Land use effects on greenhouse gas emissions from boreal inland waters

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List of papers

This thesis summarizes the following papers referred to in the text by their Roman numerals:

I. Marcus Klaus, Ann-Kristin Bergström, Anders Jonsson, Anne Deininger, Erik Geibrink, Jan Karlsson.

   Weak response of greenhouse gas emissions to whole lake N enrichment.

   In review

II. Marcus Klaus, Erik Geibrink, Anders Jonsson, Ann-Kristin Bergström, David Bastviken, Hjalmar Laudon, Jonatan Klaminder, Jan Karlsson.

   Does clearcut forestry influence aquatic greenhouse gas emissions?

   Manuscript

III. Marcus Klaus, David Seekell, William Lidberg, Jan Karlsson.

   Neglecting seasonality causes biased view of climate and forestry impacts on lake CO_2 cycling.

   Manuscript

IV. Marcus Klaus, Jan Karlsson, Erin R. Hotchkiss, Ann-Kristin Bergström, Sally MacIntyre.

   Estimates of ecosystem metabolism in unproductive lakes with inclusion of physical oxygen fluxes.

   Manuscript

Author contributions

Paper I
AB and JK designed the study. MK, EG, AJ and AD performed the fieldwork. MK analyzed the data with contributions from EG. MK wrote the manuscript. All co-authors revised the manuscript.

Paper II
JK and AB designed the study with contributions from JKl, DB and HL. MK, EG, AJ and AD performed the fieldwork. MK analyzed the data with contributions from EG. MK wrote the manuscript. All co-authors revised the manuscript.

Paper III
MK designed the study with contributions from JK and DS. MK analyzed the data with contributions from WL. MK wrote the manuscript with strong contributions from DS and JK. All co-authors revised the manuscript.

Paper IV
MK designed the study with contributions from SM and JK. MK performed the fieldwork. MK analyzed the data and wrote the manuscript with essential contributions from SM. All co-authors revised the manuscript.

Author abbreviations
MK: Marcus Klaus, AB: Ann-Kristin Bergström, AD: Anne Deininger, AJ: Anders Jonsson, DB: David Bastviken, DS: David Seekell, EG: Erik Geibrink, ER: Erin Hotchkiss, HJ: Hjalmar Laudon, JKl: Jonatan Klaminder, JK: Jan Karlsson, SM: Sally MacIntyre, WL: William Lidberg.

Abbreviations

BACI	Before-after/control-impact (experiment)
C	Carbon
CH_4	Methane
CO_2	Carbon dioxide
DIN	Dissolved inorganic nitrogen (nitrate + nitrite + ammonium)
DO	Dissolved oxygen
DOC	Dissolved organic carbon, organic molecules smaller than 0.45 µm
ER	Ecosystem respiration
GPP	Gross primary production
k_z	Eddy diffusivity, the exchange coefficient for eddy diffusion
N	Nitrogen
N_2O	Nitrous oxide
NEP	Net ecosystem production

Glossary

Actively mixing layer	Upper-most part of the water column that is directly influenced by turbulence due to surface buoyancy flux and wind stress
Advection	Bulk movement of water
Bayesian statistics	Statistical method in which evidence about the true state of a property is derived from prior results and expressed by degrees of belief
Boreal forest	Biome characterized by coniferous forest located at roughly 50°to 70°N
Buoyancy flux	Production or consumption of turbulence due to buoyancy, the property of an object that allows it to float on the water surface
Clearcutting	Forestry practice where most or all trees in a specific area are logged at a time
Diffusion	Movement of molecules or atoms from regions of high to low concentrations
Ebullition	Sudden release of methane bubbles from the water to the air
Eddy diffusion	Diffusion by eddy motion in a turbulent flow regime
Entrainment	Advective-type transport mechanism where the actively mixing layer grows in thickness by trapping water from a less mixed layer
Epilimnion	Nearly isothermal part of the water column extending from the water surface to a depth determined by the history of mixing due to wind stress and buoyancy
Flux chamber	Air-tight enclosure placed on the water surface to measure gas transfer across the air-water interface
Gas transfer velocity	Water column depth that equilibrates in gas concentrations with the atmosphere per unit of time

Headwater	Waterbody or waterway near the river source upstream any other lakes or the first confluence to higher-order streams
Hypolimnion	Part of the water column below the metalimnion that is less stratified
Internal wave	Gravity waves that oscillate within stratified waters
Inventory	Here, the amount of gas stored in the whole water column
Lake turnover	Mixing across the whole water column during isothermal conditions
Metalimnion	Part of the water column between the epilimnion and the hypolimnion with a relatively strong vertical density gradient
Riparian buffer strip	Forest along stream and lake shorelines left intact to protect waters from upslope land uses
Riparian zone	Interface between inland waters and their surrounding land
Seasonal thermocline	Lower-most extent of the actively mixing layer during a specific season
Site preparation	Measures to prepare a soil for replanting tree seedlings after clearcutting, typically by disk trenching
Structural equation model	Statistical modelling technique that simultaneously estimates relationships between multiple variables within a constructed network
Tracer gas injection	Method to measure air-water gas transfer velocities by diffusing a biologically inert gas (e.g. propane) into the water and measure changes in its concentrations over time
Unproductive lake	Clear- or brown water lake with low nutrient status and primary production

Abstract

Anthropogenic activities perturb the global carbon and nitrogen cycle with large implications for the earth's climate. Land use activities deliver excess carbon and nitrogen to aquatic ecosystems. In the boreal biome, this is mainly due to forestry and atmospheric deposition. Yet, impacts of these anthropogenically mediated inputs of carbon and nitrogen on the processing and emissions of greenhouse gases from recipient streams and lakes are largely unknown. Understanding the ecosystem-scale response of aquatic greenhouse gas cycling to land use activities is critical to better predict anthropogenic effects on the global climate system and design more efficient climate change mitigation measures.

This thesis assesses the effects of forest clearcutting and nitrate enrichment on greenhouse gas emissions from boreal inland waters. It also advances methods to quantify sources and sinks of these emissions. Short-term clearcut and nitrate enrichment effects were assessed using two whole-ecosystem experiments, carried out over four years in nine headwater catchments in boreal Sweden. In these experiments, I measured or modeled air-water fluxes of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), combining concentration, ebullition and gas-transfer velocity measurements in groundwater, streams and lakes. By using Swedish national monitoring data, I also assessed broad-scale effects of forest clearcutting by relating CO_2 concentrations in 439 forest lakes to the areal proportion of catchment forest clearcuts. To improve quantifications of CO_2 sources and sinks in lakes, I analyzed time series of oxygen concentrations and water temperature in five lakes on conditions under which whole-lake metabolism estimates can be inferred from oxygen dynamics given the perturbing influence of atmospheric exchange, mixing and internal waves.

The experiments revealed that aquatic greenhouse gas emissions did not respond to nitrate addition or forest clearcutting. Importantly, riparian zones likely buffered clearcut-induced increases in groundwater CO_2 and CH_4 concentrations. Experimental results were confirmed by monitoring data showing no relationship between CO_2 patterns across Swedish lakes and clearcut gradients. Yet, conclusions on internal vs. external CO_2 controls largely depended on whether spatially or temporally resolved data was used. Partitioning CO_2 sources and sinks in lakes using time series of oxygen was greatly challenged by physical transport and mixing processes.

Conclusively, ongoing land use activities in the boreal zone are unlikely to have major effect on headwater greenhouse gas emissions. Yet, system- and scale specific effects cannot be excluded. To reveal these effects, there is a large need of improved methods and design of monitoring programs that account for the large spatial and temporal variability in greenhouse gas dynamics and its controls by abiotic and biotic factors.

Sammanfattning

Människan påverkar jordens klimat genom utsläpp av växthusgaser. Dessa utsläpp kan också vara indirekta genom markanvändning. Markanvändning ökar ofta läckage av kol och kväve till akvatiska ekosystem. I boreala ekosystem sker detta främst genom skogsbruk och atmosfärisk deposition och kan förväntas öka växthusgasemissioner från akvatiska system. Detta har dock hittills aldrig testats på en ekosystemskala. Dessutom saknas tillförlitliga metoder för att kunna mäta metaboliska processer som konsumerar och producerar växthusgaser i låg-produktiva boreala sjöar. Experimentella och metodiska framsteg i att undersöka markanvändningseffekter på akvatiska växthusgasemissioner är essentiella för att kunna avslöja bieffekter av mänskliga aktiviteter på jordens klimat och för att kunna utveckla eventuella motåtgärder.

Den här avhandlingen undersöker hur kvävetillförseln och kalhyggesskogbruk påverkar emissioner av tre av dem viktigaste växthusgaserna, koldioxid (CO_2), metan (CH_4) och lustgas (N_2O) från boreala bäckar och sjöar. Två ekosystemexperiment genomfördes i nio skogsdominerade avrinningsområden i norra Sverige. I det första experimentet tillsattes nitrat till tre av sex sjöar. I det andra experimentet kalhöggs skogen i en del av avrinningsområdet av två av totalt fyra undersökta sjöar. Koncentrationer av CO_2, CH_4 och N_2O uppmättes varannan timme till varannan vecka ett år före och tre år efter de experimentella manipulationerna i strandnära grundvatten, sjövatten och bäckvatten. Deras emissioner till atmosfären har beräknats genom att använda modeller eller gasutbytesmätningar. För att kunna bedöma storskaliga avverkningseffekter har dessutom undersökts om det finns ett samband mellan CO_2 koncentrationer i 439 svensak skogssjöar, som provtagits i samband med den nationella miljöövervakningen, och andelen kalhygge i deras avrinningsområde. Dessutom användes högfrekventa syrgas- och temperaturprofildata från fem sjöar för att bedöma hur bra syrgaskoncentrationstidsserier lämpar sig för beräkningen av den dagliga metaboliska CO_2 omsättningen med hänsyn till fysikaliska processer som också påverkar syrgasdynamiken och därför försvårar utvärderingen av den biologiska påverkan på CO_2.

Undersökningarna visade ingen signifikant effekt av kvävetillförseln på växthusgasemissioner från sjöar. Det samma gäller för kalhyggeseffekter på växthusgasemissioner från sjöar och bäcker, detta trots att CO_2 och CH_4 koncentrationer ökade i det strandnära grundvattnet. Detta resultat bekräftades även på landskapsskala, vilket inte visade ett statistiskt samband mellan CO_2 koncentrationer i svenska skogssjöar och andelen avverkad skog i avrinningsområdet. Slutsatser angående interna kontra externa

kontrollmekanismer berodde dock till stor del på om spatialt eller temporalt högupplöst miljöövervakningsdata användes. Beräkningar av metaboliska aktiviteter i sjöar baserad på sygasdynamiken försvårades väsentligt av blandnings- och transportprocesser i vattenkolumnen. Att förstå och kvantificera dessa fysikaliska processer är därför av stor betydelse för att kunna beräkna den metaboliska CO_2 omsättningen i boreala sjöar.

