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Ecosystem-atmosphere interactions in the Arctic

Using data-model approaches to understand carbon cycle feedbacks

Efrén López-Blanco, Doctoral Thesis, 2018



Papers included in this volume:

López-Blanco, E., Lund, M., Williams, M., Tamstorf, M. P., Westergaard-Nielsen, A., Exbrayat, J. F., Hansen, B. U., and Christensen, T. R.: Exchange of CO₂ in Arctic tundra: impacts of meteorological variations and biological disturbance, *Biogeosciences*, 14, 4467-4483, 10.5194/bg-14-4467-2017, 2017.

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Using data-model approaches to understand carbon cycle feedbacks

Efrén López-Blanco, Doctoral Thesis 2018

Department of Biosciences, Aarhus University, Denmark

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Greenland Ecosystem Monitoring



Declaration

I declare that this thesis has been composed by myself and has not been submitted for any other degree. The work described is my own, except where otherwise indicated.

Efrén López-Blanco

April 2018

Data sheet

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Abstract:	<p>The terrestrial CO₂ exchange in the Arctic plays an important role in the global carbon (C) cycle. The Arctic ecosystems, containing a large amount of organic carbon (C), are experiencing ongoing warming in recent decades, which is affecting the C cycling and the feedback interactions between its different components. To improve our understanding of the atmosphere-ecosystem interactions, the Greenland Ecosystem Monitoring (GEM) program measures ecosystem CO₂ exchange and links it to biogeochemical processes. However, this task remains challenging in northern latitudes due to an insufficient number of measurement sites, particularly covering full annual cycles, but also the frequent gaps in data affected by extreme conditions and remoteness. Combining ecosystem models and field observations we are able to study the underlying processes of Arctic CO₂ exchange in changing environments. The overall aim of the research is to use data-model approaches to analyse the patterns of C exchange and their links to biological processes in Arctic ecosystems, studied in detail both from a measurement and a modelling perspective, but also from a local to a pan-arctic scale.</p> <p>In Paper I we found a compensatory response of photosynthesis (GPP) and ecosystem respiration (R_{eco}), both highly sensitive to the meteorological drivers (i.e. temperatures and radiation) in Kobbefjord, West Greenland tundra. This tight relationship led to a relatively insensitive net ecosystem exchange (NEE) to the meteorology, despite the large variability in temperature and precipitations across growing seasons. This tundra ecosystem acted as a consistent sink of C (-30 g C m⁻²), except in 2011 (41 g C m⁻²), which was associated with a major pest outbreak. In Paper II we estimated this decrease of C sink strength of 118-144 g C m⁻² in the anomalous year (2011), corresponding to 1210-1470 tonnes C at the Kobbefjord catchment scale. We concluded that the meteorological sensitivity of photosynthesis and respiration were similar, and hence compensatory, but we could not explain the causes. Therefore, in Paper III we used a calibrated and validated version of the Soil-Plant-Atmosphere model to explore full annual C cycles and detail the coupling between GPP and R_{eco}. From this study we found two key results. First, similar meteorological buffering to growing season reduced the full annual C sink strength by 60%. Second, plant traits control the compensatory effect observed (and estimated) between gross primary production and ecosystem respiration. Because a site-specific location is not representative of the entire Arctic, we further evaluated the pan-Arctic terrestrial C cycling using the CARDAMOM data assimilation system in Paper IV. Our estimates of C fluxes, pools and transit times are in good agreement with different sources of assimilated and independent data, both at pan-Arctic and local scale. Our benchmarking analysis with extensively used Global Vegetation Models (GVM) highlights that GVM modellers need to focus on the vegetation C dynamics, but also the respiratory losses, to improve our understanding of internal C cycle dynamics in the Arctic.</p> <p>Data-model approaches generate novel outputs, allowing us to explore C cycling mechanisms and controls that otherwise would not have been possible to address individually. Also, discrepancies between data and models can provide information about knowledge gaps and ecological indicators not previously detected from field observations, emphasizing the unique synergy that models and data are capable of bringing together.</p> <p>Greenland, Arctic, carbon cycle, net ecosystem exchange, photosynthesis, respiration, meteorology, biological disturbance, plant traits, observations, modelling.</p>
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Hiking trip around the Kobbefjord valley, West Greenland. Photo by Efrén López-Blanco

Preface

This thesis is the result of a three-year PhD project conducted both at Department of Biosciences and Arctic Research Centre, Aarhus University, and the School of GeoSciences, The University of Edinburgh, under the supervision of Torben R. Christensen, Mathew Williams, Magnus Lund and Mikkel P. Tamstorf. This PhD project is part of the collaborative effort from both Aarhus University and The University of Edinburgh, framed within the ExEDE (Excellence in European Doctoral Training) project. During the research period, I was based in both institutions, and the results presented here have been produced from a joint collaboration with international collages, all of whom are listed as co-authors of the respective papers.

In a way, I think I have always felt attracted and fascinated with our surrounding nature. Simple sensations such as the fresh breeze close to an open coast, the sound of zigzagging water at the top of the mountains or the hidden wildlife across a dense and humid forest early in the mornings have been somehow very rewarding. But then I got to know Greenland, with its shapes, colours, and a lot of new indescribable emerging feelings... I consider myself privileged to have explored such remote and breath-taking landscapes, almost pristine and untouched, but also to be able to work on what I like most, what make me feel pleased and passionate about. This project gave me the opportunity to travel extensively, one of my hobbies, cultivating new ideas across relevant courses all around the world and performing two exciting field campaigns in Greenland. Science is an enriching path, full of new people to meet, and with challenges awaiting at each corner, sometimes tough at first, but frequently heart-warming at the end. By better understanding how our surroundings work, we will be able to take better decisions in the future. The fact is, beyond what few individuals are still blindly denying, the Earth System is changing in an ongoing warming trend, triggering a series of processes that we do not fully understand yet. I am particularly interested in the exchange of CO₂ between the terrestrial ecosystems and the atmosphere, and how this interplay is affected by feedback changes. Therefore, in this thesis I show some of my findings, emphasizing why it is so important to keep learning from this our beloved planet.

This thesis includes an introduction to the current situation of the Arctic, the complication and difficulties about analysing feedbacks under ongoing warming conditions and the novelty of using model-data approaches. This initial part will be followed by a more specific justification of the proposed PhD thesis, including the overall aim, its specific objectives and an overview of the papers included in the thesis. Hereafter, I include two published papers, one manuscript under review and one submitted covering some of the knowledge gaps spotted in the introduction. Finally, I discuss the implications of each paper for our understanding of Arctic C dynamics, and suggest areas for further research.



View from my room in Zackenberg at 1 am, East Greenland. Photo by Efrén López-Blanco

Acknowledgement

First of all, I would like to thank all my supervisors Torben, Mat, Magnus and Mikkel for their guidance, advice, encouragement and openness throughout this project. Torben, this PhD would not have been possible without you, plus your top-level expertise in the Arctic has been invaluable for me. Mat, you have always been a great source of inspiration; your endless curiosity around the why and hows, but also the pursuit of novelty, are something that definitely have had an impact on me, a legacy. Magnus, always there and happy to help and super effective. I truly appreciate the constructive and stimulating discussions we had and I am looking forward to continue doing it in the future, plus you have been a great conference teammate at AGU. Mikkel, even though you have not been in the science game as much as you would have liked to due to your new deputy roles, your contributions have been extremely valuable and have made my work better and more detailed than it would have been otherwise. Also, your support was always great, anytime I needed something. I feel Torben, Mat, Magnus and Mikkel have been not only excellent scientific mentors, but also people that I could talk to outside the office, which I think it is very important and indispensable, too. I must admit I was a bit curious at first about the dynamics of having four supervisors and how it would work but, right from the start, it turned out to be a successful and very productive combination, each of them contributing with their specific abilities. This PhD is the result of our collaborative effort, and I am extremely grateful to you all!

Likewise, I would like to express my gratitude to the Greenland Ecosystem Monitoring programme (particularly to GeoBasis and its crew!), and to Aarhus University and the University of Edinburgh. The combination of a multicultural environment together with the possibility of geographical mobility and quality of education have made this experience incredibly enriching and fulfilling.

I am especially grateful to Jeff, Darren and Luke for their magnificent support during my stay in Edinburgh. Your contribution to my PhD is unquestionable; you were very helpful and have played an essential role in the modelling context. Thanks also to Marcin, Kirstine, Mikhail, Herbert, Janick, Lumi, Siri, Rune, Jesper and many others from the Arctic Ecosystem Ecology lab and the department of Bioscience in general (Aarhus University) as well as to Paula, Felix, Sophie, Hemanth, Pedro, Yaquing and many other Crewtons from the Attic and the Global Change Ecology lab at the department of GeoSciences (University of Edinburgh).

Last but not least. I send a special warm thank you to my family who have supported me on this motivating journey. I will forever appreciate the freedom of decision they have always granted me, which has allowed me to pursue my dreams and ambitions. I would also like to thank all my seareños friends and Carlos, Serxio, Panda, Jorge, and many others as well as my amazing housemates (specially to Victoria, Alizée and Rachel in Scotland and Gabri, Adriana and Megan in Denmark) for their daily support and positives thoughts. Isa, of course, for you goes one of the biggest thanks; I cannot express in a single sentence how much you have contributed to my well-being along these three years. Thanks a million!



On the way to the Nuuk-Kobbefjord site, West Greenland. Photo by Efrén López-Blanco

List of included papers

- Paper I** **López-Blanco, E.**, Lund, M., Williams, M., Tamstorf, M. P., Westergaard-Nielsen, A., Exbrayat, J. F., Hansen, B. U., and Christensen, T. R.: **Exchange of CO₂ in Arctic tundra: impacts of meteorological variations and biological disturbance**, *Biogeosciences*, 14, 4467-4483, 10.5194/bg-14-4467-2017, 2017.
- Paper II** Lund, M., Raundrup, K., Westergaard-Nielsen, A., **López-Blanco, E.**, Nymand, J., and Aastrup, P.: **Larval outbreaks in West Greenland: Instant and subsequent effects on tundra ecosystem productivity and CO₂ exchange**, *AMBIO*, 46, 26-38, 10.1007/s13280-016-0863-9, 2017.
- Paper III** **López-Blanco, E.**, Lund, M., Christensen, T. R., Tamstorf, M. P., Smallman, T. L., Slevin, D., Westergaard-Nielsen, A., Hansen, B. U., Abermann, J., and Williams, M.: **Plant traits are key determinants in buffering the meteorological sensitivity of net carbon exchanges of arctic tundra**, *Journal of Geophysical Research – Biogeosciences*, 123, <https://doi.org/10.1029/2018JG004386>, 2018.
- Paper IV** **López-Blanco, E.**, Exbrayat, J. F., Lund, M., Christensen, T. R., Tamstorf, M. T., Slevin, D., Hugelius, G., Bloom, A. A., and Williams, M.: **Evaluation of terrestrial pan-Arctic carbon cycling using a data assimilation system**, *Earth System Dynamics Discussions*, 2018, 1-27, 10.5194/esd-2018-19, 2018.

List of additional contributions

- Paper SI** Pirk, N., Mastepanov, M., **López-Blanco, E.**, Christensen, L. H., Christiansen, H. H., Hansen, B. U., Lund, M., Parmentier, F.-J. W., Skov, K., and Christensen, T. R.: **Toward a statistical description of methane emissions from arctic wetlands**, *AMBIO*, 46, 70-80, 10.1007/s13280-016-0893-3, 2017.

My contribution to each paper

- Paper I:** Experimental design, data preparation and analysis, fieldwork, and leading the writing of the paper.
Paper II: Flux modelling analysis and the writing of the paper.
Paper III: Experimental design, data preparation and analysis, fieldwork, and leading the writing of the paper.
Paper IV: Data preparation and analysis as well as leading the writing of the paper.
Paper SI: Data handling and the writing of the paper.

Abstract

The terrestrial CO₂ exchange in the Arctic plays an important role in the global carbon (C) cycle. The Arctic ecosystems, containing a large amount of organic carbon (C), are experiencing ongoing warming in recent decades, which is affecting the C cycling and the feedback interactions between its different components. To improve our understanding of the atmosphere-ecosystem interactions, the Greenland Ecosystem Monitoring (GEM) program measures ecosystem CO₂ exchange and links it to biogeochemical processes. However, this task remains challenging in northern latitudes due to an insufficient number of measurement sites, particularly covering full annual cycles, but also the frequent gaps in data affected by extreme conditions and remoteness. Combining ecosystem models and field observations we are able to study the underlying processes of Arctic CO₂ exchange in changing environments. The overall aim of the research is to use data-model approaches to analyse the patterns of C exchange and their links to biological processes in Arctic ecosystems, studied in detail both from a measurement and a modelling perspective, but also from a local to a pan-arctic scale.

In **Paper I** we found a compensatory response of photosynthesis (GPP) and ecosystem respiration (R_{eco}), both highly sensitive to the meteorological drivers (i.e. temperatures and radiation) in Kobbefjord, West Greenland tundra. This tight relationship led to a relatively insensitive net ecosystem exchange (NEE) to the meteorology, despite the large variability in temperature and precipitations across growing seasons. This tundra ecosystem acted as a consistent sink of C (-30 g C m^{-2}), except in 2011 (41 g C m^{-2}), which was associated with a major pest outbreak. In **Paper II** we estimated this decrease of C sink strength of 118-144 g C m^{-2} in the anomalous year (2011), corresponding to 1210-1470 tonnes C at the Kobbefjord catchment scale. We concluded that the meteorological sensitivity of photosynthesis and respiration were similar, and hence compensatory, but we could not explain the causes. Therefore, in **Paper III** we used a calibrated and validated version of the Soil-Plant-Atmosphere model to explore full annual C cycles and detail the coupling between GPP and R_{eco} . From this study we found two key results. First, similar meteorological buffering to growing season reduced the full annual C sink strength by 60%. Second, plant traits control the compensatory effect observed (and estimated) between gross primary production and ecosystem respiration. Because a site-specific location is not representative of the entire Arctic, we further evaluated the pan-Arctic terrestrial C cycling using the CARDAMOM data assimilation system in **Paper IV**. Our estimates of C fluxes, pools and transit times are in good agreement with different sources of assimilated and independent data, both at pan-Arctic and local scale. Our benchmarking analysis with extensively used Global Vegetation Models (GVM) highlights that GVM modellers need to focus on the vegetation C dynamics, but also the respiratory losses, to improve our understanding of internal C cycle dynamics in the Arctic.

Data-model approaches generate novel outputs, allowing us to explore C cycling mechanisms and controls that otherwise would not have been possible to address individually. Also, discrepancies between data and models can provide information about knowledge gaps and ecological indicators not previously detected from field observations, emphasizing the unique synergy that models and data are capable of bringing together.

Keywords: Greenland, Arctic, carbon cycle, net ecosystem exchange, photosynthesis, respiration, meteorology, biological disturbance, plant traits, observations, modelling.

Dansk sammenfatning

Den arktiske landbaserede CO₂ udveksling spiller en vigtig rolle i den globale kulstofcyklus. De arktiske økosystemer som indeholder store mængder organisk kulstof (C) er udsat for ændringer under den globale opvarmning hvilket har konsekvenser for den interne kulstof dynamik og fordeling af C. For at forbedre vores forståelse af interaktionen mellem økosystemer og atmosfæren i Arktis har et dansk-grønlandsk monitoringsprogram (Greenland Ecosystem Monitoring, GEM) målt CO₂ udvekslingen mellem land og atmosfære igennem mange år. Dette er kombineret med en række målinger på relaterede styrende parametre som samlet kan forbedre vores forståelse af de biogeokemiske kredsløb i Arktis. Selvom GEM med succes har foretaget disse kontinuerlige målinger nu igennem årtier, er disse fortsat forbundet med store udfordringer specielt når det handler om at dække de lange perioder af året uden for vækstsæsonen. Gennem at kombinere disse målinger i felt med økosystemmodeller er det muligt at arbejde med forståelsen af hele års cyklusser af kulstofudveksling og hvordan disse påvirkes af et klima i forandring. Dette studie har som overordnet formål at udnytte kombinationen af feltdata og modeller til at belyse forskellige biologiske processer i de arktiske økosystemer både på lokalt og på det store cirkumarktiske niveau.

I den første del af dette studie (**Paper I**) fandt vi kompenserende responser mellem fotosyntese (GPP) og økosystemets respiration (R_{eco}) som begge er følsomme over for de meteorologiske drivere (dvs. temperaturer, nedbør og stråling) på tundraen i Kobbefjord, Vest-Grønland. Dette nære modsatrettede forhold førte til en relativ lille påvirkning af net økosystemudvekslingen (NEE) på trods af den store variation i temperatur og nedbør henover vækstsæsonen. Dette tundraøkosystem viser sig at være en konsekvent "sink" for C (-30 g C m^{-2}), undtagen i 2011 (41 g C m^{-2}), som var forbundet med et større insektudbrud. I den næste del af studiet (**Paper II**) undersøgte vi det fald i C-sinkstyrken på $118\text{-}144 \text{ g C m}^{-2}$ i det uregelmæssige år 2011, svarende til et tab af $1210\text{-}1470 \text{ tons C}$ fra Kobbefjord-afvandingsområdet som helhed. Dette tab var forbundet med det nævnte insektudbrud. Men vi konkluderede også, at den meteorologiske følsomhed af fotosyntese og respiration fortsat var ens, og dermed kompenserende, uden dog at kunne ikke forklare årsagerne. Derfor anvendte vi i den følgende del af studiet (**Paper III**) en kalibreret og valideret version af Soil-Plant-Atmosphere-modellen til at udforske den helårlige C-omsætning for eventuelt at finde svar på koblingen mellem GPP og R_{eco} . Fra denne undersøgelse fandt vi to hovedresultater. For det første reducerede den kombinerede meteorologiske effekt på vækstsæsonen den fulde årlige C-sinkstyrke med 60%. For det andet kontrollerer planteegenskaberne den observerede kompenserende virkning mellem bruttoproduktion og økosystemets respiration. Da en enkel lokalitet ikke kan være repræsentativ for hele Arktis, undersøgte vi i den sidste del af studiet (**Paper IV**) og med afsæt i **Paper I-III** yderligere den pan-arktiske terrestriske C-omsætning ved hjælp af CARDAMOM data assimileringssystemet. Vores estimer af C fluxes, pools og omsætnings-tider er i god overensstemmelse med forskellige kilder til assimilerede og uafhængige data, både fra Arktis som helhed og fra lokale undersøgelser. Vores benchmarking-analyse med udbredt brug af Global Vegetation Models (GVM) fremhæver, at GVM-modellerne skal fokusere på vegetationens C dynamik og ydeevne, men også tabet til atmosfæren gennem respiration for at forbedre vores forståelse af den interne dynamik i C-omsætningen i Arktis.

Data-model tilgange genererer nye studiemuligheder, så vi kan udforske C omsætning og det som kontrollerer den, på en måde som ikke vil være muligt at adressere individuelt. Afvigelser mellem data og modeller kan også give oplysninger om centrale mangler i vores viden om økologiske indikatorer, der ikke tidligere er registreret i feltobservationerne, hvilket understreger den unikke synergi, som modeller og data i kombination er i stand til at samle.

Introduction

Thesis context: ongoing changes in Arctic ecosystems

Sensitivity of the Arctic to climate change - the situation

The Arctic is changing. There is strong evidence of the ongoing impacts of climate change on terrestrial ecosystems' structure (Anisimov et al., 2007; Post et al., 2009). Likewise, these changes in ecosystem function will not only continue in the future, but it will also result in cascading effects and shifts on key regional biophysical systems and cause global climatic feedbacks (Anisimov et al., 2007; Friedlingstein et al., 2006).

The Arctic terrestrial ecosystem plays a significant role in the global carbon (C) cycle despite the fact that it only contributes to 6-8 % of the global land area (AMAP, 2017; McGuire et al., 2012; van der Molen et al., 2007). Arctic organic C storage has received increased attention in recent years due to large potential for C releases following thaw. Recent reviews have estimated the Arctic terrestrial C pool to be 1400-1850 Pg C, accounting for more than twice of the atmospheric C pool and approximately 50% of the global soil organic C stocks (Hugelius et al., 2014; McGuire et al., 2009; Tarnocai et al., 2009). Most of this C is stored in soils as organic material, typically attributed to the limiting effects of cold temperatures and anaerobic conditions on decomposition (Hobbie et al., 2000; Shaver et al., 2006).

Global air surface temperatures have clearly increased since the middle of the 19th century (Jones and Moberg, 2003). However, there is a further intensified warming tendency in the Arctic (Figure 1), where temperatures have increased almost twice compared to the global average over the last 100 years (AMAP, 2017; Anisimov et al., 2007; Callaghan et al., 2012b; Serreze and Barry, 2011). Measured temperatures show an increase of 0.6 °C per decade since 1985 in latitudes above 62°N (Polyakov et al., 2002). According to the literature, the tendency will continue, and the forecasted Arctic warming is expected to be more prominent in the coming years (AMAP, 2017; Callaghan et al., 2012a; Christensen et al., 2007; Grøndahl et al., 2008; Meltofte et al., 2008). Several studies pointed out that temperatures, precipitation and growing season length

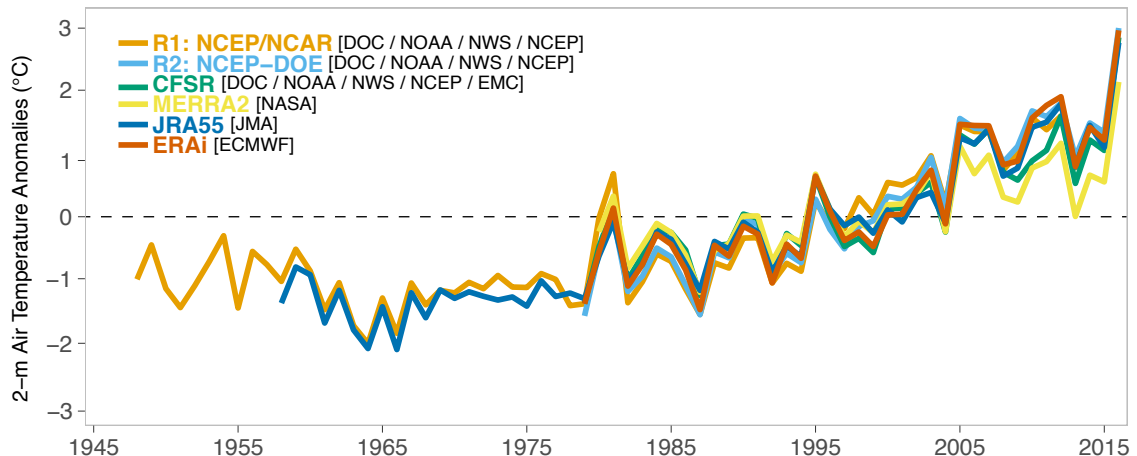


Figure 1. Annual average 2-m temperature anomalies in the Arctic (67°N+) for various reanalysis data sets. Anomalies are calculated from a 1981-2010 baseline. Data source: Zachary Lab (2017).

will likely increase in the Arctic (AMAP, 2017; Bintanja and Andry, 2017; Christensen et al., 2007; Christensen et al., 2004; IPCC, 2013). Given all these circumstances, together with the vast C pool stored in Arctic regions, the response of the C cycle to changes in climate is a major issue of global concern (McGuire et al., 2009; McGuire et al., 2012).

Uncertainty in the Arctic C cycle - the complication

In the Earth system almost everything is connected (Dopheide et al., 2012); between biosphere and atmosphere, complex mechanisms and responses interplay at multiple inter-related spatio- and temporal scales. C cycle processes interact most of the time between them all, allowing feedback loops with intricate and uncertain consequences. The C cycle is inordinately complex; relocation of C between storage pools together with turnover and decomposition rates are constant, but not at the same temporal scale, resulting from a large set of interplaying physical, biological, chemical and geological dynamics. Together these processes regulate the C balance.

The state of the C cycle in the Arctic has implications for feedback mechanisms with the climate system (Elberling et al., 2008; IPCC, 2013) and it is shaped by several actors. The likely increase of future temperature, precipitation, and growing season length may have multiple effects on CO₂ exchange, initiating a series of critical alterations in the ecosystem. On the one hand, an increase of photosynthetic C uptake can be expected by increasing plant productivity due to warmer temperatures (Street et al., 2013), earlier and longer growing seasons (Aurela et al., 2004; Black et al., 2000; Groendahl et al., 2007), enhanced nutrient availability due to more rapid N mineralization in soils (Rustad et al., 2001a), CO₂ fertilisation (Sitch et al., 2008) and shifts in vegetation dynamics such as shrub expansion and greening (Myers-Smith et al., 2011; Myneni et al., 1997).

On the other hand, these increases of C uptake may be compensated by C losses associated with drought stress on plant productivity under warmer conditions (Goetz et al., 2005; Hanis et al., 2015), microbial turnover of soil organic matter during the beginning of the cold season (Commane et al., 2017; Zona et al., 2016) but also during following summer (Helfter et al., 2015; Lund et al., 2012), higher rates of heterotrophic respiration from soil organic matter associated with warmer temperatures (Davidson and Janssens, 2006; Grosse et al., 2011; Webb et al., 2016) and substantial methane emissions (Christensen et al., 1996; Mastepanov et al., 2008; Mastepanov et al., 2012). Likewise, C releases can be boosted by the occurrence of periodic disturbances such as insect outbreaks (Callaghan et al., 2004; Heliasz et al., 2011) and severely burned landscapes (Rocha and Shaver, 2011). Finally, high latitude soil organic C may release large amount of C following permafrost thaw (Koven et al., 2011; Schuur et al., 2015) due to enhanced decomposition rates (McGuire et al., 2009), triggering the likely positive feedback of accelerating the global warming rate. These changes contribute to the increase of permafrost's temperature (Romanovsky et al., 2010) and active layer thickness (Åkerman and Johansson, 2008). These two processes affect simultaneously the (1) vegetation dynamics (Johansson et al., 2013; Myers-Smith et al., 2015), (2) hydrology by wetting-drying mechanisms (Åkerman and Johansson, 2008), (3) export and composition of dissolved organic carbon losses (Olefeldt and Roulet, 2012), (4) nutrient cycling (Rustad et al., 2001b) and (5) topography (Johansson et al., 2013).

As result of the multiple interactions between these processes, a subsequent new state (sign and magnitude) of C balance can be reached. The net ecosystem exchange (NEE) of CO₂ is the balance between

its two major modulating components: Gross Primary Production (GPP; CO₂ uptake) and Ecosystem Respiration (R_{eco}; CO₂ release), but it is also a consequence of the interplay between tissue C allocation, nitrogen (N) uptake and fixation, and decomposition of litter and soil organic matter (Thomas and Williams, 2014). Minor variations in relation to these processes can lead to changes in ecosystem C sink/source functioning, which will likely have an impact on the overall C cycle in the ecosystem (Arndal et al., 2009; Lund et al., 2010; Tagesson et al., 2012; Williams et al., 2000). Our knowledge about the exact scale and sensitivity for a phase-change of these C stocks are, however, limited. Likewise, the full implications of these changes for the regional and global terrestrial carbon dynamics remain unknown (Bloom et al., 2016; Grøndahl et al., 2008). Therefore, an improvement of our process-based understanding of CO₂ exchanges in the Arctic, and their climate sensitivity, is critical (McGuire et al., 2009).

How do we measure and model C cycling in the Arctic? - the novelty

The exchange of CO₂ between terrestrial ecosystems and the atmosphere (NEE) is a key descriptor of ecosystem functioning and it imposes a major influence on the atmospheric CO₂ concentration (Carnieli et al., 2016). Eddy covariance (EC) measurements of NEE has become a widespread technique in recent years for C flux measurements at the landscape scale (Baldocchi, 2003; Lasslop et al., 2012; Lund et al., 2012; Reichstein et al., 2005). Similarly, manual and automatic chambers (MC and AC respectively) are also primary techniques used to measure NEE (Elberling et al., 2008; Mastepanov et al., 2008; Pirk et al., 2017). For example, McGuire et al. (2012) (Supplement 1) have compiled an extensive list including ~250 observations from 120 published articles of NEE across Arctic tundra including EC and chamber methods. On the other hand NEE is frequently gap filled and separated into its two key processes, GPP and R_{eco}, to understand CO₂ flux responses to the environmental forcing (Hanis et al., 2015) using different gap-filling (Falge et al., 2001; Moffat et al., 2007; Papale et al., 2006) and partitioning approaches (Lasslop et al., 2010; Lindroth et al., 2007; Lund et al., 2010; Parmentier et al., 2011; Reichstein et al., 2005; Runkle et al., 2013). Unfortunately, these procedures present inevitable uncertainties in their estimations of C budgets and inconsistencies between approaches (Brändholt et al., 2017; Oikawa et al., 2017; Papale et al., 2006). Further, the gap-filled and partitioned products are not true observations any longer, and additional requirements need to be considered.

While the EC and AC techniques are a widely used flux monitoring approaches, their temporal and spatial coverage is limited. Likewise, the evaluation of underlying ecosystem dynamics only based on NEE and its partitioned gross fluxes is challenging. Further levels of complexity at leaf, canopy and landscape scale is desirable to better understand C related interactions and potential feedback loops. Conveniently, process oriented models have been proven capable of retrieving reasonable estimations of C cycle dynamics in Arctic ecosystems such as NEE (Williams et al., 2000), gross fluxes (Zhang et al., 2018), methane releases (Walter and Heimann, 2000), but also their feedback with permafrost (Koven et al., 2015), snow dynamics (Essery, 2015) and vegetation shifts (van der Kolk et al., 2016). However, future work is required since many biologically mediated C cycle dynamics are inadequately represented in process based modelling (Chapin et al., 2009). Some examples of these mechanisms that are currently very uncertain and unsatisfactory represented in ecosystem models are the 1) allocation of photosynthesised C to growth versus respiration, 2) litter and soil organic matter (SOM) turnover, 3) wintertime decomposition and 4) episodic disturbance events such as fires

and insect outbreaks (Chapin et al., 2009; Hobbie et al., 2000; Sitch et al., 2007). Respiration processes are complex, but they represent key elements to constrain the net C uptake uncertainty.

At coarser scales, regional to global vegetation models (GVMs) can moderately represent vegetation ecosystem processes addressing the structural (i.e. growth, competition, and turnover) and biochemical (i.e. water, carbon, and nutrients cycling) responses to climate variability (Clark et al., 2011; Friend and White, 2000; Ito and Inatomi, 2012; Pavlick et al., 2013; Sitch et al., 2003; Smith et al., 2001; Woodward et al., 1995). However, issues related to inherent differences of model structure, pre-arranged parameters derived from literature, prescribed plant-functional types (PFT) and the use of steady state assumptions contribute to large uncertainties and bias. Likewise, model intercomparison projects demonstrated a lack of consistency in prognostic estimations of terrestrial C dynamics of GVMs (Ahlström et al., 2012; Friedlingstein et al., 2014). Some other evaluation designs such as the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) (Warszawski et al., 2014) focus on the analysis of the vegetation C cycling performance. ISIMIP-related studies found that a large portion of the uncertainties in these GVMs are derived from the lack of understanding of long term C dynamics (i.e. vegetation turnover and soil decomposition) compared to photosynthetic processes (GPP and NPP). These days we find an agreement in literature suggesting that the carbon turnover in land ecosystem is a main uncertain feature of the global carbon cycle (Exbrayat et al., 2018; Friend et al., 2014; Nishina et al., 2015; Thurner et al., 2017). On top of conventional GVMs, new approaches based on Bayesian statistics and optimal parameter sets have been recently developed (Bloom et al., 2016; Bloom and Williams, 2015; Koven et al., 2015). These data-assimilation systems are becoming attractive frameworks to digest the increasing number of re-analysis products (Figure 1) (Dee et al., 2011), remote sensing- and observational-based products (Carvalhais et al., 2014; Hugelius et al., 2013a; Jung et al., 2017), which all are difficult to integrate in traditional GVMs. These model-data fusion approaches, significantly more data constrained frameworks, are suitable candidates to identify issues and bias in GVMs that need to be addressed to decrease errors and uncertainties in their forecasts.

Overall, there is an increasing tendency towards field measurements and model simulations integration to assess the consequences of climate change in the total CO₂ budget. This can be partly achieved by combining (i) ecosystem models to increase mechanistic understanding, (ii) ground plot measurements, and (iii) remotely sensed products. Certainly, model-data approaches are capable to fill important knowledge gaps learning from each other, but there are still opportunities for further enhancements.

Overview of the study area

This thesis makes particular reference to the Nuuk-Kobbefjord site (**Papers I, II, III and IV**), a research station founded under the umbrella of the Greenland Ecosystem Monitoring (GEM) program (Christensen et al., 2017). GEM is an integrated and long-term research monitoring program which seeks to contribute to the basic scientific understanding of Arctic ecosystems and their responses to climatic changes and variability as well as the potential local, regional and global implications of changes in Arctic ecosystems (Christensen and Topp-Jørgensen, 2017). The Nuuk-Kobbefjord site is located in South-west Greenland (64°07' N; 51°21' W), around 16 km from Nuuk, the capital of Greenland (Figures 2a and 2b). Kobbefjord is a low Arctic fen without permafrost in the lowland. Kobbefjord has been subjected to extensive cross-

disciplinary ecological monitoring program since 2007 within the Nuuk Ecological Research Operations (NERO, now integrated in GEM). It has been incorporated to the global data network FLUXNET, and it has been also proposed as associated station within the European research infrastructure ICOS (Integrated Carbon Observation System). The available C related datasets at high temporal resolution provide a unique opportunity to describe and analyse inter-annual variability of C dynamics where extensive environmental ancillary data, plant phenology data and ecological dynamics are also monitored. This infrastructure provides an attractive natural environment to explore C related interactions to the ongoing changes of climate in very sensitive ecosystems.

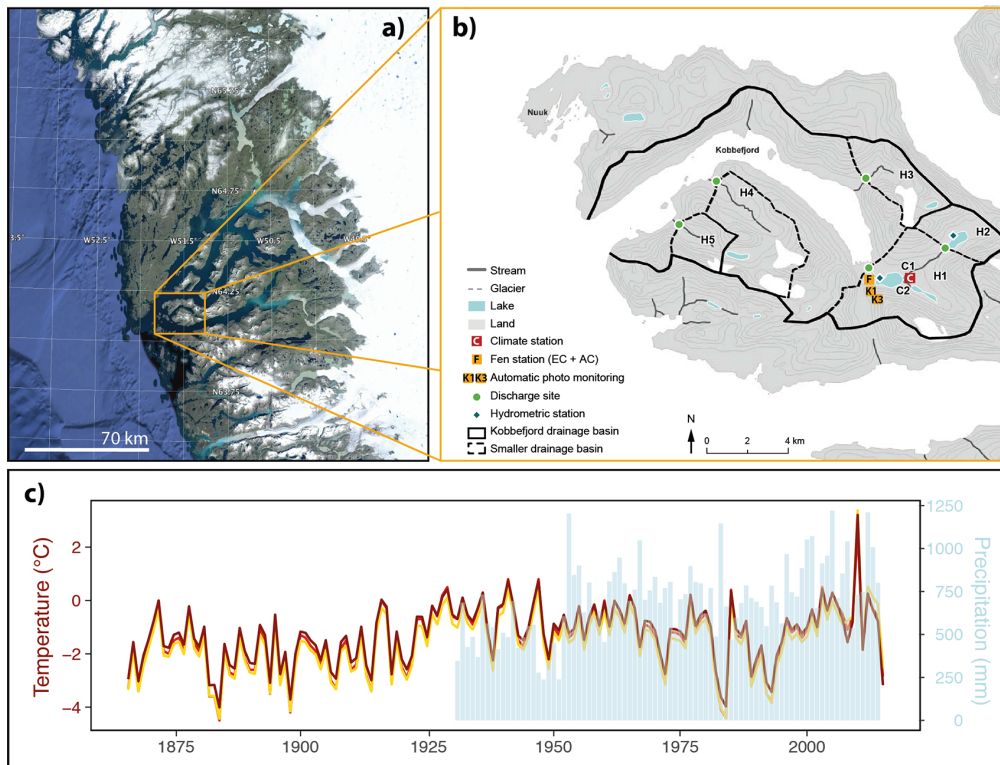


Figure 2. (a) Location of the Nuuk-Kobbefjord area in West Greenland (source: Google Earth Pro). (b) Location of Nuuk-basis instrumentation in the catchment area of Kobbefjord: the climate station, the fen station (including the EC tower and six AC), the automatic cameras (K1, K3) as well as the hydrometric (H1, H2) and diver stations (H3, H4, H5). (c) Time series of temperatures (1866-2015) from Nuuk (yellow line), Kobbefjord-Fen (red line) and Kobbefjord-weather station (orange line) together with precipitations (1931-2015) from Nuuk (light blue bar). The Kobbefjord-Fen and Kobbefjord-weather station are modelled on the basis on the long term data from Nuuk (Cappelen, 2016).

The Nuuk area presented a significant inter-annual variability with a mean annual air temperature of -1.4°C in the 1866-2015 period and a total mean annual precipitation of about 708 mm between 1932 and 2015 (Cappelen, 2016) (Figure 2c). Kobbefjord has experienced a tendency towards warmer and wetter conditions compared the long-time series considered by Cappelen (2016), except for 2011 and 2015. This large meteorological variation from year to year is likely influenced by the complex terrain, this is a coastal area surrounded by three glaciated mountains, all above 1000 m above sea level. Annual variation of the maximum snow depth also extensively fluctuated between winters; for the 2008-2015 period snow oscillated between 0.3-1.4 m of maximum height. However, it is not possible to measure C fluxes across winter seasons yet due

to the harsh conditions and remoteness, and thus it complicates the analysis of C dynamics during the cold season. There is no permafrost documented in the area, although thin lenses may remain until the growing season. The valley is dominated by three eco-types: fen (*Scirpus cespitosus*), heath (*Empetrum nigrum*, *Salix glauca*, *Vaccinium uliginosum*) and copse (*Eriophorum angustifolium*, *Salix glauca*).

Thesis rationale: a better understanding of ecosystem-atmosphere interactions in Arctic ecosystems using data-model approaches

The terrestrial C cycle is currently the least constrained component of the global carbon budget (Bloom et al., 2016; Le Quéré et al., 2013). Large uncertainties remain from poor understanding of the C cycling feedbacks to climate change as well as the magnitude, distribution and dynamics of the major terrestrial C pools. Precise estimations of the state and fluxes of the terrestrial C cycle are problematic; vegetation structure and composition together with soil properties are spatially variable (Carvalhais et al., 2014; Fischer et al., 2008; Tarnocai et al., 2009), and ecosystems in different locations have divergent characteristics. The overall aim of the proposed research is to contribute towards a better understanding of the C exchange patterns and their links to biological processes in Arctic ecosystems using data-model approaches. The research focuses on how C fluxes and stocks are influenced by meteorology, vegetation dynamics, biological disturbances, soil properties and hydrology, studied in detail both from a measurement and a modelling perspective. This thesis pivots over four themes related to each other throughout the presented papers (**Paper I, II, III, IV**): field data and modelling driven analyses, from a local to a pan-Arctic scale (Figure 3). This research covers (i) eddy flux (**Paper I, IV**) and chamber (**Paper I, II**) measurement techniques, (ii) high temporal resolution modelling with parameterization at leaf-level and prediction at canopy-level (**Paper III**), and (iii) a state-of-the-art data assimilation framework applied to the pan-Arctic region (**Paper IV**).

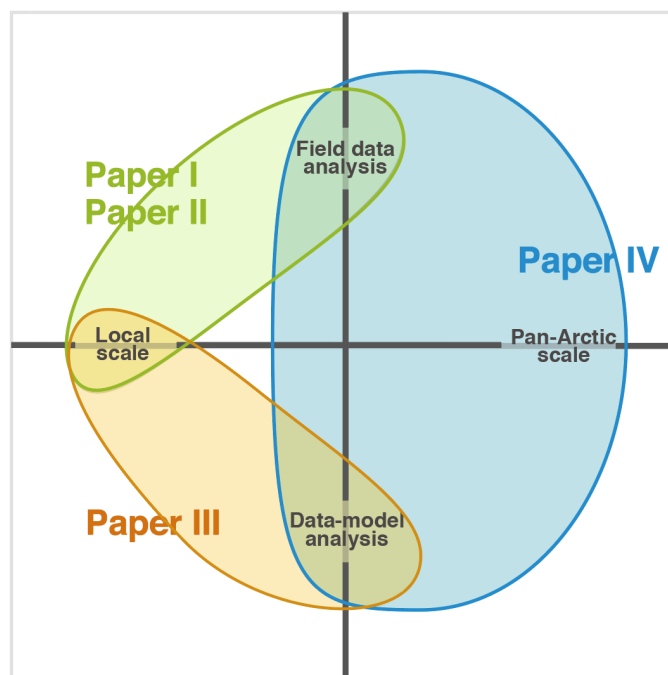


Figure 3. Conceptual diagram of the themes addressed in this PhD project including the papers involved and their inter-relationship and overlaps.

The use of long-term measurements is crucial to improve our understanding of the C exchange balance in the soil-vegetation-atmosphere continuum (Aurela et al., 2004; Christensen et al., 2012; Lafleur et al., 1997; Lund et al., 2012; Parmentier et al., 2011; Zona et al., 2014). Important synthesis processes have led to a compilation of published information regarding C cycling both in a measurement and modelling context. Nevertheless, there is a lack of reference sites from where full measurement-based data are available, documenting the basic full annual carbon fluxes, stocks and the impact of disturbance regimes at the catchment scale. With increasing temperatures, precipitations, and growing season length, tundra systems are expected to increase rates of C cycling, i.e. enhanced productivity (GPP) and respiration losses (R_{eco}). However, little is known about the responses to the meteorological variability by the C uptake and C storage interactions, and the overall influence on the net C uptake. Moreover, the C sink strength can be severely shifted by biological disturbances such as moth outbreaks, challenging the NEE forecast in the Arctic. Moth outbreaks can have extensive consequences for ecosystem productivity (decreased C uptake due to low GPP) and ecosystem functioning (i.e. canopy defoliation and reduction of biomass), leading to an increase of the total C losses (Callaghan et al., 2004; Heliasz et al., 2011; Post and Pedersen, 2008). Focus on analysis based on field observations at a small scale is required to better understand C dynamics. With **Paper I** and **II**, the intention is to elaborate on the information gathered in existing catchment scale studies making use of the extensive monitoring over the past few years under the auspices of the Greenland Ecosystem Monitoring (GEM) program.

Notwithstanding, exclusive field data analyses are insufficient to provide a complete picture of the C cycling at any scale. Field observations remain scarce and fragmented in northern latitudes due to remoteness and harsh conditions (Kwon et al., 2006; Lafleur et al., 2012; McGuire et al., 2012; Poyatos et al., 2013; van der Molen et al., 2007; Westergaard-Nielsen et al., 2013). Therefore, it is challenging to produce a comprehensive full picture of the terrestrial C cycling. The snow season and the delayed effects of wintertime variables such as the snow depth and cover are usually not considered even though these are key controllers of full annual C budgets (Aurela et al., 2002; Commane et al., 2017; Grøndahl et al., 2008; Zona et al., 2016). In addition, the linkages of the competing processes inherent to NEE with C storage in vegetation and soil remain to be fully understood. To better comprehend the dynamics controlling ecosystem respiration, a better understanding is needed in the (i) separation of R_{eco} into autotrophic (R_a ; from living C pools) and heterotrophic respiration (R_h ; from dead C pools) (Hopkins et al., 2013; Reich et al., 2008; Waring and Schlesinger, 1985; Xenakis and Williams, 2014), (ii) carbon use efficiency (CUE) (Bradford and Crowther, 2013; Street et al., 2013), and (iii) C-N relations (Thomas and Williams, 2014). Consequently, **Paper III** incorporates a process-based modelling perspective in order to fill some gaps in the current C exchange knowledge. The intention is to not only simulate the annual C budget from where there is not full annual data available using the Soil-Plant-Atmosphere (SPA) model (Williams et al., 2000; Williams et al., 1996; Williams et al., 2005), but also to take advantage of the knowledge learnt from **Paper I** and **II** to answer questions that otherwise would not have been possible to address individually.

