscaling and the impacts of natural disturbances

Kelly, Julia

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

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JULIA KELLY
ENVIRONMENTAL SCIENCE | CEC | FACULTY OF SCIENCE | LUND UNIVERSITY

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I. Challenges and best practices for deriving temperature data from an uncalibrated UAV thermal infrared camera

II. Modelling and upscaling ecosystem respiration using thermal cameras and UAVs: application to a peatland during and after a hot drought

III. Upscaling northern peatland CO_2 fluxes using satellite remote sensing data

IV. Boreal forest soil carbon fluxes one year after a wildfire: effects of burn severity and management

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Carbon exchange in boreal ecosystems: upscaling and the impacts of natural disturbances

Julia Kelly

DOCTORAL DISSERTATION

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Abstract
Boreal forests and peatlands are globally significant carbon stores but they are threatened by rising air temperatures and changes in precipitation regimes and the frequency of natural disturbances. Predicting how the boreal biome will respond to climate change depends on being able to accurately model and upscale the greenhouse gas fluxes between these ecosystems and the atmosphere. This thesis focuses on developing simple, empirical, remote sensing models of ecosystem respiration (ER) and assessing how ER varies over space and in response to natural disturbances such as drought and wildfire.

Paper I and II tested the opportunities and limitations offered by newly available, miniaturized thermal cameras, which can capture images of surface temperature at sub-decimeter resolution. Since temperature is one of the most important factors driving ER, these cameras provide an opportunity to map ER in unprecedented detail. In Paper III, satellite land surface temperature (LST) data was used to model ER across several Nordic peatland sites to examine whether remote sensing models can capture variations in ER between sites. In addition, Paper II and III highlighted the impacts of the extreme 2018 drought that affected large parts of Europe on peatland CO_2 fluxes. The drought also led to a severe wildfire season in Sweden and Paper IV investigated how the effects of fire on forest soils depended on burn severity, salvage-logging and stand age.

Producing reliable surface temperature measurements from miniaturized thermal cameras requires careful data collection and processing and one of the main outcomes of this thesis is a set of best practices for thermal camera users. Despite including larger uncertainties than traditional soil or air temperature measurements, thermal data from these cameras is suitable for modeling ER in peatland ecosystems. The ER maps that can be produced using UAV thermal cameras offer a unique resource for evaluating how ER varies within a flux tower footprint and could reveal potential biases in flux tower measurements. Indeed, this thesis demonstrated that there is substantial spatial variation in ER, both within and between peatlands. Vegetation composition played a significant role in driving this spatial variation as well as the response of peatlands to drought. Nevertheless, using only LST and the Enhanced Vegetation Index (EVI2) as model inputs captured a large proportion of the variability of daily ER across multiple peatlands. With further developments, such a modeling approach could represent a simple and effective way of estimating peatland ER across Scandinavia. In terms of wildfire impacts on boreal forest soils, stand age had a significant impact on soil respiration, nutrient availability and microclimate, whereas salvage-logging did not, in the first year after fire. Furthermore, the effects of drought and wildfire on ER depended on their severity, but during both extreme water stress in peatlands and after severe burning in forests, ER decreased. It is important that this negative feedback is accounted for in ER models to avoid overestimating carbon loss from northern ecosystems in response to disturbances and climate change.

Key words carbon fluxes, CH_4, climate change, CO_2, drought, ecosystem respiration, forest, peatland, remote sensing, temperature, thermal camera, UAV, wildfire

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II. **Kelly, J.,** Kljun, N., Eklundh, L., Klemedtsson, L., Liljebladh, B., Olsson, P-O., Weslien, P., Xie, X. 2021. *Modelling and upscaling ecosystem respiration using thermal cameras and UAVs: application to a peatland during and after a hot drought.* Agricultural and Forest Meteorology, 300, 108330.

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Author contributions

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Popular summary

Boreal ecosystems are a globally important carbon sink, currently storing at least a fifth of all the carbon contained in terrestrial ecosystems. However, the fate of this carbon sink is uncertain because rising air temperatures and changes in precipitation and the frequency of natural disturbances are impacting the movement of carbon between these ecosystems and the atmosphere. For example, although higher air temperatures may prolong the growing season, allowing plants to photosynthesize and capture carbon over a longer period each year, warmer conditions also stimulate the release of carbon by plants and by soil microbes as they decompose organic matter. The balance of these two processes, photosynthesis and ecosystem respiration (ER), determines whether ecosystems are net sinks or sources of carbon dioxide (CO_2). Being able to accurately predict photosynthesis and ER is crucial, since a change in either of these carbon fluxes has a direct impact on atmospheric carbon concentrations and the rate of climate change.

This thesis is comprised of four papers and has two main aims. The first aim was to develop new and simple methods to model ER using data collected by thermal cameras on drones and satellites. Thermal cameras take images of temperature, which is one of the main factors controlling the rate of ER. By using these cameras, temperature, and therefore ER, can be mapped over far bigger areas and in greater detail than can be measured on the ground. Attaching cameras to drones allows the collection of highly detailed data over a few hectares, whereas satellites collect data in less detail but over larger areas, from a few hectares to the whole globe. However, producing reliable temperature data from the low-cost, miniaturized thermal cameras used on drones is not straightforward. Therefore Paper I tested the performance of such a camera in the laboratory and in the field to identify the potential sources of error and quantify how much uncertainty they contributed to the temperature measurements.

Papers II and III focused on modelling the ER of peatlands, because peatlands contain dense carbon stocks that have been accumulating for thousands of years. Peatlands are also characterized by variations in microtopography that can lead to substantial differences in microclimate and vegetation species over just a few centimetres. Paper II investigated how the high resolution data from drones could be used to understand the effects of this spatial variation on carbon fluxes within a peatland, whilst Paper III focused on modelling and predicting variations in the carbon fluxes among five peatlands spread across Sweden and Finland.

The second aim of this thesis was to investigate how an extreme drought in 2018 impacted the carbon exchange of Nordic ecosystems. Peatlands are particularly vulnerable to drought because they are dependent on maintaining waterlogged conditions to slow the decomposition of their dense carbon stocks. Warmer temperatures and dry conditions are thus expected to have a large impact on their carbon emissions. The carbon flux data collected in Papers II and III provided an opportunity to test this assumption. In Sweden, the 2018 drought led to the worst wildfire season in over a century. Paper IV quantified the effects of the largest wildfire that year on forest soils, including how it affected the exchange of two greenhouse gases (CO_2 and methane), soil microclimate and chemistry. In particular, it investigated how the characteristics of the burn (burn severity), forest age and post-fire salvage-logging (versus leaving the trees standing) affected the forest soil.

There were four main outcomes from this thesis. Firstly, Paper I produced a set of best practices for using thermal cameras on drones that will benefit anyone seeking to use these cameras to record reliable temperature data. There are many applications for this type of data, from precision agriculture, where crop temperature is used to assess irrigation needs, to archaeology, where temperature maps are used to detect buried structures.

Secondly, Papers II and III showed that even simple remote sensing models could produce reasonably good predictions of peatland ER. The papers also highlighted that accounting for the spatial variability of vegetation composition and water table depth, both within and between peatlands, is key to producing accurate ER estimates. The drone data in Paper II enabled, for the first time, ER to be mapped across a peatland in high detail and such maps could be used to evaluate whether our carbon flux measurements are capturing the full range of peatland CO_2 emissions. Furthermore, the models developed in Paper III provide a foundation for estimating peatland CO_2 fluxes across the whole of Scandinavia, which could help policymakers develop sustainable management policies for these areas.

Thirdly, Papers II-IV showed that the effect of drought and wildfire on carbon exchange is closely tied to the severity of the disturbance, but that at times of very acute water stress or after a severe burn, ecosystem CO_2 emissions can decrease. The reduction of ER did not prevent peatlands from turning into net carbon sources during the 2018 drought because the drought also led to declines in photosynthesis (i.e. carbon uptake).

Nevertheless, these results suggest that some peatlands may lose less carbon than expected during extreme drought.

Finally, Paper IV showed that the amount of time between forest disturbances exerts a substantial influence on forest soils. Salvage-logging directly after a fire had no additional effects on forest soils compared to not salvage-logging, although this result was only applicable where the trees had already been killed by the fire. However, when fire occurred 12 years after a previous clear cut, the young forest had much less time to recover its soil carbon and nutrient stocks compared to stands which were mature at the time of the fire. The increasing frequency of wildfire in certain parts of the boreal region could therefore threaten the long-term carbon storage capacity of these forests.