Sammanfattningsvis är växthusgasemissioner från boreala sjöar och bäckar mest sannolik relativt opåverkad av markanvändning. Undersökningen på ekosystem- och landskapsskalan tillåter dock inga slutsatser om delprocesser som eventuellt påverkas av markanvändningen och som balanserar varandra i deras effekt på växthusgasbalansen. För att undersöka dessa effekter behövs förbättrade metoder och miljööververkningsprogram som adresserar den stora rumsliga och temporala variationen i växthusgasdynamiken och dess abiotiska och biotiska kontrollmekanismer.

Zusammenfassung

Der Mensch beeinflusst das globale Klima nicht nur durch das unmittelbare Emittieren von Treibhausgasen, sondern auch indirekt durch das Verändern von treibhausgasproduzierenden Prozessen in Ökosystemen. Landnutzung erhöht oft den Kohlenstoff- und Stickstoffeintrag in Gewässer. In borealen Breiten geschieht dies besonders duch Forstwirtschaft und atmosphärischen Niederschlag. Vermehrte Kohlenstoff- und Stickstoffeinträge können biologische (sogenannte metabolische) und Auswaschungs-Prozesse in Gang setzen die die Emission von Treibhausgasen erhöhen. Dies wurde bisher jedoch nie experimentell auf der Ökosystemkala nachgewiesen. Zudem sind bestehende Methoden zur Messung metabolischer Prozesse ungeeignet in unproduktiven Gewässern wie sie in der borealen Zone verbreitet sind. Experimenteller und methodischer Fortschritt in der Begutachtung von Landnutzungseffekten auf Treibhausgasemissionen von borealen Gewässern ist jedoch essentiell um bisher unbeachtete Nebeneffekte menschlicher Aktiviteten auf unser Klima aufzuzeigen und eventuelle Gegenmaßnahmen zu entwickeln.

Diese Arbeit untersucht den Einfluss von Stickstoffeintrag und Forstwirtschaftlichem Kahlschlag auf die Emission der drei wichtigsten anthropogenen Treibhausgase, Kohlenstoffdioxid (CO_2), Methan (CH_4) and Lachgas (N_2O), von borealen Bächen und Seen. Dazu wurden zwei großskalige Experimente in neun bewaldeten Quellgebieten Nordschwedens durchgeführt. Im ersten Experiment wurde der Eintrag von Stickstoff in drei von sechs Versuchsseen experimentell eröht. Im zweiten Experiment erhielt ein Teil des Waldes in den Wassereinzugsgebieten zweier von insgesamt vier Seen einen Kahlschlag. Ein Jahr vor und drei Jahre nach Beginn der experimentellen Eingriffe wurden alle zwei Stunden bis alle zwei Wochen die CO_2, CH_4 und N_2O Konzentrationen im strandnahen Grundwasser, Bächen und Seen gemessen und deren Emission in die Atmosphäre berechnet unter Anwendung von Gastransfermessungen und Modellen. Zur Abschätzung landschaftsskaliger Effekte wurden darüber hinaus CO_2 Konzentrationen von 439 Waldseen verteilt über ganz Schweden auf einen potentiellen Zusammenhang mit dem Anteil der Kahlschlagsfläche in deren Wassereinzugsgebieten untersucht. Schließlich wurden hochfrequente Sauerstoff- und Temperaturmessprofile in fünf Seen erstellt um zu untersuchen inwiefern Sauerstoffkonzentrationszeitreihen zur Berechnung täglicher metabolischer CO_2-Umsetzung genutzt werden können, unter dem Einfluss physikalischer Prozesse die die Sauerstoffkonzentration ebenso verändern und somit die Exraktion des metabolischen Signals erschweren.

Die Experimente erwiesen keinen signifikanten Einfluss von Stickstoffeintrag auf Treibhausgasemissionen von Seen. Kahlschlag hatte ebenso keinen Einfluss auf Treibhausgasemissionen von Seen und Bächen, trotz einer signifikanten Erhöhung von CO_2 und CH_4 Konzentrationen im Grundwasser. Dieses Ergebnis wurde auf der Landschaftsskala bestätigt, auf der es keinen statistischen Zusammenhang zwischen CO_2 Konzentrationen in schwedischen Waldseen und dem Anteil der Kahlschlagsfläche in deren Wassereinzugsgebieten gab. Schlussfolgerungen ob CO_2 Konzentrationen eher intern oder extern reguliert sind hingen fundamental davon ab, ob räumlich- oder zeitlich hochaufgelöste Umweltüberwachungsdaten genutzt wurden. Die Abschätzung metabolischer Aktivitäten in Seen anhand von Sauerstoffkonzentrationszeitreihen wurden erheblich erschwert durch Mischungs- und Transportprozesse. Deren Quantifizierung ist deshalb unabdingbar um metabolische Umsetzungsraten von CO_2 verlässlich berechnen zu können.

Zusammenfassend sind Treibhausgasemissionen von borealen Quellgewässern erstaunlich robust gegenüber Landnutzungsaktivitäten, sodass von ihnen wahrscheinlich kein zusätzlicher gewässerbedingter Einfluss auf das Weltklima hervorgeht. Auf der hier untersuchten Ökosystem- und Landschaftsskala werden jedoch Teilprozesse der Treibhausgasumsetzung, die durchaus von Landnutzung beeinflusst sein könnten und sich potentiell gegenseitig ausgleichen, nicht ersichtlich. Um diese Mechanismen aufzuzeigen bedarf es verbesserte Methoden der See- und Umweltüberwachung die explizit die enorme räumliche und zeitliche Variabilität von Treibhausgasdynamiken und deren abiotische und biotische Einflussfaktoren erfassen.

Introduction

Land use as a global climate control

Humans have been converting and managing the earth's land surface to exploit natural resources and ecosystem services (Foley et al. 2005; Goldewijk 2001). These actions have significantly and partly irreversibly perturbed earth system processes (Rockström et al. 2009). Among the most perturbed processes are the global carbon (C) and nitrogen (N) cycle that strongly regulate the global climate (Vitousek et al. 1997; Falkowski et al. 2000; Gruber and Galloway 2008). Climate controlling greenhouse gases such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) are emitted not only by fossil fuel combustion, but also by land use activities (Houghton 2003; Schlesinger 2009). These emissions are most often only quantified within the system boundaries where the land use is taking place. Yet, ecosystems are connected by hydrological or atmospheric exchange. This exchange enables land use to fuel greenhouse gas emissions in boundaring or even remote systems. Such indirect emissions are rarely accounted for, but could if included, potentially greatly change the climate impact of the land use activity in question (Haberl et al. 2012).

Intelligent land management can contribute to mitigate greenhouse gas emissions (Van Vuuren et al. 2007). Forests contribute significantly to the global C sink (Pan et al. 2011; Myneni et al. 2001; Goodale et al. 2002). Therefore, forest management is a widely used tool to maximize forest C uptake or to extract biomass as a climate-neutral energy source to replace fossil fuels (Canadell and Raupach 2008; Dixon et al. 1994; Schlamadinger and Marland 1996) in order to fulfill greenhouse gas budget commitments under the Kyoto Protocol (IGBP Terrestrial Carbon Working Group 1998). Yet, mitigation measures neglect that a significant part of terrestrial C sequestered by forests is exported to aquatic systems (Jonsson et al. 2007; Öquist et al. 2014; Battin et al. 2009), that these losses are sensitive to logging activity (Nieminen 2004; Schelker et al. 2012; Lamontagne et al. 2000), and that a major proportion of the exported C is mineralized in inland waters and emitted back to the atmosphere (Tranvik et al. 2009). Forestry induced N losses may have similar fates (Saari et al. 2010). Headwaters are by definition the first to receive land-derived subtrates. Hence, revealing potential changes in the greenhouse gas budget of headwaters downstream forest clearcuts is critical for evaluations of the overall potential of forestry to mitigate climate warming.

Role of headwaters in global greenhouse gas cycling

Inland waters are hotspots of landscape-scale C and N cycling (Seitzinger et al. 2006; Cole et al. 2007). They are often supersaturated in CO_2, CH_4 and N_2O and therefore emit these gases to the atmosphere (Cole et al. 1994; Bastviken et al. 2011; Seitzinger and Kroeze 1998). The reason for their supersaturation is that inland waters process C and N derived from land, and, importantly, most of what is mobilized by land use activities (Regnier et al. 2013; Seitzinger and Kroeze 1998; Dawson and Smith 2007). Headwaters contribute disproportionately to their size to this active role, because they are far more prevalent in the landscape than larger systems (Verpoorter et al. 2014; Bishop et al. 2008; Downing et al. 2006), more strongly connected to their catchments (Bormann and Likens 1965; Kling et al. 2000; Hotchkiss et al. 2015), and hence more strongly supersaturated in greenhouse gases (Lundin et al. 2013; Wallin et al. 2013; Holgerson and Raymond 2016).

Aquatic greenhouse gases mainly originate from microbial decomposition of organic matter (CO_2, CH_4) and microbial N transformations (N_2O). These processes can occur in soils, sediments or the water column. How sources and pathways of greenhouse gases partition in inland waters is currently subject of strong debates (Hotchkiss et al. 2015; Weyhenmeyer et al. 2015; Wilkinson et al. 2016). Sources and pathways may change quantitatively or qualitatively under the influence of land use perturbations such as forestry, with potentially large implications for the catchment-scale greenhouse gas budget.

Impacts of clearcut forestry on catchment biogeochemistry

Forestry effects on aquatic greenhouse gas emissions are unknown. Here, I attempt to hypothesize initial clearcut effects (<10 years) based on typical responses in hydrological and biogeochemical processes observed in previous forest clearcut experiments (e.g., Likens et al. 1970; Palviainen et al. 2014; Schelker et al. 2013). Here, I focus on mechanisms representative for the boreal biome where forestry is the major land use activity and clearcutting the most common logging practice (SFA 2014; Hagner 1999).