At global scale, GVMs have traditionally been used to assess vegetation C dynamics. However, forward models usually rely on predefined parameters, PFT, steady state assumptions, and different model structures, leading to large uncertainties identified in predictive estimations (Exbrayat et al., 2018; Nishina et al., 2015). Recent important studies have indicated that ecosystem turnover and decomposition are less understood than photosynthetic processes (Carvalhais et al., 2014; Friend et al., 2014) although the degree of uncertainties introduced by each component remains to be quantified. Hence, new techniques are required to benchmark the

performance with regards to ecosystem productivity and turnover from GVMs to pinpoint fixable bias, but also to efficiently assimilate the increasing volume of C related datasets available (Carvalhais et al., 2014; FAO/IIASA/ISRIC/ISSCAS/JRC, 2012; Hugelius et al., 2013a; Thurner et al., 2014). Data assimilation systems (or model-data fusion approaches) are tools developed to be constrained by data, allowing the best possible solution based on the integrated data. Recently, Bloom et al. (2016) produced global C retrievals using the state of the art CARbon DAta MOdel (CARDAMOM) framework but global point of view constrained the choice of soil organic C (SOC) data and the availability of biomass was an issue at high latitudes. The use of Arctic related products is critical to better represent high latitude characteristics such as slow turnover and decomposition processes (Hobbie et al., 2000). Therefore, in **Paper IV** we further evaluate the pan-Arctic terrestrial C cycling using the CARDAMOM data assimilation system, but incorporating new sources of Arctic-related data constraints such an innovative biomass dataset (Carvalhais et al., 2014) and the improved Northern Circumpolar Soil Carbon dataset (NCSCD) (Hugelius et al., 2013b). The CARDAMOM framework in **Paper IV** uses the same core modelling structure for C cycling utilized in **Paper III**, but **Paper IV** also links the field observation analysis back with **Paper I**, establishing also a connection with the observational and local perspective point of views.

Thesis objectives

The overall objective of this thesis is to resolve key uncertainties related to mechanisms driving the net C uptake dynamics and the interplay between photosynthetic inputs, respiratory outputs and changes of C stocks in Arctic ecosystems. This thesis involved field observations (**Paper I, II, III, IV**) and modelling simulations (**Paper III, IV**), both at local (**Paper I, II, III**) and pan-Arctic scale (**Paper IV**). Specifically, the objectives were to:

1. Investigate the impact of the environmental drivers (**Paper I**) and the biological disturbance (**Paper I, II**) over the exchange of CO₂ in Arctic tundra.
2. Investigate the compensatory effect observed and modelled between photosynthesis and respiration losses (**Paper I, III**).
3. Investigate the role of wintertime fluxes over full annual cycles (**Paper III**).
4. Evaluate the terrestrial pan-Arctic C cycle retrievals of the first 15 years of the 21st century and benchmark those retrievals with estimates from extensively used GVMs to pinpoint fixable biases (**Paper IV**).

Overview of thesis papers

The thesis is structured as a series of four papers (plus an additional side project only mentioned, not discussed), which are either published or under review process. The papers are ordered to reflect the progressive steps of the study development. This sometimes result in cross-references and overlap of content,

which is an unavoidable consequence of ensuring that the manuscripts could stand as independent research article. The content and purpose of each paper are outlined below.

Paper I - Exchange of CO₂ in Arctic tundra: impacts of meteorological variations and biological disturbance

This paper analyses the net ecosystem exchange (NEE) of CO₂ in the Nuuk-Kobbefjord site located in West Greenland tundra across eight consecutive snow-free periods. **Paper I** also characterizes the two key modulating components of NEE: gross primary productivity (GPP) and ecosystem respiration (R_{eco}). Our objectives were (i) to explore the uncertainties in NEE gap filling and partitioning, (ii) to determine how C uptake and C storage respond to meteorological variability and (iii) to identify how the environmental drivers affect not only the inter-annual variability, but also the hourly, daily, weekly and monthly variability of C fluxes. We use eddy covariance and auto-chamber data to explore different gap filling and partitioning approaches and to evaluate different sources of uncertainties derived from field measurements. We find that growing season NEE was insensitivity to meteorological variability across the 2008-2015 period. We show that the insensitivity was persistent despite the large variability in temperature and precipitation throughout the growing seasons with the exception of 2011 due to a biological disturbance caused by a moth outbreak (see also **Paper II**). The net CO₂ budget was surprisingly stable compared to the magnitude of variation of GPP and R_{eco}. Interestingly, the meteorological sensitivity of GPP and R_{eco} were similar, and thus compensatory, but we could not explain why.

Paper II - Larval outbreaks in West Greenland: Instant and subsequent effects on tundra ecosystem productivity and CO₂ exchange

This paper synthesises available information about larvae moth outbreaks in Greenland. **Paper II** also assesses the effects of the biological disturbance in the Nuuk-Kobbefjord (**Paper I**) site during 2011 and how this tundra ecosystem responds to the larval attack in the following three years. Our objective was to calculate the effects of the larval outbreak on the ecosystem productivity. We use monitoring data on land-atmosphere exchange of CO₂ from manual close chamber method, vegetation greenness derived from an automatic camera station, and remote sensing imagery to investigate possible historical outbreaks in Kobbefjord and Kangerlussuaq. We find a significant impact on vegetation productivity, with a marked decline in summertime C sink strength of 118–143 g C m⁻². Interestingly, the decrease of C sink strength was counterbalanced during the following years by the likely increase of nutrient turnover rates favouring the plant growth in the 2012-2014 period. Additionally, we show for the first time the potential for using satellite imagery to detect and map insect outbreak events in tundra ecosystems, events that can cause significant impacts on Arctic C dynamics (**Paper I**).

Paper III - Plant traits are key determinants in buffering the meteorological sensitivity of net carbon exchanges of Arctic tundra

This manuscript explores and quantifies the mechanisms that drive the interaction between photosynthesis, respiration and changes in C stocks in the Nuuk-Kobbefjord site. In **Paper I** we concluded that the meteorological sensitivity of photosynthesis and respiration were similar, and hence compensatory, but we could not explain the causes. Therefore, in **Paper III** we target some possible explanations for this behaviour, but we also explore the importance of wintertime in relation to the full annual C budgets. We use a modified, calibrated and validated version of the soil-plant-atmosphere (SPA) model to report independent predictions from observational data presented in **Paper I**. With this model version specific to high-latitude ecosystems we untangle the effects of competing ecosystem processes and their links to plant traits, testing the hypothesis that plant nitrogen and vegetation properties are important controls on the compensatory effect between GPP and R_{eco} . We find three key results in this study. First, similar meteorological sensitivity of GPP and R_{eco} leads to buffered NEE. Second, the winter season reduced full annual C sink strength by 60%. Third, plant traits control the compensatory effect observed (and estimated) between GPP and R_{eco} . We conclude that, even though the combination of data-model approaches helps to explore mechanisms that otherwise would not be possible to address individually, we still need more measurements to better constrain models and to move towards enhanced data-model integrated frameworks.

Paper IV - Evaluation of terrestrial pan-Arctic carbon cycling using a data-assimilation system

This manuscript integrates a range of data (soil organic carbon, leaf area index, biomass, and climate) to determine the most likely state of the high latitude C cycle (C fluxes, pools and transit times) for the first 15 years of the 21st century. In **Paper IV** we use an improved version of the CARDAMOM data-assimilation system, to produce pan-Arctic terrestrial C-related variables without using traditional plant functional type or steady-state assumptions. Our objectives were to (i) present and evaluate the retrievals and uncertainties of the current state of the pan-Arctic C cycle and (ii) benchmark extensively used GVMs to determine whether vegetation transit times biases are derived from productivity or vegetation stocks. We find that the pan-Arctic region was a likely sink of C, weaker in tundra and stronger in taiga, but uncertainties around the respiration losses are still large, and so the region could be a source of C. Moreover, we show that turnover time of vegetation C is poorly simulated in GVMs and is a major component of error in their forecasts. We conclude that more attention to vegetation C stocks and their change over time is required to provide better analytical constraints on the pan-Arctic predictive modelling.

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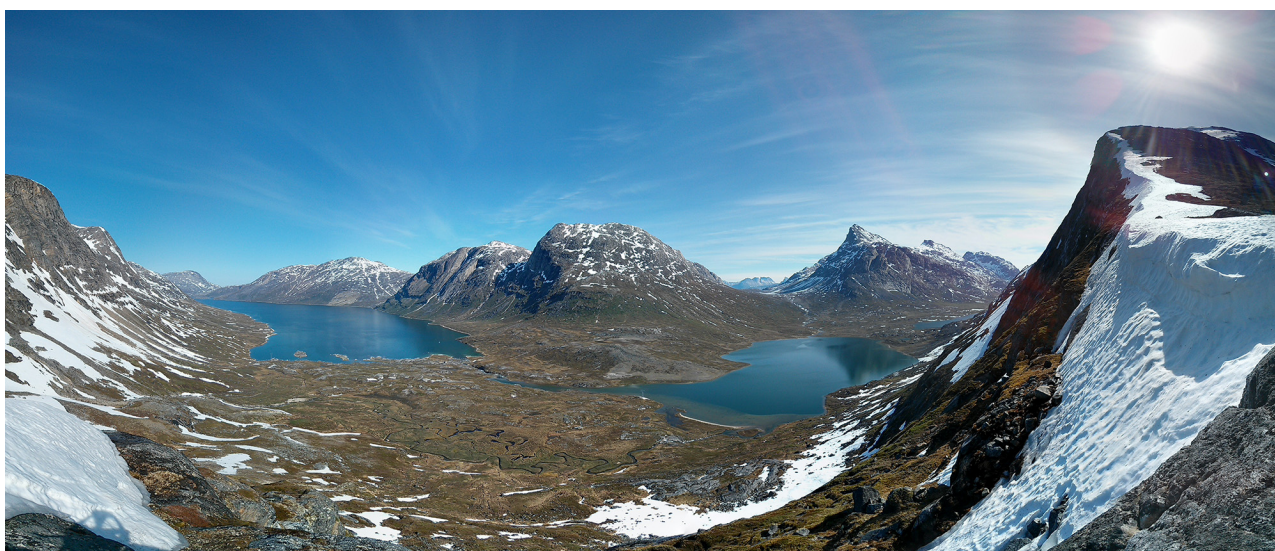
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Paper I

López-Blanco, E., Lund, M., Williams, M., Tamstorf, M. P., Westergaard-Nielsen, A., Exbrayat, J. F., Hansen, B. U., and Christensen, T. R.: **Exchange of CO₂ in Arctic tundra: impacts of meteorological variations and biological disturbance**, *Biogeosciences*, 14, 4467-4483, 10.5194/bg-14-4467-2017, 2017.



Nuuk-Kobbefjord site, West Greenland. 2015 field season. Photo by Efrén López-Blanco



Exchange of CO₂ in Arctic tundra: impacts of meteorological variations and biological disturbance

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Abstract. An improvement in our process-based understanding of carbon (C) exchange in the Arctic and its climate sensitivity is critically needed for understanding the response of tundra ecosystems to a changing climate. In this context, we analysed the net ecosystem exchange (NEE) of CO₂ in West Greenland tundra (64° N) across eight snow-free periods in 8 consecutive years, and characterized the key processes of net ecosystem exchange and its two main modulating components: gross primary production (GPP) and ecosystem respiration (R_{eco}). Overall, the ecosystem acted as a consistent sink of CO₂, accumulating -30 g C m^{-2} on average (range of -17 to -41 g C m^{-2}) during the years 2008–2015, except 2011 (source of 41 g C m^{-2}), which was associated with a major pest outbreak. The results do not reveal a marked meteorological effect on the net CO₂ uptake despite the high interannual variability in the timing of snowmelt and the start and duration of the growing season. The ranges in annual GPP (-182 to -316 g C m^{-2}) and R_{eco} (144 to 279 g C m^{-2}) were > 5 fold larger than the range in NEE. Gross fluxes were also more variable (coefficients of variation are 3.6 and 4.1 % respectively) than for NEE (0.7 %). GPP and R_{eco} were sensitive to insolation and temperature, and there was a tendency towards larger GPP and R_{eco} during warmer and wetter years. The relative lack of sensitivity of NEE to meteorology was a result of the correlated response of GPP and R_{eco} . During the snow-free season of the anomalous year of 2011, a biological disturbance related to a larvae outbreak reduced

GPP more strongly than R_{eco} . With continued warming temperatures and longer growing seasons, tundra systems will increase rates of C cycling. However, shifts in sink strength will likely be triggered by factors such as biological disturbances, events that will challenge our forecasting of C states.

1 Introduction

Quantifying the climate sensitivity of carbon (C) stocks of the terrestrial biosphere is a major challenge for Earth system science (Williams et al., 2005). In the Arctic, organic soil C storage has the potential for very large C releases following thaw (Koven et al., 2011) that could create a positive feedback on climate change and accelerate the rate of global warming. Recent reviews have estimated the Arctic terrestrial C pool to be 1400–1850 Pg C, more than twice the size of the atmospheric C pool (Hugelius et al., 2014; McGuire et al., 2009; Tarnocai et al., 2009) and approximately 50 % of the global soil organic C pool (AMAP, 2011; McGuire et al., 2009). Further, Arctic ecosystems have experienced an intensified warming tendency, reaching almost twice the global average (ACIA, 2005; AMAP, 2011; Callaghan et al., 2012c; Serreze and Barry, 2011). The projected Arctic warming is also expected to be more pronounced in coming years (AMAP, 2011; Callaghan et al., 2012a; Christensen et al., 2007; Grøndahl et al., 2008; Meltofte et al., 2008) and tem-

perature, precipitation and growing season length will likely increase in the Arctic (ACIA, 2005; Christensen et al., 2007, 2004; IPCC, 2007). Given this situation, an improvement in our process-based understanding of CO₂ exchanges in the Arctic and their climate sensitivity is critical (McGuire et al., 2009).

Measuring the interannual C exchange variability in the Arctic tundra is challenging due to extreme conditions and the patchy nature of the landscape linked to microtopography. Different eco-types are linked to different C exchange rates (Bubier et al., 2003). Synthesis studies have found a significant spatial variability in NEE (Lafleur et al., 2012; Mbufong et al., 2014) between different tundra sites (Lindroth et al., 2007; Lund et al., 2010) and also large temporal variability within sites (Aurela et al., 2004, 2007; Christensen et al., 2012; Grøndahl et al., 2008; Lafleur et al., 2012). Minor variations in the key process of photosynthesis (gross primary production, GPP) and ecosystem respiration (R_{eco}) may promote important changes in the sign and magnitude of the C balance (Arndal et al., 2009; Elberling et al., 2008; IPCC, 2007; Lund et al., 2010; Tagesson et al., 2012; Williams et al., 2000). With continued warming temperature and longer growing seasons, tundra systems will likely have enhanced GPP and R_{eco} rates, but long-term data with which to investigate and quantify these responses are rare. Further, the effects on net CO₂ sequestration are not known, and may be altered by long-term processes such as vegetation shifts and short-term disturbances like insect pest outbreaks, complicating the prognostic forecast of upcoming C states (Callaghan et al., 2012b; McGuire et al., 2012). Consequently, there is a need to understand how the C cycle behaves over timescales from days to years and the links to environmental drivers. There is a lack of reference sites in the Arctic from which full measurement-based data are available, documenting carbon fluxes at the terrestrial catchment scales. Here we investigate the functional responses of C exchange to environmental characteristics across eight snow-free periods in 8 consecutive years in West Greenland.

In recent decades, eddy covariance has become a fundamental method for carbon flux measurements at the landscape scale (Lasslop et al., 2012; Lund et al., 2012; Reichstein et al., 2005). Eddy covariance measurements of land-atmosphere fluxes or net ecosystem exchange (NEE), of CO₂ can be gap-filled and subsequently separated into the modulating components of GPP and R_{eco} using flux partitioning algorithms (Reichstein et al., 2005). These techniques are critical for providing a better understanding of the C uptake vs. C release behaviour (Lund et al., 2010), but they also allow for an examination of the environmental effects on ecological processes (Hanis et al., 2015). However, large gaps in the measured fluxes may introduce significant uncertainties in the C budget estimations. Moreover, GPP and R_{eco} estimates can be calculated in different ways. Some algorithms fit an instantaneous temperature–respiration curve to night-time data to calculate R_{eco} and estimate GPP (Lasslop

et al., 2012; Reichstein et al., 2005); others calculate R_{eco} from a light-response curve (Gilmanov et al., 2003; Lindroth et al., 2007; Lund et al., 2012; Mbufong et al., 2014; Runkle et al., 2013). Unfortunately, different interpretations of the flux gap filling and partitioning lead to different estimates of NEE, GPP and R_{eco} as well as undefined uncertainties.

The main objectives of this paper are (1) to explore the uncertainties in NEE gap filling and partitioning obtained from different approaches, (2) to determine how C uptake and C storage respond to the meteorological variability, and (3) to identify how the environmental forcing affects not only the interannual variability, but also the hourly, daily, weekly and monthly variability of NEE, GPP and R_{eco} . The intention of this paper is to elaborate on the information gathered in an existing catchment area under an extensive cross-disciplinary ecological monitoring programme in low Arctic West Greenland, established under the auspices of the Greenland Ecosystem Monitoring (GEM) (<http://www.g-e-m.dk>). Using a long-term (8-year) data set to explore uncertainties in NEE gap-filling and partitioning methods and to characterize the interannual variability of C exchange in relation to driving factors can provide our understanding of land–atmosphere CO₂ exchange in Arctic regions with a novel input. Our overarching hypothesis was that both GPP and R_{eco} would respond positively to warmer and longer growing seasons. However NEE response to warming would be more complex and variable (positive or negative) depending on subtle balances between plant and microbial climate sensitivity.

2 Materials and methods

2.1 Site description

Field measurements were conducted in the low Arctic Kobbefjord drainage basin in south-western Greenland (64°07' N; 51°21' W) (Fig. 1a). The study area is located ~ 20 km SE of Nuuk, the Greenlandic capital. Kobbefjord has been subject to extensive environmental research activities (the Nuuk Ecological Research Operations) since 2007 (<http://www.nuuk-basic.dk>). The lowland site is located 500 m from the south-eastern shore of the bottom of Kangerluarsunnguaq Fjord (Kobbefjord), and 500 m from the western shore of the 0.7 km² lake called “Badesø” (Fig. 1b). Three glaciated mountains, all above 1000 m a.s.l., surround the site. The landscape consists of a fen area surrounded by heath, copse and bedrock. The current fen vegetation is dominated by *Scirpus cespitosus*, whereas the surroundings are dominated by heath species such as *Empetrum nigrum*, *Vaccinium uliginosum*, *Salix glauca* and copse species such as *S. glauca* and *Eriophorum angustifolium* (Bay et al., 2008). Kobbefjord belongs to the “arctic shrub tundra” (bioclimate zone E) according to The Circumpolar Arctic Vegetation Map (CAVM Team, 2003; Walker et al., 2005). This map is

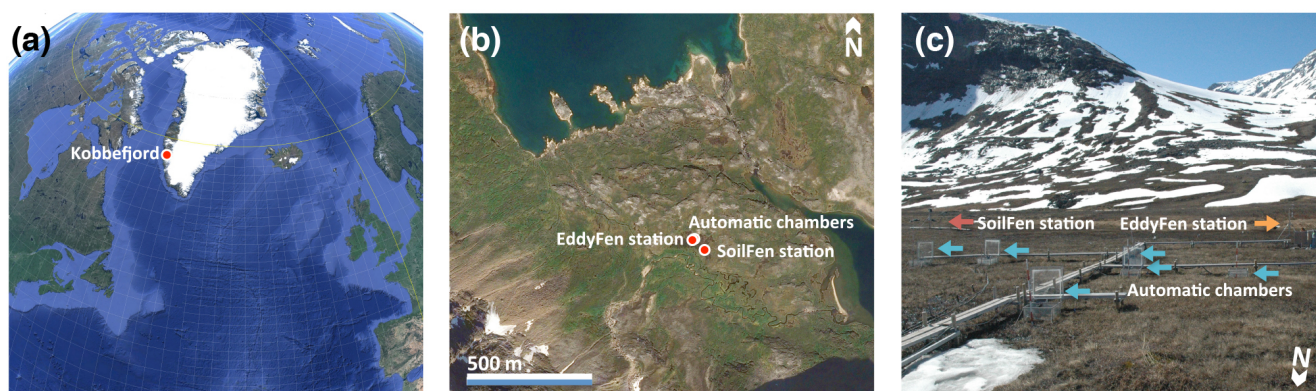


Figure 1. (a) Location of Kobbefjord in Greenland, 64°07' N; 51°21' W (source: Google Earth Pro). (b) Location of EddyFen station, automatic chambers and SoilFen station in Kobbefjord (source: Google Earth Pro, 16 July 2013). (c) Eddy covariance (orange arrow) from EddyFen station, six automatic chambers (light blue arrows) and SoilFen station (pale red arrow) (photo by Efrén López Blanco, 27 June 2015).

based on the summer warmth index (SWI), which is the sum of the monthly mean temperature above 0 °C from May to September and the southernmost bioclimatic zone E has limits of 20–35. In 2010 and 2012, the weather conditions led the area to experience temperatures from warmer climatic zones (SWI ca. 36 and 35 respectively). For the 1961–1990 period, the mean annual air temperature was –1.4 °C and the annual precipitation was 750 mm (Cappelen, 2013). The sunlight hours between May and September range from 14 to 21 h. Outcalt's frost number (Nelson and Outcalt, 1987) indicates that discontinuous permafrost should be present, although no permafrost has been found. Nonetheless, thin lenses of ice may remain until late summer.

2.2 Measurements

We have used eddy covariance (EC) data on NEE, measured during the snow-free period from 2008 to 2015. Measurements typically started around the end of the snowmelt (ca. May–June) and extended until the freeze-in period (between September and October). Once the snow melts, the growing season (i.e. the part of the year when the weather conditions allow plant growth) has been reported as the most relevant period defining both spatial (Lund et al., 2010; Mbufong et al., 2014) and temporal (Aurela et al., 2004; Groendahl et al., 2007; Lund et al., 2012) CO₂ variability. The EC measurements were conducted at the EddyFen station (Fig. 1b and c), located in a wet lowland, 40 m a.s.l. The EC tower is equipped with a closed-path infrared CO₂ and H₂O gas analyser LI-7000 (LI-COR Inc, USA) and a 3-D sonic anemometer Gill R3-50 (Gill Instruments Ltd, UK). The anemometer was installed at a height of 2.2 m, while the air intake was attached 2.0 m above terrain on the steel stand. Adjacent to the EddyFen station, an independent system (Fig. 1b and c) measures round-the-clock net CO₂ fluxes using an automatic chamber (AC) method based on Goulden and Crill (1997).

The transparent chambers, each covering a known surface area of 60 cm by 60 cm, with a height of 30 cm, can be opened and closed by the computer in succession for 10 min every hour. When the chamber closes, a CO₂ analyser (SBA-4, PP Systems, UK) monitors both the CO₂ concentration by a close loop of tubing (further information about the set up can be found in Mastepanov et al. (2013)). Nearly 20 m from the EddyFen station, the automated SoilFen (Fig. 1b and c) station provides environmental variables such as air and surface temperature (Vaisala HMP45C), soil temperature at different depths (Campbell scientific 10ST) and relative humidity (Vaisala HMP45C). Two kilometres from these stations, an automatic weather station provides complementary ancillary data such as short- and long-wave radiation (with a CNR1 instrument), photosynthetic active radiation (with a Kipp & Zonen PAR Lite instrument), precipitation (using an Ott Pluvio instrument) and snow depth (with a Campbell Scientific SR 50). The water table depth data were monitored using a piezometer located next to each of the six autochambers. Finally, a robust daily estimate of the timing of snowmelt was analysed at a pixel level from a time-lapse camera (HP e427) located at 500 m a.s.l. (Westergaard-Nielsen et al., 2013).

2.3 Data handling

2.3.1 Data collection and pre-processing

Data collection from the EddyFen station was performed using Edisol software (Moncrieff et al., 1997). Raw data files were processed using EdiRe software (version 1.5.0.32, R. Clement, University of Edinburgh) calculating the CO₂ fluxes on a half-hourly basis. The flux processing integrated despiking (Højstrup, 1993), 2-D rotation, time lag removal by covariance optimization, block averaging, frequency response correction (Moore, 1986) and Webb–Pearman–

Leuning correction (Webb et al., 1980). For more information, see Westergaard-Nielsen et al. (2013). Ancillary data (air temperature, soil temperature, incoming short-wave radiation, relative humidity, PAR and precipitation) were temporally resampled using R (R Development Core Team, 2015). Time-series-related packages such as *zoo* (Zeileis and Grothendieck, 2005), *xts* (Ryan and Ulrich, 2014) and *lubridate* (Grolemund and Wickham, 2011) were used to get the ancillary data aligned with the flux data on a half-hourly basis.

2.3.2 Generating robust and complete flux time series

Before the CO₂ flux time series were analysed, we applied three different processing techniques (u^* filtering, gap filling and partitioning) to (1) filter the NEE data for quality, (2) fill the NEE gaps and (3) separate NEE into GPP and R_{eco} . The identification of periods with insufficient turbulence conditions (indicated by low friction velocity u^*) is important for avoiding biases and uncertainties in EC fluxes. To control the data quality, the u^* thresholds were bootstrapped by identifying conditions with inadequate wind turbulence according to the method described in (Papale et al., 2006). We subsetted the data to similar environmental conditions, aside from friction velocity: 8 years and 7 temperature classes. Within each year/temperature subset the u^* threshold (5, 50 and 95 % of bootstrap) was estimated at 1000 samples per year. We used the subsequent gap filling and partitioning based on these different subsets to propagate the uncertainty of u^* threshold estimation across NEE, GPP and R_{eco} .

Our gap-filling method was similar to Falge et al. (2001), using the marginal distribution sampling (MDS) algorithm, re-adapted from Reichstein et al. (2005) in REdDyProc (Reichstein et al., 2016). MDS takes into account similar meteorological data available with different window sizes (Moffat et al., 2007). Parallel to this approach, we also gap-filled the original EC NEE data with an independent AC NEE data set (2010–2013). AC data were collected simultaneously with EC data, and so we can use them as a cross check. The EC NEE was predicted from AC NEE based on linear regression models. The subsequent product was gap-filled using the MDS algorithm (REddyProc).

We separated NEE into its two main components (GPP and R_{eco}) using two approaches: (1) the REdDyProc partitioning tool (Reichstein and Moffat, 2014) and (2) a light-response curve (LRC) approach (Lindroth et al., 2007; Lund et al., 2012). A brief description of each flux partitioning method is provided in the Supplement (Eq. S1). After the flux partitioning comparison, we used REdDyProc-based GPP and R_{eco} estimates on further analyses.

2.3.3 Flux uncertainties

In order to estimate the NEE gap-filling uncertainty, we assessed three different sources of uncertainty. First, we addressed the 95 % confidence interval of the EC prediction based on AC data. Second, we inferred the random uncertainty of filled half-hourly values from the spread of variables with otherwise very similar environmental conditions. REdDyProc uses the gap filling to also estimate an observation uncertainty for the measured NEE, by temporarily introducing artificial gaps (T. Wutzler and M. Migliavacca (BGC-Jena), personal communication). Finally, we assessed the effect of uncertainty in the estimate of the u^* threshold. In the u^* -NEE relationship we want to exclude the probably false low fluxes (absolute NEE values) at low u^* . When choosing a lower u^* threshold, the associated lower flux will contribute to the gap filling and the annual sums. Therefore, there is a tendency of a lower absolute NEE associated with lower u^* . The difference between the 5 and 95 % of bootstrap provides a means of the uncertainties based on the u^* filters. We summed and propagated all these sources of uncertainties over time. The GPP and R_{eco} uncertainties include the bias from the one-to-one flux comparison obtained from each model. The micrometeorological sign convection used in this study present uptake fluxes (GPP) as negative, while the released fluxes (R_{eco}) are shown as positive.

2.4 Identifying environmental forcing

Snow- and phenology-related variables such as the end of the snowmelt period and the start, end and length of the growing season are important components that shape the Arctic CO₂ dynamics. In this study we defined the end of the snowmelt period as the day of year when more than 80 % of the surface of the fen was considered snow free; the threshold was chosen in agreement with suggestions previously reported in Hinkler et al. (2002) and Westergaard-Nielsen et al. (2015). For the start, end and length of the growing season (GS_{start} , GS_{end} , GS_{length}); the GS_{start} and the GS_{end} were defined as the first and last days on which the consecutive 3-day NEE average was negative (i.e. CO₂ uptake) and positive (i.e. CO₂ release) respectively (Aurela et al., 2004), while GS_{length} is the number of days between GS_{start} and GS_{end} .

A random forest machine-learning algorithm (Breiman, 2001; Pedregosa et al., 2011) was utilized in a data-mining exercise to identify how the environmental controls affect the variability of NEE, GPP and R_{eco} . Random forest calculates the relative importance of explanatory variables over the response variables. Here, we use photosynthetic active radiation (PAR), air temperature (T_{air}), precipitation (Prec) and vapour pressure deficit (VPD) to explain the response of C fluxes (NEE, GPP and R_{eco}) to climate variability. Each decision tree in the forest is trained on different random subset of the same training data set. The random forest is a classifier that groups explanatory variables and, in each fi-

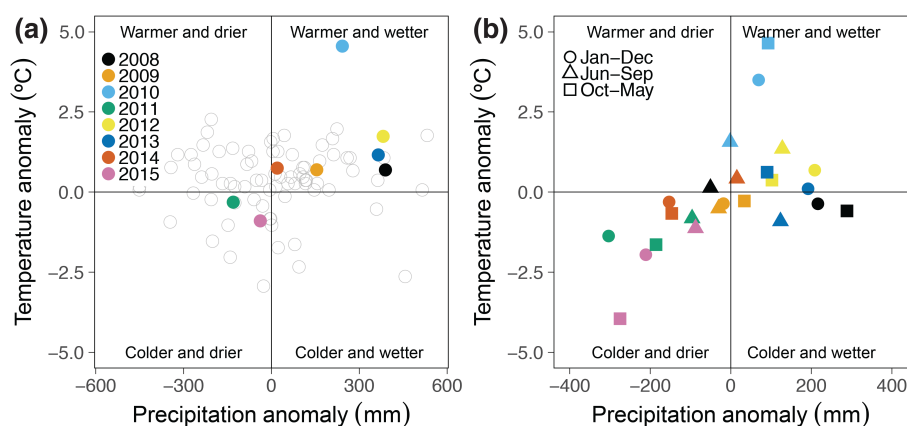


Figure 2. (a) Annual temperature (°C) and precipitation (mm) anomalies of the analysed years (2008–2015) compared to the 1866–2007 time series shown as empty circles (Cappelen, 2016), and (b) within the 2008–2015 period including annual (January to December), warm season (July to September) and cold season (October to May) averages.

nal cluster, a multiple linear regression is built to reproduce fluxes as function of driving factors. This approach has been used to extrapolate maps of biomass (Baccini et al., 2012; Exbrayat and Williams, 2015). This version of random forest sums the relative importance of each variable from 0 up to 100 %, which correspond to the fraction of decision in which a variable is involved to cluster the data. We applied random forests to assess the relative importance of PAR, T_{air} , Prec and VPD at different temporal scales (hourly, daily, weekly and monthly), aggregating them at the timescale indicated and lumping all the years together. (Table S1; Supplement). Moreover, we evaluated the diurnal, seasonal and annual pattern for each explanatory variable (data binned per hour; this is one random forest per hour of the day, day of the year and year respectively). To make sure that these results were not an artefact of the partitioning method that is based on a relationship between hourly R_{eco} and T_{air} , we performed the same analyses using daytime and night-time only hourly NEE as respective proxies for GPP and R_{eco} . Based on these results (Table S2) we concluded that the approach was robust for the Kobbefjord site.

3 Results

3.1 Interannual and seasonal variation of environmental and phenological variables

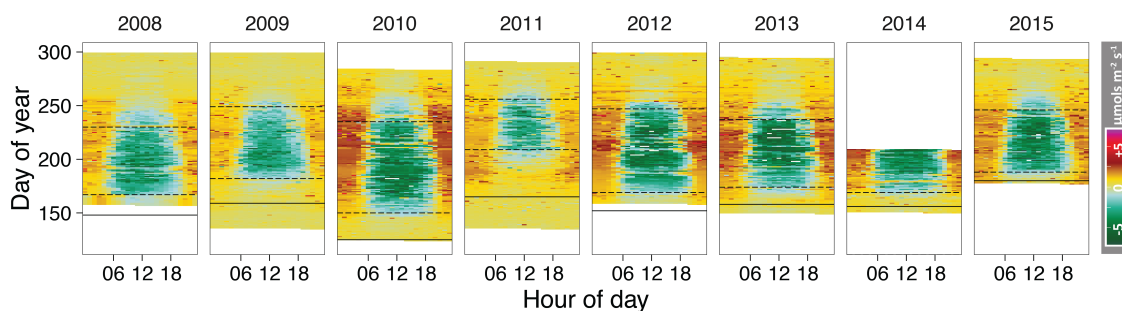
The annual mean temperature documented from Nuuk (-0.5°C) and Kobbefjord (-0.4°C) in the 2008–2015 period were generally warmer compared to the long time series between 1866 and 2007 (Cappelen, 2016; Fig. S1; Supplement), with an annual temperature average of -1.5°C . The 2008–2015 period temperature also exhibited larger variability (coefficients of variation (CV) = 283.3 %) compared to the 1866–2007 period (CV = 79.3 %). The 2008–2015 mean annual temperature measured in Kobbefjord fluctuated be-

tween -1.7°C in 2011 and 3.4°C in 2010. Moreover, the mean annual precipitation documented from the nearby station of Nuuk (885 mm) and the one measured across the 8 year-study in Kobbefjord (862 mm) were both significantly higher than the 1931–2007 mean (689 mm), although less variable (CV = 30.8 and 24.5 %). Overall, 2008, 2009, 2010, 2012, 2013 and 2014 have shown warmer and wetter anomalies while 2011 and 2015 presented colder and drier anomalies compared to the long-term mean (Fig. 2a). Among the 8 study years (Fig. 2b), the temperature and precipitation anomalies in the warm season (June to September) ranged from about -1°C (2011, 2013 and 2015) to $+1.5^{\circ}\text{C}$ (2010) and -96 mm (2011) to about $+125\text{ mm}$ (2012 and 2013). The cold season (October to May) anomalies have shown greater variability compared to the warm season, and 2010, 2012 and 2013 experienced warmer and wetter winters, while 2011 and 2015 were colder and drier.

The end of the snowmelt period and the growing season start and length presented high interannual variability (CVs were 9.5, 9.0 and 19.0 %). Kobbefjord became snow free on DOY 154 (3 June for non-leap years, SD = 15) on average. On average, the site switched from being a source of CO₂ to a sink (GS_{start}) on DOY 175 (24 June, SD = 20), and remained so (GS_{end}) until DOY 241 (29 July, SD = 8.4) (Table 1). The GS_{start} and the $\text{GS}_{\text{length}}$ did not follow a consistent pattern among the analysed years, the growing season timing have fluctuated substantially. The high interannual variability of the GS_{start} correlated with variations in temperature, end of snowmelt period and VPD ($p < 0.05$). The highest variability was observed during 2009–2012. The 2010's $\text{GS}_{\text{length}}$ was nearly twice as long as in 2011. Indeed, GS_{start} in 2011 differs only by 26 days from the GS_{end} in 2010.

Table 1. Summary of the phenology-related variables for the period 2008–2015.

	2008	2009	2010	2011	2012	2013	2014	2015
Maximum snow depth (m)	0.6	1.0	0.3	1.4	1.0	0.6	1.1	1.2
End of snowmelt period (DOY)	148	159	125	165	152	158	156	176
Beginning of growing season (DOY)	167	182	150	209	169	174	169	188
End of growing season (DOY)	230	249	235	256	247	237	–	246
Length of growing season (DOY)	63	67	85	47	78	63	–	58

**Figure 3.** Time series of gap-filled NEE (2008–2015) based on autochamber data (2010–2013) and the MDS algorithm (from REdyProc). Green represents C uptake while the orange–dark-red denotes C release. The solid lines represent the end of the snowmelt period, while the area within the dashed lines represents the period between the start and the end of the growing season.

3.2 Data processing and quality

The NEE gap filling and subsequent partitioning obtained from different approaches exposed inconsistencies in performance and specific uncertainties in the seasonal C budget calculation. During the eight study snow-free periods, data gaps made up 46.5 % of the record from the EddyFen station due to unfavourable micro-meteorological conditions, instrument failures, maintenance and calibration (Jensen and Christensen, 2014) but also due to the rejection of low-quality flux measurements or too low u^* . In 2014 a major instrument failure forced the station to stop measurements in the middle of the season. In 2010 and 2012 there were two more interruptions in the measurements (data gaps of > 20 days), although the problems could be solved before the end of the season. Such prolonged gaps led to unreliable gap-filled NEE estimates. The REdyProc MDS algorithm tended to fill these large gaps with high peaks of respiration at noontime, coercing C uptake underestimation. For this reason, an independent AC NEE data set (2010–2013) was tested to gap-fill EC data (Figs. 3 and S2). The R^2 obtained from the EC-AC correlations was always > 0.70 (2010: $R^2 = 0.80$, $p < 0.001$; 2011: $R^2 = 0.72$, $p < 0.001$; 2012: $R^2 = 0.80$, $p < 0.001$; 2013: $R^2 = 0.84$, $p < 0.001$). By using AC data, the proportion of missing data was reduced to 28 %, and we found that the random uncertainty from the combination of AC and MDS algorithm decreased by 5 % on average. By using the u^* filtering and the AC data together with EC, there was an increase in ~ 6 % in terms of C sink strength. Moreover, the propagated uncertainty in

NEE never exceeded $\pm 1.8 \text{ g C m}^{-2}$, mainly because the error related to u^* filtering was low. Further, we hypothesized that different flux partitioning approaches would lead to different estimates of GPP and R_{eco} . However, the results suggest a relatively good agreement (Fig. 4). There was a higher degree of agreement with regard to GPP ($R^2 = 0.83$) compared with R_{eco} ($R^2 = 0.30$). LRC tended to estimate 12 and 15 % larger GPP and R_{eco} respectively compared to REdyProc.

3.3 Interannual and seasonal variation of CO₂ ecosystem fluxes

Overall, land–atmosphere CO₂ exchange measured for the snow-free periods of 2008–2015, omitting 2011, acted as a sink of CO₂, taking up -30 g C m^{-2} on average (range -17 to -41 g C m^{-2}) (Fig. 5; Table 2). The cumulative NEE showed a characteristic pattern during the measurement period (Fig. 5), with an initial loss of carbon in early spring right after snowmelt (also observed in Fig. 3), followed by an intense C uptake as assimilation exceeded respiratory losses, triggered by increases in temperature, PAR and vegetation growth. This transition point matched the growing season start, when NEE switched from positive values (a net C source) to negative values (a net C sink). Eventually, the ecosystem turned again into a net C source, defining the growing season end. Even with high interannual variability in terms of the end of snowmelt time and growing season start/length (Table 1), the results do not show a marked meteorological effect on the NEE. The ranges in annual GPP (-182 to -316 g C m^{-2}) and R_{eco} (144 –

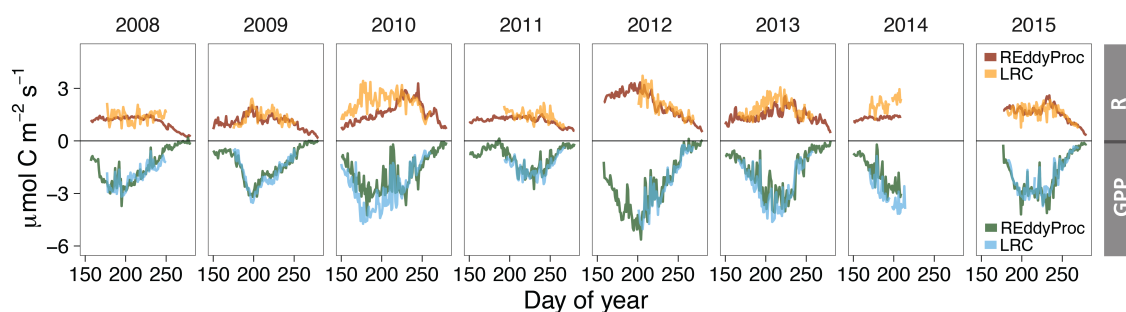


Figure 4. Time series of daily mean GPP (negative fluxes) and R_{eco} (positive fluxes) from 2008 to 2015 calculated by REddyProc (dark green and dark red) and LRC (orange and light blue).

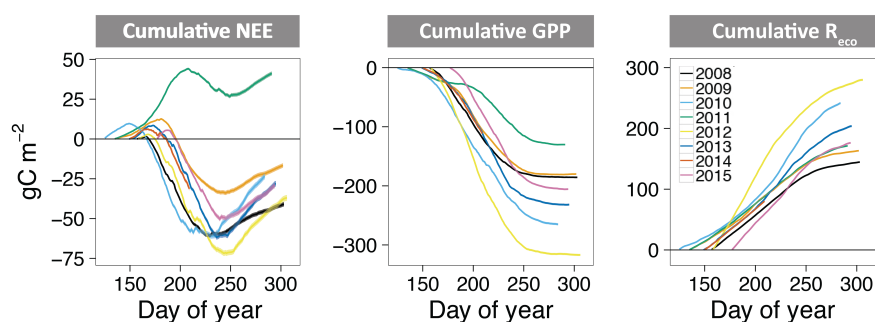


Figure 5. Cumulative NEE, GPP and R_{eco} from 2008 through 2015 including the u^* filtering and random errors.

279 gC m⁻²) (Table 2) were > 5 fold larger and more variable (CVs are 3.6 and 4.1 % respectively) than for NEE (0.7 %). There was a tendency towards larger GPP and R_{eco} during warmer and wetter years (Fig. S3), but there were no warmer and drier years during the study period. The strongest growing season CO₂ uptake occurred in 2012 (NEE = -74.2 gC m⁻²; GS_{length} = 78 days), followed by 2010 (NEE = -70.0 gC m⁻²; GS_{length} = 85 days) (Tables 1 and 2). A lengthening of the growing season did not increase the net carbon uptake in this study. In other words, an earlier end of the snowmelt resulting in a longer growing season length did not lead to a stronger carbon sink.

The anomalous year, 2011, constituted a relatively strong source of CO₂ (41 gC m⁻²) and was associated with a major pest outbreak, which reduced GPP more strongly than R_{eco} . Data on the larvae of the moth *Eurois occulta*, collected from pitfall traps in the surrounding *Salix*- and *Empetrum*-dominated plots, showed a strong peak at the beginning of the 2011 growing season (Lund et al., 2017), coinciding with high NEE and very low GPP (Fig. 4). In 2011 up to 2078 larvae were observed, while in other years only 14 (2008), 82 (2009), 186 (2010), 0 (2012) and 8 (2013) were observed. It is likely that the reduced primary production in the wetland area was a partial response to the *Eurois occulta* outbreak.

The daily aggregated NEE–GPP relationships displayed consistent linear correlation (2008–2015: $R^2 = 0.77$, $p < 0.001$) across the assessed years (Fig. 6a). The linear cor-

relations were weaker in 2010 and 2011. A hysteresis was detected in 2010 (i.e. long growing season with higher R_{eco} in autumn than in spring), while strong C releases were observed in 2011 across June and July. The relation between GPP and R_{eco} , which can be understood as the degree of coupling between inputs and outputs of C and therefore the degree of C sink strength, showed non-linear patterns (Fig. 6b). The curved behaviour is likely because GPP increased more than R_{eco} during early growing season, except for in 2011. Moreover, R_{eco} lagged behind GPP due to (1) the vegetation green-up in the first part of the growing season and (2) the higher respiration rates due to increased biomass in the second part. The years with clearer hysteresis coincide with the years with positive temperature anomalies (i.e. 2010, 2012 and 2013) of the 2008–2015 series. It is worth mentioning the different directions (clockwise or anticlockwise) in the hysteresis observed in these years between June, July and August. The data suggest that the clockwise 2012 hysteresis was due to greater gross C cycling (GPP and R_{eco}) in June and July favoured by warmer conditions, while in 2010 (anticlockwise hysteresis), the higher gross C fluxes were measured in August with warmer and wetter conditions (Fig. S4).