Introduction

Importance of boreal ecosystems in the global carbon cycle

Boreal forests are the world's second largest forest biome and 87% of the world's peatlands are found in boreal and subarctic regions (see Figure 1; Keenan et al., 2015; Vitt, 2006). These two ecosystems play a key role in the global carbon cycle, because they store at least 20% of all terrestrial biosphere carbon (and this is likely an underestimate; Bradshaw and Warkentin, 2015; IPCC, 2013). The majority of this carbon is held underground in soil and peat (Bradshaw and Warkentin, 2015). Understanding and predicting the movement of carbon between these stores and the atmosphere is critical, since these fluxes have a direct impact on atmospheric carbon concentrations and thus climate change. At the global scale, the carbon dioxide (CO_2) flux in or out of the biosphere every year is ~10 times larger than the amount of CO_2 emitted from burning fossil fuels (IPCC, 2013; Yuan et al., 2011).

The carbon balance of boreal ecosystems is largely determined by the uptake and release of CO_2, but methane (CH_4) fluxes and aquatic exports of dissolved carbon also play an important role (Chi et al., 2020; Roulet et al., 2007). Net ecosystem exchange (NEE) is the balance between gross primary production (GPP), the uptake of CO_2 during photosynthesis, and ecosystem respiration (ER), the release of CO_2 by plants as they convert the products of photosynthesis into energy (i.e. autotrophic respiration, R_a) and by soil microbes as they decompose organic matter (i.e. heterotrophic respiration, R_h). Boreal forests can be sinks or sources of CO_2 and dry upland forests tend to be CH_4 sinks (Covey and Megonigal, 2019; Dunn et al., 2007). Northern peatlands are usually CO_2 sinks and CH_4 sources (Lund et al., 2010; Turetsky et al., 2014). This thesis has primarily focused on studying peatland ER fluxes, as well as forest soil respiration and CH_4 fluxes.

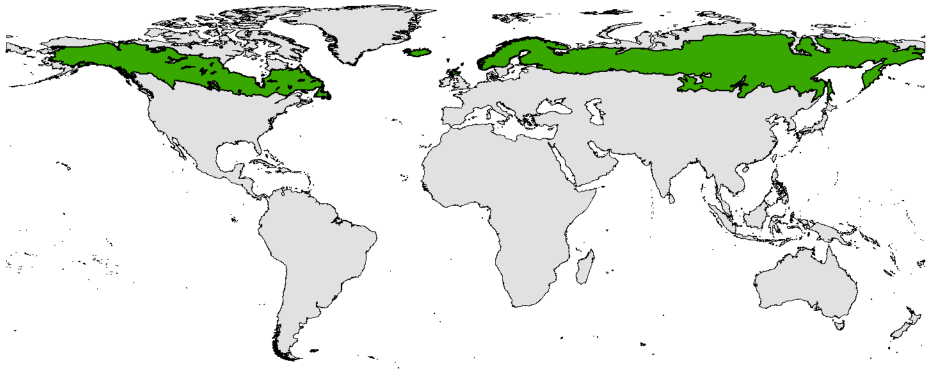

Figure 1. Location of the boreal biome (in green). Data sources: FAO (2010) and The World Bank Group (2020).

ER is particularly important in northern ecosystems, because it contributes more to NEE than GPP does, compared to the NEE of ecosystems at lower latitudes (Valentini et al., 2000). The seasonal variability of boreal ecosystem carbon fluxes is also larger than those at lower latitudes (Falge et al., 2002). As a result, boreal ecosystem NEE tends to be a small difference between two very large fluxes (GPP and ER). The ability to distinguish and separately model GPP and ER is therefore particularly important for these ecosystems, since a small change in either could result in a large change to NEE and dictate whether the ecosystem is a source or sink of carbon.

Peatlands are especially effective at storing carbon because their waterlogged conditions slow the decomposition of organic matter, allowing it to accumulate over thousands of years. Although waterlogging leads to the production of CH_4, a more potent greenhouse gas than CO_2, CH_4 does not remain in the atmosphere for as long as CO_2. As a result, over centennial to millennial timescales peatlands have had a net cooling effect on the climate (Frolking et al., 2011; Whiting and Chanton, 2001). Over decadal timescales or shorter, boreal peatlands are generally CO_2 sinks, although the NEE of a particular peatland can vary widely from year to year in response to changes in climatic variables such as air temperature, water table depth and snowmelt timing (Aurela et al., 2004; Peichl et al., 2014). Other important controls on peatland CO_2 exchange are the length of the growing season, vegetation phenology, LAI (leaf area index) and pH (Koebsch et al., 2020; Lund et al., 2010). The spatial variation of carbon fluxes within a peatland is closely related to microtopography, which is discussed later on.

Impacts of climate change, drought and wildfire on boreal ecosystem carbon fluxes

Climate change is occurring faster in the arctic and boreal regions than anywhere else on the globe: by the end of the century, these regions could become over 5 °C warmer and experience precipitation increases of between 10-50% (IPCC, 2014). Rising air temperatures can increase growing season length, stimulating carbon uptake, but also raise ER rates (Flanagan and Syed, 2011; Keyser et al., 2000). Determining the sensitivity of ER and GPP to temperature increases is thus critical for being able to predict whether boreal ecosystems will become net sinks or sources of carbon in the future.

Northern ecosystems are vulnerable not only to the direct effects of rising air temperatures, but also to the interaction of climate change with natural disturbances, such as drought, extreme heat events and wildfire. Despite the projected increases in precipitation, soil moisture availability is predicted to decline significantly in some boreal regions including Scandinavia, increasing the frequency of extreme summer drought in these areas (Cook et al., 2020). Wildfire risk is also predicted to increase in southern Sweden and across large parts of Russia and northern North America (De Groot et al., 2013; Yang et al., 2015). In 2018, persistent high temperatures and reduced precipitation led to a severe drought in central and northern Europe (Peters et al., 2020). Estimates suggest the drought was 10-100 more likely to occur as a result of anthropogenic climate change (Leach et al., 2020). Due to the unusually dry conditions, Sweden experienced an extremely severe fire season during which 25000 ha of forest burned, the largest area in 140 years (SOU, 2019). This thesis examined the impact of the drought on the CO_2 fluxes of several Scandinavian peatlands (focusing mostly on ER) and the effects of the wildfires on the soil chemistry and greenhouse gas exchange of a central Swedish forest.

Droughts and heatwaves in peatlands

The sensitivity of peatland ER to drought is not well constrained (Laiho, 2006). Both temperature, via its influence on the rate of biological reactions, and water table depth, via its influence on oxygen availability, affect ER. Therefore, many studies have shown that high temperatures and dry conditions increase peatland ER, causing a positive feedback that could increase the rate of climate change (e.g. Dorrepaal et al., 2009; Fenner and Freeman, 2011). However, others have only found weak relationships between peatland ER and water table depth, or declines in ER during water table drawdown (Lafleur et al., 2005; Sulman et al., 2010). Furthermore, since a large proportion of peatland ER is autotrophic, changes in GPP can feedback to affect ER (Crow and Wieder, 2005; Olefeldt et al., 2017). Peatland GPP may decline during drought due to water stress, or increase during moderate reductions in the water table that increase oxygen and nutrient availability to plant roots (Aurela et al., 2007; Laine et al., 2019). Vascular plants may also respond differently to drought compared to *Sphagnum*, which cannot control its water content (Strack et al., 2009; Walker et al., 2016).

The sensitivity of peatland CO_2 exchange to drought therefore depends on a number of factors including the timing and severity of the drought, mean water table depth, vegetation composition and peatland type (Aurela et al., 2007; Lund et al., 2012; Sulman et al., 2010). As a result, peatland NEE has been observed to decline or remain stable during drought, depending on how ER and GPP are affected (Aurela et al., 2007; Laine et al., 2019; Olefeldt et al., 2017). The uncertainties in our understanding and the predicted increase in drought frequency emphasize the need for more in-situ measurements of peatland CO_2 fluxes during drought.

Wildfire in forests

Wildfire is a natural disturbance in boreal forests and shapes the vegetation composition, nutrient availability and carbon balance of these ecosystems (Bond-Lamberty et al., 2007; Zackrisson, 1977). If sufficiently long time intervals occur between fires, the large amounts of carbon emitted during a fire should be recovered in the following decades as vegetation regrows and organic matter is transferred to the soil (Landry and Matthews, 2016; Yue et al., 2016). Fire also produces pyrogenic carbon that is hard to degrade and thus acts as a long-term carbon store, accounting for 12% of the total carbon emitted by fires globally every year (Jones et al., 2019). However, the predicted increases in wildfire frequency and severity could turn boreal forests from sinks to sources of carbon because there is less time for forests to recover between disturbances (Walker et al., 2019).

Wildfires cause changes in microclimate, soil physical properties, nutrient availability and vegetation composition (Bond-Lamberty et al., 2007; Certini, 2005; O'Neill et al., 2002). All of these factors have a direct impact on forest carbon fluxes. Despite higher soil temperatures (due to reductions in canopy cover, evapotranspiration and albedo), soil respiration tends to decline after fire because fire consumes soil organic matter and changes nutrient availability (Allison et al., 2010; Dooley and Treseder, 2012; Ribeiro-Kumara et al., 2020). Measurements of soil CH_4 fluxes after boreal forest wildfires are more limited and CH_4 uptake has been shown to increase, decrease or not change after fire, depending on time since fire, soil temperature and moisture (Burke et al., 1997; Köster et al., 2018, 2017).