Clearcutting effects can be broadly classified into effects on inputs to aquatic systems (loadings), metabolic processing of these inputs and loss terms to the atmosphere and sediment (Fig. 1). Downstream losses are excluded here, for simplicity. The ultimate driver of altered inputs is the reduced water uptake of a forest once it is cut. This often leads to enhanced groundwater tables and stream discharge (Andréassian 2004; Ide et al. 2013). Higher soil temperature and logging residues on clearcuts stimulate mineralization in soils and hence production of dissolved organic carbon (DOC) and CO_2 which may then be exported at elevated rates to receiving inland waters (Schelker et al. 2013; Kowalski et al. 2003; Bond-Lamberty et al. 2004). Terrestrial DOC stimulates aquatic respiration and together with enhanced soil CO_2 supply, fuels aquatic CO_2 emissions (Lapierre et al. 2013; Karlsson et al. 2007). Terrestrial C inputs may also stimulate sedimentation or methanogenic bacterial activity and CH_4 ebullition (Huttunen et al. 2003; Lundin et al. 2015). Similar to C, N is often leaking from forest clearcuts (Schelker et al. 2016; Palviainen et al. 2014; Nieminen 2004). Nitrogen may also affect greenhouse gas cycling in inland waters, yet predictions on the direction of net effects are difficult. Nitrogen inputs may suppress or stimulate CH_4 production (Liikanen et al. 2003; Bogard et al. 2014), enhance CH_4 oxidation (Deutzmann et al. 2014) and promote denitrification and N_2O emissions (Seitzinger and Nixon 1985; McCrackin and Elser 2010). Nitrogen inputs may also cause eutrophication (Bergström and Jansson 2006). Eutrophication may go along with enhanced C sequestration (Flanagan et al. 2006) or oxygen consumption which changes the balance between methanogenesis and methanotrophy (Bastviken et al. 2004) as well as nitrification and denitrification (Mengis et al. 1997). Clearcutting may also increase wind exposure (Xenopoulos and Schindler 2001; Tanentzap et al. 2008) and hence atmospheric gas transfer rates in lakes (Cole and Caraco 1998). Similarly, increased discharge may affect turbulence and hence atmospheric gas transfer rates in streams (Raymond et al. 2012).

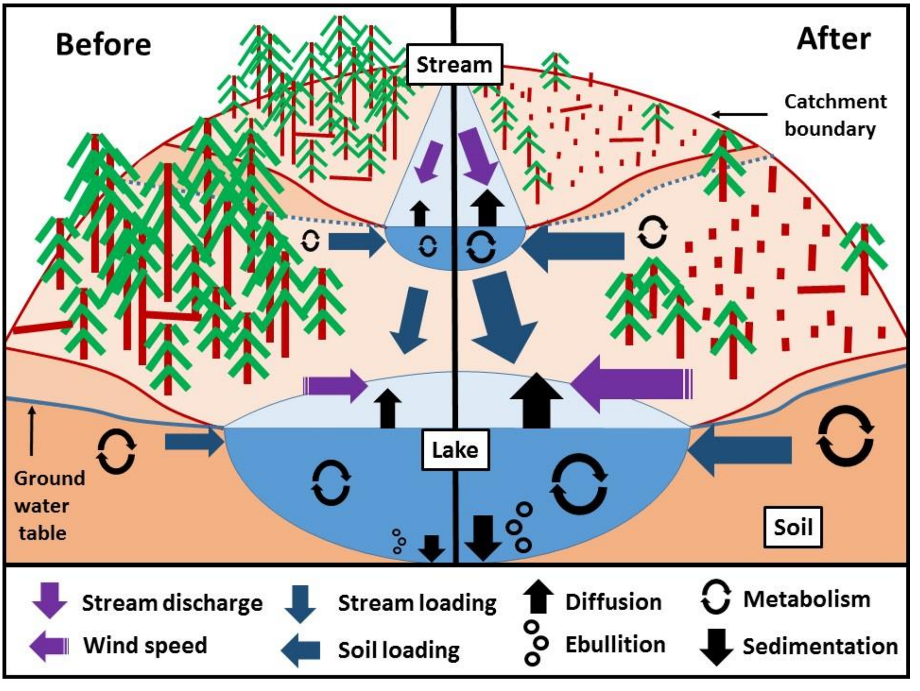

Fig 1 Conceptual figure of forest clearcutting effects on greenhouse gas cycling and atmospheric emissions in boreal headwater catchments across the soil-stream-lake continuum. Hypothetical conditions are shown for *before* and <10 years *after* clearcutting. Cross sections of a lake and its inlet stream are shown separately from each other to enhance visibility. The hypothesized size of fluxes and rates scales with symbol size.

Research needs

The complex interplay of expected hydrological, biogeochemical and physical responses to forest clearcutting can only be meaningfully studied by whole ecosystem-scale experiments across the whole groundwater-stream-lake continuum (Schindler 1998; Solomon et al. 2015). The particular complexity of potential N effects alone calls for separate experimental efforts. Whole-lake nutrient enrichment experiments are rare and have focused on combined N and phosphorous (P) effects on CO_2 emissions only (Kling et al. 1992; Findlay et al. 1999; Carpenter et al. 2001). Yet, N effects on lake ecosystems may differ from combined N and P effects, especially in boreal regions with low background N deposition (Bergström et al. 2008; Elser et al. 2009). This is highly relevant given that N and P inputs to lakes are often uncoupled when derived from forest clearcuts (Tremblay et al. 2009; Nieminen 2004). Nitrogen enrichment experiments would help to interpret outcomes of whole-catchment forest clearcut experiments. Mechanistic evidence from forest clearcut experiments are needed to validate surveys which have highlighted the sensitivity of inland water greenhouse gas cycling to changes in catchment vegetation (Urabe et al. 2011; Maberly et al. 2013), forest fires (Marchand et al. 2009) and forestry activities (Huttunen et al. 2003; Ouellet et al. 2012). Previous surveys have, however, not assessed clearcut effects at broader spatial scales at which other factors such as climate would interact with local forestry effects. These interactions are unknown but central to improve predictions of climate and land use effects on lake ecosystems and their feedback to ongoing climatic changes (Lapierre et al. 2017).

Whole-ecosystem and landscape-scale approaches would reveal net effects of forest clearcutting. However, to increase our process understanding, these approaches should be complemented with detailed studies on sources and pathways of greenhouse gases. A powerful approach to reveal these mechanisms is to model whole-ecosystem metabolism. Fundamentals to this approach and its application to CO_2 cycling in lakes are introduced in the following.

Excursus: Whole-lake metabolism modelling

The free-water oxygen technique

Estimates of gross primary production (GPP), ecosystem respiration (ER) and net ecosystem production (NEP = GPP-ER) can be derived from diel changes in concentrations of dissolved oxygen (DO) (Odum 1956). This is based on the fundamental assumption that metabolical contributions to night-time decreases in DO are due to ER alone, whereas day-time contributions are due to NEP. To track these dynamics, high frequency DO measurements are possible with free-water oxygen probes. The so-called free-water oxygen technique has become a widely applied tool to estimate whole-lake metabolism (Staehr et al. 2010). This technique can also be used to estimate rates of metabolical CO_2 cycling based on the assumption that about one mole CO_2 is produced per mole O_2 consumed and *vice versa*. However, such estimates are rare for unproductive boreal lakes, especially in those with high concentrations of colored dissolved organic matter (CDOM). In these systems, the free-water oxygen method often fails to provide meaningful metabolism estimates (Chmiel et al. 2016). Inaccuracies are due to low signal to noise ratios with physical processes greatly overriding metabolic signatures in diel oxygen cycles (Antenucci et al. 2013; Rose et al. 2014; Kemp and Boynton 1980). Therefore, efforts are required to quantify the extent to which physical transport causes changes in the magnitude and variability of metabolism estimates in these systems.

Physical transport and mixing in lakes

In lakes, DO can be exchanged with the atmosphere or other fluid parcels by diffusion, travel with the bulk water flow (advection), or be mixed into adjacent strata during entrainment. Common models to describe physical oxygen transport in lakes include diffusive gas exchange across the air-water interface as driven by wind shear (e.g. Cole and Caraco 1998). New models are now available and also take into account that near-surface turbulence, the driver of diffusive fluxes, is also enhanced by buoyancy fluxes (MacIntyre et al. 2010; Zappa et al. 2007). Buoyancy fluxes can dominate over wind shear in small, wind sheltered lakes (Read et al. 2012) and should therefore be included in any attempts to accurately model air-water gas exchange in these systems. Yet, most whole-lake metabolism models do not take advantage of these improved models of atmospheric gas exchange (but see Staehr et al. 2012).

Another factor widely neglected in whole-lake metabolism studies is vertical mixing between the upper mixed layer and lower layers (Sadro et al. 2011; Gelda and Effler 2002). Vertical exchanges within the water column can also be caused by the deepening of the mixed layer during cold fronts and the mixing induced by the breaking of internal waves (Saggio and Imberger 1998; MacIntyre et al. 1999; Boegman et al. 2005). Besides wind induced horizontal transports, advective flow is also caused by differential heating and cooling (Monismith and Morison 1990; James and Barko 1991). These transport mechanisms are most likely to confound metabolism estimates in lakes with variable thermal structure and strong oxygen concentration gradients, conditions often found in boreal unproductive brown water lakes. Erroneous metabolism estimates imply a confounded view on the sources and sinks of CO_2 in lakes. Ultimately, this makes it difficult to reveal changes in the pathways of lake carbon cycling that are potentially triggered by land use activities.

Aims and scope

This thesis consists of four chapters dealing with the effects of land use on greenhouse gas emissions from boreal inland waters. Specifically, I aim to assess:

- the effects of N enrichment on storage and emissions of CO_2, CH_4 and N_2O from six unproductive headwater lakes (Paper **I**)
- the effects of forest clearcutting on lake and stream emissions of CO_2, CH_4 and N_2O in four headwater catchments (Paper **II**)
- the role of forest clearcutting, relative to climate, for landscape-scale patterns of CO_2 concentrations in Swedish lakes (Paper **III**)
- the role of physical processes in diel oxygen dynamics in lakes and their confounding effects on whole-lake metabolism estimates that are based on the free-water oxygen method (Paper **IV**)

Together, the thesis chapters cover a large gradient of spatial and temporal scales from sub-hourly and sub-meter dynamics of in-lake processes (Paper **IV**) to multi-year and whole-ecosystem responses to land use (Paper **I-II**) and steady state effects of land use and climate at the landscape scale (Paper **III**, Fig. 2).