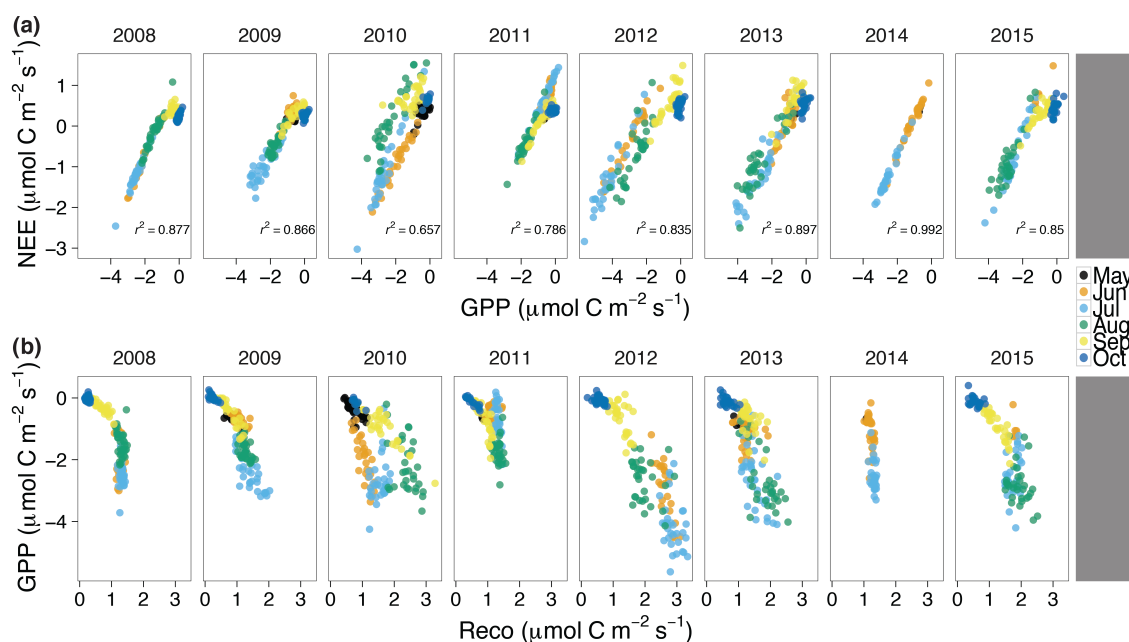
3.4 Environmental forcing

The varied importance of meteorological variables (such as PAR, T_{air} , VPD and precipitation) obtained from random forest at different temporal scales (hourly, daily, weekly and

Table 2. Summary of the measuring periods and the growing season CO₂ fluxes for the period 2008–2015.

	2008	2009	2010	2011	2012	2013	2014	2015
First measurement (DOY)	157	135	124	135	158	149	150	177
Last measurement (DOY)	303	304	282	287	305	295	209*	294
Missing data (%)	57.6	42.3	28.6	35.4	32.3	29.8	44.9*	40.0
NEE in measuring period (g C m ⁻²)	-41.3	-16.9	-24.4	40.7	-37.0	-28.1	-28.7*	-31.5
	±1.4	±1.4	±1.9	±1.3	±1.8	±1.7	±1.1	±1.6
NEE in growing season (g C m ⁻²)	-62.3	-45.9	-70.0	-16.2	-74.2	-69.7	-35.3 ^a	-55.8
Maximum daily uptake (DOY)	195	205	182	230	204	220	192 ^a	199
Maximum uptake (μmol m ⁻² s ⁻¹)	-2.4	-1.7	-3.0	-1.4	-2.8	-2.5	-1.9 ^a	-2.3
Estimated GPP (g C m ⁻²)	-185.5	-181.8	-266.1	-130.6	-316.2	-230.7	-106.8*	-206.1
	±1.4	±1.4	±1.9	±1.3	±1.9	±1.7	±1.1	±1.6
Estimated R _{eco} (g C m ⁻²)	144.2	164.9	241.6	171.3	279.2	202.6	78.1*	174.6
	±1.3	±1.3	±1.8	±1.2	±1.8	±1.7	±1.1	±1.5

Where applicable: ± sum of the autochamber, random and *u** filtering uncertainties. * incomplete growing season data set.

**Figure 6.** Interannual variability between (a) NEE–GPP and (b) GPP–*R*_{eco} relationships. The data were daily aggregated and coloured per month.

monthly) showed differences in behaviour depending on the time aggregation utilized (Fig. 7). PAR dominated NEE and GPP while *T*_{air} correlated the most with *R*_{eco} in hourly averages, whereas *T*_{air} became increasingly important at longer temporal aggregations for all the fluxes (Fig. 7). VPD and precipitation were not as important as the other variables while the use of water table depth in the analysis was discarded due to its very low impact on CO₂ fluxes. In general, NEE and GPP showed similar distributions of importance, reinforcing the linear relationships found between NEE and GPP (Fig. 6). The standard deviation of the variables' importance (across 1000 decision trees) tended to increase at coarser time aggregations.

Changes of environmental forcing (PAR, *T*_{air} and VPD) across diurnal, seasonal and annual timescales reveal patterns of functional responses to C fluxes. The diurnal cycle analyses on hourly data showed the changes in importance between day- and night-time (Fig. 8). NEE and GPP had two predominant variables (*T*_{air} and PAR) determining the variability at daytime. PAR was important at dawn (06:00 WGST) and dusk (20:00 WGST), while *T*_{air} was more important at other times. This performance indicates a threshold response to PAR, and a more continuous response to temperature. On the other hand, *R*_{eco} was mainly driven by *T*_{air} at both night-time and daytime. VPD and PAR had a negligible impact on *R*_{eco}. The seasonal pattern importance showed

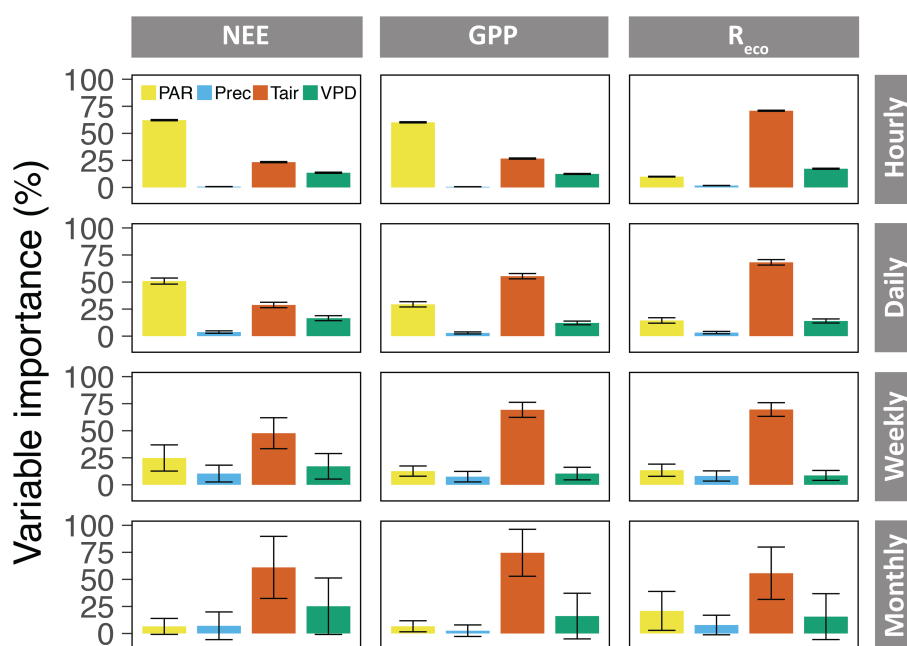


Figure 7. Importance of environmental variables PAR (yellow), T_{air} (orange), Prec (pink) and VPD (green), explaining variability in NEE, GPP and R_{eco} (partitioned by REddyproc) at different temporal aggregations (hourly, daily, weekly and monthly) when all the years were lumped together. Thick bars and error bars represent the mean \pm standard deviation of the importance across 1000 decision trees.

PAR dominating NEE and GPP from early June to early October (Fig. 8), while T_{air} and VPD became more important before and after the snow-free conditions. In terms of CO₂ emission (R_{eco}) the pattern is less clear and noisier, although T_{air} appeared to be the most important variable. Finally, the annual pattern exposes a performance in line with previous results; i.e. PAR dominated NEE and GPP while R_{eco} was more sensitive to variations of T_{air} . Interestingly, the random forest analysis revealed a decrease in PAR's importance in 2011, the same year in which the sharp decrease in C sink strength was exposed.

4 Discussion

4.1 Data processing and quality

The NEE gap filling and subsequent partitioning into GPP and R_{eco} are needed to understand the CO₂ flux responses to the environmental forcing. However, these procedures expose unavoidable uncertainties in the seasonal C budget calculation (Table 2) and partial inconsistencies between approaches (Fig. 4). In this study, we used an MDS gap-filling technique, an enhancement to the standard look-up table. Both methods have shown a good overall performance compared to other procedures such as non-linear techniques or semi-parametric models but slightly inferior to artificial neural network (Moffat et al., 2007). However, the MDS gap filling alone introduced NEE estimates out of range across the

two extensive gaps in 2010 and 2012 (Fig. S2). Quantifying the uncertainty introduced by measurement gaps is complex (Falge et al., 2001; Moffat et al., 2007; Papale et al., 2006). One possibility would be a sensitivity analysis of time series with artificially introduced gaps (Dragomir et al., 2012; Pirk et al., 2017). However, the choice of gap length and position is difficult and would render uncertainty to the uncertainty assessment itself. Instead, we used the EC prediction based on independent autochamber (AC) measurements between 2010 and 2013. The agreement between EC and AC was always $R^2 > 0.72$ and $p < 0.001$, and the 95 % confidence intervals of the predictions were reported together with the resulting uncertainties (Table 2). Although the AC data itself incorporated a new source of uncertainty in the calculations, we consider this method to be less weak than an unreliable gap-filling estimate. We used the AC as platform with which to decrease the gap length and the total random uncertainty (Aurela et al., 2002) before the MDS algorithm was applied. AC was used together with MDS and was never used as an independent gap-filling procedure.

The NEE partitioning obtained from REddyProc and LRC suggests a relatively good agreement in model performance. The one-to-one comparison between different approaches found a better agreement with regard to GPP compared to R_{eco} . In this analysis, REddyProc produced smoother R_{eco} estimates compared to the noisier GPP estimates, whereas the LRC results were the other way around. This is mainly because measurement noise goes into GPP for the REddyProc method, and into R_{eco} for the LRC method. RED-

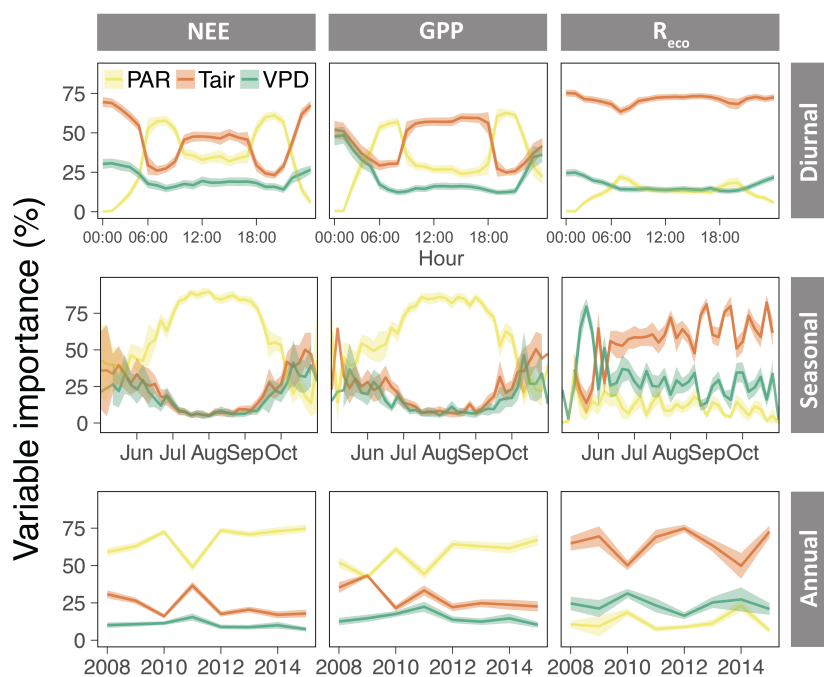


Figure 8. Diurnal, seasonal and annual importance of environmental variables PAR (yellow), T_{air} (orange), and VPD (green), explaining variability in NEE, GPP and R_{eco} . Thick lines and shading represent the mean \pm standard deviation of the importance across 1000 decision trees.

dyProc retrieves positive GPP values, whereas the LRC method results in negative R_{eco} values. Both scenarios are not fully convincing, although it is not straightforward as to how they should be treated. Removing all positive GPP/negative R_{eco} values would risk removing only one side of the extremes. Besides night-time-based (REddyProc) and daytime-based (LRC) partitioning approaches, several implementations have been proposed to improve the algorithm's performance. Lasslop et al. (2010) has modified the hyperbolic LRC to account for the temperature sensitivity of respiration and the VPD limitation of photosynthesis. Further, Runkle et al. (2013) proposed a time-sensitive multi-bulk flux-partitioning model, where the NEE time series was analysed in 1-week increments as the combination of a temperature-dependent R_{eco} flux and a PAR-dependent flux (GPP). However, it remains uncertain as to under which circumstances each partitioning approach is more appropriate, especially in the boundaries between low- and high-Arctic due to the lack of dark night during polar days (when light is not a limiting factor for plant growth). Since there are few methods with an unclear precision, an evaluation study on the effect of using different partitioning approaches along latitudinal gradients would be very beneficial to assessing the suitability for each method.

4.2 Interannual and seasonal variation of CO₂ ecosystem fluxes

The balance between the two major gross fluxes in terrestrial ecosystems, photosynthetic inputs (GPP) and respiration outputs (R_{eco}), displayed larger temporal variability than did NEE. These results suggest that both GPP and R_{eco} were strongly coupled and sensitive to meteorological conditions such as insolation and temperature (Figs. 7 and 8). Interestingly, the tendency to warmer and wetter conditions led to greater rates of C cycling associated with larger GPP and R_{eco} (Fig. S3). This result does not entirely coincide with Peichl et al. (2014), even though they performed a similar analysis for a Swedish boreal fen. This finding points towards the complexity in the response of wetland ecosystems towards changing environmental conditions. The response is dependent on many things, such as hydrological settings, and these differ between sites. In this study, larger rates of C uptake (GPP) were linked to larger rates of C release (R_{eco}), with the exception of the anomalous year 2011. The relative insensitivity of NEE to meteorological conditions during the snow-free period could be the result of the correlated response of ranked cumulative GPP and R_{eco} (Fig. 5) (Richardson et al., 2007; Wohlfahrt et al., 2008). This site likely receives more precipitation than many other tundra ecosystems and has no permafrost; thus the NEE response to climate could be less variable. However, as Kobbefjord is located in a coastal area, it is not surprising that it receives high pre-

precipitation, and other ecosystems such as coastal blanket bogs often receive even more precipitation without a clear impact of drought effect on the NEE sensitivity (Lund et al., 2015). Furthermore, permafrost adds another layer of complexity to the C dynamics (Christensen et al., 2004; Koven et al., 2011; Schuur et al., 2015). Although some studies showed similarities of CO₂ fluxes in various northern wetland ecosystems with and without permafrost (Lund et al., 2015), permafrost has a strong influence on the hydrology of peatlands (Åkerman and Johansson, 2008), and therefore their topography and distribution of vegetation (Johansson et al., 2013). Especially in the context of climate warming permafrost thaw can cause large changes to the ecosystems. Further, this study agrees with Parmentier et al. (2011) and Lund et al. (2012), who suggested that a longer growing season does not necessarily increase the net carbon uptake. Here a more negative NEE indicated a stronger C sink (i.e.) in 2012 compared to 2010. Parmentier et al. (2011) hypothesized that this behaviour is due to site-specific differences, such as meteorology and soil structure, and that changes in the carbon cycle with longer growing seasons will not be uniform around the Arctic. Thus, the effects of climate change on the tundra C balance of are not straightforward to infer.

NEE measured at Kobbefjord from 2008 to 2015 indicates a consistent sink of CO₂ (within a range of -17 to -41 g C m⁻²) with exception of the year 2011 ($+41$ g C m⁻²) (Table 2). The year 2011, associated with a major pest outbreak, reduced GPP more strongly than R_{eco} (Fig. 5) and Kobbefjord turned into a strong C source within an episodic single growing season. The return to substantial cumulative CO₂ sink rates following the extreme year of 2011 shows the ability of the ecosystem to recover from the disturbance (Lund et al., 2017). Indeed, the ecosystem not only shifted back from being a C source to a C sink, but it also changed rapidly from one year to the next. Thus we found evidence in Kobbefjord of ecosystem resilience to the meteorological variability, similar to other cases described in other northern sites (Peichl et al., 2014; Zona et al., 2014). Only a few reference sites have reported similar decreases in net C uptake, but in no case as large as the one observed here. Zona et al. (2014) described an effect of delayed responses to an unusual warm summer in Alaska. Their results suggested that vascular plants, which have enhanced their physiological activity during the warmer summer, might have difficulties readapting to cooler, but not atypical, conditions, which have provoked a significant decrease in GPP and R_{eco} the following year. In their study, the ecosystem returned to be a fairly strong C sink after 2 years, suggesting strong ecosystem resilience. Moreover, Hanis et al., 2015 have reported comparable C sink–C source variations in a Canadian fen within the growing season due to changes in the water table depth. Drier and warmer than normal conditions have triggered an increase in C source strength. Finally, during an extensive outbreak of autumn and winter moths in a sub-arctic birch forest in Sweden, Heliasz et al. (2011) observed

a similar decrease in net sink of C (most likely due to weaker GPP) across the growing season. However, the C source strength (NEE = 40.7 g C m⁻²) found in 2011 at Kobbefjord was higher compared to these other cases. To our knowledge, such abrupt disturbance concerning C sink strength in Arctic tundra has not been previously reported, excluding severely burned landscapes (Rocha and Shaver, 2011).

A combination of different factors could have led to the sharp change in C balance observed between 2010 and 2011, both physical and biological. The year 2010 had the warmest mean annual temperature (3.4 °C compared to the -0.4 °C mean annual temperature for 2008–2015) and the warmest mean wintertime temperature (-2.7 °C compared to the -6.79 °C mean for 2008–2015) (Fig. 2a). These climatic conditions generated the thinnest (maximum daily snow depth of 0.3 m compared to an average of 0.9 m) (Table 1) and shortest-lasting snowpack. Consequently, 2010 had the longest growing season (85 days) and very high growing season C uptake (-70 g C m⁻²). Increases in temperature can lead to high respiration rates during early winter (Commene et al., 2017; Zona et al., 2016) but also during the following summer (Helfter et al., 2015; Lund et al., 2012), which is related to soil temperature and snow dynamics. Further, in Kobbefjord the year 2011 had one of the lowest mean annual temperatures and mean wintertime temperatures (-1.7 and -6.1 °C respectively), which created the thickest (maximum daily snow depth of 1.4 m) and the longest-lasting snowpack, leading to the shortest growing season for the study period (only 47 days). According to Lund et al. (2012), soils will be insulated from low temperatures when below thick snowpack, which acts as a lid and prevents R_{eco} from being released to the atmosphere until the snowmelt period. Finally, an outbreak of larvae of the noctuid moth *Eurois occulta* occurred in 2011, overlapping the observed abrupt decrease in C sink strength. Although we cannot provide a quantification of change attributed to meteorological variations and biological disturbances, there is evidence showing that the moth outbreak could partially have decreased the C sink strength in Kobbefjord. In an undisturbed scenario, the meteorological conditions in 2015, colder and dryer than the mean 2008–2015 period (Fig. 2) but similar to 2011, would have stimulated similar behaviours in terms of C fluxes. However, the cumulative fluxes in 2015 (Fig. 5) followed analogous patterns compared to other years. This evidence agrees with the literature (Callaghan et al., 2012b; Lund et al., 2017) on the fact that tundra systems can fluctuate in sink strength influenced by factors such as episodic disturbances or species shifts, events which are very difficult to predict.

4.3 Environmental forcing

Our data indicate that the importance of the main environmental controls (radiation and temperature) for C fluxes did vary across diurnal, seasonal and annual cycles, but also between time aggregations. The hourly variability of NEE and

GPP (Figs. 7 and 8) was mostly dependent on PAR because of the threshold nature on radiation control on GPP. Overall, the results indicate that environmental factors that can change rapidly such as PAR will have a high influence on short timescales (Stoy et al., 2014). The increased importance of PAR at 08:00 and 20:00 h WGST coincides with the sharp gradient in light at dawn and dusk (Fig. 8). The control of PAR on GPP is not a new finding itself, but the random forest approach helps to quantify its importance. There is no GPP at night, and therefore there will be a strong increase/decrease in GPP at dawn/dusk. The seasonal pattern also showed that radiation is the single main driver for NEE and GPP between early June and early October, supported by the longer daytime. Further, PAR appeared to be a limiting factor for annual NEE in 2011, increasing further the complexity around this anomalous year. These results agree with the literature (Groendahl et al., 2007; Stoy et al., 2014), suggesting that the uptake of CO₂ is partially controlled by radiation for the photosynthetic physiology at the leaf scale. Arctic plants are usually well adapted to environments with low light levels, reporting near-maximum rates ranging from 10 to 25 °C (Oechel and Billings, 1992; Shaver and Kummerow, 1992).

Photosynthesis is restricted by low temperature, so enzymatically driven processes such as carbon fixation are more sensitive to low temperature than the light-driven biophysical reactions (Chapin et al., 2011). In this paper the daily, weekly and monthly aggregated variability of C fluxes was primarily linked to T_{air} . Moreover, the random forest analyses revealed a strong diurnal pattern with a marked contribution of T_{air} to variations in NEE and GPP (both at night-time and between 08:00 and 18:00 h WGST). These results agree with Lindroth et al. (2007), who recognized T_{air} as the key driver of NEE seasonal trends in northern peatlands. However, in this analysis both NEE and GPP had similar responses to common environmental forcing, contrary to the results in Reichstein et al. (2007). In order to circumvent the potential circularity conflicts based on the use of partitioning products, we filtered daytime NEE (true GPP) and night-time NEE (true R_{eco}), obtaining very similar results (Table S2). Further, our data also suggest that R_{eco} is often dominated by air temperature. The patterns observed here are in agreement with findings on plant respiration dynamics (Heskel et al., 2016; Lloyd and Taylor, 1994; Tjoelker et al., 2001).

In this study, environmental drivers related to water availability such as VPD and precipitation were not found to be as influential as other assessed variables. We did not find significant relationships between CO₂ fluxes and the water table depth. Thus, there was no apparent water limitation on carbon dynamics during the 8-year period. However, the complex interactions based on changes in temperature and soil moisture particularly over full annual cycles and for sites with permafrost, should be further explored. Our results contrast with Strachan et al. (2015), who described water table depth as an important driver regulating the CO₂ balance, and

others, who found that CO₂ emissions increase during dry years due to increased decomposition rates and a reduction in GPP (Aurela et al., 2007; Lund et al., 2007; Oechel et al., 1993; Peichl et al., 2014), whereas other sites act as sinks during relatively wet years (Lafleur et al., 1997). The fen in Kobbefjord is probably quite resistant to droughts since it is fed with water from the surroundings.

5 Conclusions

We have analysed eight snow-free periods in 8 consecutive years in a West Greenland tundra (64° N) focusing on the net ecosystem exchange (NEE) of CO₂ and its photosynthetic inputs (GPP) and respiration outputs (R_{eco}). Here, the NEE gap filling exposed inherent uncertainties in the seasonal C budget calculation, but there were also inconsistencies between the flux partitioning approaches used. We find that Kobbefjord acted as a consistent sink of CO₂ during the years 2008–2015, except 2011, which was associated with a major pest outbreak. The results do not show a marked meteorological effect on the net C uptake. However, the relative insensitivity of NEE during the snow-free period was driven by the correlated, balancing responses of GPP and R_{eco} , both more variable than NEE and sensitive to temperature and insolation. In this paper we show a tendency towards larger GPP and R_{eco} during wetter and warmer years. The anomalous year 2011, affected by a biological disturbance, constituted a relatively strong source of CO₂ and reduced GPP more strongly than R_{eco} . A novel analysis assessing the changes of environmental forcing across diurnal, seasonal and annual timescales unmasked patterns of functional responses to C fluxes.

Despite the fact that we analysed an 8-year data set, the results do not provide a complete picture due to the lack of year-round data (Grøndahl et al., 2008). The snow season should be taken into account for a comprehensive understanding of complete C budget (Aurela et al., 2002; Commane et al., 2017; Zona et al., 2016) and the delayed effect of wintertime-based variables such as snow depth or snow cover on the C fluxes. Because some studies have suggested that GPP and R_{eco} increase with observed changes in climate and NEE trends remain unclear (Lund et al., 2012), it is challenging to produce strong evidence while the data remains scarce and fragmented. Hence, there is a need for increased efforts in monitoring Arctic ecosystem changes over the full annual cycle (Euskirchen et al., 2012; Grøndahl et al., 2008). Future work is also required with C flux modelling in order to explore process-based insights of C exchange balance in the Arctic tundra and the interactions of photosynthesis and R_{eco} with changes in C stocks.

Data availability. Measurement data from the Greenland Ecosystem Monitoring (GEM) programme are freely available from the GEM database (<http://data.g-e-m.dk>). Post-processed data

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and scripts are available from the authors upon request (elb@bios.au.dk).

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Author contributions. EL-B, ML, MW, TRC and MPT designed the experiment. Data preparation and analysis were primarily performed by EL-B with contribution from ML (eddy covariance data processing, data quality control and LRC partitioning), MW and TRC (experimental set up), BUH (data gathering from Nuuk Ecological Research Operations, GeoBasis), AW-N (daily estimate of the timing of snowmelt) and J-FE (random forest approach). EL-B prepared the manuscript with active contributions from all co-authors.

Competing interests. The authors declare that they have no conflict of interest.

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Supplement of

Exchange of CO₂ in Arctic tundra: impacts of meteorological variations and biological disturbance

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Equations S1: Flux partitioning

The separation of NEE into its two main components (GPP and R_{eco}) was achieved applying two approaches: (1) the REddyProc partitioning tool (Reichstein et al., 2016) and (2) a light response curve (LRC) approach (Lindroth et al., 2007; Lund et al., 2012). REddyProc uses the measured night-time NEE as R_{eco} , assuming GPP close to zero. This partitioning is based on the exponential regression of night-time respiration with temperature using the Lloyd-Taylor-Function (Lloyd and Taylor, 1994):

$$R_{eco}(t) = R_{ref}(t)e^{E_0(1/(T_{ref}-T_0))-(1/(T_{air}(t)-T_0))} \quad (1)$$

where R_{ref} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the based respiration at the reference temperature (set here to 10°C), E_0 ($^\circ\text{C}$) is the temperature sensitivity, T_{air} ($^\circ\text{C}$) is the air temperature and T_0 is kept constant at -46.02°C as in Lloyd and Taylor (1994). A combined threshold of current solar radiation and potential radiation (based on exact solar time, latitude and longitude) selects night-time. REddyProc estimates temperature sensitivity E_0 from short-term periods, and the reference temperature R_{ref} based on this short-term temperature sensitivity for successive periods across the dataset. These estimates are then used to calculate the R_{eco} during day-time and night-time. GPP is calculated from the difference between NEE and R_{eco} .

On the other hand, LRC uses the Mysterlich function (Falge et al., 2001):

$$NEE = -(F_{csat} + R_d)(1 - e^{(-\alpha(PAR)/(F_{csat}+R_d)})} + R_d \quad (2)$$

where F_{csat} is the CO_2 uptake at light saturation ($\mu\text{mol m}^{-2} \text{s}^{-1}$), R_d is dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$), α is the initial slope of the light response curve ($\mu\text{mol } \mu\text{mol}^{-1}$) and PAR is the photosynthetic active radiation, ($\mu\text{mol m}^{-2} \text{s}^{-1}$). NEE and PAR feeds a 6 days moving window (time step: 1 day) to estimate a set of F_{csat} , R_d and α per day (as a response to changes in vegetation characteristics). The parameterization of the LRC was considered significant when F_{csat} , R_d and α were significantly different from zero ($p < 0.05$) (Lund et al., 2012). From the equation (2), 30 min GPP is calculated from the subtraction of R_d .

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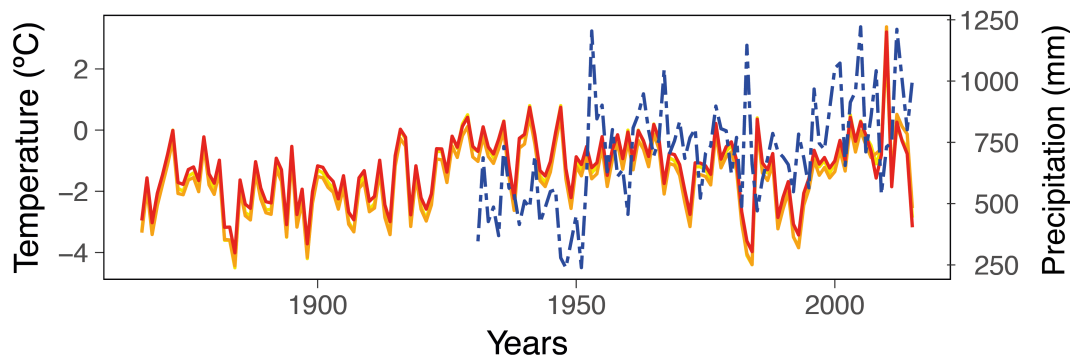


Figure S1. Time series for temperatures (1866-2015) from Nuuk, Kobbefjord-Fen and Kobbefjord-weather station (solid yellow, red and orange line respectively); and precipitations (1931-2015) from Nuuk (dashed blue line).

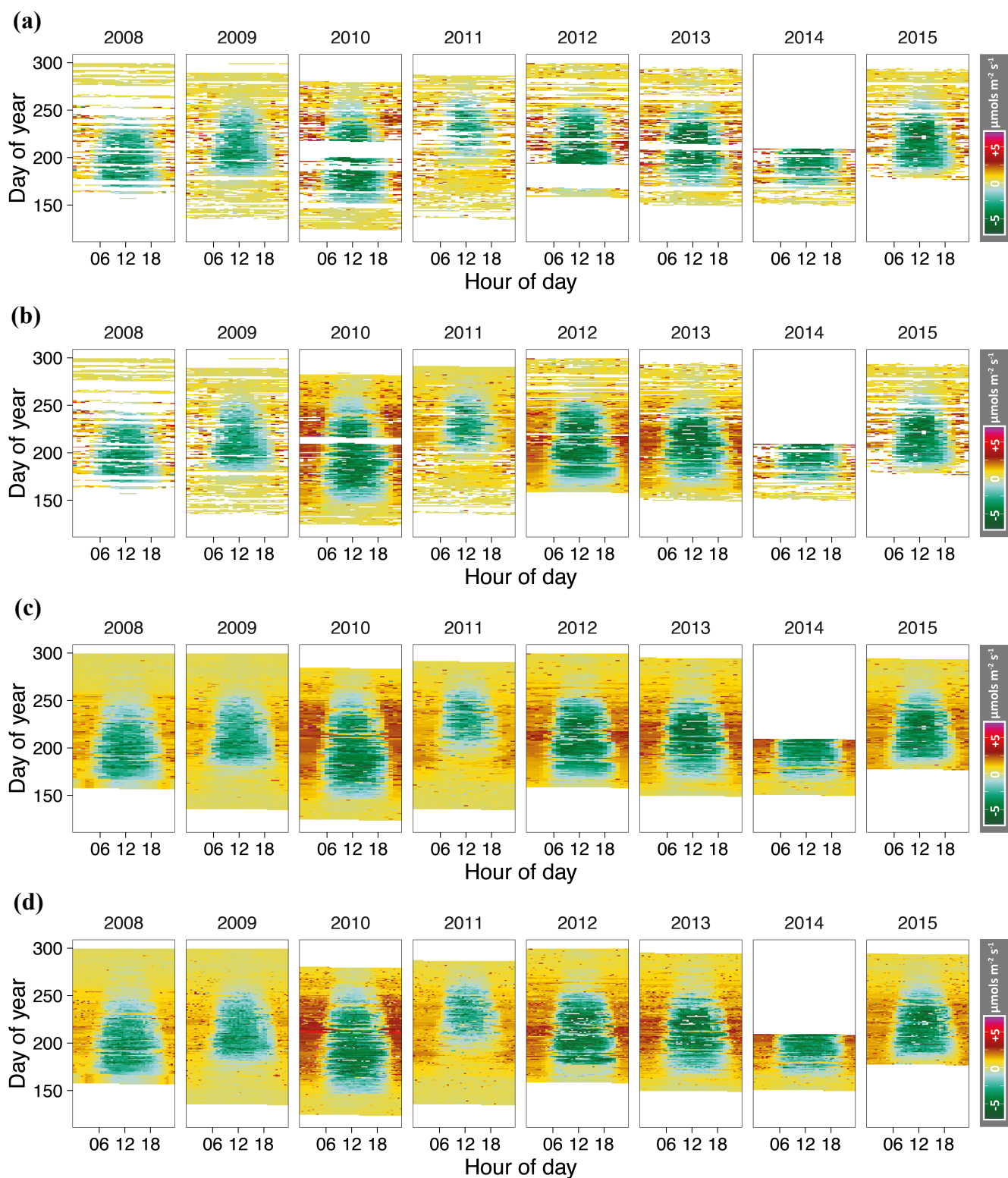


Figure S2. (a) Original NEE EC data, (b) gap-filled NEE based on auto-chamber data, (c) gap-filled product combining auto-chamber data and the MDS algorithm and (d) gap-filled product using only the MDS algorithm.

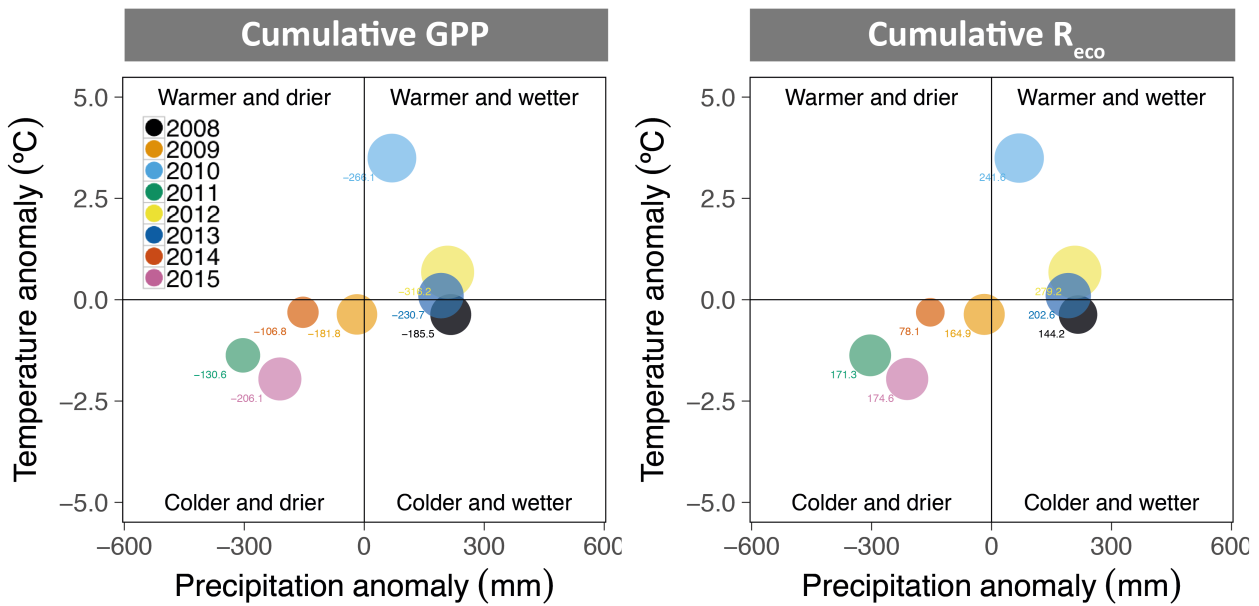


Figure S3. Annual cumulative GPP and R_{eco} defined by annual temperature and precipitation anomalies (2008-2015). The flux size is categorized depending on the flux magnitude ($g C m^{-2}$), i.e. larger diameters with greater fluxes.

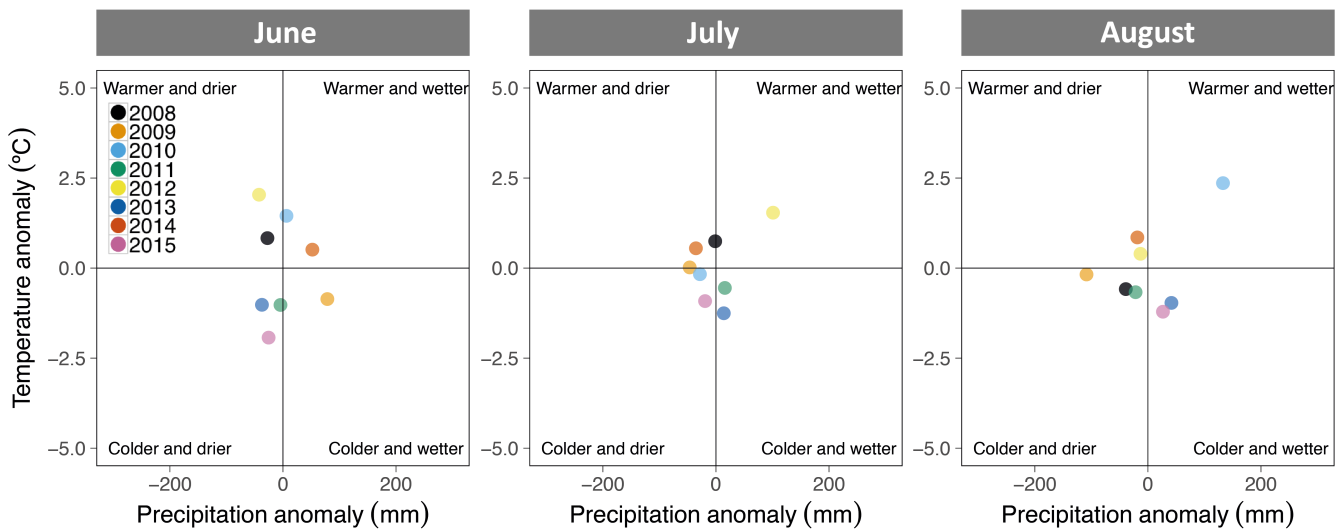


Figure S4. Temperature ($^{\circ}C$) and precipitation (mm) anomalies in June, July and August of the analysed years (2008-2015).

Table S1. Temporal scale, time aggregation, sample size and number of random forests utilized in the Random Forest analysis.

Figure	Temporal scale	Time aggregation	Sample size	Number of random forests (per variable and per flux)
7	Hourly	Hourly	24426	1
	Daily	Daily	1006	1
	Weekly	Weekly	118	1
	Monthly	Monthly	29	1
8	Diurnal	Hourly	24426	24
	Seasonal	Hourly	24426	37
	Annual	Hourly	24426	8

Paper II

Lund, M., Raundrup, K., Westergaard-Nielsen, A., **López-Blanco, E.**, Nymand, J., and Aastrup, P.:
Larval outbreaks in West Greenland: Instant and subsequent effects on tundra ecosystem productivity and CO₂ exchange, *AMBIO*, 46, 26-38, 10.1007/s13280-016-0863-9, 2017.



Nuuk-Kobbefjord site, West Greenland. 2015 field season. Photo by Efrén López-Blanco

Larval outbreaks in West Greenland: Instant and subsequent effects on tundra ecosystem productivity and CO₂ exchange

Magnus Lund, Katrine Raundrup, Andreas Westergaard-Nielsen, Efrén López-Blanco, Josephine Nymand, Peter Aastrup

Abstract Insect outbreaks can have important consequences for tundra ecosystems. In this study, we synthesise available information on outbreaks of larvae of the noctuid moth *Eurois occulta* in Greenland. Based on an extensive dataset from a monitoring programme in Kobbefjord, West Greenland, we demonstrate effects of a larval outbreak in 2011 on vegetation productivity and CO₂ exchange. We estimate a decreased carbon (C) sink strength in the order of 118–143 g C m⁻², corresponding to 1210–1470 tonnes C at the Kobbefjord catchment scale. The decreased C sink was, however, counteracted the following years by increased primary production, probably facilitated by the larval outbreak increasing nutrient turnover rates. Furthermore, we demonstrate for the first time in tundra ecosystems, the potential for using remote sensing to detect and map insect outbreak events.

Keywords Arctic · Carbon · Disturbance · Ecosystem productivity · *Eurois occulta* · Insect outbreak

INTRODUCTION

Arctic tundra ecosystems cover ca. 8% of the global land area. Yet, the vast stocks of organic carbon (C) stored in their soils make them especially important in a climate change context (McGuire et al. 2012), since increasing temperatures may result in increased emissions of carbon dioxide (CO₂) and methane (CH₄). The occurrence of periodic disturbances, such as fires, pathogens and insect outbreaks, which to a varying temporal and spatial extent

damage vegetation and affect C cycling, are also likely to change in the future (Callaghan et al. 2004; Post et al. 2009). There are, however, large gaps in our understanding of how extreme events affect ecosystem functioning and they are as such generally underrepresented in process-based ecosystem models (McGuire et al. 2012).

Insect outbreaks can have extensive consequences for ecosystem productivity and functioning in subarctic and arctic biomes (Callaghan et al. 2004; Post et al. 2009). The outbreaks may lead to local and regional canopy defoliation (Tenow and Nilssen 1990; Callaghan et al. 2004; Bjerke et al. 2014), decreased vegetation biomass (Pedersen and Post 2008; Post and Pedersen 2008), shifts in vegetation composition (Karlsen et al. 2013; Jepsen et al. 2013), decreased C uptake (Heliasz et al. 2011) as well as cascading impacts through other food web compartments (Jepsen et al. 2013). The prevalence and intensity of these disturbances are expected to increase with a warmer climate (Neuvonen et al. 1999; Callaghan et al. 2004; Chapin et al. 2004). The strong warming observed in northern high latitudes (Stocker et al. 2013) has been associated with a northward extension of outbreaks of moths and their leaf-defoliating larvae in northern Fennoscandia (Post et al. 2009; Jepsen et al. 2013), likely related to enhanced survival of overwintering eggs due to warmer winters (Callaghan et al. 2004).

There are several reports of outbreaks of the autumnal moth *Epirrita autumnata* and the winter moth *Operophtera brumata* from northern Fennoscandia, occurring at roughly decadal intervals (Tenow and Nilssen 1990; Callaghan et al. 2004; Heliasz et al. 2011; Jepsen et al. 2013; Karlsen et al. 2013). The larvae of these moth species not only defoliate forests of mountain birch *Betula pubescens*, but have also been found to feed on understorey vegetation including dwarf birch *Betula nana* and bilberry *Vaccinium*

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myrtillus (Karlsen et al. 2013). During an extensive outbreak in the lake Torneträsk catchment in subarctic Sweden in 2004, the mountain birch forest was a much smaller C sink during the growing season compared with a reference year, most likely due to lower gross primary production (Heliasz et al. 2011). Furthermore, changes in light conditions caused by defoliation and nutrient additions from larval faeces and carcasses (Karlsen et al. 2013) may alter the conditions for plant species not directly affected by defoliation.

In Greenland, outbreaks of larvae of the noctuid moth *Eurois occulta* have occasionally been reported (see “Background” section). During the 2004–2005 outbreak in Kangerlussuaq, West Greenland, the above ground biomass of all plant functional groups was reduced by up to 90% as a result of intense defoliation (Post and Pedersen 2008). However, little is known about the frequency, timing and extent of the outbreaks of *E. occulta* in Greenland. The purpose of this study is therefore to synthesize available knowledge on *E. occulta* outbreaks in Greenland and their effects on ecosystem functioning and productivity. We were fortunate to document an outbreak of *E. occulta* larvae in 2011 in Kobbefjord, West Greenland, where an extensive monitoring programme has been ongoing since 2008. We aim to quantify the effects of the larval outbreak on the ecosystem productivity by analyses of monitoring data on land–atmosphere exchange of CO₂ and vegetation greenness derived from an automatic camera setup. We study the effects of the larval outbreak over a longer time period including three years following the outbreak, allowing for an investigation of how the tundra ecosystem responds to the larval attack in subsequent years. Furthermore, we use satellite imagery to investigate possible historical outbreaks in the Kobbefjord catchment.