The magnitude of the changes in soil carbon fluxes due to fire are affected by several factors, including burn severity and forest management practices. Increasing burn severity, which is quantified based on the mortality of above- and/or belowground biomass, leads to larger reductions in soil respiration (Keeley, 2009; Ribeiro-Kumara et al., 2020). Where forests are managed for commercial production, salvage-logging (removal of burnt wood) is commonly implemented to reduce the risk of further disturbance (e.g. insect attack or fire) and recuperate usable wood. Despite the prevalence of salvage-logging, few studies have quantified its effects on soil carbon fluxes. An alternative post-fire management practice has recently emerged in Sweden: converting part of the burnt area into a nature reserve where the trees are left standing. There is thus an opportunity to compare the effects of salvage-logging versus leaving the trees standing on forest soils.

Modelling ecosystem respiration

ER is controlled by many factors including temperature, water availability, plant productivity, litter and soil organic matter quality and microbial community composition. In the gas flux and remote sensing research communities however, ER is often modelled using a simple exponential relationship to temperature (e.g. Ai et al., 2018; Lloyd and Taylor, 1994). Temperature controls the rates of reactions and also indirectly effects the majority of the other factors listed above that influence ER (Arrhenius, 1889; Davidson and Janssens, 2006; van't Hoff, 1898). The simplicity of this approach raises questions about what ER model shape should be used, especially as the predicted decomposition rates can diverge significantly at high temperatures (Sierra et al., 2016). Furthermore, since the relationship between temperature and ER is exponential or non-linear, even a small change in input temperature or model slope will lead to a large change in modelled ER. Such uncertainty is especially significant in light of the importance of ER and its temperature-sensitivity for predicting how boreal ecosystems will respond to climate change. In addition, ER models are used to partition measured NEE into ER and GPP (daytime ER can only be measured in specific cases and GPP cannot be measured directly), and thus any errors in modelled ER will be propagated to GPP and daytime ER (Lasslop et al., 2010; Reichstein et al., 2005).

Since ER is the sum of processes occurring throughout plants and the soil column, the choice of temperature metric (soil, air or surface) used to model ER is a source of ongoing discussion (Lasslop et al., 2012; Wohlfahrt and Galvagno, 2017).

Traditionally, air or soil temperature have been used because they can be accurately measured at high temporal resolution with commonly available instruments. To produce global estimates of ER using satellite data, land surface temperature data (LST) has been used but is limited by either a coarse temporal or spatial resolution (1 to 16 days, 60 m to 1 km, respectively). There is a notable sparsity of remote sensing models for estimating ER compared to GPP, but the ones that exist have used LST and spectral indices of vegetation greenness and soil moisture (Jägermeyr et al., 2014; Kimball et al., 2009).

Thermal infrared cameras

Thermal infrared cameras take images of surface temperature and as a result, they can provide higher spatial resolution data (pixel size <10 cm over areas 1-10000 m^2) than traditional air or soil measurements. Miniaturized and relatively low-cost thermal cameras are becoming increasingly available, which has opened up new possibilities for using these cameras for scientific research in the field. In particular, hand-held cameras or cameras mounted to towers or on unmanned aerial vehicles (UAVs) can provide information on how surface temperature varies across a landscape in unprecedented detail (see Figure 2). Such data may be particularly valuable for studying heterogeneous ecosystems such as peatlands, where, for example, Leonard et al. (2018) found that surface temperature varied by more than 25 °C over a 100 m^2 area.

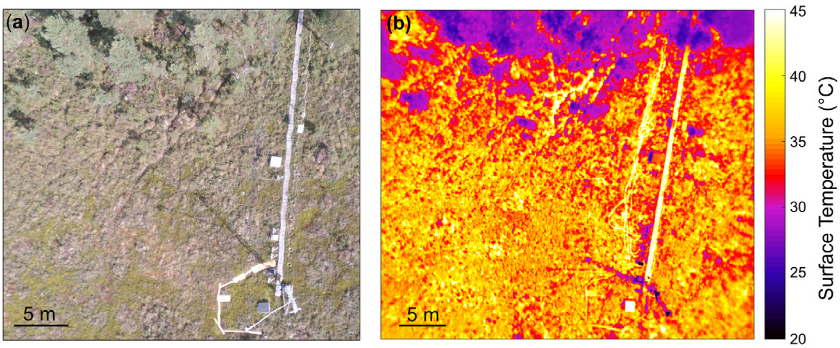

Figure 2. Comparison of UAV imagery of a peatland from (a) an RGB camera and (b) a thermal camera. The images show trees (top of frame), a boardwalk (right of frame) and the peatland surface (lower half of frame).

ER has already been successfully modelled using thermal data from satellites and aircraft. The use of higher spatial resolution data from tower-mounted or UAV-borne thermal cameras to model ER is a novel approach that deserves investigation. For instance, Pau et al. (2018) found that using thermal camera images of a rainforest canopy improved the accuracy of modelled GPP compared to using air temperature. Few studies have used thermal cameras to collect continuous time series of surface temperature in the field (Aubrecht et al., 2016). By comparison, the use of field-based spectral sensors or phenological cameras is well-established, with national and international networks promoting data collection, often in tandem with carbon flux measurements (Eklundh et al., 2011; Gamon et al., 2006; Richardson et al., 2018). Within ecology, UAV thermal data has primarily been used for monitoring crop water stress and for modelling evapotranspiration (Berni et al., 2009; Hoffmann et al., 2016).

One of the reasons that the uptake of thermal cameras has lagged behind other spectral sensors may be the more complex data collection and processing required to produce robust surface temperature data. The thermal radiation measured by a thermal camera is the product of thermal radiation from the target object, the surrounding sky or objects, the atmosphere and the camera itself. Therefore, to measure only the surface temperature of the target object, all the other sources of radiation must be corrected for. As a result, the thermal cameras designed specifically for use on UAVs can have large measurements uncertainties (e.g. ±5 °C). There is a clear need to test the performance of these cameras to assess how they can best be utilized in scientific research.

Measuring and upscaling carbon fluxes

This thesis uses two types of carbon flux measurements: chamber and eddy covariance (EC; Baldocchi et al., 1988; Livingston and Hutchinson, 1995). Using chambers allows the targeted measurement of one or a few plants or a small area of soil and thus the abiotic and biotic conditions (e.g. temperature, soil moisture and vegetation species) in those areas can be directly linked to the derived fluxes. EC measurements record greenhouse gas fluxes within an area, known as the footprint, which, for a given measurement height, changes according to the wind direction, atmospheric turbulence and the structure of the surface. The location and probability density function of the footprint can be estimated using a footprint model (Kljun et al., 2015). Since the EC data only records the aggregated flux for the whole footprint, which may contain a range of microclimatic conditions or vegetation species, it is more challenging to assess which factors are driving changes in the EC-derived fluxes compared to using chamber-derived fluxes.

The aim of upscaling is to produce large scale (from landscape to the global terrestrial surface) estimates of carbon fluxes, based on the smaller-scale measurements of these fluxes described above that are conducted at individual sites. There are several upscaling methods available (atmospheric inversions, mechanistic models, machine learning models), but this thesis focuses on using remote sensing data. Simple empirical models can be used to draw relationships between the remote sensing data, which represents the abiotic and biotic variables that influence carbon exchange, and the carbon flux measurements themselves (e.g. Olofsson et al., 2008). The accuracy of these models and the observational data they are based on is key to ensuring the robustness of the upscaled flux estimates. Having reliable, large-scale carbon flux estimates is important for assessing how ecosystems are responding to climate change. They also provide a dataset against which the results of mechanistic models can be compared, and thus help improve the accuracy of predictions of the future state of the Earth's biosphere.

One of the major challenges to upscaling is assessing how the spatial variability of soil and vegetation properties across an ecosystem affects our upscaled flux estimates. It is especially important that we understand the status of the vegetation being measured in the flux tower footprint, and can assess whether these measurements are representative of an ecosystem as a whole (e.g. Chasmer et al., 2008). Boreal peatlands are characterized by spatial variation in their microtopography that can create sunken hollows where the water table is at, or close to, the surface, and raised hummocks which sit above the water table. As a result of differences in the hydrology, microclimate and vegetation species present in these microtopographical zones, carbon fluxes can vary significantly across a peatland (e.g. Waddington and Roulet, 1996). Such spatial heterogeneity can cause mismatches between the vegetation properties being measured on the ground versus those captured by the coarse resolution satellite data used for upscaling (e.g. Gelybó et al., 2013). It is therefore crucial that our measurements and models capture the spatial variability of carbon fluxes and their drivers, so as to minimize errors in our upscaled flux estimates and improve our predictions of how an ecosystem will respond to environmental change.