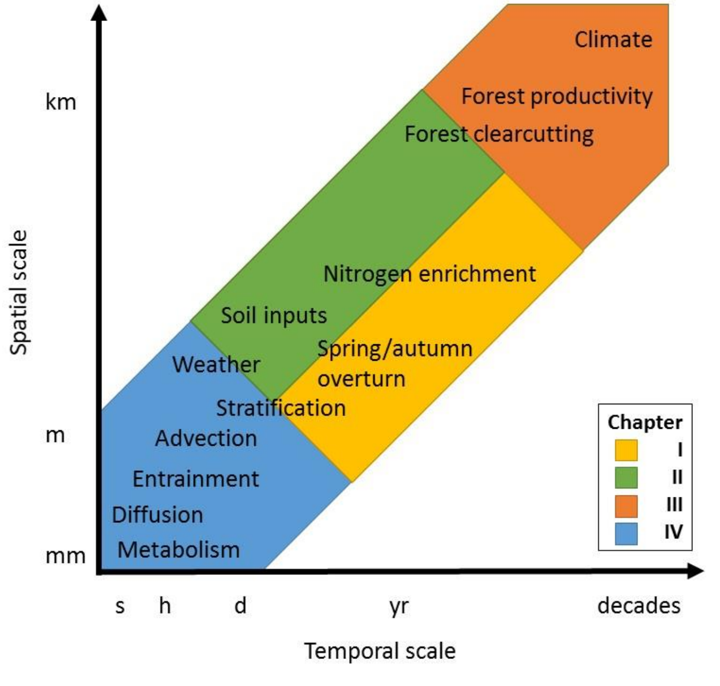

Fig 2 Stommel diagram of drivers of greenhouse gas dynamics in inland waters addressed in this thesis.

Materials and methods

This thesis combines two whole-ecosystem experiments carried out in 9 boreal headwater catchments, a global literature synthesis of 68 lakes and Swedish national lake survey data (Fölster et al. 2014) from 439 lakes of which 22 lakes were monitored seasonally (Fig. 3). Experimental research included whole-lake N enrichment (Paper **I**) and catchment forest clearcutting (Paper **II**). The spatial survey was combined with national forest inventory data to assess landscape-scale forestry effects (Paper **III**). Five of the experimental lakes were also used for physical observations to assess and further develop the free-water oxygen method (Paper **IV**).

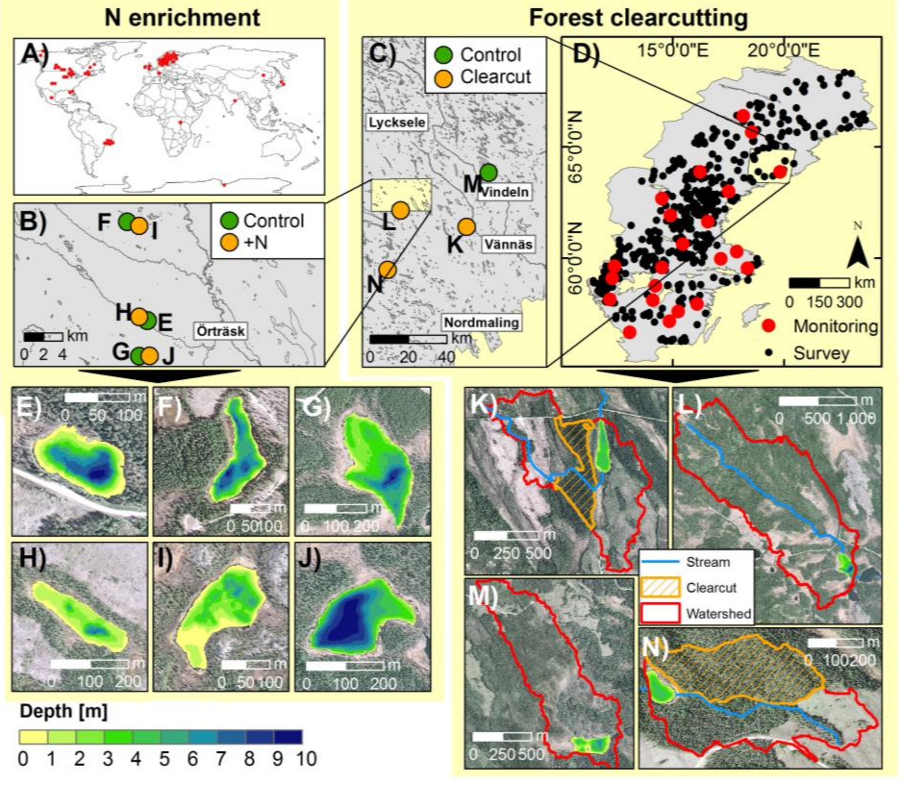

Fig. 3 Hierarchical maps of the study sites included in this thesis. Six lakes were part of N enrichment ('+N') experiments (B) embedded in a global literature synthesis of 68 lakes (A) (Paper **I**). Four lakes and three streams were included in forest clearcut experiments (C) (Paper **II**). Clearcut effects were also studied in 439 forest lakes sampled by the Swedish National lake survey (D) (Paper **III**). Detailed maps show air photos and lake bathymetry. Panel labelling is consistent across map scales and as follows: E) Nästjärn, F) Mångstenstjärn, G) Nedre Björntjärn, H) Fisklösan, I) Lapptjärn, J) Övre Björntjärn, K) Struptjärn, L), Övre Björntjärn, M) Stortjärn and N) Lillsjöliden.

Study sites

Experimental catchments

Whole-ecosystem experiments were carried out between 2011 and 2015 in nine unproductive headwater catchments located in boreal northern Sweden (Table 1, Fig. 3B, C). The annual mean air temperature and precipitation during the reference period 1960-1990 were ~1.0°C and 500-600 mm, respectively (http://www.smhi.se/klimatdata/meteorologi). Atmospheric wet deposition of dissolved inorganic N was low (< 200 kg m^{-2} yr^{-1}, Bergström et al. 2008). The catchments were mainly covered by managed coniferous forest and minor contributions from minerogenic unproductive mires. Catchment soils were typically well drained and characterized by podzol developed on glacial till and acidic bedrock. The regional hydrology was controlled by pronounced spring floods, summer and winter low flow and autumn storms. The riparian zone was characterized by organic rich peat soils. In the early 20th century, existing drainage channels were deepened and widened by ditches. Drainage channels all culminated in single lake inlets. Lakes were small, shallow and dimictic with summer stratification lasting from late-May to mid-September. Lake ice was present from late October to mid-May.

Table 1 Catchment and water characteristics of the lakes and streams studied in this thesis. Water characteristics are sampling season averages (see relevant chapter for details). Treatments refer to N enrichment (N) and forest clearcutting (C). Superscripts refer to the relevant thesis chapter.

Catchment	Treatment	Catchment area [ha]	Lake area [ha] / stream length [km]	Mean depth [m]	Water residence time [d]	DOC [mg L^{-1}]	TP [µg L^{-1}]	TN [µg L^{-1}]
Lakes								
Fisklösan[I]	N impact	9	1.7	2.1	677	7	9	284
Nästjärn[I]	N control	3	1.0	4.2	2051	7	10	329
Lapptjärn[I]	N impact	17	2.0	2.5	481	12	11	345
Mångstenstjärn[I]	N control	14	1.8	5.3	1034	10	12	317
Nedre Björntjärn[I,IV]	N impact	325	3.2	6.0	89	19	18	411
Övre Björntjärn[I,II,IV]	N+C control	284	4.8	4.0	117	23	19	466
Stortjärn[II,IV]	C control	82	3.9	2.7	95	20	13	403
Struptjärn[II,IV]	C impact	79	3.1	3.8	387	19	24	367
Lillsjöliden[II,IV]	C impact	25	0.8	3.8	115	15	19	345
439 forest lakes[III]	C survey	3-10747	0.2-3439	-	-	2-35	1-70	100-1646
Streams								
Övre Björntjärn[II]	C control	233	3.0	0.3	-	28	26	503
Struptjärn[II]	C impact	46	1.4	0.2	-	36	24	762
Lillsjöliden[II]	C impact	19	0.6	0.1	-	21	15	829

Swedish national lake survey catchments
The study area of the Swedish national lake survey covered three climate zones from cool-temperate in the South to sub-arctic in the North (56-68˚N) with mean annual temperatures ranging from -2 to 8˚C and annual precipitations of 250 to 1200 mm (Table 1, Fig. 3D). The catchments ranged from 14 to 644 m.a.s.l. Catchment soils were mainly podsols developed on glacial till and acidic bedrock. More than 90% of all forest area in Sweden is managed by clearcutting, of which 0.9% is cut annually after rotation periods of typically 70-100 years (SFA 2014). Forests covered >50% of the catchment areas and were of hemiboreal and boreal type dominated by *Picea abies* and *Pinus sylvestris*, with the exception of temperate beech forests (*Fagus sylvatica*) in the far south and subalpine birch forest (*Betula* sp.) in the far northwest. The catchment forests spanned an age range of 19-114 years. Mires covered 0-42% of catchment areas with increasing prevalence towards the northwest of Sweden. Lakes covered <1-23% of the catchment area, and were typically dimictic and ice covered for two to eight months on a gradient from south to northwest.

Field experiments

Whole-lake N enrichment experiment
Whole-lake fertilization experiments were carried out including six lakes utilizing a before-after/control-impact (BACI) design with sampling during one year *before* (2011) and three years *after* (2012-2014) onset of N enrichment. The experiment included three lake pairs similar in DOC and nutrient concentrations and water residence time (Table 1, Fig. 3E-J) and phytoplankton, zooplankton and fish communities (Deininger et al. 2017). For each lake pair, one *control* lake was left untreated and one *impact* lake was fertilized with nitrate (Fig. 5A) to simulate conditions present today in southwestern Sweden where atmospheric DIN loads are 3-4 times as high as in the study area. Nitrate was added weekly or biweekly throughout June to August 2012-2014 and twice from the ice in spring 2012 and 2013 to mimic leaching events during storms and spring floods (Bergström et al. 2008).

Whole-catchment forest clearcut experiment
Whole-catchment manipulation experiments with a BACI design were carried out, including two *impact* catchments that received a forest clearcut after one year of pre-treatment sampling and two *control* catchments that were left untreated throughout the whole study period (2012-2015, Fig. 3K-N). Clearcutting of 90-120 years old coniferous forest was performed on snow-covered frozen soil in February 2013 in the catchments of Struptjärn and Lillsjöliden by national or private forest companies according to "common practice" methods (Fig. 4). In early November 2014, clearcuts

were site-prepared by disk-trenching (Fig. 4C). Clearcut areas were 14 ha and 11 ha and corresponded to 18% and 44% of total lake watershed areas, respectively. Buffer strips of 5-60 m were left along streams and around lakes and remained largely intact throughout the study period, except of in Struptjärn were stream buffer strips were heavily damaged by a windthrow event (Fig. 4E, F).