BACKGROUND

Eurois occulta is a noctuid moth with a holarctic distribution. In Greenland, *E. occulta* is distributed northwards to Ilulissat and Qeqertarsuaq on the west coast (Mølgaard et al. 2013) and to Skjoldungen on the east coast (Fig. 1; Karsholt et al. 2015). Adult moths fly from early July to early September when they lay their eggs under stones or in moss. They hatch in fall and survive the winter as partially grown larvae underneath the snow before developing into fully grown larvae during the following spring. At this stage, they forage on green parts of the plants. In some years, *E. occulta* larvae occur in tremendous numbers (Vibe 1971).

These outbreak events have been reported to occur as far back as the late 1400 s as documented in peat cores from Ujarassuit (Iversen 1934). Since then, a number of *E.*

occulta larvae outbreaks have been reported in Greenland (Table 1), i.e. in the Kangerlussuaq inland (Fox et al. 1987; Pedersen and Post 2008; Avery and Post 2013) and in the Nuup Kangerlua area (Iversen 1934), most recently in 2010–2011 when outbreaks occurred at both locations. *E. occulta* was also found in the Disko Bay region in 2012 (Mølgaard et al. 2013). Vibe (1971) reported that outbreaks of larvae have been observed often and must be regarded as a normal phenomenon. Although this has not been determined specifically for *E. occulta*, Vibe (1971) suggested that outbreaks in Greenland occur only under the right combinations of climatic factors, e.g. temperature, solar radiation, humidity, precipitation and wind.

MATERIALS AND METHODS

Study site

This study was conducted in Kobbefjord/Kangerluarsunguaq in low Arctic West Greenland (64°08'N, 51°23'W, ca. 25 m a.s.l.), located ca. 20 km from Nuuk, the capital of Greenland (Fig. 1). This area is subjected to extensive monitoring and long-term research activities within the Greenland ecosystem monitoring (GEM) programme. The area is part of a valley system surrounded by mountains that reach up to ca. 1300 m a.s.l. The monitoring area covers 32 km² and is characterised by dwarf shrub heaths intersected with dry south-facing slopes and smaller fen areas. The heaths are dominated by *Salix glauca*, *Betula nana* and *Empetrum nigrum* (Bay et al. 2008). Long-term (1961–1990) mean annual temperature and precipitation sum for Nuuk are −1.4 °C and 750 mm, respectively (Cappelen 2012).

Monitoring data

Three terrestrial monitoring sub-programmes are operational in the Kobbefjord valley, namely BioBasis, GeoBasis and ClimateBasis (cf. Jensen and Rasch 2008); data from these programmes form the basis of this study. In 2008, an experiment was set up consisting of 18 control plots, six open-top ITEX chambers that increase temperature (cf. Henry and Molau 1997) and six plots with Hessian tents that reduce incoming light (Aastrup et al. 2015). In this study, only data from control plots were used.

Measurements of CO₂ exchange were conducted weekly to biweekly during the snow-free season 2008–2014 using the closed chamber technique. A plexiglas measuring chamber (0.33 × 0.33 × 0.34 m), equipped with a fan for air mixing and a HTR-2 probe logging photosynthetic photon flux density and air temperature, was placed on top of a fixed metal frame for three minutes and air was

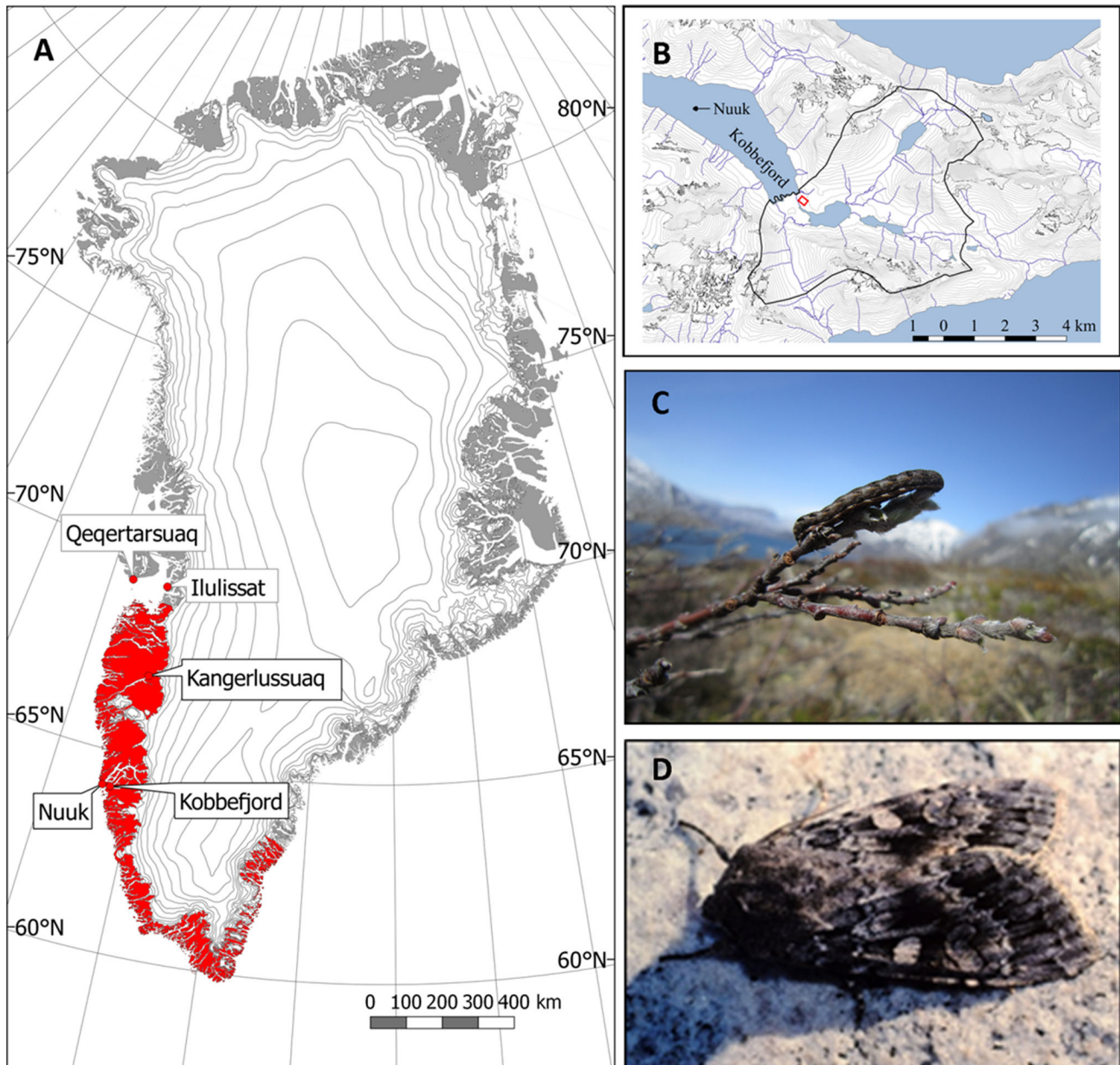


Fig. 1 **a** Updated distribution of *Eurois occulta* in Greenland. The map is modified from Jensen (2003) and includes data points from Mølgaard et al. (2013). **b** Study area in Kobbefjord. The red square indicates the approximate location of the experimental plots. The black line delineates the watershed. **c** *E. occulta* larvae. **d** Adult *E. occulta* moth, photo: J. Böcher

analysed for CO₂ concentrations using an infrared gas analyser EGM4 (PP Systems, USA). The linear change in CO₂ concentration in the transparent chamber was used to calculate net ecosystem exchange (NEE), whereas a subsequent measurement in a dark chamber was used to represent ecosystem respiration (R_{eco}). Gross primary production (GPP) was calculated as the difference between light and dark measurements ($GPP = NEE - R_{eco}$).

All taxonomic groups of arthropods were sampled on a weekly basis at four sites located within a few hundred metres of the experimental plots, each with eight pitfall

traps as specified by Aastrup et al. (2015). The traps contained ca. 200 ml water with one teaspoon of salt and two drops of detergent. The number of *E. occulta* larvae was counted at the department of Bioscience, Aarhus University, Denmark. For the purpose of this paper, samples from one site (arthropod plot 3) with vegetation composition and coverage resembling the CO₂ flux plots were included in the analyses.

Soil temperatures (ST) from a depth of 1, 5, 10 and 30 cm were measured with T107 temperature probes (Campbell Sci., UK) approximately 500 m from the

Table 1 Reported outbreaks of *Eurois occulta* in Greenland

Year	Location	Latitude	Longitude	References
1490	Ameralik	64.22	−50.00	Iversen (1934)
1932	Ameralik	64.22	−50.00	Iversen (1934)
1932	Kangerlussuaq	67.03	−50.62	Iversen (1934)
1979	Kangerlussuaq	67.03	−50.62	Fox et al. (1987)
2004	Kangerlussuaq	67.03	−50.62	Pedersen and Post (2008)
2005	Kangerlussuaq	67.03	−50.62	Pedersen and Post (2008)
2010	Kangerlussuaq	67.03	−50.62	Avery and Post (2013)
2011	Kangerlussuaq	67.03	−50.62	Avery and Post (2013)
2011	Kobbefjord	64.13	−51.37	This study
2012	Ilulissat	69.25	−50.92	Mølgaard et al. (2013)
2012	Qeqertarsuaq	69.25	−53.55	Mølgaard et al. (2013)

experimental plots. Incoming photosynthetic photon flux density (PPFD; Li-190SA, LICOR, USA) and air temperature (AT; Vaisala HMP 45D, Finland) were obtained from a weather station located ca. 2 km from the experimental plots. Daily imagery of the valley was derived from a HP E427 digital camera housed inside a weatherproof box. The box was mounted at 500 m above sea level in September 2009, and daily images were taken at noon local time (Westergaard-Nielsen et al. 2013).

Data analyses

The CO₂ flux measurements provide a snapshot of the CO₂ exchange at the specific time of the day when measurements were performed. In order to take diurnal variation into account and to estimate seasonal budgets, the following nonlinear equations (Saarnio et al. 2003; Lund et al. 2009) were parameterised for each year separately based on available monitoring data:

$$\text{GPP} = \frac{a \times \text{PPFD} \times \text{ST}}{b + \text{PPFD}} \quad (1)$$

$$R_{\text{eco}} = c \times e^{d \times \text{ST}} \quad (2)$$

where a , b , c and d are regression parameters. Initial tests indicated that ST at 30 cm provided best fits (highest r^2 values) for GPP (Eq. 1), whereas ST at 5 cm was most suitable for R_{eco} (Eq. 2). The time series of GPP and R_{eco} were constructed between 1 June and 31 August for each plot and year, and NEE was calculated as the sum of GPP and R_{eco} . The ST measurements were initiated on 25 July 2008 and thus, we did not estimate a seasonal budget for 2008.

The vegetation greenness at plant community level was evaluated from time series of RGB-images available from the fixed automatic camera overlooking Kobbefjord (Fig. 2).

In this study, snow cover fraction and green chromatic coordinate (GCC) were computed for the region covering the experimental plots from daily images through the snow melt and snow-free period. GCC has been used as a proxy for NDVI and ecosystem productivity in different ecosystems (cf. Toomey et al. 2015) including low Arctic tundra and wetlands (Westergaard-Nielsen et al. 2013) and can be extracted from digital cameras offering only red, green and blue colour channels. To enable a quantification of larval impact, the area around the head of Kobbefjord, as defined by the field of view of the camera (Fig. 2), was classified. An image from peak growing season (July 29, 2011) was selected for maximum separation between affected and non-affected vegetated areas. Prior to the classification, the image was orthorectified (Corripio 2004). Since the classification was based on high spatial resolution data with only three colour channels (RGB), a nearest neighbour classification in eCognition Developer (Trimble, Inc.) was applied, based on a processing chain of (1) a multi-resolution segmentation; (2) a spectral difference segmentation; and (3) a supervised nearest neighbour classification.

Satellite data

The MOD13Q1 vegetation index (VI) product was used to assess the spatial and temporal differences of VI signals at locations with reported larvae outbreaks. The VI product is derived from the MODIS sensor on board the Terra satellite platform. MOD13Q1 is a 16-day composite at 250 m spatial resolution based on cloud-free observations and includes, e.g. normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) measurements (Huete et al. 2002). The data were pre-processed based on the quality assessment layer, to include only observations with VI quality down to bit 1000, however, no



Fig. 2 Photos from 20 July 2011 and 21 July 2012 from the fixed automatic camera in Kobbefjord. The *red square* indicates the approximate location of the experimental plots

further processing steps to adjust for possible differences in the number of observations within each composite were taken.

The impact of larval outbreaks was examined using a window of 3×3 satellite pixels, with the centre pixel

covering the geographical coordinates of reported outbreaks (for Kobbefjord, we used the location of the experimental plots, whereas for Kangerlussuaq, we used the coordinates for site 1 in Young et al. 2016). Time-integrated NDVI and EVI, which have been found to

correlate significantly with the aboveground phytomass in the Arctic (Westergaard-Nielsen et al. 2015), were calculated using five 16-day composites during DOY 177–241 in each year. Values below 0.2 and 0.1 for NDVI and EVI, respectively, were considered erroneous and replaced by linear interpolation. This was done for Kobbefjord NDVI and EVI on DOY 193, 2004; DOY 209, 2012 and DOY 241, 2013. No values were below the thresholds for Kangerlussuaq.

RESULTS

The study years (2008–2014) were generally warmer and wetter (Table 2) than the long-term mean (see “Study site” section). The year 2010 had the highest mean annual temperature (3.4°C), mainly due to unusually high temperatures in the winter months (mean temperature for January, February and December = −1.6°C). In the summer months (June–August), mean temperatures ranged between 8.3°C (2011) and 10.5°C (2012) for all years. Snow cover varied considerably in time and space during the study period. In 2010, there was only a thin snow pack that disappeared early, whereas in 2011, maximum daily snow depth reached 1.36 m and in the experimental CO₂ flux plots, snow did not disappear until 12 June.

Larvae of the noctuid moth *E. occulta* were observed in the Kobbefjord area mainly in 2010 and 2011. The number of larvae caught in pitfall traps in 2010 was modest with 31 larvae caught during the entire season. Numbers peaked in 2011 with more than 1800 larvae caught in July, thus representing an outbreak (Fig. 3). The dwarf shrub vegetation in the experimental CO₂ flux plots was almost completely defoliated (Fig. 4). The amount of *Salix glauca* catkins was low in 2010 and non-existent in 2011, as a result of larvae feeding on the plants. Also, in 2012, when no larvae were encountered, no buds were developed.

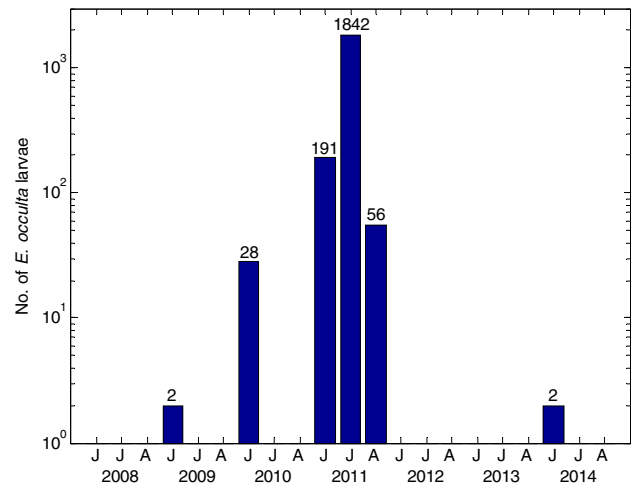


Fig. 3 Number of *Eurois occulta* larvae in arthropod plot 3 in June, July and August (J, J, A) 2008–2014

However, in the following years, the number of catkins was much higher compared with 2008–2012 (e.g. the *Salix* plants in plot 4 in Fig. 3 had 28, 21, 3, 0, 0, 143 and 73 female catkins in July 2008–2014, respectively).

The CO₂ exchange measurements showed a distinct decrease in measured fluxes in the main outbreak year (2011) compared with the other years (Fig. 5), with lower amplitude of instantaneous NEE, *R_{eco}* and GPP. There was also an apparent delay in the onset of net CO₂ uptake during 2011. However, the fluxes were higher in the years following the outbreak compared with earlier years. Based on the flux measurements and ancillary information on ST and PPF, we parameterised Eqs. 1 and 2 separately for each year (2009–2014; Table S1). However, for the outbreak year of 2011, Eq. 1 could not be fitted with the data because the larvae damaged the vegetation and severely postponed the development of the photosynthetic apparatus, which in other years correlated with the progress in ST. As an alternative, we used the green chromatic coordinate

Table 2 Meteorological characteristics during the study period in Kobbefjord including winter characteristics (Max depth, m; DOY of melt in the CO₂ flux plots, day of year), annual means (AT, air temperature, °C at 2 m; Precipitation, mm) and summer means from June, July and August (AT; Precip; PPF, photosynthetic photon flux density, μmol m⁻² s⁻¹)

Year	Snow characteristics		Annual values		Summer (JJA) values		
	Max. Depth	DOY of melt	AT	Precip	AT	Precip	PPFD
2008	n/a	n/a	−0.7	1127	9.2	140	435
2009	0.91	154	−0.6	838	8.8	135	410
2010	0.33	118	3.4	905	10.4	314	364
2011	1.36	163	−1.6	n/a	8.3	193	356
2012	1.02	152	0.5	n/a	10.5	254	373
2013	0.53	149	0.2	1046	8.4	230	377
2014	1.1	153	−0.1	709	9.0	208	391

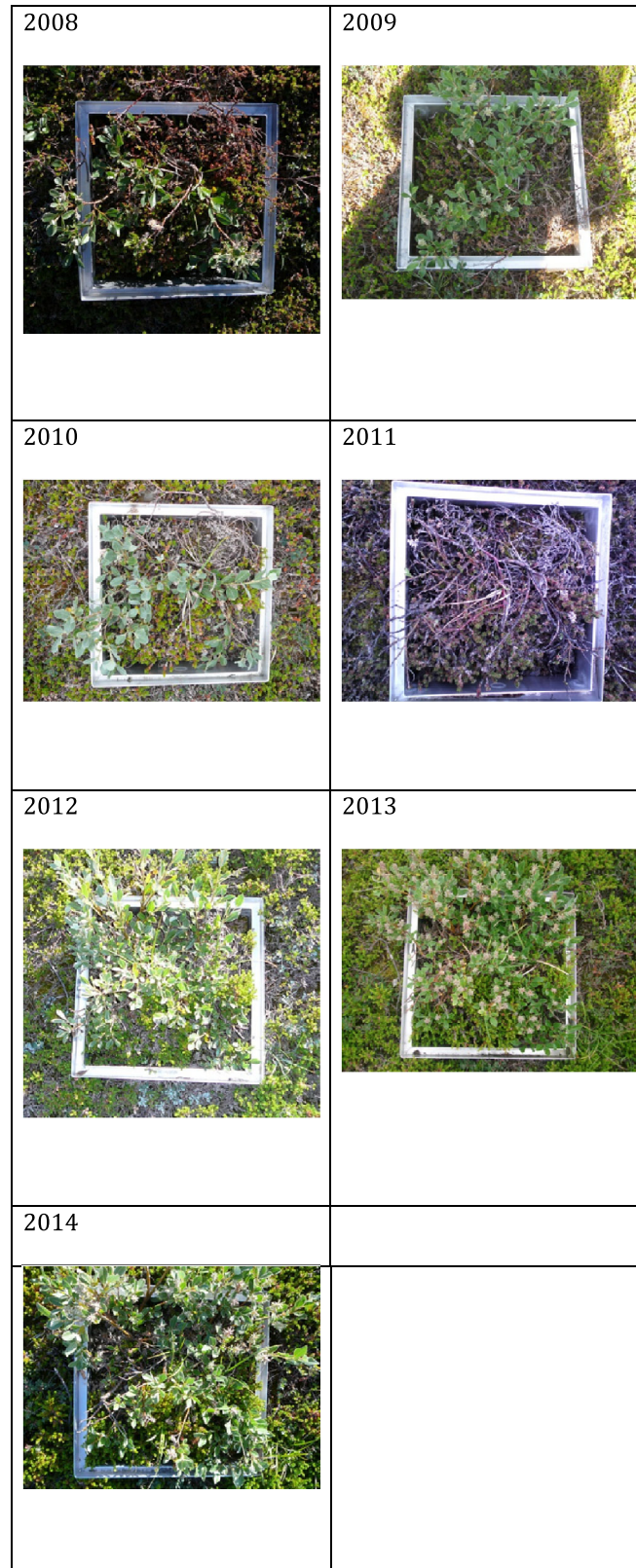


Fig. 4 Yearly photos (2008–2014) from one of the experimental plots (plot 4C) in Kobbefjord. All photos were taken between DOY 203 and 208

(GCC) as a replacement for ST in Eq. 1, to be able to estimate a C budget in 2011 (Table S1).

As for the June–August budgets (Table 3), there were significant between-year differences in all flux components (ANOVA for GPP: $F = 9.4, p < 0.001$; R_{eco} : $F = 32.3, p < 0.001$; NEE: $F = 6.3, p < 0.001$). Year 2011, the main larval outbreak year, had the lowest (i.e. least negative) GPP sums and a C sink close to zero ($NEE = 7 \pm 16 \text{ g C m}^{-2}$). However, the years following the outbreak (2012–2014) had higher (i.e. more negative) GPP sums and stronger C sink strengths compared with the years preceding the outbreak (2009–2010).

In order to estimate the C exchange in 2011, had there not been a larval outbreak, we used the parameterisations (Eqs. 1 and 2) from other years (2009, 2010, 2012–2014) with meteorological data (PPFD and ST) from 2011 (Table 4). The parameters in Eqs. 1 and 2 regulate the

sensitivity of ecosystem photosynthesis and respiration to variations in PPFD and ST, and using meteorological data from 2011, we can assess the C budget assuming that the same sensitivity can be applied to 2011. Compared with the estimated flux component budgets in 2011 (Table 3), parameterisations from other years consistently provide higher (i.e. more negative) GPP sums and stronger C sink strengths (more negative NEE).

The green chromatic coordinate (GCC) for the area of the experimental plots (indicated by the red square in Fig. 2) was lower in 2011 compared with 2010 and 2012–2014 (Fig. S1). A time integration of GCC from the end of snow melt until the end of growing season suggests a 16% decrease in greenness in 2011 compared with the 2010–2014 average. The camera-based classification of the field of view of the camera in 2011 (Fig. 2) resulted in five separable ecosystem classes with an overall accuracy of

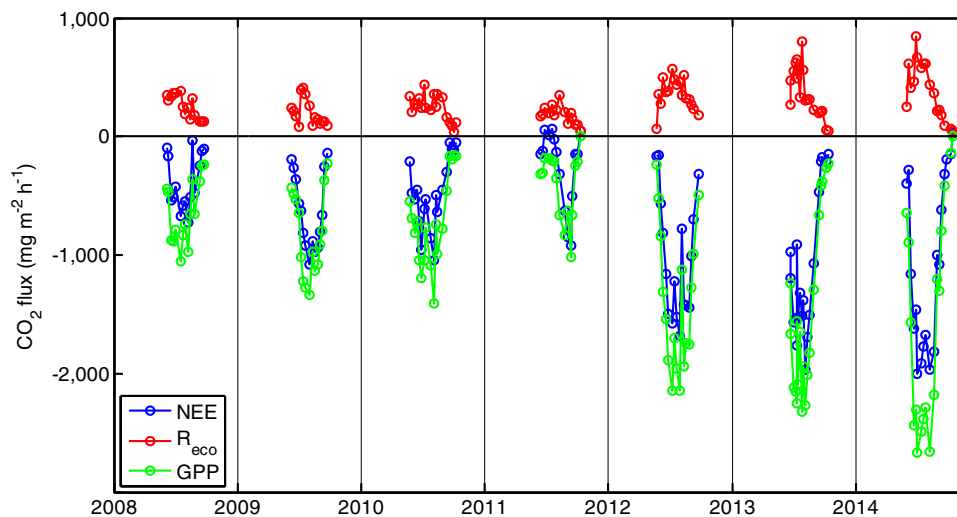


Fig. 5 Instantaneous, daytime flux measurements of net ecosystem exchange (NEE) and ecosystem respiration (R_{eco}) in the Kobbefjord experimental plots 2008–2014. Gross primary production (GPP) was calculated as the difference between NEE and R_{eco}

Table 3 Mean \pm standard error (spatial replication) of measured transparent (net ecosystem exchange, NEE) and dark (ecosystem respiration, R_{eco}) fluxes and estimated budgets of gross primary production (GPP), R_{eco} and NEE during June–August 2008–2014 in Kobbefjord. Superscript letters for the budgets columns, derived from a Tukey’s HSD multiple comparison, indicate significant differences among years. Numbers in parentheses reflect sample size (i.e. number of plots)

Year	Measurements ($\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$)		Budgets (g C m^{-2})		
	NEE	R_{eco}	GPP	R_{eco}	NEE
2008	-358 ± 81	262 ± 12	$- \pm -$	$- \pm -$	$- \pm -$
2009	-497 ± 88	216 ± 13	-252 ± 39^{abc} (14)	100 ± 5^a (16)	-150 ± 40^{abc} (12)
2010	-496 ± 77	288 ± 14	-244 ± 21^{ab} (18)	150 ± 7^b (18)	-94 ± 17^{ab} (18)
2011	-86 ± 32	236 ± 9	-104 ± 14^a (10)	110 ± 3^a (17)	7 ± 16^a (10)
2012	-1023 ± 143	406 ± 21	-399 ± 49^{bcd} (13)	200 ± 10^{cd} (18)	-216 ± 44^{bc} (13)
2013	-1164 ± 178	425 ± 27	-424 ± 44^{cd} (18)	182 ± 10^{bc} (18)	-242 ± 37^{bc} (18)
2014	-1119 ± 160	479 ± 28	-505 ± 65^d (18)	231 ± 13^d (18)	-274 ± 54^c (18)

Table 4 Estimated flux components (GPP; gross primary production, R_{eco} : ecosystem respiration, NEE; net ecosystem exchange, g C m^{-2}) in 2011 using meteorological data (photosynthetic photon flux density, PPFD and soil temperature, ST) from 2011 and parameterisations of Eqs. 1 and 2 from other years (2009, 2010, 2012–2014)

Year	GPP	R_{eco}	NEE
2009	-196 ± 31	84 ± 5	-111 ± 31
2010	-180 ± 16	119 ± 6	-61 ± 12
2012	-280 ± 34	158 ± 10	-136 ± 30
2013	-366 ± 37	170 ± 10	-196 ± 31
2014	-430 ± 57	205 ± 12	-226 ± 46

94% (Table S2); bedrock, non-attacked heath, larvae-attacked heath, fen and water (Table 5). The classification covered a total area of 2.58 km^2 , and we estimated that 0.83 km^2 consisted of heath damaged by larvae; corresponding to 32% of the area covered by the camera (Fig. 2) or 59% of the total heath area.

Time-integrated NDVI and EVI showed a marked decrease in 2011 in Kobbefjord (Fig. 6). Local minima were also observed in 2004 and 2005. Similarly, there were low values of NDVI and EVI for the area close to Kangerlussuaq for years with reported outbreaks, 2004–2005 and 2010–2011 (Table 1); however, the between-year variation was higher for this site with low time-integrated EVI and NDVI also in 2000 and 2003.

DISCUSSION

The outbreak of the noctuid moth *E. occulta* in Kobbefjord in 2011 had a strong and extensive impact on the vegetation. The production of leaves, buds and catkins or flowers in all species monitored in the area was heavily impacted and the vegetation reproduction was seriously reduced (Bay et al. 2012). Also, in the year following the outbreak, 2012, the total catkin and flower production was low (Bay et al. 2013), indicating that the plants focused their resources on establishing new leaves; a compensatory growth as a response to herbivory (McNaughton 1983). The excess energy stored in 2012 from not producing catkins resulted in a record amount of catkins in 2013 (e.g. Fig. 4).

The larvae did not forage upon leaves from all plant species, e.g. *Empetrum nigrum* was generally left untouched,

although larvae feeding on *E. nigrum* flowers were observed in the field. *E. nigrum* is generally unpalatable to herbivores and not directly defoliated during moth outbreaks (Jepsen et al. 2013; Karlsen et al. 2013); however, previous studies have discussed the possibility that starving larvae attempt to eat their leaves making them more susceptible for desiccation or infection (Jepsen et al. 2013; Karlsen et al. 2013; Olofsson et al. 2013). Plot-scale NDVI measurements showed that *E. nigrum* was notably less green in 2011 than in other years (Olsen et al. 2014), which could thus be explained by the larval outbreak. However, other adverse effects such as frost damage (Bjerke et al. 2014) during early winter 2010/2011 cannot be excluded.

In the following years, *E. nigrum* was greener than in previous years, also before the outbreak (Olsen et al. 2014). This pertained to all plant species as seen by generally higher NDVI values measured after the outbreak; an indication of good health, which may stem from higher levels of nutrients made available for the plants from decomposed larvae. Arctic tundra vegetation is generally nutrient limited (cf. Chapin and Shaver 1985) and larvae faeces and carcasses can provide a nutrient pulse to the system (Kagata and Ohgushi 2012). Also, reduced plant nutrient uptake during 2011, as a consequence of reduced growth, may have resulted in excess nutrient availability in the following years. Post and Pedersen (2008) report a fourfold increase in nitrogen (N) concentration in leaf tissues of *S. glauca* and *B. nana* at the peak of the larval outbreak in Kangerlussuaq (Table 1) along with a rapid biomass recovery following the outbreak.

There was a marked decrease in CO_2 fluxes in 2011, both in terms of instantaneous, measured fluxes (Fig. 5)

Table 5 Area coverage from camera-based classification in Kobbefjord 2011

Class	Total area coverage (km^2)	Fraction of classified area	Number of segments	Average area per segment (m^2)
Bedrock	0.30	0.12	629	483
Non-attacked heath	0.57	0.22	298	1900
Attacked heath	0.83	0.32	694	1192
Fen	0.01	0.004	24	599
Water	0.87	0.34	89	9720

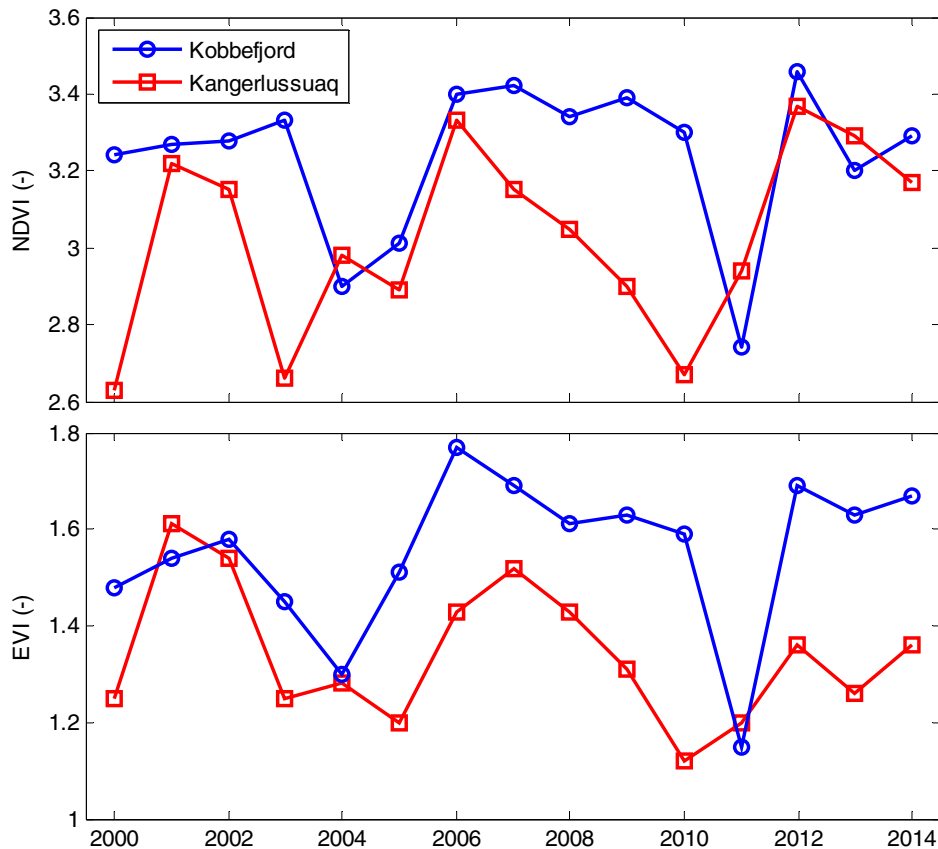


Fig. 6 Time-integrated (DOY 177–241) normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) for Kobbefjord and Kangerlussuaq (Site 1 in Young et al. 2016), respectively, derived from the MODIS sensor

and estimated summertime budgets (Table 3). Net ecosystem exchange was close to zero during June–August in 2011 (Table 3), indicating that the heath ecosystem, represented by the experimental plots, did not accumulate C during this period. The reduction in CO₂ accumulation during 2011 was caused by a significant decrease in GPP to less than half of that in other years (Table 3). However, fluxes were higher in the years following the outbreak, again indicating a rapid ecosystem recovery after the larvae attack. The increase in GPP in 2012–2014 may be explained by an increase in nutrient availability due to the larval outbreak, as discussed above, favouring vegetation growth in subsequent years.

The rapid regrowth and the increase in primary productivity indicate that the tundra ecosystem may not be as vulnerable as anticipated with respect to these outbreaks. The ecosystem may have developed a high degree of resiliency as a response to outbreak events occurring at certain intervals. Our findings, that the years following the outbreak (2012–2014) had higher GPP and stronger C sink strengths compared with the years preceding the outbreak (2009–2010), correspond to the strong biomass recovery observed in Kangerlussuaq following a larval outbreak (Post and Pedersen 2008). This indicates that the effects of

outbreaks may be counterbalanced by increased primary production in the following years. Further, the larvae appear to play a significant role by influencing nutrient dynamics and accelerating N turnover.

By using the parameterisations from other years, we estimated what the CO₂ exchange in 2011 would have been in the absence of the larval outbreak (Table 4). This approach takes inter-annual variation in meteorological characteristics into account, e.g. the impact of long-lasting snow cover in 2011 is included in these estimates. Parameters from all other years resulted in higher (i.e. more negative) GPP and stronger C sink strength, whereas the effect on R_{eco} was less consistent. The parameters from 2010 resulted in lower (less negative) GPP sum and weaker C sink strength compared with other years, which can be associated with the modest number of moth larvae affecting ecosystem productivity also in 2010 (Fig. 3). The parameters from 2013 and 2014 resulted in high GPP sums and strong C sink strengths, indicating a strong recovery from the larval attack and a potential switch to a more productive state as discussed above. As such, when assessing the effect of the larvae on vegetation productivity and C budget in 2011, it seems most reasonable to use parameters from 2009 and 2012. Although a simplification, it results in a decrease in C sink strength in

the order of 118 to 143 g C m⁻², with an associated uncertainty (combined standard error from the spatial replication) of approximately ± 47 g C m⁻². Scaling to the field of view of the camera (Fig. 2), taking the whole area of attacked heath into account (Table 5), results in a C loss of 98–119 tonnes C. However, the camera covers <10% of the entire Kobbefjord catchment (2.58 out of 32 km²) so the catchment scale C loss may be one order of magnitude larger (approximately 1210–1470 tonnes C). This approximation can be compared with a study in northern Sweden by Heliasz et al. (2011), who estimated a C loss of 29 000 tonnes C for a mountain birch forest area of 316 km² exposed to an outbreak of larvae in 2004 of the autumnal moth *E. autumnata*.

We demonstrate the potential for using satellite imagery to detect and map insect outbreaks in West Greenland. To our knowledge, this is the first time satellite data have been used to observe effects of insect outbreaks in tundra ecosystems. Both NDVI and EVI show a clear decrease in time-integrated values during 2011 in Kobbefjord, with a decrease of 15 and 26%, respectively, compared with the 2000–2014 mean (Fig. 6). A decrease of 16% in time-integrated GCC in 2011 matches this range. These estimates also match a 16–27% decrease in peak NDVI in 2012 in northern Fennoscandia during a moth larvae outbreak, compared with a 2000–2011 average (Bjerke et al. 2014). The outbreaks in Kangerlussuaq in 2004–2005 and 2010–2011 (Pedersen and Post 2008; Avery and Post 2013; Table 1) are also visible through low values of time-integrated indices (Fig. 6); however, the picture is less clear for this site with low values also in other years.

It might be suggested that outbreaks of *E. occulta* in West Greenland occur in synchrony since the satellite data indicate low NDVI and EVI in Kobbefjord also in 2004; a year with documented outbreak in Kangerlussuaq (Pedersen and Post 2008). However, as the current study is limited to the near vicinity of field investigations in the respective site, impacts on a larger scale can only be speculated upon. Nevertheless, spatial synchrony in outbreak events indicates that climatic variations play a key role in triggering outbreak events (Klemola et al. 2006; Young et al. 2014). Outbreaks of *Epirrita autumnata* and *Operophtera brumata* in northern Fennoscandia have been associated with reduced egg mortality during warm winters (Tenow and Nilssen 1990; Callaghan et al. 2004; Chapin et al. 2004; Young et al. 2014) as well as with decreased parasitoid and predator activity because of low spring and summer temperatures (Virtanen and Neuvonen 1999; Callaghan et al. 2004). However, other studies have found a positive relationship between moth outbreaks and spring and summer temperatures (Klemola et al. 2003; Young et al. 2014). In our study in Kobbefjord, the winters (December–February) of 2009/2010 and 2010/2011 were indeed the warmest on record with mean temperatures of -2.7 and -4.5 °C, respectively, compared

with a 2008–2014 mean of -6.7 °C (Table 2). Also, the summer of 2011 was relatively cold. It is also worth mentioning the importance of snow, which plays a key role in regulating Arctic ecosystem functioning (cf. Callaghan et al. 2012). There was a thick and long-lasting snow pack in the winter 2010/2011 in Kobbefjord (Table 2), which insulated and protected overwintering *E. occulta* larvae from low winter temperatures. In line with this argumentation, it can be noticed that heath vegetation on mountain slopes does not appear to be affected by the larvae (Fig. 2); these areas are generally colder and covered by less snow than the lowlands.

CONCLUSIONS

Our results indicate a marked decline in summertime C uptake during an outbreak of the larvae of *E. occulta* in 2011 in Kobbefjord. However, the years following the outbreak (2012–2014) were characterised by stronger C uptake compared with the years preceding the outbreak. This indicates that the ecosystem is well adapted to these outbreaks and that they presumably occur at certain intervals if a number of environmental conditions are fulfilled. As a consequence of the outbreaks, nutrient turnover rates increase and growth is favoured in subsequent years. As such, the outbreaks may facilitate ecosystem rejuvenation (Tenow et al. 2004).

Future studies should focus on developing tools based on remote sensing products such as the vegetation indices used here for mapping larval outbreak events in West Greenland. A spatially distributed dataset of outbreak events, as opposed to occasional observations, would be highly useful for comparisons with gridded climate data. However, satellite data can only provide landscape scale information on net effects. There is thus an urgent need to continue and expand upon in situ environmental monitoring efforts in the Arctic, in order to improve upon the process-based understanding of how climate change and associated changes in extreme events such as insect outbreaks may affect tundra ecosystem functioning and dynamics. Predicting extreme events, e.g. larval outbreaks, is difficult so in order to capture the events continuous, long-term monitoring programmes are required.

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Ambio

Electronic Supplementary Materials

This supplementary material has not been peer reviewed.

Title: Larval outbreaks in West Greenland: instant and subsequent effects on tundra ecosystem productivity and CO₂ exchange

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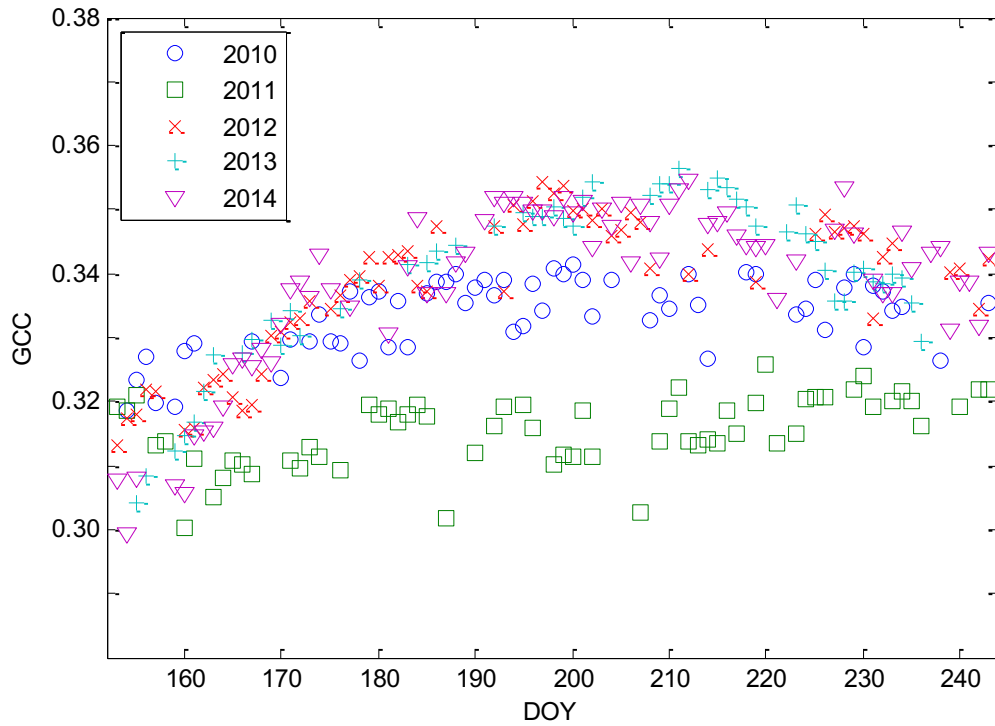


Fig. S1. The green chromatic coordinate (GCC) during June-August (DOY 152-243) in 2010-2014 for the area of the experimental plots (indicated by the red square in Fig. 2), derived from the fixed automatic camera.

Table S1. Estimated parameters from eq. 1 and eq. 2 used to construct time series of gross primary production (GPP) and ecosystem respiration (R_{eco}) for the experimental plots in Kobbefjord. Note that in 2011, the green chromatic coordinate (GCC) were used instead of soil temperature (ST) in eq. 1.