Aims

The aims of this thesis are to improve our understanding of the processes regulating carbon fluxes in boreal peatlands and forests and to test new methods to model and upscale these fluxes. In particular, this thesis focuses on ecosystem respiration (ER), its response to temperature and disturbances, and assesses how thermal imagery can be used to capture these responses at a range of spatial scales. It specifically considers how using spatial data influences our understanding of carbon exchange in boreal ecosystems. This thesis aims to answer the following research questions:

- What are the opportunities and limitations to using thermal data for modelling and upscaling ER?
- Can ER be modelled using only remote sensing data?
- How does spatial heterogeneity affect ER modelling and upscaling?
- How do wildfire and drought impact ER and CH_4 in boreal ecosystems?

Methods

Paper I

Paper I tested the performance of a miniaturized UAV thermal camera (Vue Pro 640, FLIR Systems, Inc.) in the laboratory and in the field. The aim of the paper was to assess the extent to which the signal output from the camera was affected by changes in the temperature of the camera and its surroundings. The tests were also designed to show whether a simple calibration (empirical line method) could be used to derive temperature data from the camera (the camera was not radiometrically calibrated, i.e. it only provided raw signal data in digital numbers, no temperature information). The empirical line method involves fitting a linear regression between raw spectral data and a measured variable (in this case, temperature). In the laboratory experiments, the camera took images of a blackbody (a near-perfect emitter of infrared radiation with controllable temperature) while being subjected to perturbations to simulate the effects of UAV flight, including changes in air temperature and wind speed. In the field, ground calibration plates were designed and installed that represented a range of known temperatures and could be used for an empirical line calibration. Four UAV flights (using an Explorian 8 Quadcopter, Pitchup AB) were then conducted to test the performance of the camera.

Paper II

The aim of the paper was to test the feasibility of using thermal cameras to model and upscale ER. Data were collected at Mycklemossen, a hemi-boreal peatland in south western Sweden, which is part of the Swedish Infrastructure for Ecosystem Science network (Figure 3). A thermal camera (A65, FLIR Systems, Inc.) was mounted on a tower to capture a series of high temporal (every 5 min) and spatial (<2 cm/pixel) resolution images of the surface temperature of the peatland (Figure 4). In the field of view of the camera, six collars were used to make manual dark chamber measurements of ER (June to September, 2018-2019, 516 measurements in total). The high frequency (1 Hz) measurements of CO_2 concentration were made using an

Ultraportable Greenhouse Gas Analyser (UGGA; Los Gatos Research) and converted to CO_2 flux using the ideal gas law. The collars included the two main vegetation communities in the peatland: wetter hollows dominated by *Sphagnum* and *Rynchospora alba*, and drier hummocks dominated by vascular plants (*Eriophorum vaginatum, Calluna vulgaris* and *Erica tetralix*). The measured ER and surface temperature data were used to fit an empirical ER model (Heskel et al., 2016), which was compared to model fits based on air and soil temperature data. We assessed the effects of three factors on modelled ER (ER_{mod}): vegetation community, temperature metric and the 2018 hot drought (simultaneous abnormally hot and dry conditions). ER_{mod} based on surface temperature (ER_{mod_surf}) was then upscaled to a larger area of the peatland using a land cover classification and thermal images collected during UAV flights. The thermal cameras used were a Vue Pro 640 and Vue Pro 640 R (FLIR Systems, Inc.), the latter with a ThermalCapture Calibrator (TeAx Technology GmbH) on two quadcopters: Explorian 8 (Pitchup AB) and Solo (3DR).

Figure 3. Locations of the sites used in each of the papers.

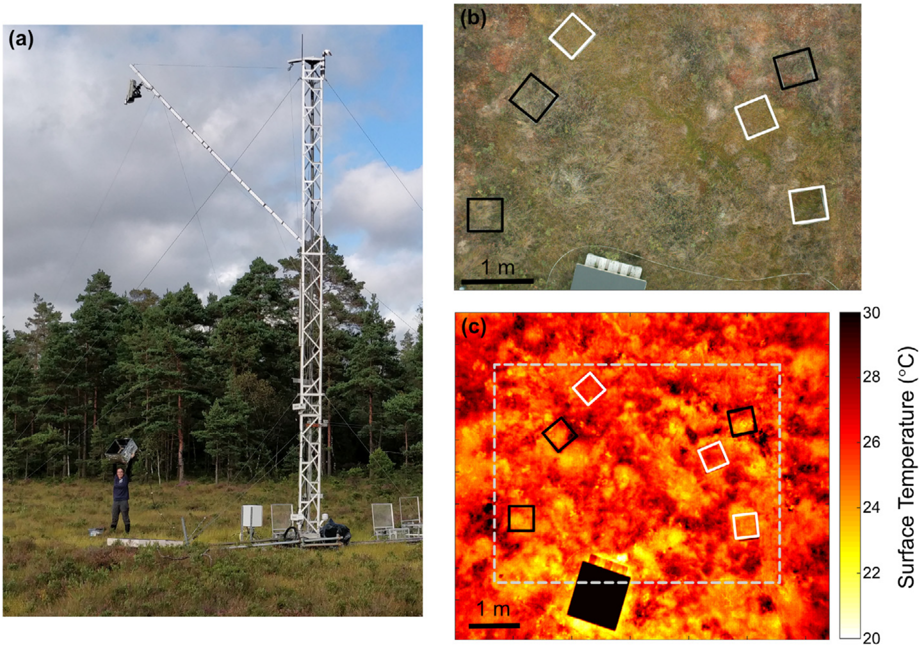

Figure 4. (a) Tower with thermal camera and author conducting ER chamber measurements (Photo: Jonas Nilsson), (b) RGB image showing the square collars (black = hummock, white = hollow) in the field of view of the thermal camera, and (c) thermal camera image, grey dashed line shows the extent of (b) and filled black square shows a temperature calibration plate used to correct the thermal images. Both (b) and (c) were taken at 11:30am on 29 August 2018 and are adapted from Paper II.

Paper III

The aim of Paper III was to model peatland CO_2 fluxes (NEE, GPP and ER) using satellite remote sensing data. EC data from five Nordic peatlands (see Figure 3) between 2017 and 2019 were used to fit the empirical flux models. The flux models were first parameterized for each site individually and then a single parameter set was generated using leave-one-out-cross-validation based on the data from all the sites. As a result, we could evaluate how well a simple model and single parameter set were able to predict the fluxes and capture spatial differences between the sites.

We used data from Sentinel-2 (10-20 m spatial resolution, 2-3 day temporal resolution) and MODIS (Moderate Resolution Imaging Spectroradiometer; 1 km spatial resolution, daily temporal resolution). The Sentinel-2 data was used to calculate EVI2 (enhanced vegetation index; Jiang et al., 2008) and NDWI (normalized difference water index; Gao, 1996), whilst the MODIS products MOD11A1 and MYD11A1 provided LST data. The remote sensing data was gap-filled and smoothed using TIMESAT (Jönsson and

Eklundh, 2004) to produce daily time series for each of the sites. The EC data was also smoothed using TIMESAT with the same settings as for the LST data. One MODIS pixel (where the tower and peak of the footprint function were located) was used to represent each site. For the Sentinel-2 data, we calculated weighted averages of the pixels that contributed to 80% of the daily EC flux footprint, which was modelled using the Flux Footprint Prediction (FFP) model (Kljun et al., 2015).

The GPP model was based on work by Schubert et al. (2010) and included EVI2, a water scalar based on NDWI and daytime LST. The ER model was based on work by Gao et al. (2015), who added a fraction of GPP to the Lloyd and Taylor (1994) equation, but in our final ER model, EVI2 was used instead of GPP. We also tested whether using EVI2 and NDWI scalars, as well as modelling the dormant and growing season separately, improved the ER model fit. We tested modelling NEE by subtracting modelled ER from modelled GPP and by parameterizing the ER and GPP models together.

Paper IV

The aim of the paper was to assess the effect of wildfire on soil respiration, CH_4 fluxes, microclimate and nutrient availability. Specifically, we wanted to test whether significant differences in any of these four properties occurred as a result of differences in burn severity, salvage-logging (versus leaving the burnt trees standing) and stand maturity at the time of the fire. Data were collected from five Scots pine (*Pinus sylvestris*) forests burned by the 2018 Ljusdal fire in central Sweden, the largest area burned that year (8995 ha; see Figure 3 and Figure 5). To analyse the effects of burn severity, we compared an unburnt mature site (UM), a low severity burn mature site (LM, almost 100% tree survival) and a high severity burn mature site (HM, 100% tree mortality). To analyse the effects of salvage-logging, we compared the HM site (unlogged) to a salvage-logged high severity burn mature site (SHM). To analyse the effects of stand maturity, we compared the HM site (~100 years old) with a high severity burn young site (HY; 10 years old).