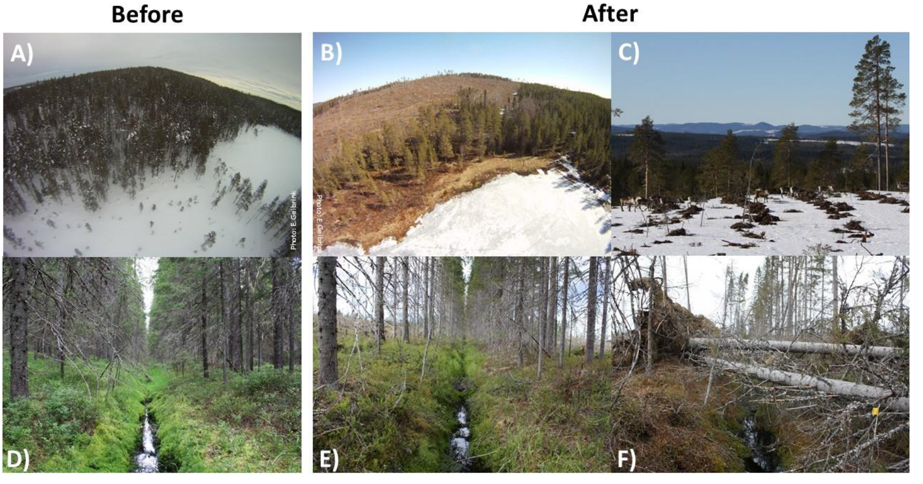

Fig. 4 Forest-stream-lake continuum before and after clearcutting in lake Lillsjöliden (here ice-covered) (A-C) and the inlet of Struptjärn (D-F). Note the soil trenches (snow free patches) after site preparation (C) and the storm damage of the riparian buffer vegetation (F). Figure redrawn from Paper **II**.

Field sampling

In the whole-ecosystem experiments, concentrations of CO_2, CH_4 and N_2O were monitored 2-hourly to biweekly in surface lake water (Papers **I**, **II**) and stream and hillslope-groundwater (Paper **II**). In the N enrichment experiment, I also measured gas concentrations monthly along depth profiles to calculate whole-lake inventories. Gas concentrations were measured using non-dispersive infrared gas analyzers (Johnson et al. 2010) (Fig. 5B) or by gas chromatography of headspace gas extracted from water injected into air-tight acidified glass vials, or using the headspace equilibrium technique (Fig. 5D). Spatial variability was accounted for in the clearcut experiment by sampling multiple locations within each lake and stream. In addition, CH_4 fluxes across the air-water interface (diffusion + ebullition) was sampled weekly using 115 floating chambers placed along depth transects (Bastviken et al. 2010) (Fig. 5E). To model air-water gas-transfer velocities and surface energy budgets in lakes, I measured weather variables every 5 min using meteorological stations (Fig. 5G). To estimate air-water gas-transfer velocities in streams, I performed 282 static flux chamber measurements (Fig. 5I) and 23 propane injection experiments (Wallin et al. 2011) (Fig. 5J). To infer diel oxygen dynamics across the mixed layer and thermocline, profiles of temperature and oxygen concentrations were measured every 5 min for 2-8 weeks at 0.5 m depth intervals (Fig. 5C).

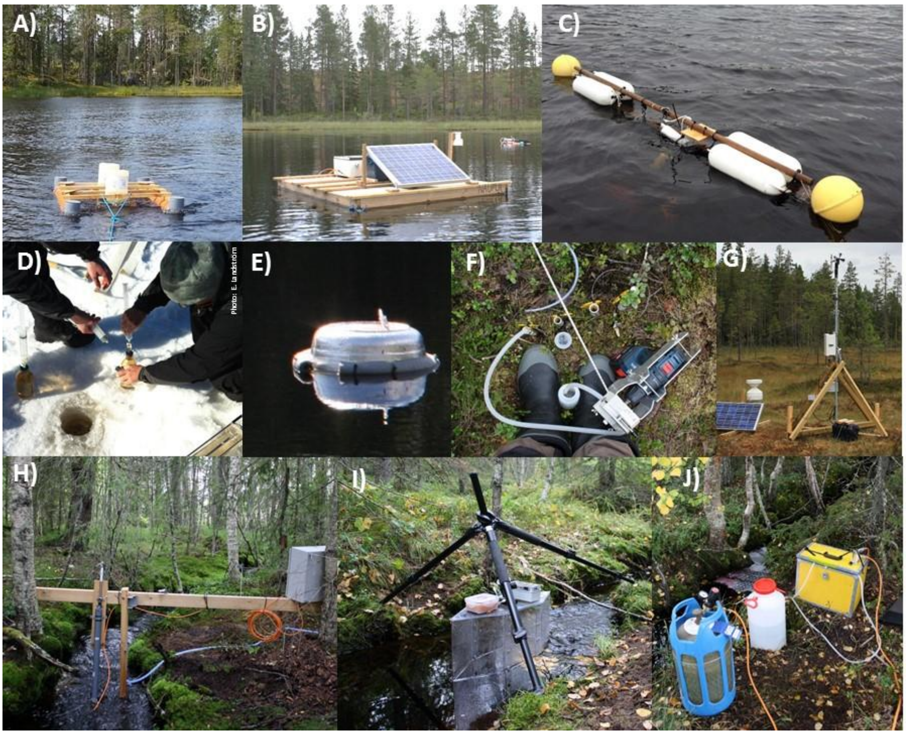

Fig. 5 Selection of field methods used in this thesis: A) whole-lake N enrichment (**I**), B) automated lake CO_2 concentration measurements (**I,II**), C) automated oxygen concentration and temperature profiling (**IV**), D), spot measurements of gas concentrations (**I, II**), E) floating chamber deployment, F) groundwater wells (**II**), G) weather station (**I, II, IV**), H), automated stream water height and CO_2 concentration measurements (**I, II**), I) flux chamber for gas transfer velocity measurements in streams (**II**), J) propane injection for gas transfer velocity measurements in streams (**II**).

Gas flux calculations

Diffusive gas fluxes across the air-water interface or across water layers of different density were calculated based on surface-water concentrations and gas transfer velocities using Fick's first law (Fick 1855). One exception here is diffusive fluxes across the air-water interface during spring- and autumn turnover that were inferred from declines of whole-lake inventories over times (Paper **I**). Gas transfer velocities for lake-air exchange were modeled based on wind speed (Cole and Caraco 1998) (Paper **I,II,IV**) or near-surface turbulence caused by wind shear and buoyancy flux (Zappa et al. 2007; MacIntyre et al. 2010) (Paper **IV**). Gas transfer velocities for air-stream exchange were modeled based on stream discharge, using empirical relationships established by the propane-injection experiments and flux chamber measurements (Paper **II**). Total fluxes of CH_4 were estimated from concentration increases in floating chambers over time (Bastviken et al. 2004) (Paper **II**).

To estimate physical oxygen fluxes in lakes that may bias metabolism estimates based on the free-water oxygen method (Paper **IV**), I developed a conceptual framework shown in Fig. 6. Within this framework, I modeled eddy diffusivities, the gas transfer velocity for exchange across water layers of different densities, as a function of depth following MacIntyre et al. (2009) using the surface energy budget method (Jassby and Powell 1975) or using the energy dissipation method (Osborn 1980). Entrainment of water during deepening of the actively mixing layer was calculated based on a volumetric mass-balance approach.

Metabolism modelling

I calculated GPP and ER based on diel dynamics in DO concentrations using an inverse modelling approach adapted from Van de Bogert et al. (2007) and solved by Bayesian parameter estimation (Hotchkiss and Hall 2014) (Paper **IV**). This approach reconstructs time series of DO at time t, based on DO at time t-1 and adding contributions from GPP, ER and physical oxygen fluxes, including air-water gas exchange, eddy diffusion and entrainment. To investigate the effect of physical oxygen fluxes on GPP and ER estimates, three model runs were performed, first, including air-water gas exchange only based on a wind based model, second, including air-water gas exchange only based on the surface renewal model and, third, including air-water gas exchange based on a wind based model, diffusion and entrainment. In addition, I applied the metabolism model separately to raw time series of DO and time series that were median filtered to remove sudden nocturnal drops in DO during low wind speeds likely related to transport of low-oxygen water by internal waves or lateral advection (Fig. 6).

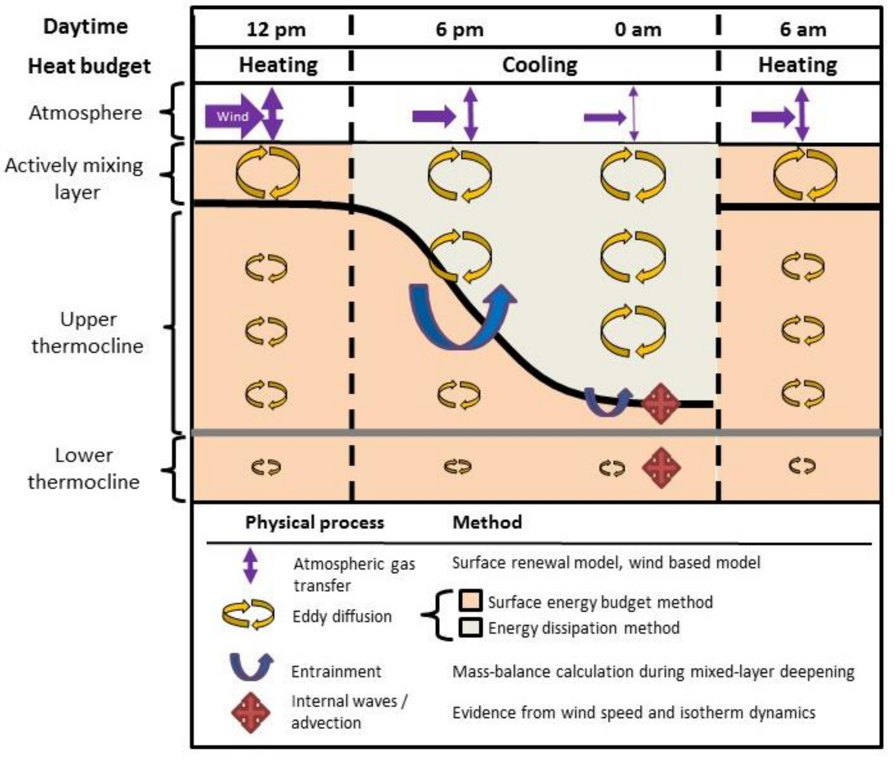

Fig. 6 Conceptual model of diel variations in physical processes that control oxygen fluxes across concentration gradients in the mixed layer and the thermocline of lakes. Wind speed is assumed largest during day time and to taper at night. Atmospheric gas transfer coefficients will be larger when winds are higher. The vertical mixing due to wind shear and shear associated with internal waves will drive mixing during stratification, with larger eddy diffusivities (k_z) near the surface and smallest k_z where stratification is greatest. I compute k_z from the surface energy budget method for conditions with red shading. Under cooling, turbulence is caused by wind induced shear near the surface and by large eddies from convection thoughout the water column. I compute k_z under cooling from dissipation rates for conditions with grey shading. When the mixed layer deepens, vertical fluxes are computed based on the change in mixed layer depth. When winds are light, as before sunrise, oxygen concentrations may change due to internal waves, the shift from a downwelled thermocline to an upwelled one or due to flows from differential cooling which transport oxygen from littoral regions offshore (Figure redrawn in simplified form from Paper **IV**).