Year	Plot no.	GPP parameterization (eq. 1)					R_{eco} parameterization (eq. 2)				
		a	b	r2	RMSE	n	c	d	r2	RMSE	n
2009	1	-145	310	0.86	146	15	65	0.10	0.53	55	15
	2	-183	192	0.76	287	14	54	0.11	0.40	75	14
	3	-63	260	0.31	123	13	17	0.20	0.66	61	13
	4	-	-	-	-	-	7	0.30	0.93	65	13
	5	-	-	-	-	-	53	0.12	0.53	76	14
	6	-143	33	0.59	371	14	53	0.14	0.54	108	14
	7	-62	391	0.69	83	14	30	0.13	0.49	37	14
	8	-211	509	0.76	304	14	-	-	-	-	-
	9	-52	89	0.46	123	14	14	0.22	0.71	67	14
	10	-62	47	0.32	146	13	23	0.19	0.60	91	13
	11	-122	199	0.54	360	13	40	0.16	0.79	66	13
	12	-	-	-	-	-	28	0.16	0.62	67	14
	13	-36	168	0.72	55	14	12	0.21	0.69	42	14
	14	-202	134	0.63	392	15	74	0.10	0.39	85	15
	15	-47	215	0.40	99	14	45	0.14	0.47	92	14
	16	-65	85	0.47	149	14	19	0.20	0.63	92	14
	17	-56	132	0.33	149	14	-	-	-	-	-
	18	-	-	-	-	-	27	0.16	0.69	55	14
2010	1	-123	200	0.63	228	17	72	0.11	0.66	57	18
	2	-189	533	0.45	460	17	84	0.10	0.42	89	17
	3	-66	196	0.71	99	17	41	0.14	0.49	69	17
	4	-140	198	0.78	259	17	48	0.17	0.81	76	17
	5	-174	369	0.76	278	15	66	0.13	0.63	86	15
	6	-93	178	0.86	101	17	74	0.11	0.64	67	17
	7	-46	88	0.78	64	18	35	0.14	0.85	26	18
	8	-203	588	0.83	239	16	79	0.09	0.40	76	18
	9	-90	220	0.80	83	17	63	0.13	0.66	77	18
	10	-81	116	0.71	142	17	50	0.15	0.79	58	17
	11	-84	198	0.88	73	15	65	0.11	0.63	65	15
	12	-145	161	0.76	273	17	152	0.08	0.41	131	17
	13	-49	139	0.76	81	17	64	0.11	0.77	36	18
	14	-244	682	0.64	424	18	79	0.12	0.43	115	18
	15	-73	163	0.39	274	16	61	0.14	0.69	74	18
	16	-76	125	0.77	101	17	46	0.14	0.76	53	17
	17	-38	94	0.34	123	13	34	0.16	0.67	70	15
	18	-83	617	0.82	92	17	109	0.06	0.34	72	17
2011	1	-84	67	0.66	114	12	66	0.12	0.74	45	14
	2	-	-	-	-	-	68	0.09	0.43	49	12

	3	-97	647	0.54	96	13	89	0.08	0.58	43	14
	4	-122	640	0.22	263	10	64	0.12	0.71	64	11
	5	-	-	-	-	-	121	0.06	0.41	80	10
	6	-	-	-	-	-	106	0.07	0.42	65	11
	7	-	-	-	-	-	41	0.13	0.64	33	12
	8	-	-	-	-	-	36	0.18	0.65	62	12
	9	-130	693	0.36	107	14	55	0.14	0.83	42	14
	10	-61	75	0.37	97	11	65	0.11	0.71	46	12
	11	-	-	-	-	-	108	0.07	0.58	56	11
	12	-	-	-	-	-	-	-	-	-	-
	13	-30	142	0.18	43	13	61	0.12	0.76	36	14
	14	-110	46	0.53	419	11	26	0.19	0.58	71	12
	15	-147	1369	0.80	57	13	47	0.15	0.95	22	14
	16	-175	775	0.69	60	13	27	0.19	0.92	32	14
	17	-	-	-	-	-	93	0.09	0.64	64	12
	18	-133	1571	0.31	147	11	132	0.05	0.51	46	12
2012	1	-193	368	0.86	197	17	84	0.12	0.57	104	17
	2	-239	245	0.87	282	17	152	0.06	0.25	131	17
	3	-113	129	0.75	127	16	97	0.10	0.77	59	16
	4	-	-	-	-	-	200	0.07	0.52	107	15
	5	-	-	-	-	-	95	0.12	0.45	106	12
	6	-	-	-	-	-	102	0.11	0.75	72	15
	7	-83	244	0.70	138	16	103	0.06	0.27	80	16
	8	-333	257	0.84	472	17	122	0.09	0.60	91	17
	9	-113	105	0.63	147	15	126	0.09	0.42	117	15
	10	-139	318	0.26	328	15	119	0.09	0.38	127	15
	11	-153	162	0.72	262	11	135	0.08	0.26	88	11
	12	-	-	-	-	-	257	0.06	0.51	99	14
	13	-73	71	0.71	142	16	148	0.05	0.32	71	17
	14	-276	294	0.89	294	14	130	0.09	0.53	104	14
	15	-	-	-	-	-	94	0.12	0.45	131	14
	16	-118	111	0.65	163	15	57	0.14	0.56	105	15
	17	-90	145	0.71	226	11	13	0.25	0.61	134	12
	18	-103	153	0.48	217	14	116	0.08	0.39	71	14
2013	1	-188	175	0.82	230	16	65	0.14	0.70	77	16
	2	-481	758	0.94	299	15	31	0.23	0.66	158	16
	3	-143	64	0.77	124	15	68	0.15	0.76	89	15
	4	-374	369	0.81	478	16	103	0.15	0.61	200	16
	5	-390	325	0.83	470	14	162	0.11	0.52	203	15
	6	-227	281	0.91	191	16	46	0.19	0.70	137	16
	7	-95	321	0.84	104	15	47	0.14	0.82	37	16
	8	-453	374	0.89	499	14	109	0.10	0.65	89	15
	9	-172	328	0.75	142	15	81	0.15	0.76	102	15
	10	-146	158	0.81	134	15	93	0.13	0.57	138	15

11	-264	415	0.92	214	15	67	0.15	0.67	136	15	
12	-397	390	0.87	410	15	117	0.13	0.70	142	16	
13	-86	163	0.67	131	15	96	0.09	0.55	68	16	
14	-427	736	0.88	409	15	47	0.19	0.82	87	15	
15	-95	7	0.71	148	16	54	0.18	0.81	94	16	
16	-164	317	0.79	156	15	52	0.18	0.52	166	15	
17	-121	323	0.86	137	15	40	0.16	0.73	84	15	
18	-147	404	0.84	153	15	87	0.11	0.42	136	15	
2014	1	-223	247	0.67	356	15	163	0.08	0.27	142	15
	2	-331	186	0.64	731	16	174	0.08	0.42	155	16
	3	-159	201	0.46	343	13	111	0.12	0.69	129	13
	4	-340	145	0.57	743	12	116	0.14	0.52	252	12
	5	-371	52	0.70	565	12	247	0.09	0.38	285	12
	6	-237	122	0.82	314	13	95	0.12	0.78	94	13
	7	-114	306	0.83	123	16	75	0.12	0.78	50	16
	8	-506	446	0.75	779	15	101	0.13	0.59	134	15
	9	-144	293	0.33	351	16	93	0.13	0.59	148	16
	10	-152	226	0.61	237	12	99	0.13	0.42	251	13
	11	-231	224	0.87	225	13	99	0.13	0.70	140	13
	12	-349	48	0.71	632	12	274	0.07	0.36	186	12
	13	-112	427	0.75	139	15	95	0.10	0.56	80	16
	14	-319	318	0.73	501	15	178	0.08	0.31	169	16
	15	-120	303	0.45	175	15	100	0.12	0.89	61	15
	16	-136	120	0.59	203	13	82	0.13	0.87	59	13
	17	-111	163	0.70	191	13	107	0.10	0.48	139	13
	18	-144	53	0.66	199	11	166	0.08	0.42	123	11

Table S2. Error matrix from the ecosystem classification. The classification is the result of an automated multiresolution segmentation process (eCognition Developer 9.0.2, Trimble) with primary weight on segment size (scale parameter set to 500) as well as shape (set to 0.1) and compactness (set to 0.5). The generated segments were subsequently used as training data (15 segments per class). The classification was based on a supervised maximum likelihood algorithm, trained with aforementioned selected segments. Each class was tested with approx. 30 independent ground control points generated from in-situ registrations (more than 10 control points per class) and visual inspection of the imagery. The high accuracy is due to the limited number of classes, the limited areal coverage, and a significant percentage of the area being covered by user-selected segments.

Class	Affected heath	Fen	Bedrock	Water	Non-affected heath
Affected heath	29	0	0	0	1
Fen	0	29	0	0	1
Bedrock	0	0	28	0	2
Water	1	0	0	28	1
Non-affected heath	3	0	0	0	27
Overall accuracy	0.94				

Paper III

López-Blanco, E., Lund, M., Christensen, T. R., Tamstorf, M. P., Smallman, T. L., Slevin, D., Westergaard-Nielsen, A., Hansen, B. U., Abermann, J., and Williams, M.: **Plant traits are key determinants in buffering the meteorological sensitivity of net carbon exchanges of arctic tundra**, *Journal of Geophysical Research–Biogeosciences*, 123, <https://doi.org/10.1029/2018JG004386>, 2018.



Nuuk-Kobbefjord site, West Greenland. 2015 field season. Photo by Efrén López-Blanco



RESEARCH ARTICLE

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Key Points:

- We calibrated and validated an ecosystem model using field data to predict carbon dynamics over 8 years in West Greenland tundra
- Similar meteorological sensitivity of GPP and R_{eco} leads to buffered NEE
- Plant traits control the compensatory effect observed (and estimated) between gross primary production and ecosystem respiration

Supporting Information:

- Supporting Information S1

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Plant Traits are Key Determinants in Buffering the Meteorological Sensitivity of Net Carbon Exchanges of Arctic Tundra

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Abstract The climate sensitivity of carbon (C) cycling in Arctic terrestrial ecosystems is a major unknown in the Earth system. There is a lack of knowledge about the mechanisms that drive the interactions between photosynthesis, respiration, and changes in C stocks across full annual cycles in Arctic tundra. We use a calibrated and validated model (soil-plant-atmosphere; SPA) to estimate net ecosystem exchange (NEE), gross primary production (GPP), ecosystem respiration (R_{eco}), and internal C processing across eight full years. SPA's carbon flux estimates are validated with observational data obtained from the Greenland Ecosystem Monitoring program in West Greenland tundra. Overall, the model explained 73%, 73%, and 50% of the variance in NEE, GPP, and R_{eco} , respectively, and 85% of the plant greenness variation. Flux data highlighted the insensitivity of growing season NEE to interannual meteorological variability, due to compensatory responses of photosynthesis and ecosystem respiration. In this modelling study, we show that this NEE buffering is the case also for full annual cycles. We show through a sensitivity analysis that plant traits related to nitrogen are likely key determinants in the compensatory response, through simulated links to photosynthesis and plant respiration. Interestingly, we found a similar temperature sensitivity of the trait-flux couplings for GPP and R_{eco} , suggesting that plant traits drive the stabilization of NEE. Further, model analysis indicated that wintertime periods decreased the C sink by 60%, mostly driven by litter heterotrophic respiration. This result emphasizes the importance of wintertime periods and allows a more comprehensive understanding of full annual C dynamics.

1. Introduction

The Arctic tundra, an important element of the global carbon (C) cycle (AMAP, 2017; Hugelius et al., 2014; McGuire et al., 2009; Tarnocai et al., 2009; Williams & Rastetter, 1999), is expected to experience changes in the current global warming context (ACIA, 2005; AMAP, 2017; Callaghan et al., 2012; Christensen et al., 2007; Grøndahl et al., 2008; Meltote et al., 2008; Serreze & Barry, 2011). The likely increase of future temperature, precipitation, and growing season length (Arctic Climate Impact Assessment, 2005; Bintanja & Andry, 2017; IPCC, 2013) may have multiple effects on CO₂ exchange. Increases in plant productivity are expected in response to rising temperatures (Street et al., 2013), under joint warmer and wetter conditions (López-Blanco et al., 2017), or with earlier and longer growing seasons (Aurela et al., 2004; Black et al., 2000; Groendahl et al., 2007). These gains may be counterbalanced by C losses associated with microbial decomposition of soil organic matter during early winter (Commane et al., 2017; Zona et al., 2016) but also during following summer (Helfter et al., 2015; Lund et al., 2012), drought stress on plant photosynthesis under warmer conditions (Goetz et al., 2005; Hanis et al., 2015), higher rates of microbial oxidation of soil organic matter associated with warmer temperatures (Webb et al., 2016), decreases in photosynthesis due to biological disturbances (Heliasz et al., 2011; López-Blanco et al., 2017; Lund et al., 2017), permafrost thaw (Koven et al., 2011; Schuur et al., 2015), or severely burned landscapes (Rocha & Shaver, 2011). Minor variations in relation to these processes can lead to changes in ecosystem C sink functioning.

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It is still a key challenge to understand the interannual variation in net ecosystem exchange (NEE) between the Arctic tundra and the atmosphere due to the large uncertainties between photosynthesis and respiration interactions (McGuire et al., 2012), and how these gross fluxes connect with C storage in vegetation and soil. The task is challenging because of insufficient coverage of measurement sites in the Arctic, particularly across annual cycles. The extreme conditions and remoteness of the Arctic (Kwon et al., 2006; Lafleur et al., 2012; McGuire et al., 2012; Poyatos et al., 2013; van der Molen et al., 2007; Westergaard-Nielsen et al., 2013), but also instrument failures, make automatic and continuous measurements difficult, especially during wintertime (Lund et al., 2012). Frequent gaps in data sets, and the inevitable bias attached to their gap filling (Falge et al., 2001; Moffat et al., 2007; Papale et al., 2006), complicate subsequent analysis because of increased uncertainty. The analysis of the annual impact of driving variables on C fluxes becomes problematic without year-round data (Grøndahl et al., 2008; López-Blanco et al., 2017; van der Molen et al., 2007), and the discussion of C source/sink dynamics is compromised without taking into account nongrowing season processes (Aurela et al., 2004; Commane et al., 2017; Zona et al., 2016).

The process-based understanding of the mechanisms driving the interplay between NEE's competing processes are not yet fully understood. Likewise, there is a lack of knowledge about each of the sub-components contributing to the respiratory losses during both the growing season and the wintertime periods (Hobbie et al., 2000). NEE is usually separated into its two key processes: photosynthesis (gross primary production [GPP]) and ecosystem respiration (R_{eco}) (Lasslop et al., 2010; Reichstein et al., 2005). Similarly, the respiratory loss splits between autotrophic respiration (R_{a} ; the sum of growth [R_{g}] and maintenance [R_{m}] respiration from leaves, stems, and roots) and heterotrophic respiration (R_{h} ; litter and soil organic matter decomposition) (Waring & Schlesinger, 1985). These components change not only within seasons but also from year to year, in response to both biotic and abiotic drivers, and can vary among tissue types (Hopkins et al., 2013; Reich et al., 2008; Tjoelker et al., 2001; Waring & Schlesinger, 1985). The decomposition of gross fluxes in Arctic ecosystems remains unquantified at such high levels of complexity (McGuire et al., 2012). Furthermore, terrestrial ecosystem models frequently assume fixed values of carbon use efficiency (CUE), the proportion of GPP allocated to growth, usually based on a predefined fraction of GPP respired as R_{a} . CUE needs to be sensitive to biological states (such as tissue N concentration), and environmental conditions (Bradford & Crowther, 2013). Without accurate estimates of current carbon fluxes from the Arctic, predicting the response of these systems to global change is challenging (Hobbie et al., 2000). Therefore, studies on C storage and turnover controls are needed and special attention must be paid to dynamic systems including positive feedbacks, which will ultimately lead into a more comprehensive picture of the Arctic ecosystem-atmosphere interactions.

We have previously found that eddy covariance (EC) derived ecosystem flux data suggest an insensitivity to meteorology of growing season NEE across interannual variability (López-Blanco et al., 2017). This insensitivity was despite large variability in temperature and precipitation through the growing seasons. The net CO_2 budget was surprisingly stable compared to the magnitude of variations in GPP and R_{eco} inferred from the eddy flux data. We concluded that the meteorological sensitivity of photosynthesis and ecosystem respiration were similar, and hence compensatory, but we could not explain the causes. This research led to two key questions. First, is this meteorological buffering of NEE also the case over full annual cycles? Second, what determines the meteorological insensitivity of NEE? We hypothesize that plant traits, particularly foliar N, are critical in causing the similar meteorological sensitivities of photosynthesis and respiration. Foliar N mediates both photosynthesis and a major fraction of autotrophic respiration.

In this study we applied a process-based terrestrial ecosystem model, combined with extensive field measurements to simulate year-round C fluxes (and hence CUE) and C stocks in plants and soils, and address these questions. We used the modified, calibrated and validated soil-plant-atmosphere (SPA) model (Williams et al., 1996) to report independent predictions from observational data measured by the Greenland Ecosystem Monitoring (GEM) program (<http://g-e-m.dk/>) in West Greenland tundra (64°N), across 8 years between 2008 and 2015. The Kobbefjord site is currently the southernmost station in the low Arctic Western Greenland equipped for measurement of terrestrial CO_2 exchange. Our aim using this data-model framework was to quantify (1) how realistically the SPA model can simulate growing season C fluxes in Arctic tundra, and the sensitivity of key parameters in calibrating the model; (2) the role of the winter period on the full annual-cycle C balance, to determine if NEE is insensitive to meteorology over full annual cycles;

and (3) untangling the effects of competing ecosystem processes and their links to plant traits, testing the hypothesis that plant N and vegetation properties are important controls on the tight link between GPP and R_{eco} , through the role of N in metabolic processes. Ultimately, discrepancies between model and data emerging from these questions can provide helpful information about knowledge gaps and ecological indicators not previously detected from field observations, emphasizing the unique synergy that models and data are capable of bringing together.

2. Materials and Methods

2.1. Site Description

Kobbefjord is a valley system located in the low Arctic in Western Greenland (64°07'N; 51°21'W). The study area is located ~20 km from Nuuk, Greenland's capital, and has been subjected to extensive environmental research activities since 2007 within the Nuuk Ecological Research Operations program under the auspices of the GEM program (<http://g-e-m.dk/>). The Kobbefjord area presents high meteorological variability from year to year, with a mean annual air temperature of -0.4 °C (ranging between -1.7 °C in 2011 and 3.4 °C in 2010) and a total annual precipitation of about 862 mm between 2008 and 2015 (López-Blanco et al., 2017). There is no continuous permafrost at the site and the annual variation of the maximum snow depth observed in our measurement period was 0.4 to 1.4 m. The water table in Kobbefjord fluctuated between $+0.53$ cm (sign of water abundance at the end of the growing season) and -18 cm (sign of water stress at the peak of the growing season) in the 2010–2015 period. However, no apparent water limitation on C dynamics has been found in the ecosystem, likely resistant to drought due to the water from the surroundings (López-Blanco et al., 2017). The vegetation in the key study site—a fen ecosystem—is dominated by *Eriophorum angustifolium* and *Scirpus caespitosus*, and it is surrounded by heath species such as *Empetrum nigrum*, *Vaccinium uliginosum*, and copse species as *S. glauca* and *Eriophorum angustifolium* (Bay et al., 2008). For more information, see López-Blanco et al., 2017.

2.2. Field Observations: Model Forcing, Calibration, and Validation

First, this research used data from the meteorological towers located at the Kobbefjord site during the 2008–2015 period to drive the SPA model to estimate C fluxes and stocks. The ancillary data (air temperature [T_{air} ; °C], vapor pressure deficit [VPD; kPa] shortwave radiation [SWR; W/m^2], photosynthetic active radiation [PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$], total precipitation [P; mm], and snow coverage [S; %]; Figure S1; hereafter, S denotes additional information) presented gaps no larger than 0.3% for T_{air} and VPD and 10% for SWR, PAR, and P due to poor weather and instrument malfunction. Since the model requires gap-filled inputs, we gap filled the meteorological data using daily ERA-Interim reanalysis (Dee et al., 2011) products (T_{air} , dew point temperature [T_{dp}], P and SWR). The T_{air} and T_{dp} consist of data at 00Z, 06Z, 12Z, and 18Z (instantaneous values). P and SWR consist of data at 00Z and 12Z (totals for the previous 12 hr). We used a weather generator code (full description can be found in Text S1) to apply a diurnal cycle to the T_{air} and SWR variables. PAR was calculated to be twice the SWR. Finally, we resampled the data set from hourly to half-hour temporal resolution for the SPA model.

Further, we performed a 4-week fieldwork campaign between June and July 2015 to obtain site-specific measurements on local aboveground vegetation and soil structure. The footprint analysis performed by Westergaard-Nielsen et al. (2013) suggested an overall contribution of fen (63.9%), heath (23.7%), copse (9.0%), and bedrock (3.4%) to the EC measurements. Therefore, we intentionally selected five plots in the fen site together with three and two more plots from the surrounding heath and copse, respectively. We sampled the aboveground vegetation from 10 plots of $10 \text{ cm} \times 10 \text{ cm}$ square area, and the soil underneath at a maximum depth of 20 cm, within a 100-m radius of the location of the EC tower. The samples were collected on 12 August (1 week earlier than GPP at maximum capacity), frozen, and shipped to the laboratory. In the laboratory, we (1) separated the different tissue types by hand (i.e., leaves, stems, roots, litter, and mosses) from the aboveground biomass and roots from the soil cores, (2) measured the leaf area index (LAI) using Image J (Schneider et al., 2012), (3) dried at 70 °C until constant weight during ~48 hr, (4) weighted the resulting dry samples, (5) subsampled each stock before the carbon and nitrogen (CN) analysis, (6) finely grinded using a ball mixer at maximum frequency (25 Hz) during 2 min, and (7) measured total CN contents using a NC 2500 analyzer. After this, we calculated the leaf mass per area (LMA), total foliar nitrogen and total leaf, stem, root, and litter C content at the harvesting date (Figure S2). Stem here does not strictly refer to

woody material; it is just structural biomass that is not photosynthetic (leaves) or absorbing water/nutrients from the soil (roots). Since our aim was to simulate the observations from the fen site, only data from this eco-type was used to calibrate the vegetation parameters in the model initialization.

We manually calibrated the last 4 years of the time series (2012–2015) and then validated the initial 4 years (2008–2011) including the anomalous year 2011, ensuring that both the calibration and validation data sets do not overlap. The calibration period was specifically selected to exclude the moth outbreak in 2011 to quantify the model-data mismatch introduced by the biological disturbance, which is not represented in the model. The state variables for the earlier 4 years were calibrated based on matching to stocks the final 4 years. The calibration procedure of the model parameters used field data, values retrieved from literature and tuning of turnover rates of the C stocks (Table 1) to match the stock data for the calibration years. Moreover, we targeted NEE, GPP, R_{eco} , and LAI as key variables aiming for a defined, acceptable degree of statistical agreement. The statistical metrics we considered acceptable were (1) $R^2 \geq 0.7$ for NEE, GPP, and LAI (compared with % of Greenness) and ≥ 0.5 for R_{eco} ; (2) $\text{RMSE} \leq 1 \text{ g C m}^{-2} \text{ year}^{-1}$, and (3) mean bias $\leq 1 \text{ g C m}^{-2} \text{ year}^{-1}$ for the simulated period for these four variables.

We used NEE data during the final 4 years for calibration, then used to testing the first 4 years. We processed, gap filled, and partitioned EC data on NEE measured during eight snow-free seasons across the 2008–2015 period. The measurement season is typically scheduled between the snow melt period in spring and the snow freeze-in period at the end of summer. The end of the snow melt period and the growing season start and length present high interannual variability (López-Blanco et al., 2017). In 2014 the EC station suffered a major instrument failure that translated in the loss of half of the growing season data. The EC tower is equipped with a closed-path infrared CO_2 and H_2O gas analyzer LI-7000 (LI-COR Inc., USA) and a 3-D sonic anemometer Gill R3-50 (Gill Instruments Ltd, UK). We processed NEE gap-filled and partitioned NEE using ReddyProc's technique (López-Blanco et al., 2017). In this study, we used the meteorological sign of convention representing uptake and release of C with negative and positive values, respectively.

Moreover, we used a daily estimate of the timing of snowmelt and freeze-in period to constrain the soil temperature during the wintertime, as well as the % of greenness to determine the phenology timing (seasonality) at a pixel level from a time-lapse camera (HP e427) located at 500 m asl. (Westergaard-Nielsen et al., 2013). We used % of greenness to constrain and validate model estimations. Percent of greenness data were used as input in the last 4 years (calibration set) to tune the decay slope after the peak of the growing season of LAI, then used as an independent test only in 2010 and 2011 due to the lack of greenness data in 2008 and 2009. The % of greenness, an index based on the three colors in a digital camera, RedGreenBlue, was computed as $G/(R + G + B)$, which normalizes for changes in illumination. It was recently found that the physical reason for the % of greenness signal was a mix of leaf color, LAI, and the background (Keenan et al., 2014). Additionally, the seasonal greening of the vegetation was measured using a SpectroSense 2+ handheld system with two mounted sensors, which calculates the greening index (normalized difference vegetation index—NDVI) to cross check the % of greenness data from the automatic photo camera in the fen site. Measurements were made 4–5 times across snow-free periods.

2.3. Model Description

This study utilizes process-based modeling at leaf-level scale (parameterization) and canopy-level scale (prediction). The SPA model (Figure 1; Williams et al., 1996) uses a multiple canopy layer approach (up to 10 layers) linking each canopy layer independently to root accessible soil layers (up to 20 layers; Williams et al., 1996). SPA estimates ecosystem fluxes of C, water and energy coupling its leaf level C, water and energy cycles through eco-physiological principles. SPA has been already validated against EC observations in Arctic tundra (Williams et al., 2000) but also in tropical rain forest (Williams et al., 1998), temperate deciduous forests (Williams et al., 1996), or temperate evergreen forests (Williams et al., 2001). The model requires a simple set of measurable meteorological-related variables together with vegetation- and soil-related parameters, completely independent of flux data, against which the model can be compared (Williams et al., 2000). SPA uses a multilayer canopy radiative transfer scheme accounting for both sunlit and shaded leaf area (Williams et al., 1998). Photosynthesis is simulated using a detailed representation of carboxylation (Farquhar & von Caemmerer, 1982). The critical V_{cmax} and J_{max} parameters are linearly related to foliar N. Moreover, the evaporative fluxes (wet surface, soil, and transpiration) are based on the Penman-Monteith model (Jones, 1992). Photosynthesis and transpiration are linked through a stomatal optimization scheme, which aims to

Table 1
Ranking Table Listing the S-Indices (SI) for NEE, GPP, and R_{eco} Subject to the Average $\pm 10\%$ Change of Each of the 36 Ecosystem Parameters in SPA

Parameter	Unit	Function	Value	Source	SI-NEE	SI-GPP	SI- R_{eco}
Initial autotrophic respiration C	g C m ⁻²	IC	0	Field data	0.000	0.000	0.000
Initial foliage C	g C m ⁻²	IC	0	Field data	0.000	0.000	0.000
Root biomass to reach 50% of max depth	g m ⁻²	SS	50	Smallman et al., 2013	0.000	0.000	0.000
Turnover rate of autotrophic respiration pool	hr ⁻¹	CC	0.07	Smallman et al., 2013	0.000	0.000	0.000
Water retained by canopy	mm	WC	1	Williams et al., 1996, 2000	0.000	0.000	0.000
Leaf capacitance	mmol m ⁻² leaf area MPa ⁻¹	CS	4000	Smallman et al., 2013	0.004	0.000	0.001
Stem conductivity	mmol m ⁻¹ s ⁻¹ MPa ⁻¹	CS	5	Smallman et al., 2013	0.008	0.002	0.002
Maximum root depth	m	SS	0.5	Smallman et al., 2013	0.015	0.000	0.002
Minimum temperature threshold	deg C	PH	10	van der Kolk et al., 2016	0.031	0.008	0.006
Minimum leaf water potential	MPa	WC	-1.5	Williams et al., 2000	0.037	0.008	0.004
Turnover rate of wood	hr ⁻¹	CC	0.000008	Tuned	0.045	0.000	0.005
Precipitation that penetrates canopy	fraction	WC	0.7	Williams et al., 1996, 2000	0.048	0.000	0.006
Root resistivity	MPa s g mmol ⁻¹	CS	20	Smallman et al., 2013	0.049	0.005	0.000
Initial wood C	g C m ⁻²	IC	70	Field data	0.070	0.000	0.008
Width of leaf	m	CS	0.02	Williams et al., 2000	0.078	0.022	0.015
GDD threshold	deg C	PH	10	Shulski and Wendler, 2007	0.092	0.021	0.014
Decomposition rate	hr ⁻¹	CC	0.000004	Smallman et al., 2013	0.155	0.000	0.018
Initial labile C	g C m ⁻²	IC	13	Tuned	0.176	0.056	0.043
Turnover rate of foliage	hr ⁻¹	CC	0.0029	Hobbie et al., 2000	0.324	0.084	0.058
Respiratory cost of labile transfers	fraction	CC	0.129	Smallman et al., 2013	0.373	0.058	0.023
Stomatal efficiency parameter	$\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O m}^{-2} \text{ s}^{-1}$	WC	1.007	Smallman et al., 2013	0.407	0.059	0.010
Turnover rate of fine roots	hr ⁻²	CC	0.000009	Sloan et al., 2013	0.440	0.036	0.089
Initial litter C	g C m ⁻²	IC	60	Field data	0.499	0.000	0.056
Mineralization rate of litter	hr ⁻¹	CC	0.000055	Tuned	0.585	0.000	0.065
Turnover rate of labile pool	hr ⁻¹	CC	0.0022	Tuned	0.629	0.131	0.075
NPP allocated to foliage	fraction	CC	0.7	Smallman et al., 2013	0.713	0.147	0.084
Fraction of leaf loss to litter	fraction	CC	0.3	Tuned	0.963	0.166	0.077
NPP allocated to roots	fraction	CC	0.7	Smallman et al., 2013	1.052	0.033	0.080
Mineralization rate of SOM	hr ⁻¹	CC	0.000001	Tuned	1.259	0.000	0.140
Rate coefficient for V_{cmax}	$\mu\text{mol C g N}^{-1} \text{ s}^{-1}$	PT	14	Smallman et al., 2013	1.334	0.227	0.104
Initial SOM C	g C m ⁻²	IC	4800	Hugelius et al., 2013	1.346	0.001	0.150
Initial root C	g C m ⁻²	IC	200	Field data	1.584	0.047	0.124
Average foliar nitrogen	g N m ⁻²	CS	1.61	Field data	3.154	0.916	0.667
Maximum foliar carbon stock	g C m ⁻²	CC	28	Field data	3.868	0.922	0.595
Rate coefficient for J_{max}	$\mu\text{mol C g N}^{-1} \text{ s}^{-1}$	PT	36	Smallman et al., 2013	4.432	0.786	0.369
Leaf mass per area	g C m ⁻²	CS	56.27	Field data	4.546	1.137	0.769

Note. The table orders the S-indices (NEE) starting with the lowest value and increasing to the highest value. The function column classifies the parameters based on their role, that is, photosynthetic (PT), C cycle (CC), water cycle (WC), initial conditions (IC), canopy structure (CS), soil structure (SS), and phenology (PH). The colors represent how sensitive the parameter is to the response variable: green = little sensitive; red = very sensitive. A further test of the four most sensitive parameters is proposed in Figure 6 (pink highlight).

maximize C accumulation within SPA's hydraulic limitations. SPA simulates both the vertical distribution and movement of water and heat through the soil profile. A detailed overview of SPA can be found in Smallman et al. (2013). Plant phenology and carbon dynamics are simulated using a box carbon model, the Data Assimilation Linked Ecosystem Carbon model imbedded within the SPA framework, which simulates the states and dynamics of ecosystem C stocks (foliage, structural/wood carbon, fine roots, labile carbon, soil organic matter (SOM), and surface litter) (Williams et al., 2005). In SPA, the unique allocations groupings are (1) foliar allocation is a fixed fraction from NPP (Table 1; NPP allocated to foliage), dependent on growing degree day summation, restarting from the snow melt period (retrieved from the photo monitoring) and (2) stem and root allocation are dependent on a fixed fraction from NPP (Table 1; NPP

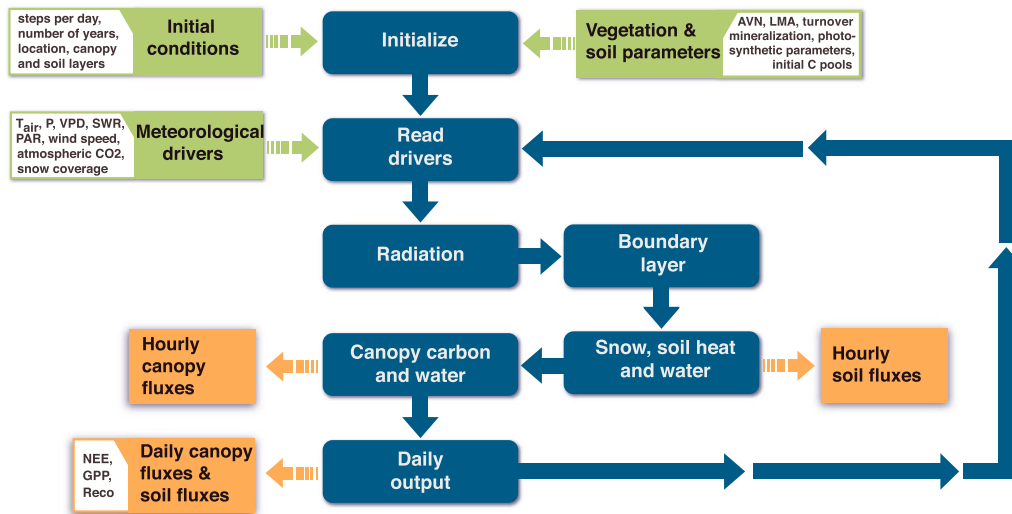


Figure 1. Schematic description of the soil-plant-atmosphere model. The blue boxes represent the key model components, while the green boxes the model inputs and the orange boxes the model outputs.

allocated to roots, while NPP allocated to stems is 1-NPP allocated to roots). The plant phenology in SPA is entirely driven by meteorological forcing unless stated otherwise. The unique turnover groupings are (1) foliar turnover, driven by a minimum temperature threshold (Table 1) and a predefined day at the end of August and (2) roots and stem represented as a constant loss fraction assuming first-order kinetics. Litter decomposition to SOM, litter mineralization ($R_{h \text{ litter}}$) and SOM mineralization ($R_{h \text{ som}}$) follow a similar continuous decay process with exponential temperature adjustment. Leaves and fine root mortality is directly input to the litter stock, while woody mortality is directly input to the SOM stock. Thus we assume different labilities for the dead organic C depending on tissue source. The collected data were used to parameterize and evaluate the Arctic specific branch in SPA in order to simulate the full range of biogeochemical feedbacks in West Greenland.

The model has been modified to introduce a revised C allocation approach, which separately estimates respiration associated with growth (R_g) and maintenance (R_m) respiration. Growth respiration is assumed to be a fixed fraction of C allocated to each tissue using the following equations:

$$R_{g \text{ leaf}} = (GPP_{\text{leaf}} * R_g \text{ frac}); NPP_{\text{leaf}} = \text{alloc}_{\text{leaf}} - R_{g \text{ leaf}} \quad (1)$$

$$R_{g \text{ root}} = (GPP_{\text{roots}} * R_g \text{ frac}); NPP_{\text{root}} = \text{alloc}_{\text{roots}} - R_{g \text{ root}} \quad (2)$$

$$R_{g \text{ stem}} = (GPP_{\text{stem}} * R_g \text{ frac}); NPP_{\text{stem}} = \text{alloc}_{\text{stem}} - R_{g \text{ stem}} \quad (3)$$

where R_g is assumed to be a fixed fraction of C allocated (alloc) to a given tissue ($R_g \text{ frac}$) equivalent to 21% of NPP (Waring & Schlesinger, 1985). Further, maintenance respiration (R_m) has been calculated based on a modified version of the Reich et al. (2008) calculation in SPA, which demonstrated a strong respiration-nitrogen (N) relationship among tissue types (leaves, stems, and roots). The R_m in leaves has been calculated based on air temperature, average foliar N, leaf C per area, and LAI, only when the air temperatures $>0^\circ\text{C}$. R_m in roots was calculated based on soil temperatures at 10 cm depth, the C:N relation in roots and the root C stock, following the same freezing point limitation. Finally, a brief description of the equations showing the different components of the C fluxes related to each other is provided in the supporting information equation S1.

The snowpack thickness has a direct influence on soil temperatures and consequently on respiration processes. Therefore, we also implemented a snow cover subroutine in order to constrain soil temperature across wintertime periods. We used snow fraction information (Figure S3) recorded from the camera pointing towards the fen site (Westergaard-Nielsen et al., 2013) to inform a simplified version of the snow scheme by

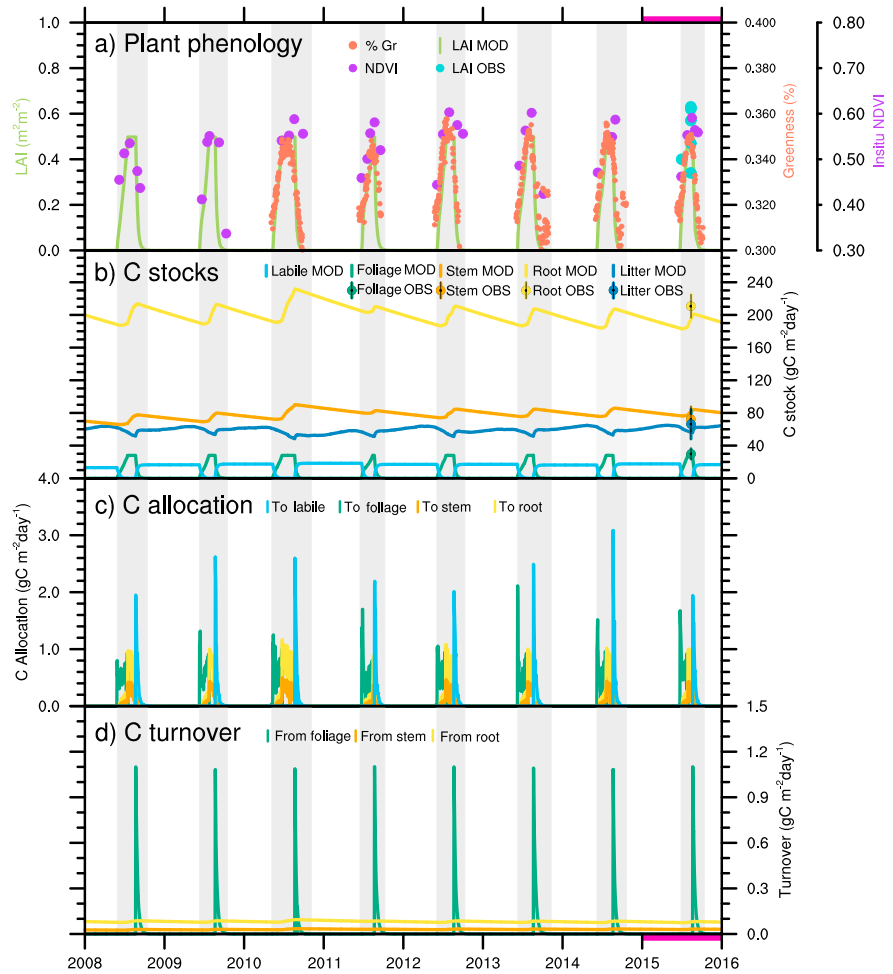


Figure 2. Time-series of observed (OBS) and predicted (MOD) plant phenology (%Gr, % of greenness; NDVI, in situ normalized difference vegetation index; LAI, leaf area index) (a) and C stocks (labile, foliage, stem, root, and litter) (b), as well as simulated C allocation (to labile, foliage, stem, and root) (c) and C turnover [from foliage, stem, and root] (d). The gray shading denotes the snow-free period reported in López-Blanco et al. (2017). The 2015 C dynamics (pink highlights) are presented in detail in Figure S5.

Essery (2015). The modified snow scheme used snow fractional cover to update the soil surface energy balance including albedo, evaporative, and sensible heat exchanges.

2.4. Sensitivity Analysis

We conducted a sensitivity analysis of the vegetation related parameters used in SPA to determine how critical each is to the estimation of NEE, GPP, and R_{eco} . By identifying how sensitive NEE, GPP and R_{eco} are to changes in each of the 36 parameters, we identify potential model limitations of the simulated C dynamics (e.g., C allocation, C turnover, phenology, and seasonality). The sensitivity analysis also helps to test the robustness of model outputs in presence of uncertainty. We first determined 36 nominal parameters values (Table 1) and confirmed that these generate reasonable model fluxes compared to the flux tower data. We decided our response variables for the sensitivity analysis as total annual NEE, GPP, and R_{eco} . In sequence, we modified each parameter $\pm 10\%$. We evaluated the percentage change in the response variable. The ratio of the % change in response variable to % change in parameter is the sensitivity index (SI), such that if $|SI| > 1$ [$|SI| = \text{magnitude of } S$], the parameter is very sensitive to the response variable; close to 0 means little sensitivity. We tested the sensitivity analysis for the entire data set and for each year independently. Additionally, we assessed the relationships between the four most sensitive parameters in the model

Table 2

Statistics of Linear Fit Between the SPA Model (Independent) and the Field Observations (Dependent) per Individual Year and for the Entire 2008–2015 Period

Statistics	Validation set					Calibration set	
	2008	2009	2010	2011	2008–2011	2012	
NEE	Intercept	−0.12 (−0.16/−0.07)	−0.12 (−0.16/−0.08)	−0.23 (−0.29/−0.18)	−0.16 (−0.21/−0.1)	−0.17 (−0.19/−0.14)	−0.08 (−0.12/−0.04)
	Slope	0.66 (0.59/0.72)	0.83 (0.76/0.9)	0.63 (0.57/0.69)	0.52 (0.42/0.62)	0.65 (0.61/0.68)	0.52 (0.48/0.56)
	R ²	0.72	0.76	0.74	0.42	0.7	0.8
	RMSE	0.28	0.26	0.35	0.31	0.31	0.24
	Bias	−0.02	−0.1	−0.18	−0.28	−0.15	0.03
GPP	Intercept	0.06 (−0.06/0.18)	0.24 (0.13/0.35)	0.16 (0.01/0.31)	0.12 (−0.02/0.26)	0.15 (0.09/0.22)	0.16 (0.05/0.27)
	Slope	0.96 (0.89/1.04)	1 (0.97/1.13)	0.95 (0.88/1.03)	0.88 (0.74/1.02)	0.97 (0.93/1.01)	0.59 (0.54/0.63)
	R ²	0.82	0.8	0.79	0.51	0.77	0.84
	RMSE	0.46	0.47	0.54	0.54	0.51	0.43
	Bias	0.11	0.19	0.23	0.21	0.19	1.01
Reco	Intercept	−0.28 (−0.35/−0.2)	−0.19 (−0.23/−0.14)	−0.14 (−0.22/−0.07)	−0.29 (−0.34/−0.25)	−0.21 (−0.24/−0.18)	−0.18 (−0.25/−0.12)
	Slope	0.88 (0.79/0.97)	0.88 (0.82/0.94)	0.7 (0.63/0.77)	0.79 (0.73/0.85)	0.78 (0.74/0.81)	0.43 (0.39/0.47)
	R ²	0.52	0.72	0.55	0.66	0.59	0.56
	RMSE	0.36	0.26	0.42	0.22	0.33	0.35
	Bias	−0.37	−0.26	−0.42	−0.44	−0.37	−0.96
LAI	Intercept	—	—	0.31 (0.31/0.31)	0.32 (0.31/0.32)	0.31 (0.31/0.32)	0.32 (0.31/0.32)
	Slope	—	—	0.06 (0.06/0.07)	0.06 (0.05/0.06)	0.06 (0.06/0.06)	0.07 (0.06/0.08)
	R ²	—	—	0.90	0.75	0.83	0.88
	RMSE	—	—	0.00	0.01	0.01	0.01
	Bias	—	—	0.03	0.11	0.06	0.07

Note. The data set was divided into a calibration set (2008–2011) and a validation set (2012–2015). The presented statistics are from a model run entirely driven by environmental data, based on growing degree day summation restarted from the snow melt period and minimum temperature threshold, both calculated from soil temperatures at 10 cm depth. The parentheses represent the 95% confidence interval for the intercepts and slopes. The units for RMSE and bias are $\text{g C m}^{-2} \text{ year}^{-1}$ in NEE, GPP, and R_{eco} , and $\text{m}^2 \text{ m}^{-2}$ in LAI.

against mean annual temperature. This assessment tested whether the sensitivity of both GPP and R_{eco} to plant traits is coupled or decoupled across meteorological variation. We hypothesized that the metabolic processes (photosynthesis and autotrophic respiration) that are coupled by plant traits in the model would have similar temperature sensitivity.

3. Results

The SPA model performed well in simulating the observed plant phenology (Figure 2a and Table 2) and C fluxes (Figure 3 and Table 2), tracking the variations observed across multiseasonal and multiannual periods. We modelled full annual C dynamics despite the lack of field observations during winter by implementing a snow cover subroutine constrained by snow fraction data (Figure S3). The data constraint improved substantially soil temperature estimations (Figure S4), and as such it enhanced confidence across the wintertime period. We found that SPA supports the main finding from our previous analysis on flux responses to meteorological variations and biological disturbance using observational data only (López-Blanco et al., 2017). In this study, large meteorological variability across the full annual 2008–2015 period led to a strong coupling between modelled photosynthetic inputs and respiration outputs and thus also stability of net C uptake (Figure 4). Wintertime plays an important role in the annual C budget by decreasing the C sink strength, mainly through sustained R_{eco} rates driven by C litter decomposition. We also note evidence that heterotrophic respiration dominates the shoulders of the growing seasons (wintertime, early spring, and late autumn), while growth and maintenance respiration are more important between greenup and greendown (Figure 5). From our sensitivity analysis of vegetation-related input parameters, it emerges that plant traits are important controllers in the interannual gross flux variability (Table 1). Also, we found that the sensitivity of both GPP and R_{eco} to changes in plant traits was coupled across meteorological variation (Figure 6).