At each site, flux data were derived from manual dark chamber measurements (using an UGGA, Los Gatos Research) at 10 collars during June to September 2019, the first growing season after the fire. Soil temperature and water content were measured at the same time. In May 2019, 20 soil samples (turned into 4 composite samples) were collected at each site to provide information on the soil chemistry including pH and carbon, nitrogen, ammonium (NH_4^+), nitrate (NO_3^-) and phosphorus (P) content. We used linear mixed effects models to test whether there were significant differences in the soil CO_2 and CH_4 fluxes between the sites.

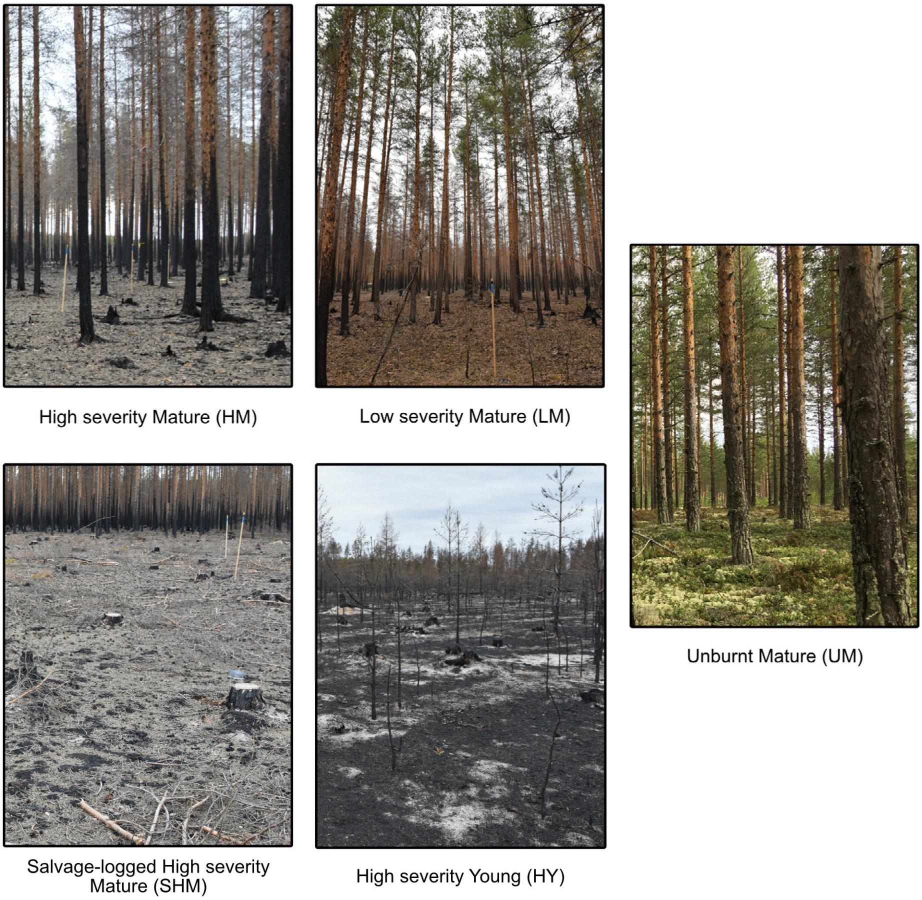

Figure 5. Adapted from Paper IV, photos of the five sites used in Paper IV to study the effects of the Ljusdal fire.

Results and discussion

Best practices for using thermal cameras

In Paper I, the performance of a miniaturized, low-cost UAV thermal camera was tested in the laboratory and in the field. Our results showed good accuracy (±0.5 °C) under stable laboratory conditions. However, measured surface temperature increased by more than 2 °C min^{-1} when the camera was exposed to wind in the laboratory experiments and during the UAV flights. We also found large temperature variations across individual frames (up to 2.6 °C difference between the centre and the edge of the frame, an effect known as 'vignetting') and during the first 15 minutes after switching on the camera. We estimated that the accuracy of the camera during UAV flight was approximately ±5 °C when compared with measurements from a tower-mounted thermal camera, although due to the temperature drift we observed, this was likely a best-case estimate.

Our observations are emblematic of the challenges to using thermal cameras in the field. The sensors of these uncooled microbolometer cameras are sensitive to changes in their own temperature and that of the camera (Budzier and Gerlach, 2015). Our results showed that the automated corrections made by the camera to minimize these issues were not sufficient to cope with the rapid changes in camera temperature during UAV flight. Future work seeking to use thermal cameras should therefore carefully consider whether a) spatial temperature data is vital to answering the research question and b) if the need to collect such data outweighs the potentially significant time and effort required to conduct additional corrections and post-processing.

Developing best practices, corrections or calibration procedures for field-based thermal camera measurements is therefore key to ensuring that these cameras can be used effectively in scientific research. Methods for UAV data collection and processing have been reviewed in Aasen et al. (2018) and Assmann et al. (2019) but they focused primarily on multispectral imagery. In Paper I, we contributed by distilling the results of our experiments and previous literature into a set of practical steps for robust data collection focusing specifically on thermal UAV cameras (see Figure 6). There are many applications of UAV thermal cameras that will benefit from these best practices.

Examples include assessments of crop water stress in precision agriculture, the detection of buried archaeological structures, and ecological studies monitoring the effects of microclimate on fauna and flora (Casas-Mulet et al., 2020; Messina and Modica, 2020; Walker, 2020).

By combining these best practices for data collection, with work by, for example, Faye et al. (2016) and Senior et al. (2019) to produce workflows and standardized data processing routines, thermal data will become more reliable and large-scale thermal data collection will become more feasible. For example, establishing a network of thermal cameras similar to the PhenoCam and other spectral networks, would open up numerous opportunities for investigating microclimate, phenology, plant physiology, the surface energy balance, carbon and water fluxes in high spatial and temporal resolution (Still et al., 2019).

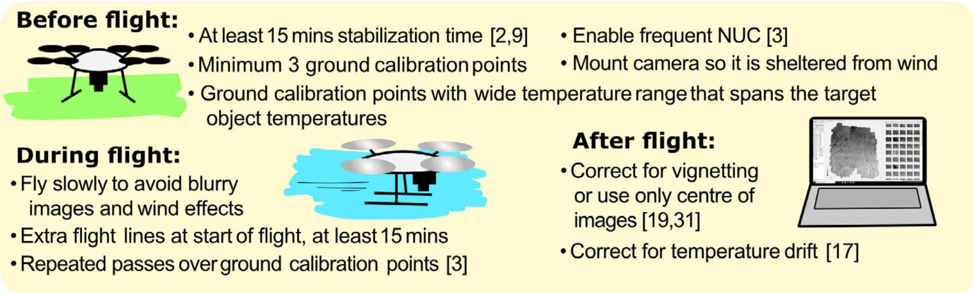

Figure 6. Reproduced from Paper I, best practices for using UAV thermal cameras. Numbers in square brackets are references, please see Paper I for details.

Modelling ER with thermal camera data: opportunities and challenges

In Paper II, we tested the feasibility of using data from thermal cameras on towers and UAVs to model and upscale ER. When compared to models derived using air or soil temperature, surface-temperature modelled ER (ER_{mod_surf}) had similar accuracies: mean R^2 = 0.55, 0.44 and 0.54, and mean normalized root mean square error = 46%, 52% and 47% (NRMSE, normalized using mean observed ER) for air, soil and surface temperature derived ER_{mod}, respectively. Our findings support the use of thermal data for modelling and upscaling ER. In Paper III, we also tested ER models based only on satellite LST data across several Nordic peatland sites that produced R^2 between 0.69-0.86, depending on the site and model used. Although it is a simple approach, our results confirm that good fits can be achieved using surface temperature alone when modelling ER from a single peatland site because temperature is one of the main drivers of the temporal variation in peatland ER (Sonnentag et al., 2010).

We demonstrated the capabilities of thermal data for upscaling ER by producing high resolution (pixel size <7 cm) UAV-derived maps of ER_{mod_surf} in Paper II. These maps represent a powerful new resource to assess how ER varies across an ecosystem and a similar upscaling approach could be applied to map other carbon fluxes or evapotranspiration (cf. Wang et al., 2019). Such maps can help assess how variations in measured fluxes correspond to variations in their driving variables, locate hotspots of carbon emission and show whether existing flux measurements are representative of the ecosystem as a whole. Ultimately, the high temporal resolution data from the tower-mounted thermal camera could be used to gap-fill data between UAV flights, to enable the production of detailed ER maps at any point in time.

To proceed further, the upscaled ER_{mod_surf} maps need to be validated using flux tower data (accounting for the flux tower footprint) and/or chamber measurements. The upscaling method could also be further developed. An analysis of the ER maps showed that not accounting for the differences in ER between hollows and hummocks and their spatial distribution led to over- or underestimates of the mean ER_{mod_surf} by up to 18%. Clearly, using separate ER models and high resolution land cover classifications to account for the different vegetation communities present in peatlands is key to accurate upscaling. However, our binary classification did not reflect the gradient of microtopographical locations and associated vegetation communities within a peatland which may introduce biases into the upscaled flux estimations (Korrensalo et al., 2019; Moore et al., 2019; Waddington and Roulet, 2000). Future ER modelling and upscaling approaches may benefit from accounting for the variability in factors such as leaf area index or water table level within each vegetation class and across an ecosystem using, for example, a Bayesian hierarchical modelling approach (Levy et al., 2020). In addition, our approach did not account for the R_a from the trees scattered across the peatland. In order to extend the upscaling approach to forest ecosystems or treed peatlands, the surface temperatures of the soil, understory and tree canopy would need to be measured separately.