Swedish national lake survey

I extracted alkalinity and pH data from the Swedish National lake inventories carried out in the autumns of 2000 and 2005 (SLU 2014). Based on this data, I calculated CO_2 concentrations following Stumm and Morgan (1995) for 439 forest lakes distributed equally across lowland Sweden (Fig. 3D). To explain spatial patterns in CO_2 concentrations, I used data on annual mean air temperature, precipitation and wind speed from a mesoscale climate model (Landelius et al. 2016) and forest productivity and the areal percentage of forest clearcuts from gridded Swedish National forest survey data (SLU 2005), calculated for each lake catchment delineated from a national 2m elevation model (Swedish National Land Survey 2015). To assess how representative forestry effects revealed from autumn snap-shot samplings were for the annual scale, I explored drivers of seasonal variability of CO_2 in a subset of 22 monitoring lakes.

Global literature synthesis

To set results from the N-enrichment experiment in a global context, I compiled all peer-reviewed original studies listed on ISI Web of Knowledge which assess the effects of nutrient enrichment (with N or P alone or with N and P combined) on CO_2, CH_4 or N_2O concentrations or emissions in standing inland-waters. Here, nutrients have to be explicitly shown or discussed to be a driving factor, e.g. by adding them to the system or by establishing gradients in space or time. Studies in reservoirs, temporal analysis of seasonal variability and spatial analyses of within-lake variability were excluded. I summarized outcomes in contingency tables counting the number of studies that showed a significant increase, decrease or no significant change in response to nutrients according to (1) the spatiotemporal scale of the system (multi-annual trends, spatial surveys, whole-lake experiments, mesocosm experiments, sediment incubations) or (2) whether lakes were enriched in N or P alone or N and P combined.

Statistical analyses

The effects of experimental N enrichment and forest clearcutting were statistically tested following the paired BACI approach of Stewart-Oaten et al. (1986) using linear mixed-effects models. Treatment effects were analyzed in terms of effect sizes, defined as the *before-after* change in the differences between paired *impact*- and *control* systems.

To evaluate forestry effects on CO_2 concentrations in Swedish survey lakes and to isolate these effects from potential other factors such as climate, I used structural equation modelling. This is a common approach based on defining plausible causal relationships between variables and then evaluating the most likely direct and indirect paths of causality based on data. Here, I based model fitting on a piecewise approach where each equation is solved separately (Lefcheck 2016).

Major results and discussion

This thesis demonstrates by two independent whole-ecosystem experiments and a spatial survey that N enrichment and forest clearcutting has only weak effects on greenhouse gas emissions from boreal inland waters (Table 2). The results emphasize that the climate change mitigation potential of forestry activities is unlikely to be confounded by previously overlooked effects of carbon and nitrogen losses on aquatic greenhouse gas emissions.

Nitrogen effects

Despite a significant increase in dissolved inorganic nitrogen (DIN) concentrations, N enrichment did not affect lake-atmosphere fluxes and summer and winter inventories of CO_2, CH_4 and N_2O (Paper **I**). These findings contrast with results from previous whole-lake experiments (Kling et al. 1992; Carpenter et al. 2001; Findlay et al. 1999) that have been limited to combined N and P effects on CO_2 emissions only. Yet, they confirm the picture of the global literature synthesis which revealed that nutrient enrichment effects varied significantly between habitat-specific studies, whole-lake experiments and spatial surveys and depended on the type of nutrient enrichment (N, P or N+P). Combined, these results demonstrate the scale and context dependence of greenhouse gas emissions to N enrichments.

The lack of a clear response in the N enrichment experiment and the wide range of responses in previous studies can be explained by two hypotheses:

(1) The potential stimulation of metabolical gas production or consumption was negligible compared to other factors that control in-lake gas dynamics. This was likely the case for CO_2. The non-significant CO_2 decrease (-3.8 mmol m^{-2} d^{-1}) in response to N addition corresponded well to the net increase in pelagic GPP (3.2 mmol m^{-2} d^{-1}) measured during the experiment (Deininger et al. 2017, unpubl.). Yet, primary production-driven CO_2 declines can only cause a maximum decrease in summer CO_2 emissions by 15%, because their contribution was largely masked by external CO_2 inputs (Striegl and Michmerhuizen 1998; Wilkinson et al. 2016) or mineralization of terrestrial DOC (Karlsson et al. 2007; Vachon et al. 2017; Lapierre et al. 2013). In previous mesocosm and whole-lake experiments, stronger CO_2 declines may have been due to the larger importance of C uptake by primary producers for the whole-lake C budget or due to stronger stimulation of GPP by combined N and P enrichment. Therefore, even a clear GPP response following N enrichment does not necessarily translate into similar clear responses in lake-atmosphere CO_2 fluxes.

(2) The potential stimulation of metabolical gas production or consumption was counteracted by other processes that control in-lake gas dynamics. This was especially relevant for the CH_4 cycle which includes many components of which only some may be involved in the system studied (Bastviken et al. 2004). For example, freshly produced biomass as a result of nutrient addition typically stimulates methanogenesis (DelSontro et al. 2016; Bogard et al. 2014) but does not necessarily cause measurable changes in diffusive CH_4 fluxes because it is efficiently oxidized on its way to the lake-air interface (West et al. 2016). Methane oxidization can even occur under the enhanced supply of nitrate that provides additional electron acceptors for CH_4 oxidizing bacteria (Deutzmann et al. 2014). Similarly, N_2O production, typically stimulated by N addition in laboratory experiments, may have been limited in my whole-lake experiment because nitrate was added to the oxic epilimnion where N_2O production during denitrification is inefficient (Mengis et al. 1997). Clearly, all relevant components of CO_2, CH_4 and N_2O cycling should be measured in future experiments to reveal mechanisms behind nutrient enrichment effects on whole-lake greenhouse gas emissions.

Clearcut effects

Clearcutting experiment

Forest clearcutting did not change groundwater levels, stream discharge, nutrient and DOC concentrations and greenhouse gas emissions from inland waters (Table 2, Fig. 7A, Paper **II**). These results, consistent across both streams and lakes over a three-year post-treatment period, suggest that the generally strong effects of forest clearcutting on terrestrial hydrology and C and nutrient cycling are not necessarily translated into effects on recipient downstream aquatic ecosystems.

Table 2 Summary of land use effects on greenhouse gas dynamics in inland waters as demonstrated in the different thesis chapters. Abbreviations: “o”=no response, “+”=significant increase. NA=Not available.

					Response		
Chapter	System	Treatment	Approach	Parameter	CO_2	CH_4	N_2O
I	Lake	N enrichment	Experiment	Flux	o	o	o
I	Lake	N/P enrichment	Various*	Flux / Concentration	o	o	+
II	Lake	Clearcut	Experiment	Flux	o	o	o
II	Stream	Clearcut	Experiment	Flux	o	o	o
II	Groundwater	Clearcut	Experiment	Concentration	+	+	NA
III	Lake	Clearcut	Survey	Concentration	o	NA	NA

*Summarized from the global literature synthesis

The lack of a clear response in groundwater levels, stream discharge and nutrient and DOC concentrations in the clearcutting experiment can be explained by the following hypotheses:

(1) The areal proportion of forest cut was below critical threshold levels above which significant changes in water chemistry can be expected. The areal proportion of forest cut in my experimental catchments was 18-44%, confirming regional threshold levels of 30% (Schelker et al. 2014; Palviainen et al. 2014).

(2) The time it takes for the system to respond exceeded the experimental period. Relatively long water residence times in the soils of my gently sloping catchments would support this hypothesis (Kreutzweiser et al. 2008). Longer-term experiments in lowland areas have indeed shown that it may take up to 4 years for ground-, stream- or lake water chemistry to change measurably (Schelker et al. 2012; Palviainen et al. 2014; Futter et al. 2010). These studies demonstrated also that responses are often triggered by site preparation which occurred in my experiment only after the second of three post-treatment years.

(3) Forestry effects on aquatic systems are negligible in unproductive forests. Due to their tight nutrient cycling, unproductive forests loose only little amounts of DIN to aquatic systems after clearcutting (Futter et al. 2010). Forests in my catchments were relatively unproductive with a timber growth rate of 2-3 m^3 ha^{-1} yr^{-1} (SLU 2005). In another paired-catchment study in my study region, forest clearcutting caused substantial DIN leaching (Schelker et al. 2016), suggesting that even within regions of similar forest productivity, clearcut effects can be highly site-specific.

(4) *Interannual variation in weather conditions have masked or delayed forest clearcutting effects*. Precpitiation was ~250 mm yr^{-1} higher in the *before*-period relative to the *after*-period. Even extreme clearcut treatments do not cause changes of more than 200 mm yr^{-1} in boreal forests (Ide et al. 2013). Any clearcut effect is therefore likely masked by natural variability, a common observation in long-term clearcut experiments (Buttle and Metcalfe 2000; Schelker et al. 2013; Kreutzweiser et al. 2008).

The absence in water chemical and hydrological responses may explain why forest clearcutting did not affect aquatic greenhouse gas emissions, given that CO_2, CH_4 and N_2O are often derived from bacterial processing of catchment-derived DOC (Bogard and del Giorgio 2016; Peura et al. 2014; Hotchkiss et al. 2015) and DIN (Seitzinger 1988; McCrackin and Elser 2010).