3.1. Sensitivity and Quality of Modelled C Fluxes and Stocks

In this study, % of greenness data were used to constrain LAI simulated in SPA, defining the timing of the plant phenology at the beginning and at the end of the growing season (Figure 2a and Table 2). The % of

Table 2 (continued)

Statistics	Calibration set				Total	
	2013	2014	2015	2012–2015	2008–2015	
NEE	Intercept	−0.1 (−0.14/−0.07)	0.02 (−0.05/0.1)	−0.1 (−0.15/−0.05)	−0.09 (−0.11/−0.06)	−0.13 (−0.15/−0.11)
	Slope	0.55 (0.51/0.59)	0.67 (0.59/0.75)	0.62 (0.56/0.68)	0.56 (0.54/0.59)	0.6 (0.57/0.62)
	R ²	0.85	0.82	0.8	0.81	0.73
	RMSE	0.21	0.25	0.25	0.24	0.29
	Bias	−0.02	0.19	−0.01	0.02	−0.07
GPP	Intercept	0.28 (0.2/0.36)	0.6 (0.35/0.85)	0.25 (0.12/0.38)	0.17 (0.11/0.24)	0.08 (0.02/0.13)
	Slope	0.8 (0.75/0.84)	1.1 (0.95/1.2)	0.75 (0.69/0.81)	0.69 (0.66/0.72)	0.76 (0.73/0.79)
	R ²	0.91	0.84	0.83	0.81	0.73
	RMSE	0.31	0.41	0.4	0.45	0.55
	Bias	0.59	0.47	0.67	0.73	0.42
Reco	Intercept	−0.28 (−0.33/−0.24)	−1.1 (−1.22/−0.95)	−0.23 (−0.27/−0.18)	−0.2 (−0.23/−0.16)	−0.16 (−0.18/−0.14)
	Slope	0.73 (0.68/0.77)	1.4 (1.3/1.6)	0.6 (0.56/0.64)	0.53 (0.5/0.56)	0.59 (0.56/0.61)
	R ²	0.73	0.56	0.7	0.52	0.5
	RMSE	0.24	0.34	0.24	0.34	0.36
	Bias	−0.51	−0.66	−0.57	−0.67	−0.52
LAI	Intercept	0.31 (0.31/0.31)	0.31 (0.31/0.32)	0.31 (0.31/0.32)	0.31 (0.31/0.31)	0.31 (0.31/0.31)
	Slope	0.07 (0.07/0.08)	0.07 (0.07/0.08)	0.07 (0.07/0.08)	0.07 (0.07/0.08)	0.07 (0.06/0.07)
	R ²	0.87	0.88	0.90	0.88	0.85
	RMSE	0.01	0.01	0.00	0.01	0.01
	Bias	0.12	0.08	0.12	0.10	0.08

greenness is only shown within the snow-free period, defined by the gray boxes across the entire time series. The modelled LAI was able to represent ~85% of the % of greenness variability (Table 2). The calibration set (2012–2015) has larger degree of agreement ($R^2 = 0.88$) compared to the validation set (2010–2011; $R^2 = 0.83$). NPP allocated to foliage, photosynthetic parameters, turnover rate of foliage, and maximum foliar carbon stock were key parameters used to fit the observations (Table 1). The modelled C stocks obtained from the labile, foliage, stem, root, and litter stocks and the observational data points from the field campaign in 2015 are included as mean \pm range (Figure 2b). The field data on C stocks was used to establish a benchmark for each C stock at the modelled time step, assuming steady state conditions. The manual calibration aimed to have the modelled C stock inside the observations' ranges. Estimated C foliage, C stem, C roots, and C litter were within the observed thresholds (Figures 2b and S5). NPP allocated to foliage and roots (Figure 2c), as well as all the turnover rate parameters (Figure 2d) and the initial C stocks were key to estimating ecosystem C stocks.

The SPA estimates of C fluxes across eight snow-free periods were validated against the flux data presented in López-Blanco et al. (2017; Figure 3). The model represented ~73%, ~73%, and 50% of the variability in NEE, GPP, and R_{eco} , respectively (Table 2). The calibration set has a larger degree of agreement ($R^2 = 0.81, 0.81$ and $RMSE = 0.24, 0.45$ for NEE and GPP, respectively) compared to the validation set ($R^2 = 0.70, 0.77$ and $RMSE = 0.24, 0.45$), except for R_{eco} ($R^2 = 0.52$ in calibration versus $R^2 = 0.59$ in validation; Table 2). The mean annual NEE during the 2008–2015 period was -17.2 g C m^{-2} (range -33.8 to 5.3 g C m^{-2}), while mean GPP was $-147.9 \text{ g C m}^{-2}$ (-92.8 to $-219.4 \text{ g C m}^{-2}$) and mean R_{eco} was 130.7 g C m^{-2} (98.1 to 185.6 g C m^{-2} ; Table 3). In general, the model captured the initial respiration peak of the growing season (Figure 3a) and the beginning of the growing season ($R^2 = 0.85, p < 0.001$), followed by a short but intensive C uptake period (Figures 3a and 3c). However, Figures 3b and 3d also show the biases observed due to difference in timing (shifts of peak of the growing season in 2010 R_{eco} and 2011 NEE for example) and differences in flux magnitudes (such as 2012 GPP and R_{eco}). Overall, SPA tended to overestimate NEE (i.e., higher C uptake) by 13%, while GPP and R_{eco} were underestimated (i.e., lower photosynthetic and respiration rates) by 28% and 36%, respectively.

LMA, rate coefficient for J_{max} (J_{max}), maximum foliar mass, and foliar nitrogen (N) are the four most sensitive parameters in SPA for the simulation NEE, GPP, and R_{eco} under the current setup (Table 1). For example, the S-

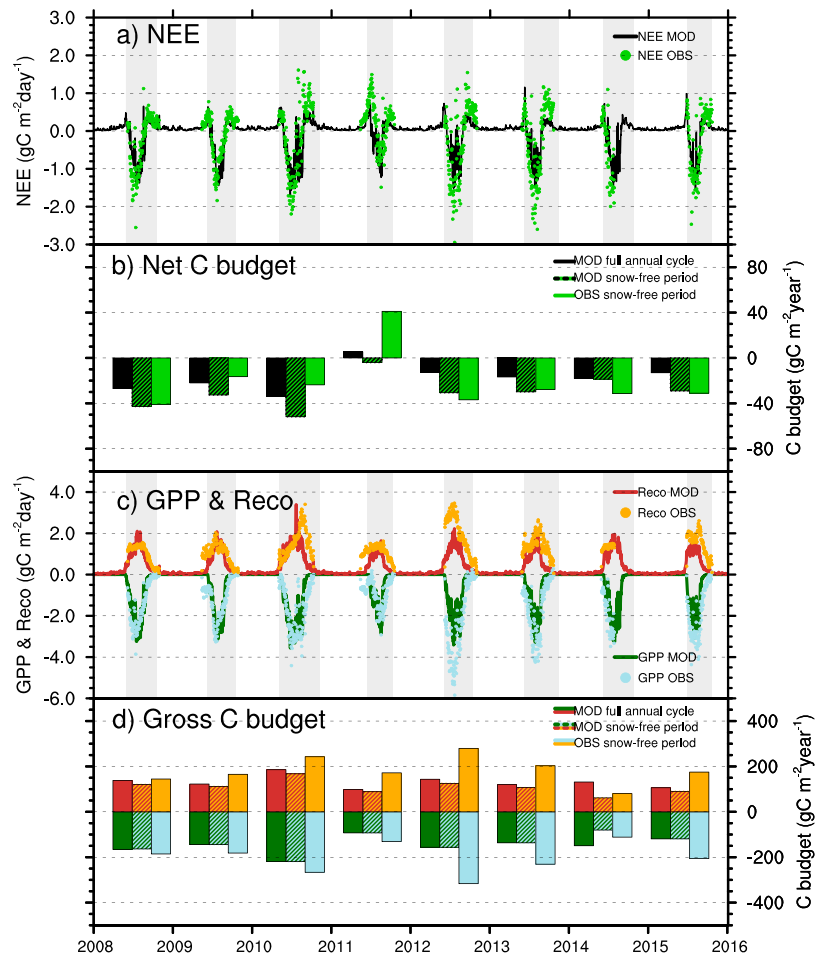


Figure 3. Time series (a and c) and full annual budgets (b and d) of observed (OBS) and predicted (MOD) C fluxes (NEE, net ecosystem exchange; GPP, gross primary production; and R_{eco} , ecosystem respiration).

index of LMA ($SI-NEE = 4.55$) denotes that if this parameter increases 1%, C fluxes will experience a shift of 4.55%. Interestingly, NEE, GPP, and R_{eco} experienced a similar sensitivity pattern, and $SI-GPP$ and $SI-R_{eco}$ were in the same order of magnitude. LMA, maximum foliar mass, and foliar N are field observations collected in the 2015 field campaign; thus, this sensitivity analysis demonstrates how field data can help to improve the model certainty over key parameters. However, there are other calibrated parameters such as mineralization rate of SOM or fraction of leaf loss to litter that are relatively sensitive for the modelled C fluxes, denoting site-specific characteristics with likely high uncertainty if they are applied to different conditions/locations. Ideally, the calibrated parameters need to be replaced by field measurements from similar conditions to improve the certainty around the SPA runs in case model is to be applied to other sites.

3.2. The Role of the Winter Period on the Full Annual-Cycle C Balance

The SPA model quantifies the wintertime period in the annual C budget. The addition of the respiratory losses across wintertime periods shifted NEE significantly by decreasing the C sink strength $\sim 60\%$ (Figures 3b, 3d, and 4) and increasing 22.7% the annual soil respiration ($R_{g\ root} + R_{m\ root} + R_{h\ litter} + R_{h\ soil\ organic\ matter}$) excluding the June–September period. Interestingly, the partitioning of these wintertime respiration losses indicates that $R_{h\ litter}$ was the largest contributor with 43.3% to the annual budget. During winter, the only two flux contributions to NEE were derived from litter and SOM decomposition, both parts of the heterotrophic

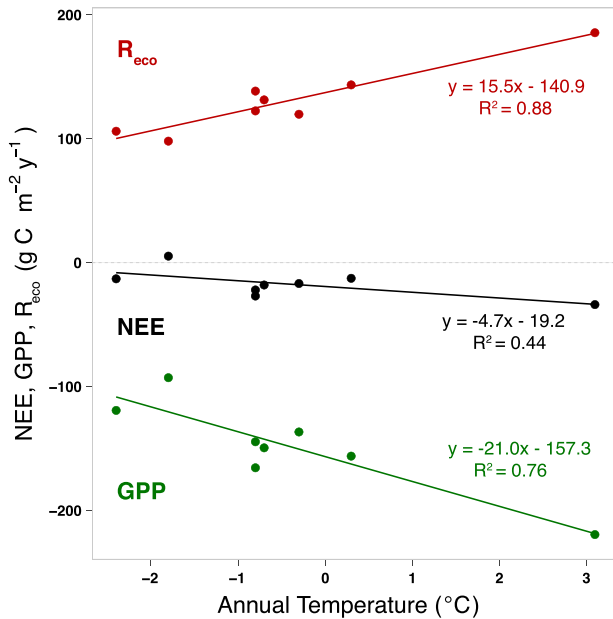


Figure 4. The relationship between estimated annual NEE (black), GPP (dark green), R_{eco} (dark red) ($\text{g C m}^{-2} \text{ year}^{-1}$) and mean annual temperature ($^{\circ}\text{C}$) for the years 2008–2015. Linear regressions are shown for each flux against temperature, including equations and R^2 values.

respiration (R_h ; Figure 5a; Equation S1). The contribution from litter decomposition to the annual budget is 2-fold larger than from SOM (27% versus 15%). Moreover, in Arctic ecosystems there are two key periods with large respiratory losses (i.e., large positive NEE) in the transition between summer and the shoulder seasons (Figure 3a). The first peak is between the end of the snow melt period and the beginning of growing season, while the second one is observed between the end of the growing season and the freeze-in period. The model suggests that the first peak of positive NEE was driven by air temperature ($R^2 = 0.77, p < 0.001$), while the second peak was driven by the accumulation of litter stock ($R^2 = 0.74, p < 0.001$). These two processes occurred in spring and fall together with the respiration produced by litter and SOM in winter are the main contributors to the decrease of C sink strength.

Since the validation of wintertime fluxes remains challenging due to the lack of field data, we constrained the snow cover, one of the most important controllers of the wintertime period in Arctic ecosystems, and its direct influence on soil temperature and therefore the C fluxes. The agreement between observed and modelled soil temperatures at 10 cm depth was $\sim 94\%$ with snow cover routine employed and $\sim 65\%$ without (Figure S4). The major improvement on the model simulations was for wintertime soil temperatures, which on average increased from -9.1 to -0.6 $^{\circ}\text{C}$ (observations were -0.3 $^{\circ}\text{C}$) for the January–April period and from -0.6 $^{\circ}\text{C}$ to $+2.4$ $^{\circ}\text{C}$ (observations were $+2.8$ $^{\circ}\text{C}$) for the November–December period. Moreover, these changes in soil temperature (i.e., warmer temperatures in wintertime) have increased R_h (litter + SOM) $\sim 8\%$

due to the insulation effect from snow.

3.3. Partitioning the Processes Contributing to NEE and Their Meteorological Sensitivity

We found that SPA supports the main finding from our previous analysis on flux responses to meteorological variations and biological disturbance (López-Blanco et al., 2017). The net C uptake insensitivity found across meteorologically diverse growing seasons and full annual cycles here is also driven by the compensation between photosynthesis (GPP) and the sum of respiration losses (R_{eco} ; Figures 4 and 5). The model suggests stronger and steeper correlations between annual GPP ($R^2 = 0.75$, slope = $21 \text{ g C m}^{-2} \text{ year}^{-1} \text{ }^{\circ}\text{C}$) and R_{eco} ($R^2 = 0.88$, slope = $15 \text{ g C m}^{-2} \text{ year}^{-1} \text{ }^{\circ}\text{C}$) with annual temperatures compared to NEE-temperature ($R^2 = 0.44$ and slope = $5 \text{ g C m}^{-2} \text{ year}^{-1} \text{ }^{\circ}\text{C}$; Figure 4). These results reinforce previous findings demonstrating a relative insensitivity of NEE to meteorological drivers, due to the compensatory effect between GPP and R_{eco} shown here. A linear regression of annual R_{eco} on GPP shows a strong correlation, $R^2 = 0.96$. We note evidence that R_h dominates the outer shoulders (wintertime, early spring, and late autumn), while R_g and R_m are more important during the growing season (Figure 5a). In summer, plant growth increased R_a . Annually aggregated data suggest that when R_a was dominating over R_h , there was a tight link between GPP and R_{eco} . The annual data also reflect a strong relationship between GPP and R_a ($R_m + R_g$) ($R^2 = 0.97, p < 0.001$). Phenology drivers such as beginning of the growing season ($R^2 = 0.88$ and $0.82, p < 0.001$) and snow melt period ($R^2 = 0.82$ and $0.89, p < 0.001$) played an important role in the GPP and R_a dynamics, respectively (Figure S6). We also found a significant correlation between GPP and R_h ($R^2 = 0.89, p < 0.001$), influenced by the amount of litter deposited each year (proportional to GPP), as noted from the major contribution from litter decomposition to R_h . Overall, annual photosynthetic inputs dominate the sum of the respiration outputs ($R_g + R_m + R_h$) except in 2011 (Figure 5b).

Interestingly, the model quantified a decrease of 20% in the annual CUE for 2011. This decrease was directly related to a significant decrease of GPP (40%) and R_a (34%) compared to the rest of the years (Table 3). Moreover, annual R_h increased its contribution to NEE $\sim 18\%$ in 2011, likely induced by the late snow melt period. These estimations are the result of a marked variability of meteorological conditions between 2010 and 2011. Even though the Kobbefjord area was associated with a major larvae outbreak (Lund et al., 2017), the

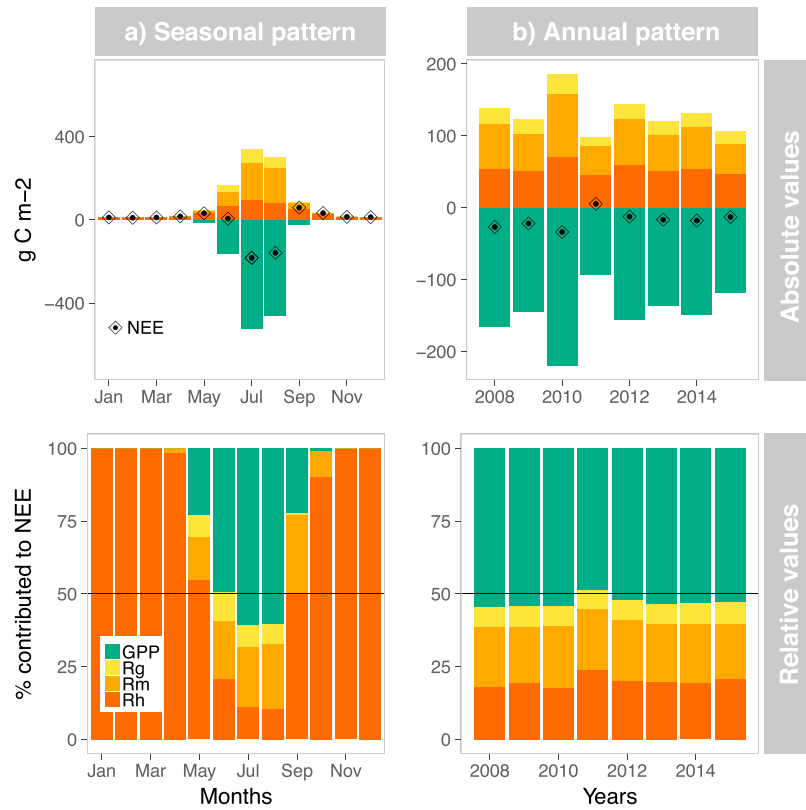


Figure 5. Seasonal (a) and annual (b) partitioned modelled gross fluxes (GPP, gross primary production; R_g , growth respiration; R_m , maintenance respiration; and R_h , heterotrophic respiration). The upper set shows absolute values including superimposed monthly and annual NEEs. The bottom set shows relative values (i.e., the % contributed of gross fluxes to NEE) highlighting the balance between inputs (productivity) and outputs (respiration).

model unexpectedly captured the seasonality of NEE without any prescription in the model structure on biological disturbances. The model was able to estimate similar NEE ($R^2 = 0.76$, $p < 0.001$), GPP ($R^2 = 0.80$, $p < 0.001$) and R_{eco} ($R^2 = 0.65$, $p < 0.001$) in 2011 when we run the C uptake seasonality in SPA forced by the % of greenness data instead (compared to the regular set up; $R^2 = 0.42$, 0.51 and 0.66 , $p < 0.001$ respectively; Table 2). The NEE estimates from this synthetic setup (18 g C m^{-2}) were still not close to the field measurements (40 g C m^{-2}), but they were better than environmental driven runs (5 g C m^{-2}). Therefore, SPA quantifies the likely effect on 2011 NEE as 45% meteorological driven and 55% contributed by the moth outbreak in 2011 from the difference between the phenology driven run and the field observations. This finding suggests a joint, relatively equal influence from both the meteorological drivers and the biological disturbance.

3.4. The Plant Traits Effect on Buffering the Interannual NEE Variability

We found that both GPP and R_{eco} are sensitive to annual temperature variability, while NEE is much less sensitive due to compensatory effects (Figure 4). In order to understand the reason of this compensation, we hypothesized that plant traits couple the two processes closely and lead to compensation. Plant traits such as LMA, rate coefficient for J_{max} , maximum leaf mass, and foliar N are the most sensitive controls on both GPP and R_{eco} shown by the sensitivity analysis (Table 1), which provides some support for our hypothesis. For further testing, we repeated the sensitivity experiments for individual years (2008–2015) and these four plant traits (Figure 6). We assessed the regression lines describing the change in GPP and R_{eco} trait sensitivity to mean annual temperature using two analysis of covariance tests with and without the interaction between GPP and R_{eco} . The models with interaction were not significantly different, which suggests the slopes of the relationships do not differ between GPP and R_{eco} fits. Thus, the emergent relative temperature sensitivity of

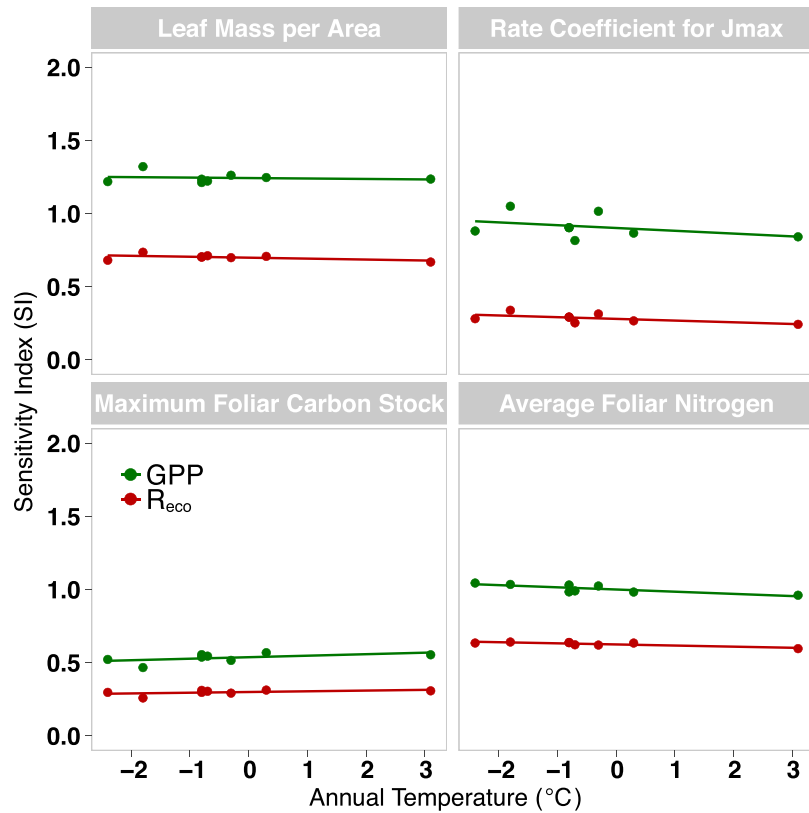


Figure 6. Sensitivity variability of the four most sensitive parameters in soil-plant-atmosphere (shown in Table 1) compared to the mean annual temperature through the analyzed years (2008–2015).

these processes, and therefore compensation, is maintained despite potential year to year or spatial differences in plant traits.

4. Discussion

The SPA model has been implemented, calibrated, and validated to explore the challenges in process based understanding of C cycling in Arctic ecosystems at high temporal resolution (i.e., half-hourly time

Table 3
Annual Average of Main Ecosystem C Fluxes NEE, GPP, NPP and R_{eco}

Years	NEE	GPP	NPP	R _{eco}	R _m leaf	R _m root	R _g leaf	R _g root	R _g stem	R _h litter	R _h som	CUE
2008	-26.9	-165.5	-80.8	138.5	43.4	19.2	7.8	9.2	4	36.1	18.8	0.49
2009	-22	-144.5	-70.4	122.5	34.7	16.4	7.8	8.2	3.5	34.2	17.6	0.49
2010	-33.8	-219.4	-104.8	185.6	59.9	27.2	7.8	13.6	5.8	43.7	27.5	0.48
2011	5.3	-92.8	-35.2	98.1	25	15.3	7.8	3.1	1.3	29.6	16	0.38
2012	-12.6	-156.1	-71.5	143.5	43.1	20.5	7.9	8.4	3.6	38.1	21.9	0.46
2013	-16.8	-136.6	-64.3	119.8	35.1	15.7	7.8	7.3	3.1	33.1	17.5	0.47
2014	-18	-149.4	-70	131.4	39.5	17.7	7.8	8.1	3.5	35.2	19.5	0.47
2015	-13	-119.2	-56.9	106.1	28.2	14.3	7.8	6.3	2.7	31	15.9	0.48
Mean 2008–2015	-17.2	-147.9	-69.2	130.7	38.6	18.3	7.8	8.0	3.4	35.1	19.3	0.47
Min 2008–2015	-33.8	-219.4	-104.8	98.1	25.0	14.3	7.8	3.1	1.3	29.6	15.9	0.38
Max 2008–2015	5.3	-92.8	-35.2	185.6	59.9	27.2	7.9	13.6	5.8	43.7	27.5	0.49

Note. NPP is defined as $NPP = GPP - R_g$. R_{eco} sub-subcomponents split between the autotrophic respiration (R_g; the sum of growth (R_g) and maintenance (R_m) respiration from leaves, stems and roots) and heterotrophic respiration (R_h; litter and soil organic matter decomposition). Carbon use efficiency (CUE) is defined as $CUE = 1 - ((R_m + R_g)/GPP)$. The units for all variables are g C m⁻² year⁻¹ except for CUE (dimensionless).

steps). The model captured well multiseason and multiannual variability of plant phenology and C dynamics compared to field observations. The results here are in line with a previous study showing meteorology driven insensitivity of NEE based on the coupling between GPP and R_{eco} , also throughout full annual cycles. However, the results from this paper also point to plant traits as key controls in the compensatory effect between GPP and ecosystem respiration. This study emphasizes the significance of integration between field observations and process-based modeling to advance our understating of ecosystem carbon dynamics.

4.1. Quality and Limitations of Modelled C Fluxes and Stocks

The SPA model demonstrated a coherent performance of basic C fluxes, stocks and plant phenology against the independent in situ data provided by the GEM program (Figures 2a and 2b, Figure 3, and Table 2). In this modeling exercise, three important sources of data are vital for model performance: (1) plant phenology (i.e., the % of greenness; Figure 2a and Table 2); (2) the snow fraction information (Figure S3), both derived from an inexpensive optical camera (Westergaard-Nielsen et al., 2013; Westergaard-Nielsen et al., 2017); and (3) the foliar N content and LMA data from the field campaign (Figure S2 and Table 1). On the one hand, the fit between observed and modeled beginning of the growing season ($R^2 = 0.92$; $p < 0.001$) was a major challenge, and it has been found very sensitive for the simulated C budget. Mismatches on growing season start/end led to significant biases, both positive and negative (Table 2), likely shaped by the high meteorological interannual variability observed in Kobbefjord (López-Blanco et al., 2017). For example, the model underrepresented phenology dynamics between years 2010 and 2011, with a subsequent impact on C budget estimations. In 2010, the warmest summer with the longest growing season triggered an excessive C uptake, while in 2011 the colder June followed by the cloudier July likely led to a delayed growing season, not well captured in SPA. By forcing SPA's beginning of the growing season in 2011 with the % of greenness data (rather than environmentally forced), the agreement improved from a $R^2 = 0.4$ to $R^2 = 0.76$ for NEE, and an increase of 18 g C m^{-2} respired. Along these lines, this is also an indirect validation of the phenology methodology and its links to C dynamics.

On the other hand, three of the most sensitive parameters used in the model runs (LMA, J_{max} , and maximum foliar mass) were derived from field observations (Table 1). The terrestrial carbon cycle is currently the least constrained component of the global carbon budget (Bloom et al., 2016; IPCC, 2013). From a modeling perspective, more field measurements are required to better constrain the ecosystem model performances of C cycling in changing environments. We consider that more observations on plant phenology, photosynthetic parameters (Albert et al., 2011; Boesgaard et al., 2012; Rogers et al., 2017), plant structure (Carnieli et al., 2013; Van Wijk et al., 2004), C and N stocks at different stages of the season (Arndal et al., 2009), C storage and turnover (Cornelissen et al., 2007; DeMarco et al., 2014; Hobbie et al., 2000; Sloan et al., 2013) will improve modeling robustness based on enhanced calibrations. The discussion around variable selection, experimental design, and data suitability needs to be agreed both by field and model researchers. The incorporation of field observations into models can lead to improvements in modelled ecosystem processes, while models can inform on data collected in field campaigns.

The SPA model outputs, which has been manually parameterized (Table 1), could benefit from model data fusion approaches based on Bayesian statistics and optimal parameter sets (Bloom et al., 2016; Bloom & Williams, 2015; Williams et al., 2005). Additionally, we have neglected important components and processes shaping more complete C dynamics in northern latitudes. First, mosses should be considered in Arctic tundra modeling studies (Uchida et al., 2016) as they are a representative vegetation type in Arctic ecosystems and have important implications for CUE and soil temperature insulation (Bradford & Crowther, 2013; Street, Stoy, et al., 2012; Street et al., 2013; Williams et al., 2000). Second, methane (CH_4) is another important contributor to the total C budgets in these ecosystems (Mastepanov et al., 2008, 2012; Tagesson et al., 2012; Zona et al., 2016). However, CH_4 modeling is challenging due to its different transport mechanisms, but possible (Kaiser et al., 2017; Walter et al., 2001; Walter & Heimann, 2000), and some studies can be used to set up future modeling efforts at this site (Pirk et al., 2017). Third, permafrost dynamics brings an additional layer of complexity to the C exchange (Åkerman & Johansson, 2008; Koven et al., 2011; Schuur et al., 2015) and its application and modeling is required due to the increased permafrost thaw in warmer temperatures (Rasmussen et al., 2017; Riseborough et al., 2008). Fourth, dissolved organic carbon losses by runoff can represent 12–35% of NEE in similar latitudes (Olefeldt et al., 2012; Roulet et al., 2007), and fen sites have been found to have higher export

rates than bogs or palsa environments (Olefeldt & Roulet, 2012). Finally, vegetation shifts feedbacks in response to changing temperature, precipitation, snow dynamics, and permafrost thaw are critical (Andrew et al., 2017; Myers-Smith et al., 2015), and its modeling has been proved implementable (van der Kolk et al., 2016).

4.2. The Role of the Winter Period on the Full Annual-Cycle C Balance

Recent studies have emphasized the relevance of the incorporation of wintertime periods to gain a more comprehensive understanding of the C sink/source dynamics in Arctic terrestrial ecosystems (Commane et al., 2017; Zona et al., 2016). The response of decomposition processes to temperature across long and cold winters is critical, especially when low but constant rates of respiration contribute to the annual budget under changing snow packs (McGuire et al., 2000). Thick snow packs insulate the soil from low temperatures and can at the same time act as a lid preventing respiration losses from reaching the atmosphere until snowmelt period (Lund et al., 2012). In this study, we included snow fraction data (Figure S3) to constrain soil temperature (Figure S4), so the representation of heterotrophic respiration derived from roots, litter and SOM decomposition in the outer shoulders (Figure 3) is more realistically simulated. Hobbie et al. (2000) indicated that winter activity can influence both the magnitude and the direction of annual C fluxes, and they reported winter activity to represent 61–81% of annual NEE (Oechel et al., 1997) and ~20% of annual soil respiration (Schimel & Klein, 1995). Here we quantify a decrease of the C sink strength (NEE) of 62% and an increase of 22.7% of the annual soil respiration. This result suggests a nontrivial contribution of the cold period to the year-round CO₂ exchange in this tundra site. The challenges now remain on wintertime-based field campaigns, similar to Pirk et al. (2016), to measure soil CO₂ data for validation with certain temporal coverage. To better constrain the decomposition rates and their feedbacks with snow regimes and soil temperatures controlling the wintertime C dynamics in Arctic ecosystems, it is essential to increase efforts on monitoring the changes occurring over full annual cycles (Euskirchen et al., 2012; Grøndahl et al., 2008), and at a deeper level of complexity (Cornelissen et al., 2007; DeMarco et al., 2014).

4.3. Quantifying the Contributing Processes to NEE, Their Meteorological and Biological Sensitivity, and Links to Leaf Traits

The SPA model has proven capable of effectively simulating Arctic C cycling (Table 2) at a very high temporal resolution as a result of its parameterization at leaf-level scale (Table 1), unravelling deeper levels of complexity at canopy-level scale (Table 3). In SPA, the net C uptake was calculated from the balance between the photosynthetic inputs (GPP) and respiration outputs (R_{eco} ; Figure 3), and the respiration losses are separated into its finer components (R_g , R_m , and R_h) (Figure 5). In the biosphere, stock dynamics are connected (Dopheide et al., 2012), and these fluxes are the result of the allocation (Figure 2c) of NPP to the various identifiable stocks of biomass (foliage, labile, stems, roots, litter, and SOM) together with their turnover rates and decomposition (Figure 2d). SPA captures all these fluxes within the same framework, and Figure 7 is an illustration of the terrestrial C cycling in Kobbefjord the period 2008–2015. Figure 7 synthesizes annual ranges of C stocks, allocation, turnover, and fluxes shown previously in Figures 2, 3, 4, and 5b and Table 3. The sensible balance between the components (Figure 7) can be highly dependent on meteorological variability but also biological disturbances (López-Blanco et al., 2017). In fact, one can positively feedback on the other. For example, in 2010, Kobbefjord experienced the warmest July–September period, and this anomaly was followed by a colder and drier October–May period, producing the thickest snowpack (Figure S1) on record. Additionally, the delayed beginning of the growing season in 2011 was characterized by a colder June, a cloudier (low PAR) July (Table S1) and larvae moth feeding on vegetation surrounding the fen (Lund et al., 2017). This succession of meteorological and biological events may have favored (1) optimal conditions for the moth outbreak, facilitating the survival of larvae eggs over winter due to the warmer soil temperatures under a very thick snowpack and (2) minimal conditions for plant growth agreeing with the significant decrease in GPP (Figure 5b) and subsequent decrease of CUE (Table 3). This study demonstrates that shifts in growing season timing can lead to large changes in net C exchange, thus delayed effects can severely affect the following years' performance.

However, SPA representation of process interactions agrees with the analyses realized by López-Blanco et al. (2017), suggesting that large interannual growing season variability of GPP and R_{eco} are also compensatory, and so NEE remained stable across meteorologically diverse years (Figure 4 and 5b). This result can be compared with the findings from Westergaard-Nielsen et al. (2017) in Zackenberg, Northeast Greenland, where

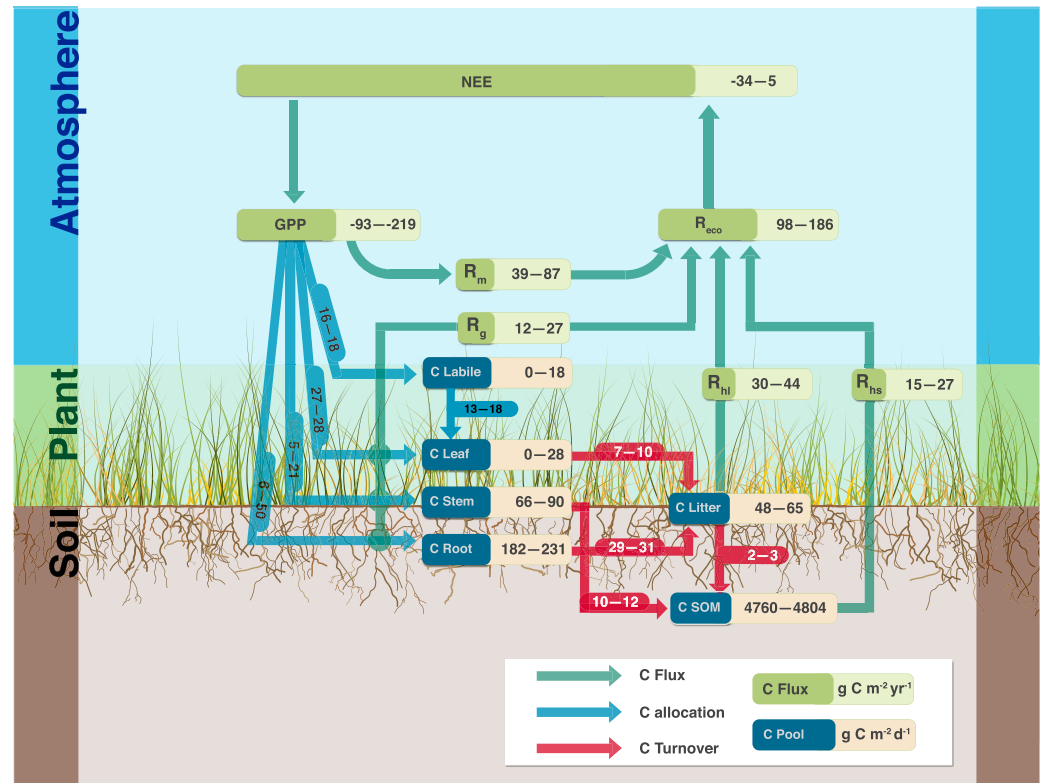


Figure 7. Schematic diagram of the terrestrial C processes modelled in SPA for the Kobbefjord (fen) site across the soil-plant-atmosphere continuum. C processes represented include flows for C fluxes in green (NEE, net ecosystem exchange; GPP, gross primary production; R_{eco} , ecosystem respiration; R_g , growth respiration; R_m , maintenance respiration; and R_h , heterotrophic respiration), C allocation in light blue (to labile, leaf, stem, and root), C turnover in dark red (from leaf, stem, root, and litter) and C stocks in dark blue (labile, leaf, stem, root, litter, and SOM). The ranges delimit minimum and maximum values.

the vegetation compensated the shorter growing season by having fast greenup and a tendency to higher peak in greenness, which links to GPP. We use the modeling to explore the mechanisms driving this compensatory effect. We implemented tissue-level respiration-nitrogen relationships from Reich et al. (2008) and fixed fractions of C allocated following Waring and Schlesinger (1985) to dynamically calculate R_m and R_g , respectively (Figure 5). During the June–August period, R_a contributed 69.8% to all respiratory losses (R_{eco} ; $R_g = 18.5\%$; $R_m = 51.25\%$; Figure 5a) while annually, 58.3% ($R_g = 14.8\%$; $R_m = 43.5\%$; Figure 5 b). These results suggest that the plant respiration is dominated by nitrogen-related dynamics (R_m) rather than the production of new biomass (R_g). The parameterization used here has been already reported based on plant C stock size and on the magnitude of GPP (Hopkins et al., 2013; Thornton & Rosenbloom, 2005). However, reports of explicit partitioned respiration components in the Arctic are missing, so field measurements are required for validation. Overall, this implementation provided a better understanding of the CUE responses to environmental change, and CUE estimations are more abundant in literature. The CUE around the sub-Arctic tundra has been reported ~ 0.47 , but mosses could increase it up to 0.71–0.81 (Bradford & Crowther, 2013; Street et al., 2013). Here we reported CUE, estimated from first principles of modeling GPP and R_a , of ~ 0.5 except in 2011 (Table 3). We found CUE to be sensitive to the events described this year, decreasing from ~ 0.5 to 0.4 (Table 3). A value of 0.4 indicates that 40% of gained C is allocated to biomass, and thus the $GPP - R_{eco}$ compensation was disrupted by an unusual meteorology and the biological disturbance. CUE is sensitive to temperature and nitrogen concentration (cold temperatures and large N availabilities will increase CUE; Bradford & Crowther, 2013). In likely warming scenarios the CUE is hypothesized to decrease, favoring respiration losses (Street et al., 2013); therefore, this fact may affect the future coupling. Further modeling studies can investigate this likelihood.

From the sensitivity analysis (Table 1), similar responses of NEE, GPP, and R_{eco} have emerged to changes in plant traits and vegetation properties. In fact, the correlation of GPP and R_{eco} sensitivity to the same key parameters was strong ($R^2 = 0.84$), supporting the compensatory effect revealed by GPP and R_{eco} ($R^2 = 0.95$; Table 3). Reichstein et al. (2014) suggested that a significant part of the large unexplained variance of ecosystem functional properties and their environment is related to variation in plant traits. Additionally, the same authors suggested that ecosystem properties such as GPP or R_a could be derived from plant traits, claiming also a stronger integration of plant traits and ecosystem-atmosphere exchange. Here LMA, the rate coefficient for J_{max} , maximum foliar mass, and foliar N were found to be very important elements for the model parameterization (Table 1). We also found that these four most sensitive N-related plant traits in SPA presented a similar temperature sensitivity for GPP and R_{eco} across full annual cycles (Figure 6). This evidence supports our hypothesis that plant traits drive stabilization of NEE (Figure 4), through temperature-sensitive compensation between GPP and R_a . We find that GPP is more sensitive to temperature than R_{eco} , so compensation is not completely balanced between GPP and R_{eco} . But both fluxes have similar trait-temperature sensitivity, and so compensation is relatively insensitive to temperature changes. There is evidence that plant traits are potentially key controllers in the gross flux coupling and that they can explain other ecosystem functional properties, including allocation, respiration and decomposition and stabilization of carbon in the soil. Street, Shaver, et al. (2012) pointed to very robust relationships between total foliar nitrogen and LAI across multiple different Arctic regions, despite their large variability in C uptake and plant functional types. The role of functional properties seems very important to interannual variability, even to biological disturbance, which suggests ecosystem resilience to changes (Reichstein et al., 2014). Further testing of the hypothesis presented here could involve a comparison of flux measurements from other high-latitude sites with similar climate but differing dominant vegetation communities, with different plant traits.

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5. Conclusions

The SPA model captures well high temporal C dynamics and plant phenology in high-latitude ecosystems. Using a process model, we have explored the role of the wintertime period on NEE and decomposed the compensatory effects buffering NEE to meteorological variability. Wintertime heterotrophic respiration decreased the annual C sink strength mostly through litter decomposition, highlighting the importance of the cold period to the year-round CO_2 exchange in Arctic tundra. The modeling suggests that GPP and R_{eco} sensitivities to meteorology are similar and therefore compensatory, due to the key role that plant N content has on both processes, leading to a NEE stability across climatically diverse full annual cycles. Here plant traits and vegetation properties seem to be relevant controllers of the gross flux coupling. Continued exploration of flux time series is required to investigate the robustness of this meteorological buffering. Special attention needs to be paid to disturbance events such as the 2011 anomaly where the interplay between unusual meteorology and moth outbreak can break down the photosynthesis-respiration compensation.

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**Plant Traits are Key Determinants in Buffering the Meteorological Sensitivity of
Net Carbon Exchanges of Arctic Tundra**

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Introduction

This supporting information provides additional details regarding the weather generator script used to gap-fill meteorological forcing (**Text S1**), the C flux partitioning and carbon use efficiency equations utilized in the study (**Equations S1**), the meteorological drivers used in the SPA framework after the model initialization (**Figure S1**), the carbon (C) and nitrogen (N) content of the three plant ecotypes sampled during the field campaign in 2015 (**Figure S2**), the snow coverage data used to constrain the snow subroutine introduced in SPA (**Figure S3**), the observed and modelled soil temperature before and after the implementation of the snow cover subroutine (**Figure S4**), a zoom-in on 2015 data presented in Figure 2 (**Figure S5**), the correlation matrix showing the Pearson correlations and significance between partitioned C fluxes- and phenology-related variables (**Figure S6**), and the air temperature and photosynthetic active radiation anomalies of the analyzed years (**Table S1**).

Text S1: Description of Weather Generator v1

Authors: Oliver Browne, T. Luke Smallman & Mathew Williams

The weather generator uses simple empirical approach to use daily information (max / min / mean, day of year and latitude) to estimate hourly time step information for incoming shortwave radiation, air temperature, relative humidity, precipitation, wind speed and atmospheric CO₂ concentration. A wide range of statistical and machine learning approaches are available to perform downscaling or gap-filling of time series; however, the explicit aim of the weather generator is to utilise a minimum of input information to allow for provision of consistent meteorological inputs in a data-sparse environment. The process of downscaling daily information to hourly will be briefly outlined in the following paragraphs, including a quantification of the weather generator's errors in downscaling meteorology. Wind speed and atmospheric CO₂ concentration are currently assumed to be equal to their daily mean values for each hour. The code is written in Fortran (including a control interface written in R), is fully commented and is freely available to download.

Hourly incoming shortwave radiation is estimated based on day length (estimated as a function of latitude and day of year), the daily time course of solar geometry and mean daily incoming shortwave. Day length is assumed to be equally distributed before and after noon, thus estimating the hour of sunrise and sun set. Solar radiation is then distributed over the daily time course based on the magnitude of the cosine solar zenith angle.