Papers I-III highlighted two challenges to using thermal data to model ER. The first concerns the relatively high uncertainty of thermal data (from field-based cameras) compared to air or soil temperature measurements, which is propagated to estimates of ER_{mod_surf}. The impact of this challenge is at least partially mitigated by the lower temperature-sensitivity of ER_{mod_surf} compared to ER modelled with air or soil temperature. Furthermore, when we tested the impacts of the uncertainties in the thermal camera measurements on estimates of modelled ER in Paper II, we found that the magnitude and direction of the error in ER depended on the shape of the ER model and mean temperatures being measured. It is therefore challenging to draw broader conclusions about how these uncertainties affect the use of thermal camera data, as the magnitude of the errors will be case specific. In any case, users will benefit from technological developments of these cameras which improve their accuracy specifications.

The second challenge concerns whether it is appropriate to use surface temperature to model ER from a biophysical perspective. In Paper II, we found that during the peak of the hot drought in 2018, mean monthly surface temperatures reached almost 41 °C and became uncoupled from the underlying peat temperatures. In Paper III, models based only on LST often predicted a seasonal pattern of ER that was shifted in time (too early) compared to the EC data because LST started increasing earlier than ER in the spring. Furthermore, all the ER models we tested failed to capture winter ER fluxes, when R_h may continue but LST is coolest, which can contribute significantly to annual peatland NEE (Aurela et al., 2002). At a daily time scale, Paper II showed that surface temperature is coolest at night and thus would be unable to capture the midnight ER peak which has been observed in a northern Swedish peatland and corresponds to the nighttime peak in peat temperature (Järveoja et al., 2020).

Nevertheless, temperature is an important variable needed for predicting ER and thermally-derived surface temperature is the only way it can be measured using remote sensing. An advantage of using LST data in remote sensing carbon flux models is that it can help capture temporal variations in the fluxes at a higher resolution (weekly to daily scale) than commonly used vegetation indices which vary at the seasonal scale. Abiotic variables such as LST are particularly important for capturing variations in peatland carbon fluxes during the peak of the growing season, when vegetation and phenology indices remain constant (Peichl et al., 2015). To address the limitations raised above, surface temperature could be used as an input to a peat or air temperature model, separate ER models or parameterizations could be developed for different parts of the year or day, or additional variables could be added to ER models that help capture the temporal variation in ER and its temperature sensitivity.

Modelling ER: moving beyond temperature

Apart from temperature, water table depth also plays an important role in influencing the temporal and spatial variability of peatland ER. In Paper II, ER increased as water table depth declined, particularly for hollows (mean R^2 = 0.74 and 0.41 for hollows and hummocks, respectively). However, the 2018 hot drought led to declines in the ER of both communities compared to 2019 when weather conditions were closer to the long-term average. In Paper III, precipitation and water table depth explained some of the variability in cumulative and peak ER among the sites (R^2 between 0.25-0.33). Future work could therefore focus on integrating soil moisture or water table depth into ER modelling and upscaling. ER models that include soil moisture availability already exist (Reichstein and Beer, 2008). The question remains as to whether these models can be successfully applied using only remote sensing estimates of soil moisture, which would thus make it possible to use them to upscale ER. Another open question is whether remote sensing estimates of soil moisture work in peatlands.

In Paper III, we integrated water availability by following an approach used to model GPP with remote sensing data: multiplying an ER model by a water scalar based on the maximum growing season NDWI (Gao, 1996). The NDWI is related to vegetation water content and has been shown to relate to peatland water table (Kalacska et al., 2018; Meingast et al., 2014). However, using the water scalar had very little impact on the modelling results, which is likely due to the fact that the NDWI and water scalar showed a weak relationship with precipitation and water table depth across the sites (R^2 between 0.06-0.18).

Previous work has had mixed results estimating peatland water table depth or peat water content using satellite remote sensing data (Burdun et al., 2020; Meingast et al., 2014). In field trials, the simple ratio water index and shortwave infrared water stress index, have shown promising results and should be tested using MODIS data at the ecosystem level to see if they could further improve the ER modelling approach in Paper III (Meingast et al., 2014). Narrow-band indices based on hyperspectral data, as well as synthetic aperture radar (SAR) data have also shown strong correlations to *Sphagnum* water content and water table depth, respectively (Harris and Bryant, 2009; Kasischke et al., 2009). Approaches which use data from hand-held spectrometers, UAV or airborne data to estimate peatland vegetation water content or water table depth appear to work well (Harris and Bryant, 2009; Rahman et al., 2017). This is in part because higher spatial resolution data can directly target patches of *Sphagnum* (an indicator species for peat moisture content) or open water (to derive water table depth). Extending the ER modelling approach in Paper II to use UAV-derived estimates of water availability could therefore be a promising avenue for improving estimates of upscaled ER.

In Paper III, we included EVI2 as a proxy for vegetation productivity in the ER model, which improved the model's ability to capture the magnitude and timing of peak growing season ER compared to using temperature alone. There are many studies showing a link between ER and productivity or phenology, including in peatlands (Davidson and Janssens, 2006; Peichl et al., 2015). R_a is dependent on the supply of products from photosynthesis, and has been shown to be the dominant contributor to, and driver of the temporal variation in, peatland ER (Järveoja et al., 2018). R_h is also linked to vegetation productivity because plant litter and root exudates provide the substrates needed for decomposition (Crow and Wieder, 2005). Our work demonstrated that using EVI2 to model ER was just as effective, whilst also minimizing the propagation of uncertainty and model complexity, compared to using modelled GPP as an input.

The mean R^2 and NRMSE of the final ER model in Paper III, using a single parameter set for all sites, were 0.57 and 15%, respectively, whilst site-based parameter sets produced a mean R^2 and NRMSE of 0.86 and 9% (RMSE was normalized using the range of the observed ER). Our site-based model parameterizations produced the same accuracy as those of Schubert et al. (2010), who used MODIS LST data to model Swedish peatland ER, although we used higher temporal resolution data (daily compared to 16-day composites) and more sites (five compared to two). Our results confirm that simple, purely remote-sensing based models can capture a large proportion of the temporal variability of northern peatland ER, even using a single parameterization across multiple sites.

However, when we applied a single model parameterization to all five peatland sites, we found that the model predicted similar maximum ER at all the sites despite considerable differences in the EC-derived ER fluxes. Differences in maximum ER between the sites were only weakly related to variables that have already been discussed above: temperature, moisture availability and light availability (the latter was likely important due to its effects on vegetation productivity). Kross et al. (2013) noted that peatland nutrient status and vegetation composition can also impact the relationship between remote sensing vegetation indices and EC-derived GPP fluxes. Similarly, our results suggest that peatland type is an important variable that should be considered in future modelling approaches because the ER model accuracy (when using a single model parameterization for all the sites) was considerably lower at Abisko-Stordalen, the only ombrotrophic bog in our study, compared to all the other sites which were fens. EVI2 is not a biophysically-based index; in other words, it captures a composite of many factors that affect plant greenness (e.g. leaf area index, productivity, species). Finding spectral variables which are more closely related to specific vegetation characteristics (e.g. species, biomass) as well as peatland hydrology may help distinguish between peatland types and better capture the influence of vegetation composition on peatland CO_2 fluxes.

The effects of drought on peatland ER

In Paper II, we conducted chamber measurements of peatland hummock and hollow ER during the growing seasons of 2018 (a hot drought) and 2019 (climate conditions closer to the long-term average). Mean growing season hummock ER was almost 50% lower, and hollow ER 15% lower, in 2018 compared to 2019. In both years, there was a significant difference in mean ER between the hummocks and hollows. These results are significant because they are based on direct measurements of ER in situ and capture the response of the peatland to a real extreme event (as opposed to an experimentally simulated drought). They suggest that we cannot assume the existence of a positive feedback loop between drought, high air temperatures and increased decomposition in peatlands. These results also highlight that peatland carbon loss during droughts and heatwaves is strongly linked to vegetation composition.