Yet, aquatic greenhouse gas emissions are also fueled by direct catchment inputs of gases (Rasilo et al. 2017; Striegl and Michmerhuizen 1998; Öquist et al. 2009). Shallow (~40cm) groundwater concentrations of CO_2 and CH_4 in fact increased by 52% and 820% in response to the clearcutting treatment, relative to reference conditions (Table 2). Despite that shallow groundwater is a hotspot for riparian greenhouse gas export to headwater streams in my study region (Leith et al. 2015), increased gas supply in these layers has apparently not translated into enhanced aquatic emissions. This mismatch leads me to two additional hypotheses.

(5) Groundwater-derived greenhouse gases were transport-limited. Even though external sources often dominate CO_2 and CH_4 emissions in headwater streams (Hotchkiss et al. 2015; Öquist et al. 2009; Jones and Mulholland 1998b) headwaters may be only weakly connected to their surrounding soils during summer low flow conditions (Dinsmore et al. 2009; Rasilo et al. 2017). Such conditions were often prevalent during the relatively dry post-treatment period, suggesting that greenhouse gases in groundwaters were transport-limited. Clearly, hydrologic connectivity between aquatic systems and their catchment is a key to understand and predict forest clearcut effects (Fraterrigo and Downing 2008; Ecke 2009; Kreutzweiser et al. 2008).

(6) The riparian zone effectively buffered clearcutting effects. Greenhouse gases may be altered in their concentrations during transport across the hillslope-riparian-open-water continuum, a phenomenon often observed in boreal headwater catchments (Leith et al. 2015; Rasilo et al. 2017, Rasilo et al. 2012). This may especially apply to methane which would be strongly affected by the large redox gradients in riparian zones. Despite lacking more detailed mechanistic understanding of the function of the riparian buffer zones in my catchments, I can conclude from groundwater, stream and lake observations that they are likely to have effectively prevented increases in aquatic greenhouse gas emissions.

Broad-scale clearcut effects

According to national inventory data from 439 Swedish forest lakes, forest clear-cutting effects did not imprint in landscape-scale CO_2 patterns (Fig. 7B, Table 2, Paper **III**). This pattern was consistent across a relatively wet year (2000) and a relatively dry year (2005) and even if accounting for between-lake differences in catchment-to-lake-area ratios, forest productivity and climate variables such as air temperature and precipitation.

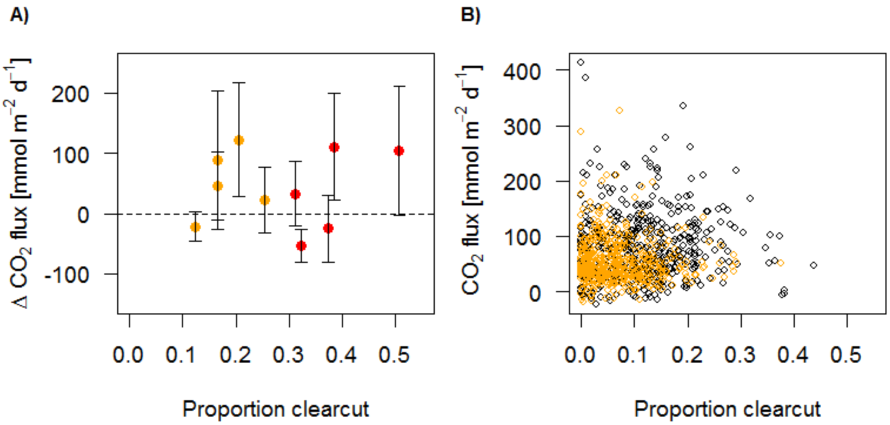

Fig. 7 Absence of any forest clearcut effect on CO_2 fluxes across the air-water interface in A) two experimental streams and B) 439 Swedish forest lakes. Panel A) shows the effect size in two streams that received a forest clearcut (orange circles = Struptjärn, red circles = Lillsjöliden). Effect sizes were measured at 5 sites with a different areal proportion of clearcuts in their catchment areas. Error bars show propagated standard errors (reproduced from Paper **II**). Panel B) shows CO_2 fluxes in autumn 2000 (black circles) and autumn 2005 (orange circles) in lakes with different areal proportions of clearcuts in their catchment, calculated from alkalinity, pH and the gas transfer velocity model by Vachon & Prairie (2013) (Figure derived from data presented in Paper **III**).

Broad-scale patterns were based on single snap-shot samplings during autumn turnover. Autumn conditions may not be representative for the whole open-water period, given the typically strong seasonality of CO_2 concentrations in boreal lakes (Åberg et al. 2010; Huotari et al. 2009). However, even CO_2 concentrations averaged over the whole open-water period measured in 22 monitoring lakes did not show any indications of clearcut effects. The same was true for effects on CDOM concentrations (but see Paper **III** for interactions with catchment-to-lake-area ratios). Hence, clearcut-induced increases in DOC concentrations often found in local-scale studies (Winkler et al. 2009; Bertolo and Magnan 2007; Schelker et al. 2012) may be diluted in Swedish catchments at larger spatial scales (Schelker et al. 2014). Combined, my spatially and temporally resolved datasets suggest that forest clearcutting does not control CO_2 cycling in Swedish lakes at broad spatial scales. However, given that forest clearcutting increases lake DOC concentrations at the landscape-scale in Canada (France et al. 2000), I cannot upscale my findings to boreal forests in general.

Interestingly, I found that trends in CO_2 concentrations along climate and forestry gradients did not always correspond between autumn and open-water season averages in monitoring lakes. According to spatially resolved data, autumn CO_2 concentrations increased with mean annual air temperature but were not coupled to CDOM concentrations. In contrast, open-water season averaged CO_2 concentrations were constant across temperature gradients but increased with CDOM. These antagonistic results suggest that our fundamental understanding of the controls of CO_2 in lakes depends on whether spatially or temporally resolved data are used. Without carefully designed sampling programs, accounting for seasonal variability, it is therefore likely that we misinterpret the controls of lake CO_2 dynamics and make inaccurate predictions of future conditions.

Whole-lake metabolism

My combined analysis of dynamics in thermal structure and oxygen concentrations clearly demonstrates the need to account for physical oxygen fluxes when using the freewater-oxygen method to model metabolism in unproductive lakes with strong vertical gradients in oxygen concentrations (Paper **IV**). Across five of my experimental lakes GPP, ER and NEP ranged from 0 to 0.9, -0.3 to -2.5 and -0.2 to -1.6 g C m^{-3} d^{-1}, respectively. These estimates differed by 0-25% depending on the atmospheric gas transfer model used and by 0-120% depending on whether fluxes from mixing were considered or not. Biases did not vary systematically across depth gradients and seasons because vertical DO gradients were usually large when transport and mixing processes were small and vice versa (Table 3). The above mentioned errors in metabolism estimates were as large or larger than errors found in other unproductive lakes (Staehr et al. 2012; Sadro et al. 2011a; Antenucci et al. 2013). However, my observations revealed yet another, previously undescribed error source: metabolism estimates varied by up to 400% if oxygen changes likely caused by internal waves and thermocline dynamics were ignored.

Specifically, I observed frequent night-time decreases in oxygen concentrations that would imply night-time respiration rates of up to 24 g C m^{-3} d^{-1}, which were two orders of magnitude higher than pelagic respiration I have measured independently using laboratory incubations. The estimates exceeded even the highest rates measured globally with the free-water oxygen method (Solomon et al. 2013). Based on detailed analysis of the lake thermal structure in relation to weather conditions, I explain the observed oxygen changes to be mainly caused by the upwelling of water from deeper layers with relatively lower oxygen concentrations triggered by internal waves or during relaxation of thermocline tilting when winds ceased during nights (see also Deshpande et al. 2015). To remove the associated oxygen changes, I used a time series filtering approach. However, lateral advection during differential cooling may also have contributed to the observed oxygen changes. Installations of near-shore temperature and oxygen arrays would be needed to confirm this alternative hypothesis.

Table 3 Potential bias of metabolism estimates based on the free-water oxygen technique caused by physical oxygen fluxes, shown for different depth layers and seasons. “+++”=strong bias, “++”=intermediate bias, “+”=small bias, “o”=no bias.

Layer	Atmospheric gas transfer	Eddy diffusion	Entrainment	Internal waves / Advection
Depth layer				
Actively mixing layer	++	+	o	+
Upper thermocline	+	+	+	+++
Lower thermocline	o	o	o	+++
Season				
Spring	+	+	o	+++
Summer	+	+	o	+++
Autumn	+	o	+	+

My dataset also allowed me to evaluate metabolism estimates based on the magnitude of measured physical oxygen fluxes. Specifically, I found that diel cycles in physical oxygen fluxes were enhanced by up to 300% when metabolism estimates were unreasonable (GPP<0 or ER>0) relative to when metabolism estimates were biologically meaningful (GPP≥0 or ER≥0). This supports previous findings that the free-water oxygen method is often constrained to calm conditions (Rose et al. 2014). However, in addition, it proofs mechanistically that failure of current metabolism models to derive meaningful metabolism estimates is due to the confounding effect of physical oxygen fluxes. Importantly, in unproductive lakes, it is often not clear if temporal variability in metabolism estimates is true or instead simply reflects variation due to physical processes (Beck et al. 2015; Richardson et al. 2016; Giling et al. 2017). Explicitly accounting for physical oxygen fluxes could therefore greatly increase the potential of the freewater-oxygen method to relate whole-lake metabolism to causal factors.

Taken together, rigorous accounting for vertical oxygen fluxes combined with time series filtering could help to more accurately resolve temporal patterns in metabolism, especially during storm events when metabolic signals are masked by transport and mixing of oxygen. During such conditions, GPP and ER may be affected by catchment-derived nutrient and C inputs (MacIntyre et al. 2006; Koch et al. 2012; Sadro and Melack 2012; Klug et al. 2012; Tsai et al. 2008). Revealing such responses would not only greatly reduce the current bias of the free-water oxygen method towards calm conditions, but also improve our understanding of whole-lake greenhouse gas cycling under the perturbing influence of land use activities.