Downscaling air temperature requires input of daily minimum, maximum and mean air temperature (note daily mean temperature could be approximated as the mean of the minimum and maximum). The daily minimum temperature is assumed to occur at dawn while the maximum temperature is assumed to occur at midday plus an assumed lag value (currently assumed to equal 1 hour). The daily temperature curve is divided into three linear sections spanning midnight to dawn, dawn to the daily maximum temperature and daily maximum to midnight. The midnight temperature is calculated to maintain the desired daily mean temperature. At high latitudes when periods of 24-

hour darkness / light are possible the temperature time course is assumed to be equal to the daily mean. The hourly time course of relative humidity is assumed to be anti-correlated with that of temperature. The daily minimum and maximum relative humidity are assumed to occur at the same time as the maximum and minimum temperatures respectively.

The timing of precipitation is challenging to simulate due to complex processes requiring detailed information from the wider atmospheric conditions. Here, we have two simple assumptions available. First to distribute precipitation uniformly over the day. Second, to concentrate rainfall to a four-hour period targeted to begin when relative humidity is at its maximum.

Equations S1: Flux partitioning and carbon use efficiency.

The different components of the carbon budget considered in this study are related to each other as follows:

$$NEE = GPP - R_{eco} \quad (1)$$

where NEE is Net ecosystem exchange, GPP is gross primary production and R_{eco} is the ecological respiration. R_{eco} is defined as:

$$R_{eco} = R_a + R_h \quad (2)$$

where R_a is autotrophic respiration, and R_h is heterotrophic respiration. R_a and R_h are separated further down as:

$$R_a = R_g + R_m = (R_{g \text{ leaf}} + R_{g \text{ root}} + R_{g \text{ stem}}) + (R_{m \text{ leaf}} + R_{m \text{ root}}) \quad (3)$$

$$R_h = R_{h \text{ litter}} + R_{h \text{ soil organic matter}} \quad (4)$$

where R_g is growth respiration, R_m is maintenance respiration, and R_h is heterotrophic respiration. Each of these respiratory losses are split by C pools.

The carbon use efficiency (CUE) is defined as:

$$CUE = 1 - ((R_m + R_g) / GPP) \quad (5)$$

where CUE is 1 minus the ratio of carbon losses through autotrophic respiration (R_a), split between growth (R_g) and maintenance (R_m), and gross primary productivity (GPP).

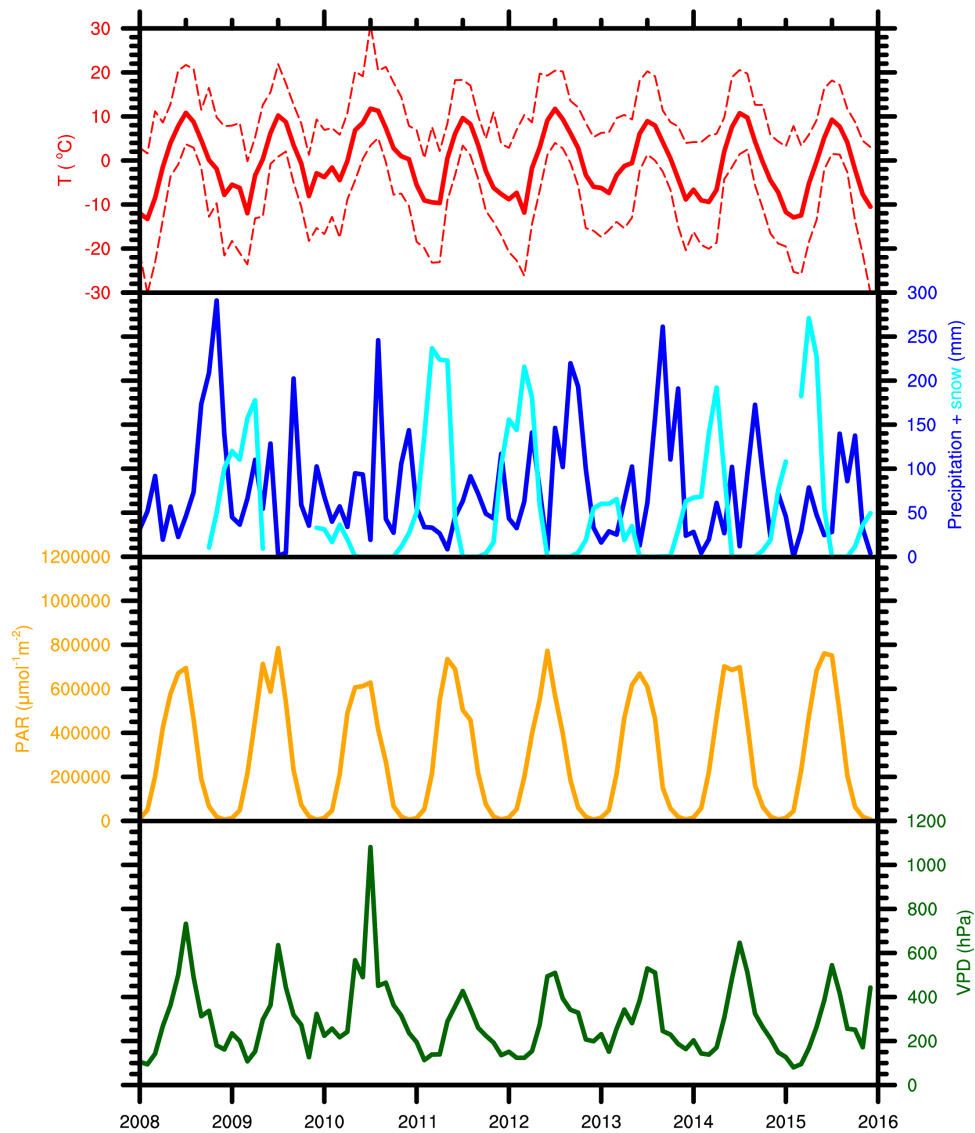


Figure S1. Time series of the monthly averaged drivers read in the SPA framework after the initialization of initial conditions and the vegetation and soil parameters. The meteorological drivers represented are **(a)** minimum, mean (solid line), minimum and maximum (dashed line) air temperature ($^{\circ}\text{C}$), **(b)** cumulative precipitation and snow depth (mm), **(c)** photosynthetic active radiation ($\mu\text{mol}^{-1} \text{m}^{-2}$), and **(d)** vapor pressure deficit (hPa).

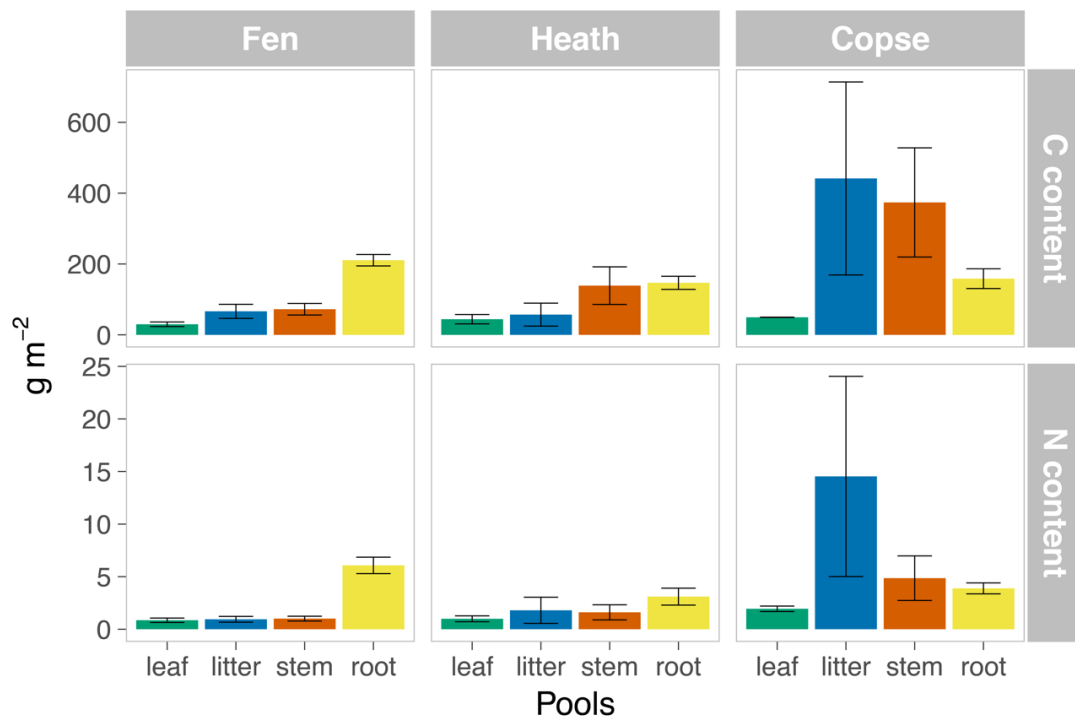


Figure S2. Carbon (C) and nitrogen (N) content (g m^{-2}) of the three plant ecotypes sampled (fen, heath and copse) around the eddy covariance tower, separated by pools (leaf, litter, stem and roots). The error bars summarize the standard deviation from the CN analysis' replicates and the variability between samples.

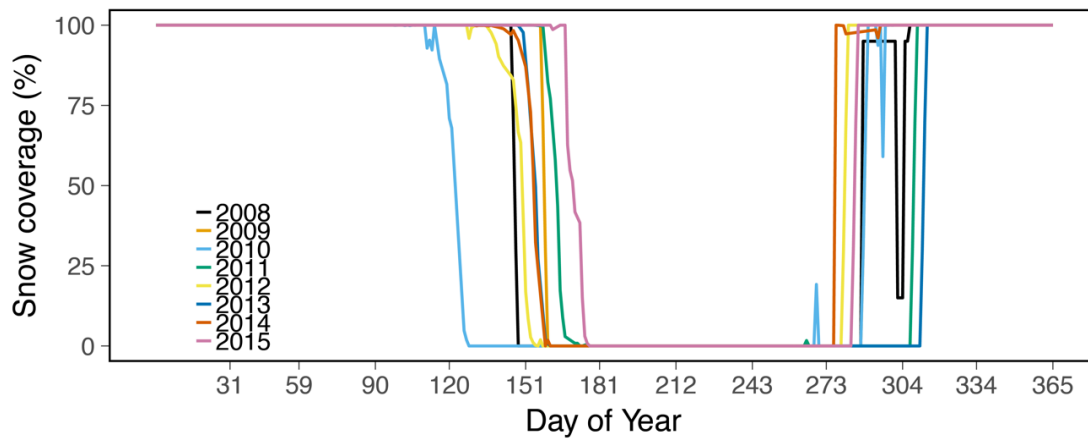


Figure S3. Snow coverage data used to constrain the snow subroutine introduced in SPA following Essery (2015).

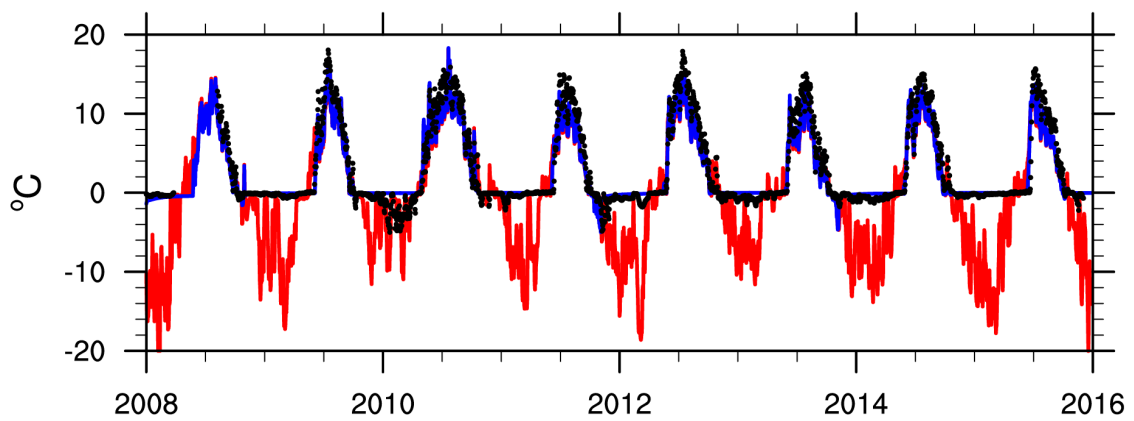


Figure S4. Time series of the observed and modelled soil temperature before (red) and after (blue) the implementation of the snow cover subroutine. The outputs shown are at a depth of 10 cm across the period 2008-2015.

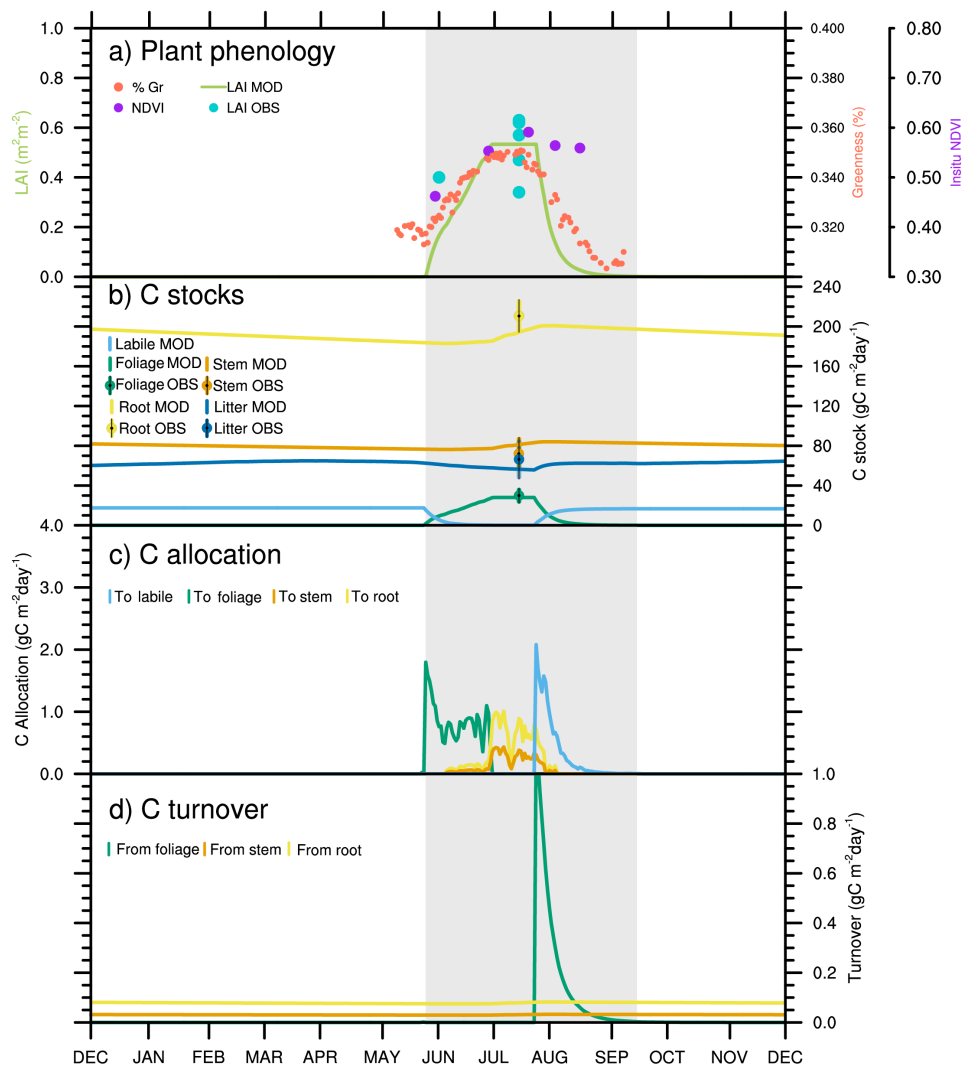


Figure S5. Zoom-in on 2015 data presented in Figure 2. Observed [OBS] and predicted [MOD] plant phenology [%Gr, % of greenness; NDVI, in-situ Normalized Difference Vegetation Index; LAI; Leaf Area Index] (a) and C pools [labile, foliage, stem, root, litter] (b), as well as simulated C allocation [to labile, foliage, stem and root] (c) and C turnover [from foliage, stem and root] (d).



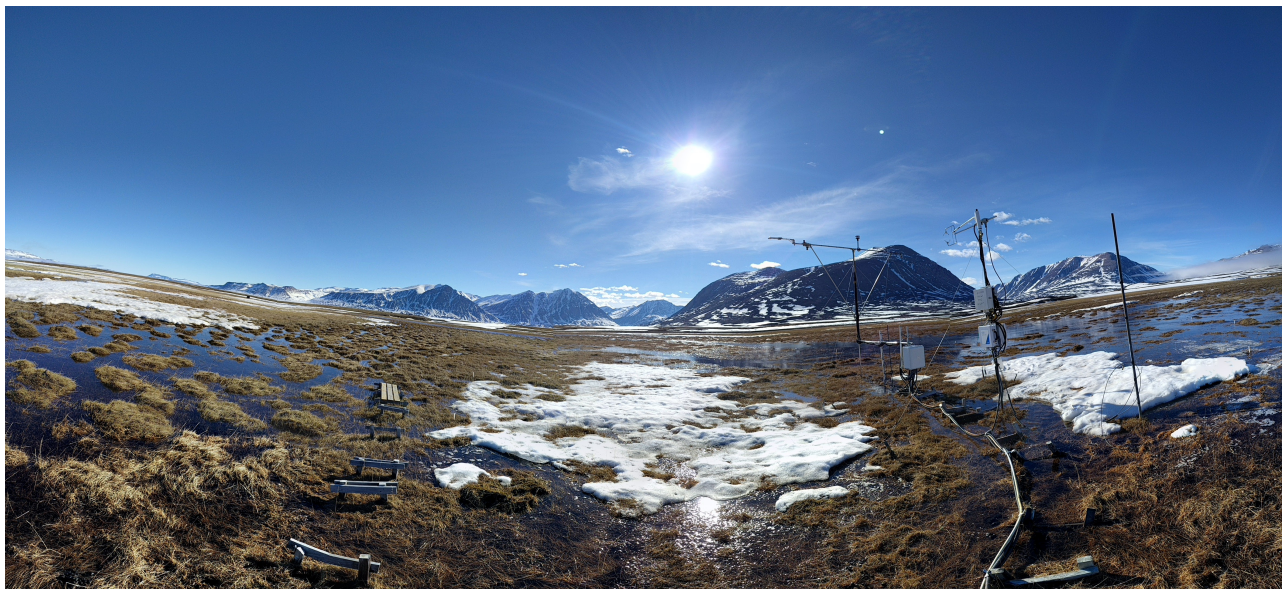
Figure S6. Correlation matrix showing the Pearson correlations and significance between NEE, Net Ecosystem Exchange; GPP, Gross Primary Production; Rg, Growth respiration; Rm, Maintenance respiration; Rh, Heterotrophic respiration; CUE, Carbon Use Efficiency; SM, Snow Melt period; bGS, beginning of the Growing Season; IGS, length of the Growing Season.

Table S1. Monthly air temperature (T_{air} ; °C) and photosynthetic active radiation (PAR; $\mu\text{mol}^{-1} \text{m}^{-2}$) anomalies of the analyzed years (2008-2015)

Year	Period	T_{air} anomalies	PAR anomalies
2008	June	0.22	279.32
2008	July	3.20	177.38
2008	August	0.61	-21.79
2008	September	-3.63	-221.43
2009	June	-1.47	96.99
2009	July	2.47	216.15
2009	August	1.01	11.08
2009	September	-4.21	-203.20
2010	June	0.84	96.04
2010	July	2.29	88.75
2010	August	3.55	-69.35
2010	September	-0.35	-174.46
2011	June	-1.64	159.61
2011	July	1.90	2.68
2011	August	0.52	-40.69
2011	September	-4.21	-213.61
2012	June	1.42	231.68
2012	July	3.99	56.20
2012	August	1.59	-74.82
2012	September	-1.70	-237.46
2013	June	-1.63	165.36
2013	July	1.20	96.87
2013	August	0.22	-19.09
2013	September	-3.55	-252.28
2014	June	-0.10	176.50
2014	July	3.01	157.98
2014	August	2.04	-33.68
2014	September	-3.41	-245.56
2015	June	-2.54	250.73
2015	July	1.54	140.38
2015	August	-0.02	-45.38
2015	September	-3.61	-228.75

Paper IV

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Zackenberg site, East Greenland. 2017 field season. Photo by Efrén López-Blanco

Evaluation of terrestrial pan-Arctic carbon cycling using a data-assimilation system

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Keywords: Arctic tundra, Arctic taiga, Net Ecosystem Exchange, Gross primary production, Ecosystem Respiration, carbon stocks, transit times, field observations, global vegetation models.

Abstract. There is a significant knowledge gap in the current state of the terrestrial carbon (C) budget. The Arctic accounts for approximately 50% of the global soil organic C stock, emphasizing the important role of Arctic regions in the global C cycle. Recent studies have pointed to the poor understanding of C pools turnover, although remain unclear as to whether productivity or biomass dominate the biases. Here, we use an improved version of the CARDAMOM data-assimilation system, to produce pan-Arctic terrestrial C-related variables without using traditional plant functional type or steady-state assumptions. Our approach integrates a range of data (soil organic C, leaf area index, biomass, and climate) to determine the most likely state of the high latitude C cycle at a 1° x 1° resolution for the first 15 years of the 21st century, but also to provide general guidance about the controlling biases in the turnover dynamics. As average, CARDAMOM estimates 513 (456, 579), 245 (208, 290) and 204 (109, 427) g C m⁻² yr⁻¹ (90% confidence interval) from photosynthesis, autotrophic and heterotrophic respiration respectively, suggesting that the pan-Arctic region acted as a likely sink -55 (-152, 157) g C m⁻² yr⁻¹, weaker in tundra and stronger in taiga, but our confidence intervals remain large (and so the region could be a source of C). In general, we find a good agreement between CARDAMOM and different sources of assimilated and independent data at both pan-Arctic and local scale. Using CARDAMOM as a benchmarking tool for global vegetation models (GVM), we also conclude that turnover time of vegetation C is weakly simulated in vegetation models and is a major component of error in their forecasts. Our findings highlight that GVM modellers need to focus on the vegetation C stocks dynamics, but also their respiratory losses, to improve our process-based understanding of internal C cycle dynamics in the Arctic.

1 Introduction

Arctic ecosystems play a significant role in the global carbon (C) cycle (Hobbie et al., 2000; McGuire et al., 2009; McGuire et al., 2012). Slow organic matter decomposition rates due to cold and poorly drained soils in combination with cryogenic soil processes have led to an accumulation of large stocks of C stored in the soils, much of which is currently held in permafrost (Tarnocai et al., 2009). The permafrost region soil organic C (SOC) stock is more than twice the size of the atmospheric C stock; and accounts for approximately half of the global SOC stock (Hugelius et al., 2014; Jackson et al., 2017). High latitude ecosystems are experiencing a temperature increase that is nearly twice the global average (AMAP, 2017). The expected future increase of temperature (IPCC, 2013), precipitations (Bintanja and Andry, 2017), and growing season length (Aurela et al., 2004; Groendahl et al., 2007) will likely have consequences in the Arctic net C balance. As high latitudes warm, C cycle dynamics may lead to an increase of carbon dioxide (CO₂) emissions through ecosystem respiration (R_{eco}) driven by for example larger heterotrophic respiration (Commane et al., 2017; Schuur et al., 2015; Zona et al., 2016), drought stress on plant productivity (Goetz et al., 2005) and episodic disturbances (Lund et al., 2017; Mack et al., 2011). However, temperature-induced vegetation changes may counterbalance those effects by photosynthetic enhancement (Forkel et al., 2016; Graven et al., 2013; Lucht et al., 2002; Zhou et al., 2001; Zhu et al., 2016). Two examples are the increase of gross primary productivity (GPP) due to extended growing seasons, nutrient availability and CO₂ fertilization (Abbott et al., 2016; Myers-Smith et al., 2015; Myneni et al., 1997) and the shifts in vegetation dynamics such as shrub expansion (Myers-Smith et al., 2011). Consequently, phenology shifts may feedback on climate with unclear magnitude and sign (Anav et al., 2013; Murray-Tortarolo et al., 2013; Peñuelas et al., 2009). As a result of the significant changes that are already affecting the structure and function of Arctic ecosystems, it is critical to understand and quantify the C dynamics of the terrestrial tundra and taiga and their responses to climate change (McGuire et al., 2012).

Although the land surface is estimated to offset 30% of anthropogenic emissions of CO₂ (Canadell et al., 2007; Le Quéré et al., 2018), the terrestrial C cycle is currently the least constrained component of the global C budget and vast uncertainties remain (Bloom et al., 2016). Despite the importance of Arctic tundra and taiga biomes in the global land C cycle, our understanding of controls interacting between the allocation of C from net primary productivity (NPP), C stocks (C_{stock}), and transit times (TT), is deficient (Carvalhais et al., 2014; Friend et al., 2014; Hobbie et al., 2000). The TT is a concept that represents the time it takes for a particle of C to persist in a specific C stock and it is defined by the C stock and its outgoing flux, here addressed as $TT = C_{\text{stock}} / NPP$. According to a recent study by Sierra et al. (2017), TT is an important diagnostic metric of the C cycle and a concept that is independent of model internal structure and theoretical assumptions (steady state for example) for its calculation. Terms such as turnover time (Carvalhais et al., 2016), residence time (Friend et al., 2014), and turnover rate (Thurner et al., 2016) are used in the literature to represent the concept of TT (Sierra et al. 2017). The spatial variability with climate has been more studied for ecosystem productivity than for C transit time dynamics (Friend et al., 2014; Nishina et al., 2015; Thurner et al., 2016; Thurner et al., 2017). Friend et al., 2014 detailed that transit time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO₂. They found a 30% larger variation in modelled vegetation C change than response of NPP. Nishina et al. (2015) also suggested that long term C dynamics within ecosystems (vegetation turnover and soil decomposition) are more critical factors than photosynthetic processes (i.e. GPP or NPP). The respective contribution of bias from biomass and NPP to biases in transit times remain unquantified. Without an appropriate understanding of current state of basic components of the C cycle, the understanding of C cycle feedbacks to climate change remains highly uncertain (Hobbie et al., 2000; Koven et al., 2015b).

There are these days important efforts incorporating both in-situ and satellite-based datasets to assess C cycle retrievals and to reduce the uncertainties. At local scale, the net ecosystem exchange (NEE) of CO₂ between the land surface and the atmosphere is usually measured using eddy covariance EC techniques (Baldocchi, 2003). International efforts have led to the creation of global networks such as FLUXNET (<http://fluxnet.fluxdata.org/>) and ICOS (<https://www.icos-ri.eu/>), to harmonise data and support the reduction of uncertainties around the C cycle and its driving mechanisms. However, upscaling field observations to estimate regional to global C budget presents important challenges due to insufficient spatial coverage of measurements and heterogeneous landscape mosaics (McGuire et al., 2012). Furthermore, harsh environmental conditions in high latitude ecosystems and their remoteness complicates the collection of high quality data (Grøndahl et al., 2008; Lafleur et al., 2012). Given the lack of continuous, spatially distributed ground-based scale observations of NEE in the Arctic, it remains a challenging task to calculate with certainty whether or not the Arctic is a net C sink or a net C source, and how the net C balance will evolve in the future (Fisher et al., 2014). Over the past decade, an increasing number of regional to global datasets has improved our understanding of the terrestrial C dynamics, including global scale vegetation dynamics. These range from machine-learning based upscaling of FLUXNET data (Jung et al., 2017), remotely-sensed biomass products (Carvalhais et al., 2014; Thurner et al., 2014) and the creation of a global soil database (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). However, important limitations in data availability still remain in difficult measured drivers such as soil-plant turnover and soil respiration responses to climate, especially for a highly influential and understudied region like the Arctic.

Conveniently, Global Vegetation Models (GVM) have been developed to determine global terrestrial C cycles and represent vegetation ecosystem processes including the structural (i.e. growth, competition, and turnover) and biochemical (i.e. water, carbon, and nutrients cycling) responses to climate variability (Clark et al., 2011; Fisher et al., 2014; Friend and White, 2000; Ito and Inatomi, 2012; Pavlick et al., 2013; Sitch et al., 2003; Smith et al., 2001; Woodward et al., 1995). The advantage of using process-based models to measure C dynamics is that processes which drive ecosystem-atmosphere interactions can be simulated and reconstructed when data is scarce. However, C cycle modelling in GVMs typically relies on pre-arranged parameters retrieved from literature, prescribed plant-functional-type (PFT) and spin-up processes until the C stocks (biomass and SOC) reach their steady state. Further, inherent differences of model structure contribute more significantly to GVM uncertainties (Exbrayat et al., 2018; Nishina et al., 2014), than from differences in climate projections (Ahlström et al., 2012). Many model intercomparison projects have demonstrated a lack of coherence in future projections of terrestrial C cycling (Ahlström et al., 2012; Friedlingstein et al., 2014). Recent studies have used simulations from the first phase of the Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP) (Warszawski et al., 2014) to evaluate the importance of key elements regulating vegetation C dynamics, but also the estimated magnitude of their associated uncertainties (Exbrayat et al., 2018; Friend et al., 2014; Nishina et al., 2014; Nishina et al., 2015; Thurner et al., 2017). An important insight is that the TTs in land ecosystem are a main uncertain feature of the global C cycle and, despite the increasing volume of C-cycling related products, GVMs do not provide estimates of the internal dynamics which regulate the C cycle and its response to changes.

An approach to circumvent these issues is to integrate models and data to estimate these dynamics in agreement with observations. Integrating available climatic, ecological and biochemical data from field experiments, flux towers and remote sensing observations using data assimilation system (e.g. ensemble Kalman filter, Bayesian technique) can reduce uncertainties in parameter estimation and improve calculation of C cycle dynamics (Fox et al., 2009; Luo et al., 2009; Williams et al., 2005). Here, we use the CARbon DAta MOdel framework (CARDAMOM) (Bloom et al., 2016; Smallman et al., 2017) to retrieve the pan-Arctic terrestrial carbon cycle for the 2000-2015 period in agreement with gridded observations of LAI,

in some locations. Additionally, we selected variable u^* threshold to identify insufficient turbulence wind conditions from year to year similar to López-Blanco et al. (2017). For readability purposes, in this data-model comparison we included the median (P50) \pm the 50% confidence interval (percentile 25th to 75th; (P_{25}^{75})) including both random and u^* filtering uncertainty following the method described in Papale et al. (2006). Some of the sites lack wintertime measurements and we filtered out data for months with less than 10 % observations. We performed a point-to-grid cell comparison to assess the degree of agreement between each flux magnitude and seasonality calculating the statistics of linear fit (slope, intercept, R^2 , RMSE, and bias) per flux and site between CARDAMOM and FLUXNET2015 datasets.

2.4 Benchmark of Global Vegetation Models

We examined the pan-Arctic annual changes in net primary production (NPP), vegetation biomass carbon stocks (C_{veg}) and vegetation transit times (TT_{veg}) using CARDAMOM as benchmark tool for six participating GVMs in the ISI-MIP comparison project (Warszawski et al., 2014). In this study we have considered HYBRID (Friend and White, 2000), JeDi (Pavlick et al., 2013), JULES (Clark et al., 2011), LPJmL (Sitch et al., 2003), SDGVM (Woodward et al., 1995), and VISIT (Ito and Inatomi, 2012). The specific properties and degree of complexity of each ISI-MIP model are summarized in Table S4, and more detailed information can be found in Friend et al. (2014) and Thurner et al. (2017). In this study, each model simulation has been conducted under multiple General Circulation Models (GCMs). Here we included HadGEM2-ES (Collins et al., 2011), IPSLCM5A-LR (Dufresne et al., 2013), MIROC-ESM-CHEM (Watanabe et al., 2011), GFDL-ESM2M (Dunne et al., 2012), and NorESM1-M (Bentsen et al., 2013) GCMs from the fifth phase of the Coupled Model Intercomparison Project (CMIP5) experiment (Arora et al., 2013; Taylor et al., 2012), which are temperature and precipitation bias corrected following Hempel et al. (2013). The comparisons with CARDAMOM for each GVM included the mean ensemble of all GCM forcings. The comparisons have been performed under the same spatial resolution as the CARDAMOM spatial resolution for the 2000-2004 period ($1^\circ \times 1^\circ$ resolution). We estimated the degree of agreement using the statistics of linear fit (slope, intercept, R^2 , RMSE, and bias) per variable and model between CARDAMOM and GVMs, but also their spatial variability including stipples where the GVM datasets are within the CARDAMOM's 90% confidence interval.

3 Results

3.1 Pan-Arctic retrievals of C cycle

Overall, we found that the pan-Arctic region (Figure 1 and Table 1) acted as a small sink of C (area-weighted P50) over the 2000-2015 period with an average of -55.8 ($_{-260.5}^{1158.1}$) $\text{g C m}^{-2} \text{yr}^{-1}$, P50 ($_{P05}^{P95}$), although the 90% confidence intervals remain large (and so the region could be a source of C). Tundra regions presented a weaker sink compared to taiga regions, this is -13.0 ($_{-158.5}^{1107.7}$) and -104.1 ($_{-375.4}^{1215.0}$) $\text{g C m}^{-2} \text{yr}^{-1}$ respectively, but also lower uncertainties with nearly $1265.5 \text{ g C m}^{-2} \text{yr}^{-1}$ between P05 and P95 in tundra. In general, the photosynthetic inputs exceeded the respiratory outputs ($\text{GPP} > \text{R}_{eco}$; Table 1), although the much larger uncertainties stemming from R_{eco} , and more specifically from R_h , compared with GPP complicate the net C sink/source estimate beyond the median's average ensembles. In the pan-Arctic region approximately half of GPP is autotrophically respired resulting in an NPP of 263.3 ($_{177.4}^{376.6}$) $\text{g C m}^{-2} \text{yr}^{-1}$. Carbon use efficiency (NPP/GPP) averages 0.51 ($_{0.46}^{0.55}$), and marginally varied across tundra 0.50 ($_{0.46}^{0.54}$) and taiga 0.52 ($_{0.46}^{0.56}$). Despite these apparent small variations, tundra

biomass and SOC stocks. In this paper, we compare analyses of C dynamics of Arctic tundra and taiga against (a) global products of GPP (Jung et al., 2017) and heterotrophic respiration (R_h) (Hashimoto et al., 2015); (b) NEE, GPP and R_{eco} field observations from 8 sub- and high- Arctic sites included in the FLUXNET2015 dataset, and (c) 6 extensively used GVMs from the ISI-MIP comparison project (Warszawski et al., 2014). Our objectives are to (1) present and evaluate the retrievals and uncertainties of the current state of the pan-Arctic terrestrial C cycling using a model-data fusion system, (2) quantify the degree of agreement between our better constrained product with local to global scale sources of available data available, and (3) use CARDAMOM as a benchmarking tool for the ISI-MIP models to provide general guidance towards GVM improvements. Finally, we suggest future work to be done in the context of pan-Arctic C cycling modelling at the global scale.

2 Data and methods

2.1 Pan-Arctic region

The spatial domain we considered in this study (Figure S1) corresponds to the extent of the Northern Circumpolar Soil Carbon Database version 2 (NCSCDv2) dataset (Hugelius et al., 2013a; Hugelius et al., 2013b), bounded by latitudes 44°N - 80°N and longitudes 180°W - 180°E, and at a spatial resolution of 1° x 1°. This area of study totals 18.7 million km² of land area. We used the GlobCover vegetation map product developed by the European Space Agency (Bontemps et al., 2011) to separate regions dominated by non-forested and forested land cover types (hereafter referred as tundra and taiga, respectively) (Figure S1). The differentiation between tundra and taiga grid cells is in agreement with the tree line delimited by Brown et al. (1997) together with the tundra domain defined from the Regional Carbon Cycle Assessment and Processes Activity reported by McGuire et al. (2012). However, the tundra region extends into taiga regions without presence of trees in some areas such as the extensive grasslands in South Russia and Mongolia (Figure S1). This classification of tundra and taiga totals 9.0 and 9.7 million km² of land area, respectively.

2.2 The CARbon DAta MOdel framework

Here we use the CARbon DAta MOdel framework (CARDAMOM; Bloom et al., 2016) (list of acronyms can be found in Table S1) to retrieve terrestrial C cycle dynamics, including explicit confidence intervals, in the pan-Arctic region. CARDAMOM is centred around the Data Assimilation Linked Ecosystem Carbon version 2 (DALEC2), to simulate land-atmosphere C fluxes and the evolution of six C stocks (foliage, labile, wood, roots, soil organic matter (SOM) and surface litter) and corresponding fluxes (Bloom and Williams, 2015; Williams et al., 2005). DALEC2 includes 17 parameters controlling the processes of plant phenology, photosynthesis, allocation of primary production to respiration and vegetation carbon stocks, plant and organic matter turnover rates, all established within specific prior ranges based on ecologically viable limits (Table S2). DALEC2 simulates GPP and its allocation to the four plant stocks and autotrophic respiration (R_a) as time-invariant fraction. Plant C decays into litter and soil stocks where microbial decomposition generates heterotrophic respiration (R_h). In each plant, litter and soil stock turnover is simulated using temperature dependent first-order kinetics. The Net Ecosystem Exchange (NEE) is calculated as the difference between GPP and the sum of the respiration fluxes ($R_{eco} = R_a + R_h$), while Net Primary Productivity (NPP) is the difference between GPP and R_a . Only NEE follows the standard micrometeorological sign convention presenting the uptake of C as negative (sink), and the release of C as positive (source); both GPP and R_{eco} are reported as positive fluxes.

CARDAMOM is driven by climate data from the European Centre for Medium-Range Weather Forecast Reanalysis interim (ERA-interim) dataset (Dee et al., 2011) for the 2000-2015 period. A Bayesian Metropolis-Hastings Markov chain Monte Carlo (MHMCMC) algorithm is used to retrieve the posterior distribution of 17 process parameters according to observational constraints and Ecological and Dynamic constraints (EDCs; Bloom and Williams, 2015). EDCs ensure that DALEC2 simulates the terrestrial carbon cycle in agreement with ecological theory. Observational constraints include monthly time series of Leaf Area Index (LAI) from the MOD15A2 product (Myneni et al., 2002), estimates of vegetation biomass and soil organic carbon content. In this paper, there are two main differences with the global approach described in Bloom et al. (2016). First, the biomass constraints used by Bloom et al. (2016) only cover tropical regions. Instead, here we use global biomass estimates from Carvalhais et al. (2014) which are based on remotely-sensed forest biomass (Turner et al., 2014) and upscaled GPP based on data driven estimates (Jung et al., 2011) covering the pan-Arctic domain. Second, we constrained the storage of SOC in the 0-1 m topsoil from the Circum-Arctic permafrost region (Brown et al., 1997) using the NCSCD spatial explicit product (Hugelius et al., 2013a; Hugelius et al., 2013b) instead of the Harmonized World Soil Database (HWSD) (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). While we report results using this configuration, we provide estimates of the sensitivity of retrievals to the choice of SOC database and the inclusion or omission of C_{veg} prior (global biomass product) in the Supplement.

We apply the setup described above to 3433 $1^\circ \times 1^\circ$ pixels (1815 in tundra; 1618 in taiga) using a monthly time step. Each pixel is treated independently without assuming a prior land cover type. Prior values for two parameters (fraction of GPP respired and canopy efficiency) are set according to Bloom et al. (2016). The MHMCMC is performed three times until convergence and a total of 1500 parameter sets is sampled from the posterior distribution of parameter sets which allow producing corresponding density function of all C fluxes and stocks. In the following we report highest confidence results (median; P50) and the uncertainty represented by the 90% confidence interval (5th percentile to 95th percencile, (P_{05}^{95})). We aggregated the different C stocks into photosynthetic (C_{photo} ; leaf and labile), vegetation (C_{veg} ; leaf, labile, wood and roots) and soil (C_{dom} ; litter and SOM) C stocks.

2.3 Model evaluation at local and pan-Arctic scales

At the pan-Arctic scale, we compared our CARDAMOM GPP with FLUXCOM dataset from Jung et al. (2017). FLUXCOM is based on a machine-learning approach to upscale local GPP data from eddy-covariance towers and provide gridded estimates of monthly fluxes at $0.5^\circ \times 0.5^\circ$ resolution. FLUXCOM has been used in previous studies as a benchmark for simulated GPP (Exbrayat et al., 2018; Slevin et al., 2017). We also compared our CARDAMOM R_h with the global spatiotemporal distribution of soil respiration from Hashimoto et al. (2015) calculated by a climate-driven empirical model. To assess the degree of statistical agreement we calculated linear goodness-of-fit (slope, intercept, R^2 , RMSE, and bias) between CARDAMOM and the two independent datasets. The mapping includes stipples representing locations where the independent datasets are within the CARDAMOM's 90% confidence interval.

At a local scale, we compare CARDAMOM NEE and its partitioned components GPP and R_{eco} estimates against monthly aggregated values from the FLUXNET2015 sites. We selected 8 sites (Belelli Marchesini et al., 2007; Bond-Lamberty et al., 2004; Goulden et al., 1996; Ikawa et al., 2015; Kutzbach et al., 2007; López-Blanco et al., 2017; Lund et al., 2012; Sari et al., 2017) located across sub- and high-Arctic latitudes, covering locations with different climatic conditions and dominating ecotypes (Table S3). For this evaluation, we compared the same years for both observations and CARDAMOM, and we selected data using daytime method (Lasslop et al., 2010) due to the absence of true nighttime period during Arctic summers

photosynthesized and respired (respectively $315.0^{(450.1)}_{(226.9)}$ and $300.0^{(1515.0)}_{(119.3)}$ g C m⁻² yr⁻¹) approximately half as much as the Taiga region ($736.5^{(940.9)}_{(564.9)}$ and $618.98^{(2106.3)}_{(276.6)}$ g C m⁻² yr⁻¹).

The total size of the pan-Arctic soil C stock (C_{dom}) averaged $24.4^{(47.6)}_{(10.3)}$ kg C m⁻², an estimate 94% greater than the vegetation C stock (C_{veg}), $1.4^{(6.0)}_{(0.5)}$ kg C m⁻². The soil C stock (fresh litter and SOM) is clearly dominated by C_{som} , accounting for the 98.8%, which also dominates the total terrestrial C stock in the pan-Arctic. Among the living C stocks, 91% of the C is allocated to the structural stocks (wood and roots; $1.3^{(5.8)}_{(0.4)}$ kg C m⁻²) compared to 9% to the photosynthetic stock (leaves and labile; $0.1^{(0.1)}_{(0.1)}$ kg C m⁻²). On average, the total ecosystem C stock is $26.2^{(51.1)}_{(11.7)}$ kg C m⁻² in the pan-Arctic region, with slightly lower stocks in tundra ($24.6^{(50.7)}_{(10.8)}$ kg C m⁻²) than taiga ($28.0^{(52.0)}_{(12.8)}$ kg C m⁻²). In general, the taiga region accumulated on average ~44 %, ~55 % and ~10 % more C than tundra region in photosynthetic, structural and soil C stocks, respectively. In other words, taiga accumulates ~12 % more total C than tundra. Uncertainties in estimates of soil C stock are notably higher than for living C stocks, highlighting the lack of observational and mechanistic constraint on heterotrophic respiration.

The global mean C transit time is $1.4^{(2.2)}_{(0.9)}$ years in leaves and labile plant tissue (TT_{photo}), $4.3^{(15.3)}_{(1.6)}$ years in stems and roots (TT_{veg}), and $129.3^{(981.1)}_{(10.9)}$ years in litter and SOM (TT_{dom}). The total C transit time (TT_{tot}) ($142.5^{(1089.4)}_{(11.9)}$ years) is clearly dominated by the soil C stock, highlighting the very long periods of times that C particles persist in Arctic soils. CARDAMOM calculated 60% longer TT_{dom} in tundra compared to taiga, but also significantly greater uncertainties likely echoing from the caviates found in C_{dom} and R_{h} due to the limitations of data constraints. Longer transit times are likely affected at some degree by low temperatures, wet soils, and thus slower decomposition processes.

3.2 Data assimilation and evaluation: from global to local scale

Our analysis indicates that the assimilated data by the CARDAMOM framework are in good agreement with priors of SOC and, in a lesser degree, biomass. The agreement for the SOC dataset by Hugelius et al. (2013a) is a 1:1 relationship ($R^2 = 1.0$; RMSE = 0.97 kg C m⁻²) (Figure 2). The biomass product from Carvalhais et al. (2014) led to a tendency towards ~28% higher accumulation of C in the vegetation (leaf, labile, wood and roots) C stocks compared to the assimilated biomass in CARDAMOM ($R^2 = 0.97$; RMSE = 0.46 kg C m⁻²). The understanding of ecological dynamics implemented in CARDAMOM cannot fully resolve Carvalhais et al. (2014) biomass in agreement with other products of LAI and SOC.