Nevertheless, to fully evaluate the impact of the 2018 drought on peatland CO_2 exchange, the response of GPP and, in particular, NEE must be considered. In Paper III, we presented EC data from the same peatland (Mycklemossen) as well as from Degerö, Siikaneva, and Lompolojänkkä, all of which are featured in the Rinne et al. (2020) analysis of the impact of the 2018 drought on Nordic peatlands. They concluded that summer NEE at Mycklemossen, Degerö and Siikaneva had been reduced (i.e. less C uptake) due to the drought, but that it had no impact on the water table or carbon fluxes at Lompolojänkkä. Indeed, the annual cumulative NEE sums in Paper III showed that those three sites became CO_2 sources in 2018, whilst Lompolojänkkä and Abisko-Stordalen remained CO_2 sinks. If the mean GPP and ER are calculated for June-September (the same period measured in Paper II), GPP is lower in 2018 than in 2017 at all three sites whilst ER is lower at Degerö and Mycklemossen but higher at Siikaneva in 2018 compared to 2017. These results suggest that declines in GPP may be more important than changes in ER for determining the response of peatland NEE to drought, which is supported by observations from Peichl et al. (2014) and Sonnentag et al. (2010).

Warmer temperatures and increased oxygen availability during drought have often (but not consistently) been found to increase peatland ER (Dorrepaal et al., 2009; Fenner and Freeman, 2011; Laiho, 2006). It is therefore interesting that the ER data presented in Papers II and III was not consistently higher in 2018 than in the surrounding years. However, both R_a and R_h decline under water stress and there is evidence that extreme and prolonged drought may decrease peatland ER. The varied response of ER at the three sites to the 2018 hot drought is likely a result of differences in the magnitude of the water table drawdown (Peichl et al., 2014) and vegetation composition (Jassey et al., 2018). At Mycklemossen, our observations of reduced ER in 2018 compared to

2019 in Paper II were attributed to the intensity and long duration of the hot drought (Strack et al., 2009). As a result, any labile C exposed by the lowered water table may have been used up at the beginning of the drought, thus slowing R_h rates during the rest of the summer (Laiho, 2006). The declines in GPP modelled from the EC data also lend support to our theory that the priming effect of vegetation on R_h would have been reduced as plant productivity declined during the drought. Since the hummocks had more plant biomass than the hollows, declines in R_a and R_h linked to reduced plant photosynthesis would have had more impact on hummock ER than hollow ER. The water table is also generally lower in hummocks than in hollows, and thus further lowering of the water table during the drought may have had less impact (in terms of exposing organic matter for decomposition) on hummock ER compared to hollow ER. These differences between the two vegetation communities may explain why ER was lower in hummocks than in hollows during the 2018 hot drought.

The effects of wildfire on forest soil carbon fluxes

The extremely warm and dry conditions during summer 2018 led to a severe wildfire season in Sweden: the total area burned in 2018 (25000 ha) was approximately 10 larger than the annual average during the early 2000s (SOU, 2019). Paper IV examined the impact of the Ljusdal fire on forest soils, focusing specifically on the effects of burn severity, salvage-logging and stand age.

None of these factors had a significant impact on soil CH_4 uptake, except burn severity, which led to significantly different CH_4 uptake between a high and low severity burn though not compared to an unburnt site (Figure 7d-f). Soil moisture, one of the most important factors affecting CH_4 uptake in soils, was generally unaffected by burning, as was the mineral soil layer where most CH_4 uptake takes place. It is therefore unsurprising that the CH_4 fluxes were similar among the five sites.

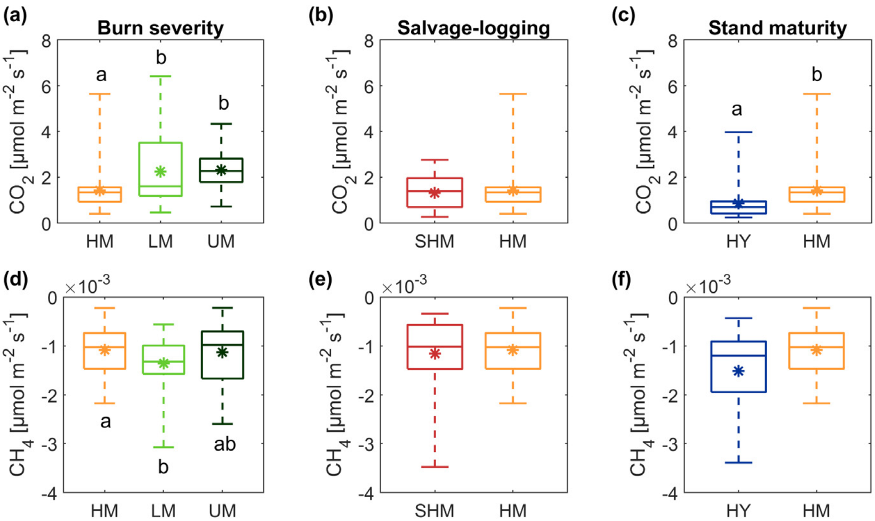

Figure 7. Reproduced from Paper IV, the observed soil respiration and CH_4 fluxes at the five sites grouped according to the factor of interest (burn severity, salvage-logging or stand maturity). Significant letters above/below the boxplots indicate significant differences in the fluxes between the sites based on an Analysis of Variance and Tukey's post-hoc tests. The boxplots show the median, interquartile range and maximum and minimum data values, with the star representing the mean. Site acronyms: High severity Mature (HM), Low severity Mature (LM), Unburnt Mature (UM), Salvage-logged High severity Mature (SHM), High severity Young (HY).

A high severity burn led to significantly lower soil respiration compared to a low severity burn and unburnt site (Figure 7a). This was likely due to the shutdown of R_a (complete tree and ground vegetation mortality) and a decline in R_h, as a result of the combustion of the soil organic layer and the cessation of the supply of root exudates from the trees. Yet despite an estimated 75% loss of the organic layer at the low burn severity site, soil respiration was similar at this site compared to the unburnt site. Our results thus suggest that tree root respiration is one of the main drivers of post-fire soil respiration in mature stands, which agrees with findings by Singh et al. (2008) who observed that root biomass was positively correlated with soil respiration after Canadian forest fires. Furthermore, we speculated that at the low burn severity site, tree fine root growth and R_h may have increased in the months after the fire (which occurred in the middle of the growing season) as a result of the increased nutrient availability (bioavailable P, NO_3^- and effective cation exchange capacity) and soil pH (Bryanin and Makoto, 2017; Maynard et al., 2014; Yuan and Chen, 2010). The increased fine root turnover and R_h may thus have compensated for any initial R_h reductions due to the consumption of the organic layer.

After a high severity burn, salvage-logging had no significant impact on soil respiration, microclimate and soil chemistry, compared to leaving the dead trees standing (Figure

7b). The soil conditions at the salvage-logged and unlogged sites were similar, i.e. there was only a small amount of woody debris on the ground and no soil compaction due to the salvage-logging operation near our collars at the salvage-logged site, which helps explain why we found no substantial differences in the soil CO_2 fluxes between the two sites. However, the interaction of salvage-logging and burn severity deserves further study. It is likely that salvage-logging after a low severity burn (where the trees survive) would cause a significant decline in soil respiration due to the shutdown of autotrophic respiration, and even greater changes to the total ecosystem CO_2 fluxes. The differences in the carbon exchange and nutrient availability between the salvage-logged and unlogged sites are likely to become more important in the long-term (discussed further in the next section).

Stand age at the time of the fire had a clear impact on post-fire soil conditions. The young site stood out from the mature site (HM) in terms of microclimate (warmer and drier soils), its lower soil respiration and nutrient concentrations and thinner organic layer depth (Figure 7c). Soil respiration was also significantly less temperature-sensitive at the young site than at the mature site, suggesting that it was substrate-limited due to the lack of available organic matter and labile C. Soil respiration would likely have been lower at the young site than at the mature site even before the fire, because of the thinner organic layer and smaller tree root biomass, but the fire would have exacerbated the differences between the two sites. The reduced soil nutrient availability at the young site compared to the mature site may also be the result of the clearcutting and soil scarification which occurred at the young site 12 years before the fire (Örlander et al., 1996; Thiffault et al., 2007).

Ultimately, our observations at the young site indicate that the time available for the accumulation of the soil organic layer between disturbances is an important variable for determining the effects of a disturbance on forest soils. These results confirm that shorter return intervals between disturbances are likely to impede the ability of forests to retain soil nutrients and act as long-term carbon stores. These findings have important implications given predictions that the frequency of wildfires will increase across many parts of the boreal region (De Groot et al., 2013).

Environmental science perspective

Response of boreal peatland CO_2 fluxes to climate change

Climate change is one of the greatest societal challenges of the 21st century. Predicting how ecosystems will respond is crucial for understanding the magnitude and direction of feedbacks between the biosphere and the climate. The results of Paper II suggest that, in some cases, ER declines at high temperatures and that ecosystems may lose less carbon than expected during extreme heat and drought events. We also found evidence of a negative feedback mechanism described by Kettridge and Waddington (2014), whereby desiccated *Sphagnum* acts as an insulating barrier, minimizing water loss during drought, which demonstrates the resilience of peatlands to water table drawdown. Nevertheless, these results must be considered alongside those of Paper III, which showed that the three peatlands that were affected by the 2018 drought were net carbon sources that year due to reductions in GPP and/or increases in ER. Increases in the frequency or longevity of summer droughts could therefore still lead to a net increase in CO_2 emissions from peatlands and a positive feedback to climate change. Ultimately, predicting the future CO_2 balance of peatlands depends not only on being able to model how they behave during short-term extreme events, but on understanding how they will respond to long-term trends of rising temperatures and changing precipitation regimes. Predicting the full carbon balance of peatlands will also require combining the models developed in Paper III with models that estimate CH_4 fluxes and aquatic carbon exports.