Conclusions

Summary

Based on unique ecosystem-scale experiments and national-scale lake and forest surveys, this thesis demonstrates that N enrichment and forest clearcutting do not affect greenhouse gas emissions from boreal headwaters. This lack of response is because aquatic greenhouse gas cycling involves a large number of processes whose individual responses may offset each other over time and space, or are of minor importance for the ecosystem-scale greenhouse gas budget. For example, significant increases in primary production in response to N enrichment did not significantly decrease CO_2 emissions, emphasizing the modest role of biological C fixation for the CO_2 dynamics of boreal lakes, greatly masked by effects of terrestrial inputs of organic matter. Surprisingly, these inputs did not change in response to forest clearcutting, leaving an important source for aquatic greenhouse gas production unaffected. Even the significantly increased supply of CO_2 and CH_4 in clearcut-affected hillslope groundwater did not leak into streams and lakes, emphasizing the potentially effective role of riparian buffer strips to prevent clearcut-induced pulses of aquatic greenhouse gas emissions. This was even shown at a national scale where CO_2 concentrations in 439 Swedish forest lakes did not vary with the areal percentage of forest clearcuts in their catchments. Together, my experimental and observational findings provide evidence that current forestry practices in Sweden do not affect greenhouse gas emissions of downstream headwaters. Therefore, aquatic greenhouse gas emissions are less likely to confound the climate change mitigation potential of clearcut forestry than initially hypothesized. However, my findings should be extrapolated with caution to other environments. Here, site-specific conditions make my study system representative for systems where clearcutting causes a limited initial impact on catchment hydrology and biogeochemistry. In this regard, my study must be regarded as a forerunner of longer-term experiments that include the whole hillslope-riparian zone-stream-lake continuum to fully evaluate forest clearcut effects on aquatic greenhouse gas emissions.

Besides ecosystem-scale experiments, I call for improved methods and design of monitoring programs to better reveal the mechanisms that act on aquatic greenhouse gas dynamics. I demonstrated that our understanding of fundamental broad-scale controls on lake carbon cycling depends on wether spatially or temporally resolved monitoring data were used. Developing sampling programs that explicitly account for the large spatial and temporal variation of greenhouse gases is therefore critical to advance our mechanistic understanding and predictions of climate and land use effects on aquatic greenhouse gas emissions.

Outlook

Analyses ahead of this thesis

Given the lack of an overall net-response of greenhouse gas emissions from lakes and streams to N enrichment and forest clearcutting, an emerging key question is whether individual processes would respond and, in systems other than the ones studied in this thesis, contribute to significant changes in the ecosystem-scale greenhouse gas budget. Revealing such mechanisms would be essential for extrapolating results from this thesis, restricted to boreal inland waters, to other aquatic ecosystems. A way forward is provided by the free-water oxygen technique. This technique allows us to derive whole-ecosystem metabolism as a source or sink of CO_2 emissions from lakes that potentially responds to land use related N and C inputs. I assessed the existing free-water oxygen technique in terms of its accuracy in unproductive boreal lakes where oxygen dynamics are largely driven by physical transport and mixing of oxygen. My assessment revealed that metabolism estimates can be biased by up- and downwelling of the thermocline, internal waves, lateral advection, atmospheric gas exchange, eddy diffusion and dynamics in the depth of the actively mixing layer. These processes have to be explicitely considered in models to infer accurate metabolism estimates. Most importantly, I recommend to evaluate freewater-metabolism estimates by carefully analyzing dynamics in the thermal structure of the water column and argue for the need of three-dimensional approaches to infer metabolism estimates from free-water oxygen time series in unproductive stratified lakes. I suggest taking advantage of process-based models in physical limnology in order to enlarge the range of conditions under which the free-water oxygen method is currently applicable. I additionally recommend that studies include multiple temperature and oxygen arrays such that the causes of the horizontal flows are understood and to enable spatial averaging.

In future, oxygen probes that have been deployed in all lakes and streams during the clearcut experiment will allow me to calculate whole-ecosystem metabolism and to assess its response to the forest clearcutting. Another analysis ahead of this thesis involves the assessment of clearcut effects during seasons other than the ice-free season I focused on in this thesis. Data on gas concentrations under the lake ice and in streams during spring flood is available and will provide novel insights in the response of annual greenhouse gas emissions to forest clearcutting that may differ from summer responses. In addition, sediment traps were deployed to assess if C sedimentation rates have responded to clearcutting.

Take home questions – from applied science to philosophy

The overall aim of this thesis topic, to evaluate the effect of forestry as a measure to mitigate climate change, is not fully accomplished yet. My thesis has just touched upon the linkages between forests and aquatic ecosystems in terms of their individual metabolic balance and downstream transport and processing of mass and energy. I would therefore like to conclude with an, admittedly, rather speculative view on the biogeochemical couplings between terrestrial and aquatic ecosystems that we are probably just beginning to explore in their full dimension. My bold vision is that the greenhouse gas budget of aquatic ecosystems mirrors the greenhouse gas budget of its catchment throughout cycles of catchment disturbance and recovery (Table 4, Fig. 8). Just as the C balance of forests evolves throughout a rotation period, so could the C balance of downstream aquatic ecosystems. After initial clearcut-induced C losses, younger, more productive forests bind more C than older, less productive forests (Goulden et al. 2011). Yet, they also loose more C to the soil (Högberg et al. 2001; Peichl et al. 2007; Peterson and Lajtha 2013) that is eventually transferred to inland waters acting as vents to the atmosphere (Jones and Mulholland 1998a; Maberly et al. 2013). The opposite may be true in old-growth forests that may bind C more strongly within the terrestrial environment (Luyssaert et al. 2008; Peichl et al. 2007; Czimczik et al. 2006; Wang et al. 2002) and leave less to be processed in and emitted from downstream aquatic systems. Hence, aquatic ecosystems may provide a feedback mechanism that buffers, on a catchment-scale, the forest C balance throughout disturbance-succession cycles. Given that repeated disturbance decrease soil C sequestration (Gough et al. 2008; Noormets et al. 2012), forestry effects on aquatic ecosystems may ultimately depend on the forest disturbance history.

All these hypotheses address exciting unkowns. They hold potential to not just shed new light on the discussion on the efficiency of forestry as a tool to mitigate climate change, but also to open opportunities to evaluate more general phenomena in earth system science suggested by the Gaia hypothesis (Lovelock 1979): the potential of compartments of the earth system to interact with each other in such a way that disturbances in the greenhouse gas balance of one system are counteracted by opposite responses in another tightly connected system, which, at sufficiently large spatial and temporal scales, contributes to keep the global climate in relative balance.

Table 4 Outlook on research questions that address the potential role of inland waters in modifying the effect of clearcut forestry to mitigate climate change.

Applied question	Theoretical consideration
Is the enhanced CO_2 uptake by young forests counteracted by enhanced leakage to and emissions from aquatic systems?	Soil respiration increases with forest productivity. CO_2 emissions from inland waters scale with catchment soil respiration.
How do clearcut effects compare between pristine catchments with primary forest cut compared to catchments with secondary forest cut?	Responses decrease with the number of times an ecosystem has been disturbed due to gradual impoverishment of soil organic matter stocks.
How do greenhouse gas dynamics in inland waters change throughout the rotation period of the catchment forest?	The metabolism of aquatic and terrestrial ecosystems is linked throughout disturbance-succession cycles. Land-atmosphere C exchange is in balance over sufficiently large spatiotemporal scales.

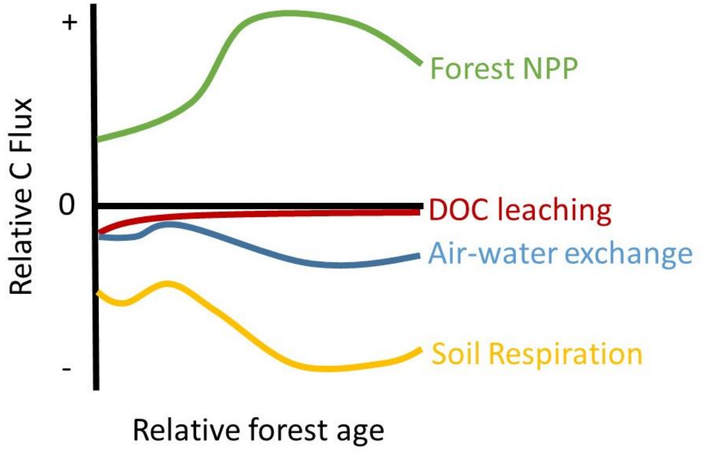

Fig. 8 Hypothesized trends in C fluxes across the terrestrial, aquatic and atmospheric environment during forest succession. Fluxes include forest net primary production (NPP), autotrophic and heterotrophic soil respiration (from Goulden et al. 2011), DOC leaching from forest soils to inland waters (from Peichl et al. 2007), and speculated C exchange across the air-water interface in inland waters. Fluxes are specific to the area of the respective ecosystem.

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Lapptjärn sampling at its best

Epilogue

Rocket Science

by Coco Jet

Intro
Bbm Eb F/A Bbm

Pre-verse
Bbm F
Funding, funding, funding, funding ....

Verse I
   Bbm   F
Another disappointment, another kick-off
thriller
   Bbm   F
Another headless plan, another project
killer
   Bbm   F
Another meeting - no results, another time
for fillers
   Bbm   F
Another research plan delay and no one
watch's the mirror

Pre-chorus
Bbm   C7
Welcome to the forefront of Science
      Bbm   C7   Ab7
The benchmark is set, the goal defined!

Chorus
Bbm   Fm
Is this the world that you had in your
mind?
    Db   C
Is this the progress needed or a hidden
contract signed?
      Bbm   Fm
The entrance card - is your CV
    Eb
a publication record:
Db   C
opening doors to the next degree
Db   C
towards an impact factor 33

Verse II
   Bbm   F
Another ghost co-authorship, another
review to be joined
   Bbm   F
Another flashy title found, another
midnight-powerpoint
   Bbm   F
Another deadline passed, another sample
goes to hell
   Bbm   F
Another course disaster - and where is the
rebell?

Pre-chorus
Bbm   C7
Welcome to the forefront of Science
Bbm   C7   Ab7
The benchmark is set, the goal defined!

Chorus
Bbm   Fm
Is this the world that you had in your
mind?
    Db   C
Is this what really saves the world or does
it make us blind?
      Bbm   Fm
the choice is yours - to play the game or
not
Eb
Rat race for fame
       Db   C
Or funding is given to the next that came
     Db   C
A rocket science record that is pimped with
flames

Solo

Chorus
Bbm   Fm
Is this the world that you had in your
mind?
    Db   C
Is this what really saves the world or does
it make us blind?
      Bbm   Fm
the choice is yours - to play the game or
not
     Eb
or stand up, step back:
   Db   C
allow yourself the time to relax your brain
          Db   C
'cause brilliant ideas don't pop up under
strain

Outro
Bbm Eb F/A