Value of modelling boreal peatland CO_2 fluxes

Robust measurements or models of carbon fluxes are a crucial step towards predicting how ecosystems will respond to future environmental change. The global network of flux towers is especially important because flux towers provide our primary source of direct measurements of ecosystem greenhouse gas fluxes (Running et al., 1999). The upscaling method piloted in Paper II provides a tool to analyse these measurements, assess how carbon fluxes vary across an ecosystem and evaluate whether flux tower data is representative of the surrounding ecosystem. In addition, the models developed in Paper III, which were parameterized using flux tower data, could provide a foundation for estimating the CO_2 fluxes of intact peatlands across the whole Nordic region. Such estimates provide a valuable data source against which the results of more complex mechanistic models can be compared and could inform policymaking related to the sustainable management and conservation of peatlands.

Impacts of management on boreal peatland CO_2 fluxes

It is important to acknowledge that boreal forests and peatlands contribute many services to humankind beyond carbon storage, including water regulation, supporting biodiversity, providing raw materials as well as non-material contributions that enhance people's quality of life. Nevertheless, focusing on their significance as carbon stores, is particularly relevant in light of current debates about how ecosystems could be sustainably managed to retain or increase their carbon storage potential.

There are many natural limitations on the amount of carbon that ecosystems can store (see e.g. Baldocchi and Penuelas, 2019), and certain management practices can place further constraints on carbon storage or lead to significant carbon losses. For example, in the Nordic and Baltic regions, nearly half of all peatlands have been drained, and the CO_2 emissions from these drained areas are equivalent to a third of all other CO_2 emissions from these countries (excluding from land use; Barthelmes et al., 2015). Typically, peatland drainage for agricultural, forestry or peat extraction stops the accumulation and promotes the decomposition of organic matter, thus decreasing the amount of carbon stored. Although this thesis only studied intact peatlands, the impacts of the 2018 drought captured in Paper III illustrated the short-term effects of peatland drainage on CO_2 fluxes: rapid conversion from being carbon sinks to sources.

Rewetting drained peatlands is a management strategy which can turn degraded peatlands into CO_2 sinks by reducing decomposition (although increasing their CH_4 emissions; Wilson et al., 2016). Within Sweden, rewetting is advocated as part of the government's first climate policy action plan to meet national and international climate change mitigation goals (Miljödepartementet, 2019). On a global scale, Leifeld and Menichetti (2018) demonstrated that restoring degraded peatlands is a more effective management strategy, in terms of the amount of carbon stored per unit land area and the additional nutrient inputs needed, than strategies focused on increasing the carbon storage potential of mineral agricultural soils. Deciding which peat areas to rewet requires careful consideration. For example, drained boreal peatlands used for forestry can continue to act as carbon sinks even several decades after drainage and during drought periods, so rewetting them may have limited benefits (Minkkinen et al., 2018). The CO_2 flux models and upscaling approaches developed in Papers II and III, if parameterized using fluxes from rewetted peatlands, could provide useful tools to evaluate the carbon sink strength of these areas. Such an application emphasizes the need to further develop the models to include water table depth or soil moisture data, since this is the main environmental condition being manipulated during peatland rewetting.

Impacts of management on boreal forest carbon fluxes

Predicted increases in forest fire frequency make it especially important to assess how management decisions affect the recovery of forests after fire. Paper IV focused specifically on the effects of salvage-logging, a common practice after many forest disturbances (e.g. fire, wind throw, insect outbreaks). The differences in soil conditions between a salvage-logged and non-logged site were not significant in the first growing season after the fire, but are likely to become significant over the long-term. Salvage-logging removes burnt wood, which provides an important source of nutrients that outlasts the short-lived ash nutrient pulse but also leads to increased CO_2 emissions as it decomposes over many years following a fire (Amiro et al., 2006; Marañón-Jiménez et al., 2013). The alterations to site microclimate following salvage-logging can also impact vegetation establishment, which influences the rate of carbon uptake and is important for commercial forestry production. Maximum soil temperature was 4 °C higher and there was a larger soil temperature range at the salvage-logged compared to the unlogged site. In the temperature-limited boreal region, increases in soil temperature may favour seedling growth, although the few existing studies of salvage-logging effects on microclimate (beyond the boreal region) suggest that the harsher microclimate is detrimental to seedling growth (Leverkus et al., 2021).

Ultimately, the decision over whether to replant a commercial forestry monoculture (as occurred in 2020 for the salvage-logged site) versus allowing natural regeneration to occur (as is the case at the unlogged high burn and low burn severity sites which are now part of a nature reserve) after fire may have a stronger impact on the ecosystem carbon balance than the act of salvage-logging. Three years after a major Swedish forest fire, Gustafsson et al. (2019) found that a replanted site was moving towards net CO_2 uptake faster than a natural regeneration site. The evidence from this fire and fires in Alaska shows an interaction between burn severity, microclimate and tree establishment: deciduous broadleaf trees tend to establish in high burn severity areas where the remaining soil organic layer is very thin, whereas coniferous species tend to establish in moister sites burned at lower severity (Johnstone et al., 2010). It is thus feasible that the high severity burn mature site will be colonized by broadleaf species, a stark contrast to the pine monoculture that was planted at the salvage-logged site. These changes in the vegetation composition could lead to significant differences between the two sites in terms of their CO_2 fluxes, surface energy balance, biodiversity and soil nutrient availability (Gaumont-Guay et al., 2009; Johnstone et al., 2010). Paper IV established a baseline against which such future changes at the sites can be evaluated, and the ongoing data collection at the sites will provide a long-term perspective of the implications of the management decisions taken immediately after the Ljusdal fire.

Conclusions

Studying ecosystem carbon fluxes is a vital part of environmental science because it can help assess the impacts of climate change on terrestrial ecosystems, quantify ecosystem-atmosphere feedbacks and support decision-making for sustainable management. This doctoral thesis has contributed to environmental science in two ways: by developing and refining methods to upscale peatland ecosystem respiration (ER) and by consolidating our understanding of the factors driving carbon exchange in boreal ecosystems.

In terms of methodology, this thesis has demonstrated how the spatial temperature data from miniaturized thermal cameras can be used to map peatland ER at sub-decimetre resolution. Such maps provide a novel resource to estimate ER at the ecosystem scale and to evaluate the representativeness of our current carbon flux measurements. The robustness of this approach is dependent, among other things, on minimizing the uncertainties associated with thermal camera data, and the best practices suggested in this thesis contribute towards achieving this goal.

This thesis has also shown that estimating peatland ER over larger areas at daily resolution with satellite remote sensing data is possible using a simple model driven by land surface temperature and EVI2. The accuracy of these estimates is greatest when growing season ER fluxes are estimated using a model parameterized for a single peatland site. Finding variables or model formulations that can capture the differences in peak growing season ER across multiple peatlands is the main challenge to making accurate regional estimates of ER. Future work should focus on including information on vegetation composition and water table depth in ER models, because these factors play an important role in driving the spatial variability of ER, both within and between peatlands. Not accounting for this spatial heterogeneity can lead to significant biases in upscaled estimates of ER and mask important information about how peatlands respond to natural disturbances.

The 2018 drought provided a natural experiment for studying the effects of combined high air temperatures and reduced water availability on boreal ecosystem carbon fluxes. Although the drought turned many Nordic peatlands from CO_2 sinks to sources, the positive feedback loop between higher temperatures, lower water table and increased

CO_2 emissions may not be as strong as expected during extended periods of severe water stress. The impact of drought was also dependent on vegetation composition, emphasizing the importance of accounting for this source of spatial heterogeneity when modelling peatland CO_2 exchange.

The drought led to an exceptional number of forest fires in Sweden during the summer of 2018. Analysing the forest soils affected by the Ljusdal fire provided important insights into the roles of burn severity, salvage-logging and stand age in determining post-fire soil carbon fluxes. Salvage-logging a mature stand had no additional effects on forest soils after a high severity burn but long-term monitoring is needed to fully assess the implications of this management practice on the ecosystem carbon balance. The Ljusdal fire investigation highlighted that the forests most vulnerable to soil carbon and nutrient losses after fire are young stands burned at high severity that have been affected by multiple disturbances within a few years.

The results presented here confirm that the predicted increase in the frequency of drought, wildfire and other stand replacing disturbances threatens the long-term carbon storage capacity of boreal ecosystems. Reliable models and upscaled estimates of carbon exchange are therefore essential to help track the changes in the boreal carbon sink and inform sustainable management strategies.

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