On the other hand, we compared our estimates of GPP and R_{h} with independent datasets to evaluate the model performance (Figure 3). We found GPP to be well correlated ($R^2 = 0.81$; RMSE = 0.43 kg C m⁻²), but significantly lower (~51%) compared to Jung et al. (2017)'s GPP estimates. The areas with larger agreement, this is where FLUXCOM falls within CARDAMOM's 90% confidence interval, are in taiga regions rather than in tundra (Figure 3). We found the R_{h} product from Hashimoto et al. (2015) is less consistent with our estimates ($R^2 = 0.38$; RMSE = 0.09 kg C m⁻²), presenting a tendency towards lower values in tundra pixels and higher values in taiga pixels. R_{h} falls only within the 90% confidence interval of CARDAMOM in Central Northern Canada and Eurasia as well as the grasslands in South Russia and Mongolia (Figure 3). The spatial variability of R_{h} is considerably smaller in Hashimoto et al. (2015) compared to our CARDAMOM estimates. This findings confirm the uncertainties previously noted in modelled respiratory processes (Table 1) where the upper P95 in R_{h} dominated NEE's uncertainties, but also the soil C stocks and transit times.

In order to get also a comparison with direct ground observations from the FLUXNET2015 dataset, we report here monthly aggregated P50 ± P25-75 estimates of NEE, GPP and R_{eco} to show timing and magnitudes, but also to diagnose

whether CARDAMOM is in general agreement with flux tower data. Overall, CARDAMOM performed well in simulating observed NEE ($R^2 = 0.66$; $RMSE = 0.51 \text{ g C m}^{-2} \text{ month}^{-1}$; $Bias = 0.16 \text{ g C m}^{-2} \text{ month}^{-1}$), GPP ($R^2 = 0.85$; $RMSE = 0.89 \text{ g C m}^{-2} \text{ month}^{-1}$; $Bias = 0.5 \text{ g C m}^{-2} \text{ month}^{-1}$) and R_{eco} ($R^2 = 0.82$; $RMSE = 0.63 \text{ g C m}^{-2} \text{ month}^{-1}$; $Bias = 0.35 \text{ g C m}^{-2} \text{ month}^{-1}$) across 8 sub-Arctic and high-Arctic sites from the FLUXNET2015 dataset (Figure 4; Table 2). CARDAMOM NEE is 25% lower than FLUXNET2015, while GPP and R_{eco} are 30% and 10% higher, respectively. This mismatch is important in the context of the FLUXCOM GPP upscaling, 50% lower than CARDAMOM. Some sites such as Hakasia, Samoylov, Poker Flat and Manitoba (NEE $R^2 = 0.73$; GPP $R^2 = 0.92$ and $R_{eco} R^2 = 0.88$) represent better the seasonality and the magnitude of the C fluxes than the rest, i.e. Tiksi, Kobbefjord, Zackenberg and UCI-1998 (NEE $R^2 = 0.58$; GPP $R^2 = 0.67$ and $R_{eco} R^2 = 0.67$). In general, CARDAMOM captured the beginning and the end of the growing season (Figure 4), although the assimilation system have important bias due to (1) difference in timing (e.g. earlier shifts of peak of the growing season in Manitoba GPP and R_{eco} and earlier end of the growing season in Poker Flat NEE) and (2) differences in flux magnitudes (such as in Hakasia GPP and R_{eco} and Kobbefjord NEE).

3.3 Benchmarking ISI-MIP with CARDAMOM

We used our highest confidence retrievals of NPP, C_{veg} and TT_{veg} (i.e. retrievals including assimilated LAI, biomass and SOC) to benchmark the performance of the GVMs from the ISI-MIP project. In this assessment we compared not only their spatial variability across the pan-Arctic, tundra and taiga region (Figure 5), but also the degree of agreement between their mean model ensemble within the 90% confidence interval of our assimilation framework (Figure 6, Table 3). Overall, ISI-MIP models are more in agreement with CARDAMOM's NPP estimates ($RMSE = 0.3 \text{ kg C m}^{-2} \text{ yr}^{-1}$; $Bias = 0.1 \text{ kg C m}^{-2} \text{ yr}^{-1}$) than C_{veg} ($RMSE = 2.8 \text{ kg C m}^{-2}$; $Bias = 1.7 \text{ kg C m}^{-2}$) and TT_{veg} ($RMSE = 15.0 \text{ years}$; $Bias = 3.5 \text{ years}$). Moreover, the assessed GVMs consistently estimated 36% and 53% higher NPP and C_{veg} and 45% longer TT_{veg} than CARDAMOM across the entire pan-Arctic domain (Figure 5 and 6). HYBRID overestimated CARDAMOM NPP and C_{veg} more clearly than any other model by 70% and 75%, but only 36% for TT_{veg} . This is a representative example of compensating errors that may reduce the apparent bias in the inner dynamics. In other word, HYBRID TT_{veg} is simply the result of a systematic overestimation of NPP and C_{veg} . On the other hand, JeDi and SDGVM are the models in closer agreement with CARDAMOM (Table 3; Figure 5 and 6).

Finally, we apportioned the error contribution to TT_{veg} by applying an attribution analysis in order to identify the origin of the bias, this is NPP or C_{veg} . Interestingly, we found that C_{veg} is weakly simulated in GVMs and is a major component of error in their forecasts (Figure 7). We used CARDAMOM to calculate two hypothetical TT_{veg} (i.e. $TT_{veg} = \text{CARDAMOM } C_{veg} / \text{ISI-MIP NPP}$ and $TT_{veg} = \text{ISI-MIP } C_{veg} / \text{CARDAMOM NPP}$) and then identify the largest difference with CARDAMOM's reference TT_{veg} . We estimated the hypothetical TT_{veg} for each pixel in each model, and derived a pixel-wise measure of the contribution of biases in NPP and C_{veg} to biases in TT_{veg} by overlapping their distribution functions (Figure 7). The distribution of the differences relative to CARDAMOM revealed that the highest error (i.e. the lower overlapped area, and by extension the largest contributor to TT_{veg} biases) comes from C_{veg} with only a 29% agreement in the distribution.

4 Discussion

4.1. Pan-Arctic retrievals of C cycle

The CARDAMOM framework has been used to evaluate the terrestrial pan-Arctic C cycling in tundra and taiga at coarse spatio-temporal scale (at monthly and annual time steps for the 2000-2015 period and at $1^\circ \times 1^\circ$ grid cells). Overall, we found that the pan-Arctic region (1) was most likely a consistent sink of C (weaker in tundra and stronger in taiga), although the large uncertainties derived from respiratory processes (Table 1) strongly increase the 90% confidence interval uncertainty; (2) accumulated most of the C in the soil C stock (both fresh litter and SOM, but dominated by the latter with a contribution of about 97%); and (3) experienced longer transit times litter and SOM C stock in tundra compared to taiga.

In general, we found a reasonable agreement between CARDAMOM and different sources of assimilated and independent data at both pan-Arctic and local scale. CARDAMOM retrievals of assimilated data are in agreement with the SOC and biomass constraints (Figure 2). The simulation of TT_{dom} is weakly constrained - our analysis adjusts TT to match mapped stocks, hence the strong match of modelled to mapped SOC. So, independent data on TT_{dom} data (e.g. ^{14}C) is required across the pan-Arctic region to provide stronger constraint on process parameters. Further, the retrievals presented here exhibited a modest performance compared to independent global GPP (Jung et al., 2017) and R_h products (Hashimoto et al., 2015) (Figure 3). The uncertainties in CARDAMOM R_h are substantially larger than for CARDAMOM GPP, and that echoes in the large uncertainty found in NEE (Table 1). One difference between these two models is the lack of moisture limitation on respiration in CARDAMOM. Conversely, GPP is relatively well-constrained through the assimilation of LAI and a prior for productivity (Bloom et al., 2016), although an important mismatch has been found: CARDAMOM GPP is 50% lower than FLUXCOM, but 30% higher than FLUXNET2015 EC data.

Interestingly, the agreement between earth observation data and EC data is surprisingly good given the vast scale difference. However, a direct point-to-grid cell comparison with local observations derived from the FLUXNET2015 dataset (Figure 4, Table 2) is challenging and always difficult. CARDAMOM outputs covers $1^\circ \times 1^\circ$ grid cells, whereas local eddy covariance flux measurements are in the order of 1-10 hectares. Thus, for observational sites located in areas with complex terrain, such as Kobbefjord in coastal Greenland, the agreement can be expected to be low. For inland forest sites, such as Poker Flat in Alaska, there may be less differences in vegetation characteristics and local climatology between the local scale measurement footprint and the corresponding CARDAMOM grid cell. This scaling issue is likely to have a larger impact on flux magnitudes compared with seasonal dynamics. In general, CARDAMOM captured the seasonal dynamics in NEE, GPP and R_{eco} well (Figure 4, Table 2). There was, however, a consistent timing-mismatch in early season flux increase, where CARDAMOM predicts earlier growing season onset compared with observations. This is likely due to the impact of snow cover, which is not explicitly included in the CARDAMOM framework.

At broader scales CARDAMOM demonstrates that an assimilation system can certainly be a robust and useful tool to assess large scale C cycle dynamics in the Arctic - its retrievals are in agreement with several outcomes from relevant papers such as the (I) C flux observations and model estimates reported in McGuire et al. (2012); (II) C stocks and transit times described by Carvalhais et al. (2014), and (III) NPP, C stocks and turnover rates stated in Thurner et al. (2017).

- I. The CARDAMOM NEE estimates reported in this study for the tundra domain are inside the variability comparison of values compiled by McGuire et al. (2012) considering field observation, regional process-based models, global-process based models and inversion models. The authors reported that Arctic tundra was a sink of CO_2 of $-150 \text{ Tg C yr}^{-1}$ ($SD=45.9$) across the 2000-2006 period over an area of $9.16 \times 10^6 \text{ km}^2$. Here, CARDAMOM NEE estimated -

125 Tg C yr⁻¹ over an area of 9 x 10⁶ km² for the same period. This exhaustive assessment of the C balance in Arctic tundra included approximately 250 estimates using the chamber and eddy covariance method from 120 published papers (McGuire et al., 2012; Supplement 1) with an area-weighted mean of means of -202 Tg C yr⁻¹. The regional models, including runs from LPJ-Guess WHyMe (Wania et al., 2009a, b), Orchidee (Koven et al., 2011), TEM6 (McGuire et al., 2010), and TCF model (Kimball et al., 2009), reported a NEE of -187 Tg C yr⁻¹ and GPP, NPP, R_a and R_h of 350, 199, 151 and 182 g C m⁻²yr⁻¹, respectively. GVMs applications such as CLM4C (Lawrence et al., 2011), CLM4CN (Thornton et al., 2009), Hyland (Levy et al., 2004), LPJ (Sitch et al., 2003), LPJ- Guess (Smith et al., 2001), O-CN (Zaehle and Friend, 2010), SDGVM (Woodward et al., 1995), and TRIFFID (Cox, 2001) estimated a NEE of -93 Tg C yr⁻¹ and GPP, NPP, R_a and R_h of 272, 162, 83 and 144 g C m⁻²yr⁻¹. For the same period, CARDAMOM has estimated 318, 161, 154 and 148 g C m⁻²yr⁻¹ respectively for the same gross C fluxes.

- II. Carvalhais et al. (2014) estimated a total ecosystem carbon (C_{tot}) of 20.5_(8.0)^(52.5) kg C m⁻² for tundra and 24.8_(15.2)^(58.0) kg C m⁻² for taiga, while CARDAMOM tundra was 24.6_(18.3)^(33.0) kg C m⁻², while 28.0_(21.5)^(36.1) kg C m⁻² in taiga (Figure 5; Table 1) for the same area. In other words, Carvalhais et al. (2014)'s C_{tot} product stored only 17% and 12% less carbon in tundra and taiga respectively than CARDAMOM. Overall, CARDAMOM calculated 20% and 6% longer transit times for tundra and taiga respectively, with average values of 80.8_(21.8)^(195.2) years in tundra and 51.2_(22.1)^(109.3) years in taiga (Table 1) compared to the 64.4_(25.7)^(259.8) years in tundra and 48.2_(24.9)^(111.6) years in taiga in Carvalhais et al. (2014). These numbers have been retrieved from the same biome classification and they include the 90% confidence interval of the assessed spatial variability. Both datasets agree on the fact that high (cold) latitudes, first tundra, and second taiga have the longest transit times in the entire globe (Bloom et al., 2016; Carvalhais et al., 2014).
- III. A recent study from Thurner et al. (2017) assessed temperate and taiga-related TTs presenting a 5-year average NPP dataset applying both MODIS (Running et al., 2004; Zhao et al., 2005) and BETHY/DLR (Tum et al., 2016) products and an innovative biomass product (Thurner et al., 2014) accounting for both forest and non-forest vegetation. Our estimate of TT_{veg} for the exact same period is 5.2_(1.9)^(17.8) years, very close to Thurner et al. (2017)'s TT, 8.2_(5.5)^(11.5) years using MODIS and 6.5_(4.2)^(8.7) years using BETHY/DLR. A note of caution here, the number reported by the authors are turnover rates, which are inferred to transit times by just applying the inverse of turnover rates (TT_{veg}=1/turnover rates). Additionally, their NPP estimates, 0.35 and 0.45 kg C m⁻² yr⁻¹ from both MODIS and BETHY/DLR, is only 5% more productive as average than CARDAMOM NPP estimate, 0.4_(0.3)^(0.5) kg C m⁻² yr⁻¹; and the biomass derived from Thurner et al. (2014), 3.0 ± 1.1 kg C m⁻², is 23% lower than CARDAMOM C_{veg}, 2.3_(1.2)^(4.9) kg C m⁻², calculated for the same period and for the same taiga domain.

4.2. CARDAMOM as a benchmarking tool

The CARDAMOM framework has proven capable of effectively simulating Arctic C cycling dynamics in the entire pan-Arctic region, but also to partition it in its two main biomes, i.e. tundra and taiga (Figure 2, 3, 4, Table 1, Discussion 4.1). We used our data assimilation system as a benchmarking tool for six GVMs and we found that productivity (NPP) processes are more in agreement with CARDAMOM than biomass (C_{veg}), and thus biomass is the largest contributor to the bias governing C transit time (TT). This finding suggests also that there is a need to improve simulations of vegetation C stocks in Earth System models and to calculate more robust inner dynamics. Recent studies used the same GVM inter-comparison models we

used here raising strong arguments about the differences in model formulations and their impact on calculations, significant uncertainties and poor representation of C stocks dynamics at global scale (Exbrayat et al., 2018; Friend et al., 2014; Nishina et al., 2014; Nishina et al., 2015; Thurner et al., 2017). Here, we present a considerably more data-constrained and data-integrated approach than traditional GVMs to calculate C dynamics. Consequently, we believe CARDAMOM is a good candidate to use as benchmark approach to pinpoint caveats of model performance. For example, Exbrayat et al. (2018) found that ISI-MIP models are less in agreement for NPP in boreal latitudes compared to global CARDAMOM retrievals addressed in Bloom et al. (2016), lacking the biomass constraint in boreal regions. In this study, we incorporated two new and critical layers of data constraints suitable for high latitudes (Carvalhais et al., 2014; Hugelius et al., 2013b) compared to the previous CARDAMOM version, and we found that NPP has one of the best agreements among the assessed variables (compared to C_{veg} and TT_{veg}), but also slightly better performance in tundra than in taiga (Bias = 9 and 19 g C m⁻² yr⁻¹ respectively) (Figure 5 and 6; Table 3).

Furthermore, recent studies have emphasized the significance and need for model comparison of variables such as transit times (Ceballos-Núñez et al., 2017; Sierra et al., 2017), a diagnostic metric independent of model internal structure. From a modelling point of view, it remains unclear why transit times differ (Figure 5 and 6) and whether NPP or C_{veg} dominates the biases. Based on Figure 5 and 6, biases in biomass C stocks likely dominate the error in transit times. Consequently, we used CARDAMOM to calculate the relative contribution of productivity and biomass to the transit times bias by applying a simple attribution analysis (Figure 7). We concluded that the largest bias to transit times are originated by a deficient understanding of the biomass component. Therefore, this study agrees with previous studies (Friend et al., 2014; Nishina et al., 2014; Thurner et al., 2017) highlighting the deficient representation of transit times/turnover dynamics, but we further suggest that GVM and ESM modellers need to focus on the vegetation C stocks dynamics calculations to improve inner C dynamics.

4.3 Outlook

Although CARDAMOM estimates for pan-Arctic C cycling are in moderately good agreement with observations and data constraints, we have not included important components controlling ecosystem processes that could potentially improve our understanding on C feedbacks, and with emphasis for high latitude ecosystems. For example, thaw and release of permafrost C is not represented in CARDAMOM, but the influence on vegetation dynamics, permafrost degradation and soil respiration is critical in high latitudes (Koven et al., 2015a; Parazoo et al., 2018). Also, Koven et al. (2017) shown that soil thermal regimes are key to getting the long-term vulnerability of soil C right. Moreover, we have not characterized snow dynamics and the insulating effect of snow affecting respiratory losses across wintertime periods either (Essery, 2015; López-Blanco et al., 2018). Further, methane emissions, another important contributor to total C budget (Mastepanov et al., 2008; Mastepanov et al., 2012; Zona et al., 2016), was neglected from this modelling exercise and it is not easy to model due to its complex transport mechanisms (Kaiser et al., 2017; Walter et al., 2001).

In order to decrease uncertainties around the balance of photosynthetic inputs and respiratory outputs, future explorations on SOC decomposition by microbial activity (Xenakis and Williams, 2014), nutrient interactions with carbon (Thomas and Williams, 2014), plant traits relationships across pan-Arctic regions (Reichstein et al., 2014; Sloan et al., 2013), mechanisms driving carbon use efficiency (Bradford and Crowther, 2013; Street et al., 2013), drivers of gross flux coupling (López-Blanco et al., 2017), and effect of fine-scale disturbances such as moth outbreaks (Heliasz et al., 2011; López-Blanco et al., 2017; Lund et al., 2017) should be addressed at the coarse pan-Arctic scale. From a modelling perspective, we consider

that more field observations are crucial, specifically on plant and soil decomposition (C stocks turnover rates)(He et al., 2016) and respiratory processes (partitioning of R_{eco} into R_a and R_h) (Hobbie et al., 2000; McGuire et al., 2000), not only across the growing season, but also during wintertime (Commane et al., 2017; Zona et al., 2016). An improved data-model integration will move towards enhanced model robustness and the decrease of model uncertainties.

5 Conclusions

The Arctic is experiencing rapid environmental changes, which are expected to significantly influence the global C cycle. Using a data-assimilation framework we have evaluated the current state of key C flux, stocks and transit time variables for the pan-Arctic region. We found that the pan-Arctic region was a likely sink of C, weaker in tundra and stronger in taiga, but uncertainties around the respiration losses are still large, and so the region could be a source of C. Comparisons with global and local scale datasets demonstrate the advantageous capabilities of CARDAMOM assessing the C cycling in the Arctic domain. Moreover, CARDAMOM is a more data-constrained and data-integrated approach than any GVMs available, thus data-assimilation systems are good candidates to benchmark a forward model's performance and pinpoint issues that need attention. We found better agreement for NPP estimates than for biomass, which is the main contributor to transit time bias. Improved mapping of vegetation C stocks and change over time is required for better analytical constraint. Moreover, future work is required with modelling of soil thermal regimes, permafrost and snow dynamics to improve accuracy and decrease uncertainties. This work establishes the baseline for more process-based ecological analyses using the CARDAMOM data-assimilation system as a promising technique to constrain the pan-Arctic C cycle.

Data availability

CARDAMOM output used in this study is available from Exbrayat and Williams (2018) from the University of Edinburgh's DataShare service at <http://dx.doi.org/10.7488/ds/2334>.

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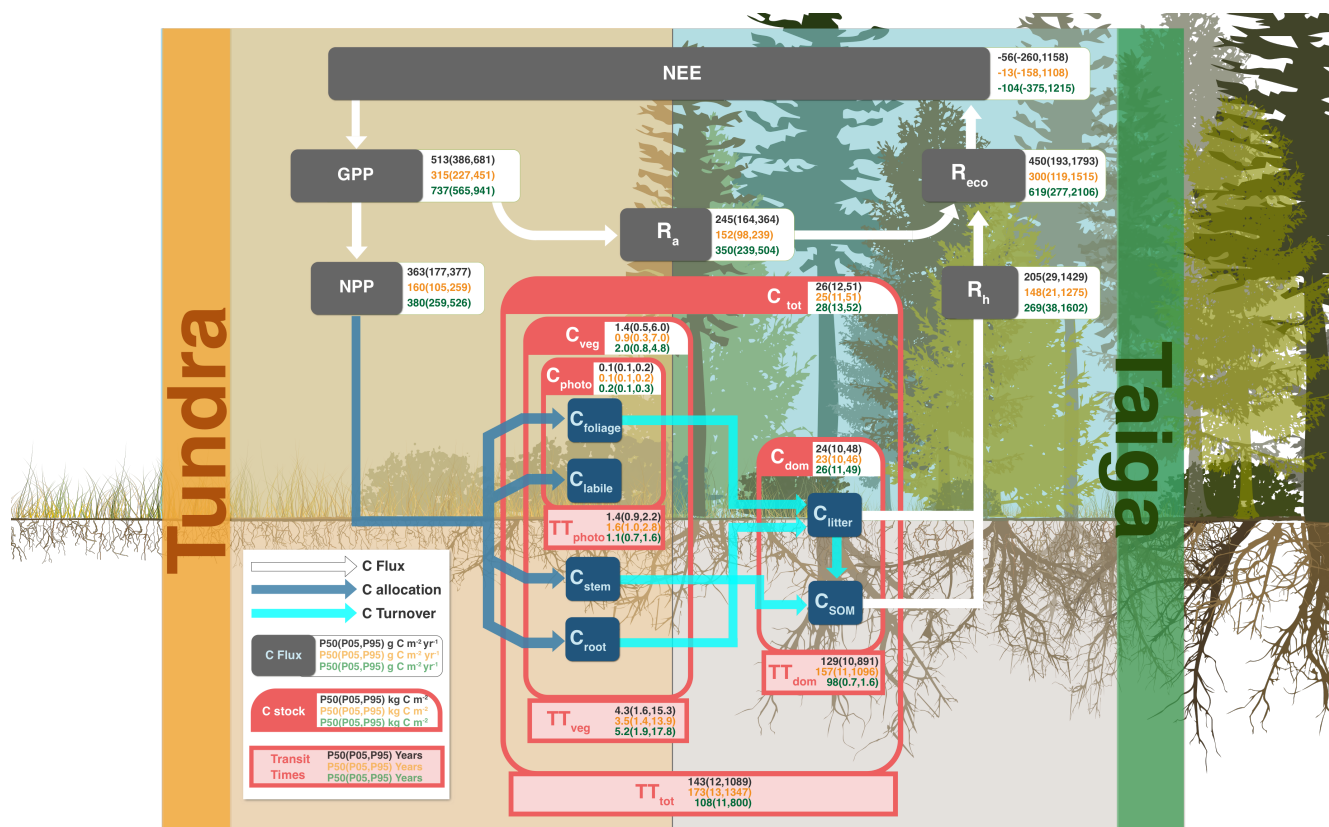


Figure 1. Schematic diagram of the terrestrial C processes modelled in CARDAMOM for the pan-Arctic (black values), tundra (yellow values) and taiga (green values) domains. The values characterize the median for the 2000–2015 period and the parentheses delimit the 90% confidence interval. C processes represented include flows for C fluxes in white [NEE, Net Ecosystem Exchange; GPP, Gross Primary Production; NPP, Net Primary Production; R_{eco}, ecosystem Respiration; R_a, autotrophic Respiration; R_h, heterotrophic Respiration], C allocation in blue [to labile, leaf, stem and root], and C turnover in cyan [from leaf, wood, roots and litter] . C stocks are represented in dark blue boxes [labile, leaf, stem, root, litter and SOM, Soil Organic Matter] and aggregated into photosynthetic (C_{photo} = leaf + labile), vegetation (C_{veg} = leaf + labile + wood + roots), soil (C_{dom} = litter + SOM) and total (C_{tot} = C_{photo} + C_{veg} + C_{dom}) C stocks in red boxes. Analogy, transit times (TT) are also aggregated into photosynthetic (TT_{photo} = leaf + labile), vegetation (TT_{veg} = leaf + labile + wood + roots), soil (TT_{dom} = litter + SOM) and total (TT_{tot} = TT_{photo} + TT_{veg} + TT_{dom}) C transit times.

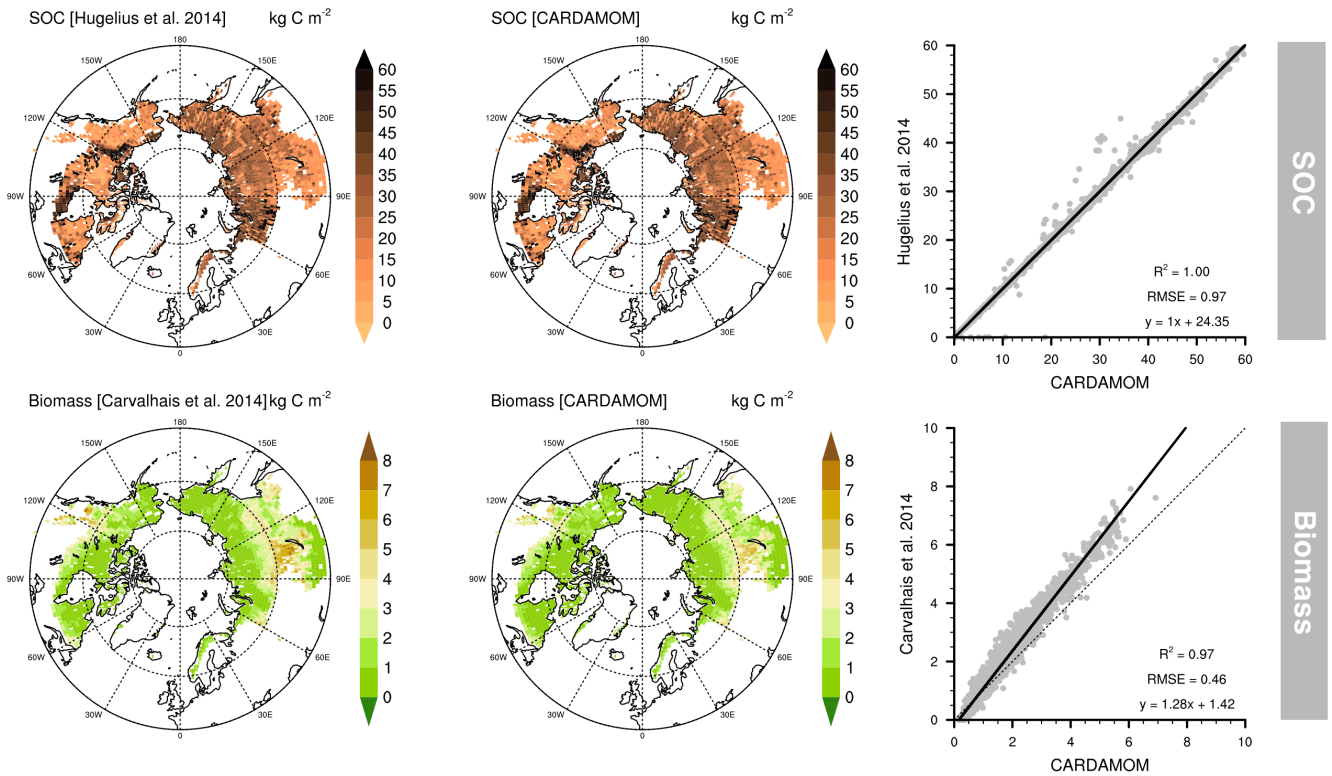


Figure 2. Original soil organic carbon [SOC; Hugelius et al., 2014] and biomass [Carvalhais et al., 2014] datasets used in the data assimilation process within the CARDAMOM framework (left hand side), assimilated SOC and biomass integrated in CARDAMOM (center), and their respective goodness-of-fit statistics between original and assimilated datasets (right hand side).

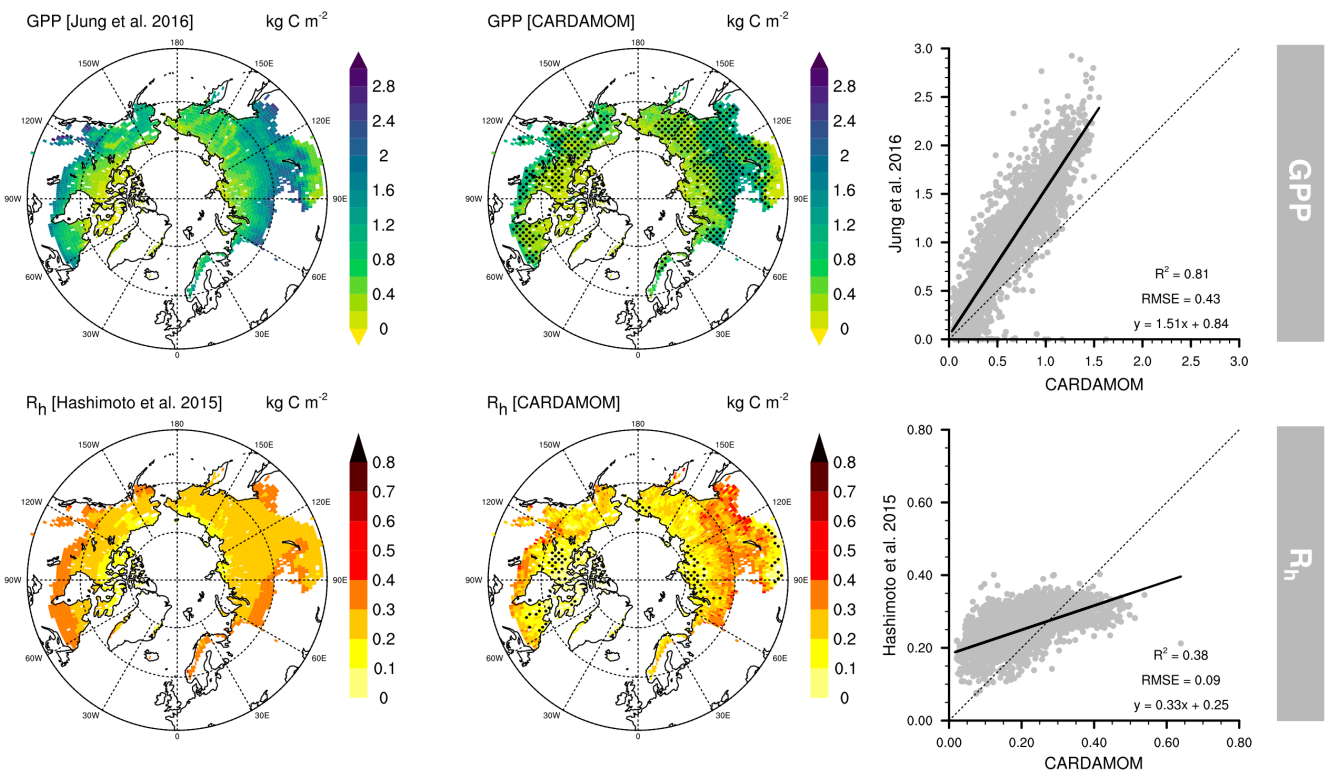
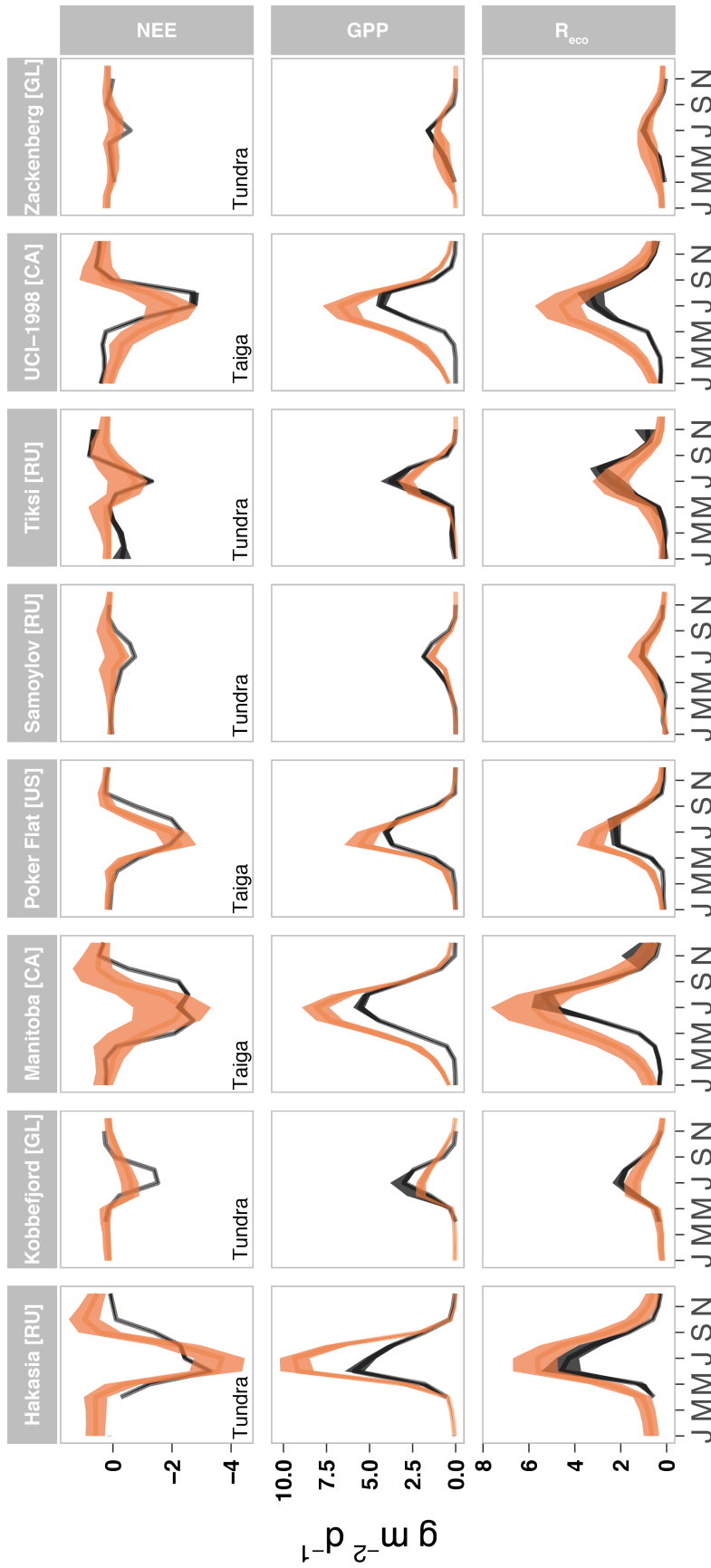


Figure 3. Original gross primary productivity [GPP; Jung et al., 2016] and heterotrophic respiration [R_h ; Hashimoto et al., 2015] datasets used in the data validation process (left hand side), estimated GPP and R_h by CARDAMOM (center), and their respective goodness-of-fit statistics between original and assimilated datasets (right hand side). Stippling indicates locations where the independent datasets are within the CARDAMOM's 5th and 95th percentiles.



■ FLUXNET2015 ■ CARDAMOM

Figure 4. Monthly-aggregated seasonal variability of observed [FLUXNET2015] and modelled [CARDAMOM] C fluxes [NEE, Net Ecosystem Exchange; GPP, Gross Primary Production; R_{eco} , ecosystem Respiration] across eight low- and high-Arctic sites [Hakasia, Kobefjord, Manitoba, Poker Flat, Samoylov, Tiksi, UCI-1998 and Zackenberg]. Each of these sites, located in different countries [RU-Russia, GL-Greenland, CA-Canada, US-United States,] feature different meteorological conditions and vegetation types (Table S2). Uncertainties represent the 25th and 75th percentiles of both field observations and the CARDAMOM framework.

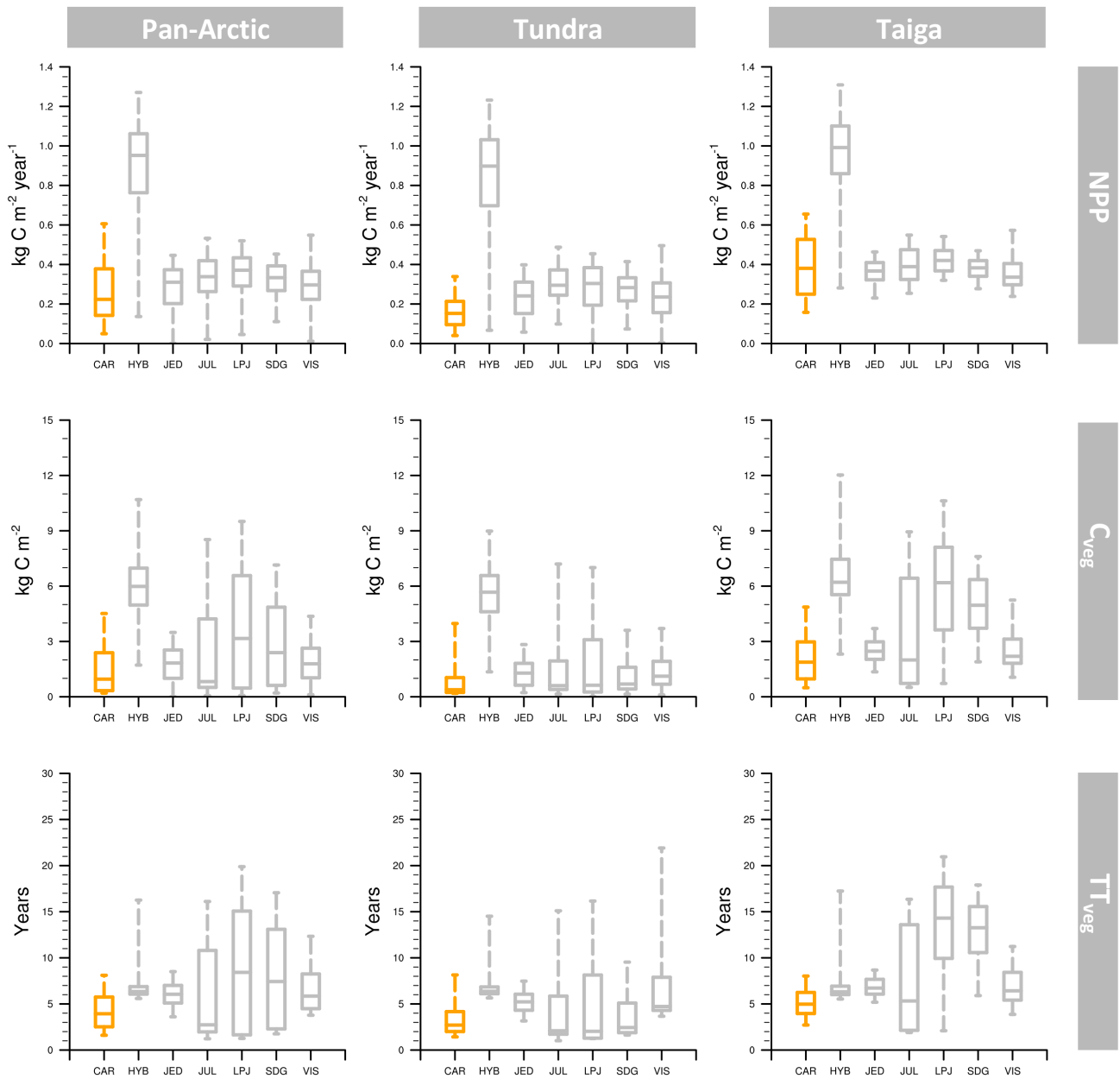


Figure 5. Central tendency and variability of NPP [Net Primary Production], C_{veg} [Vegetation C pool], TT_{veg} [Vegetation transit time] in the Pan-Arctic, tundra and taiga regions. The box whisker plots comprises the estimations between the 5th and 95th percentiles, and the box encompasses the 25th to 75th percentiles. The line in each box mark the median of studied variables in each region.

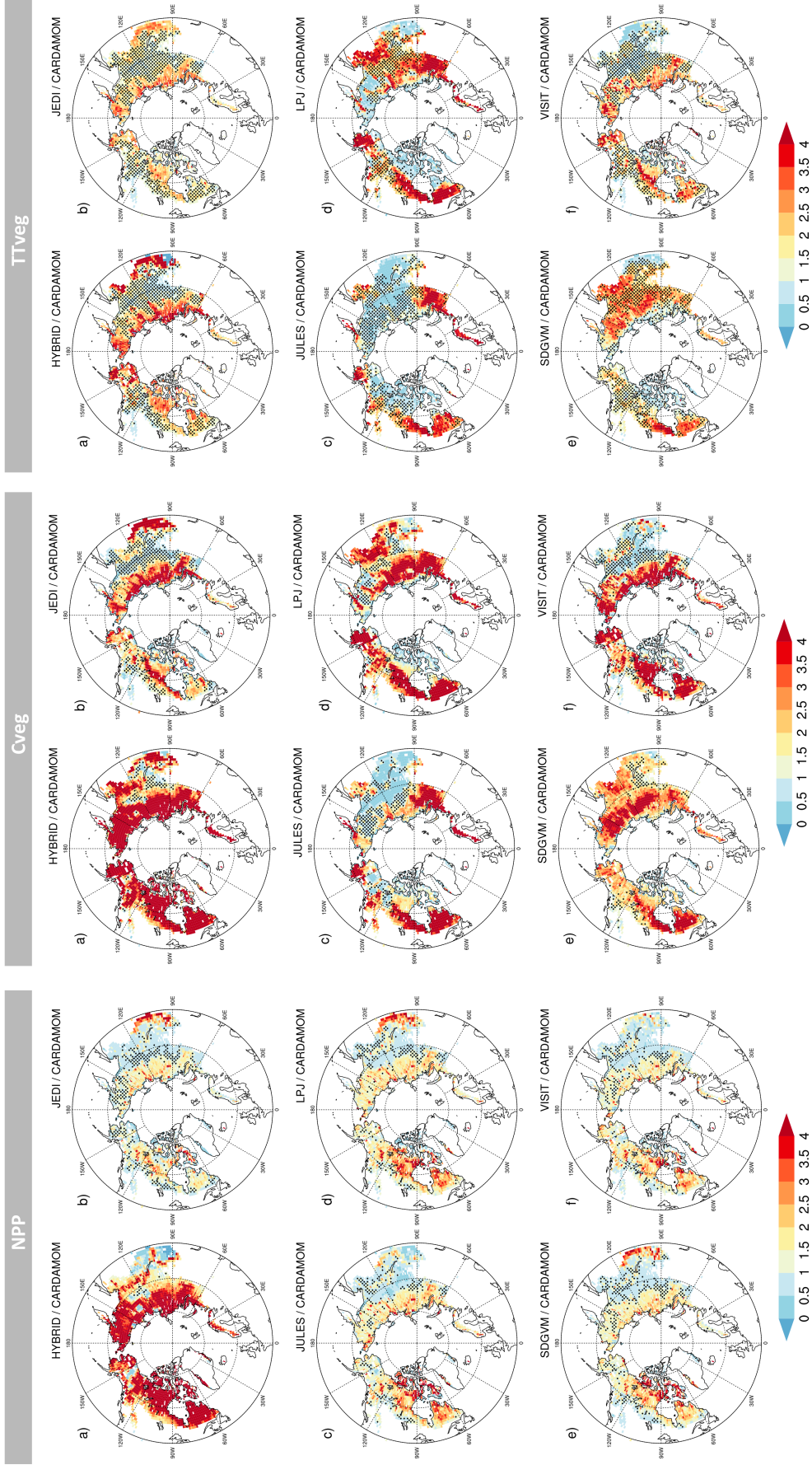


Figure 6. NPP [Net Primary Production], Cveg [Vegetation C pool] and TTveg [Vegetation transit time] ratios between ISI-MIP model ensembles [HYBRID, JEDI, LPJ, SDGVM and VISIT] and CARDAMOM. Stippling indicates locations where the ISI-MIP model mean is within the CARDAMOM's 5th and 95th percentiles.

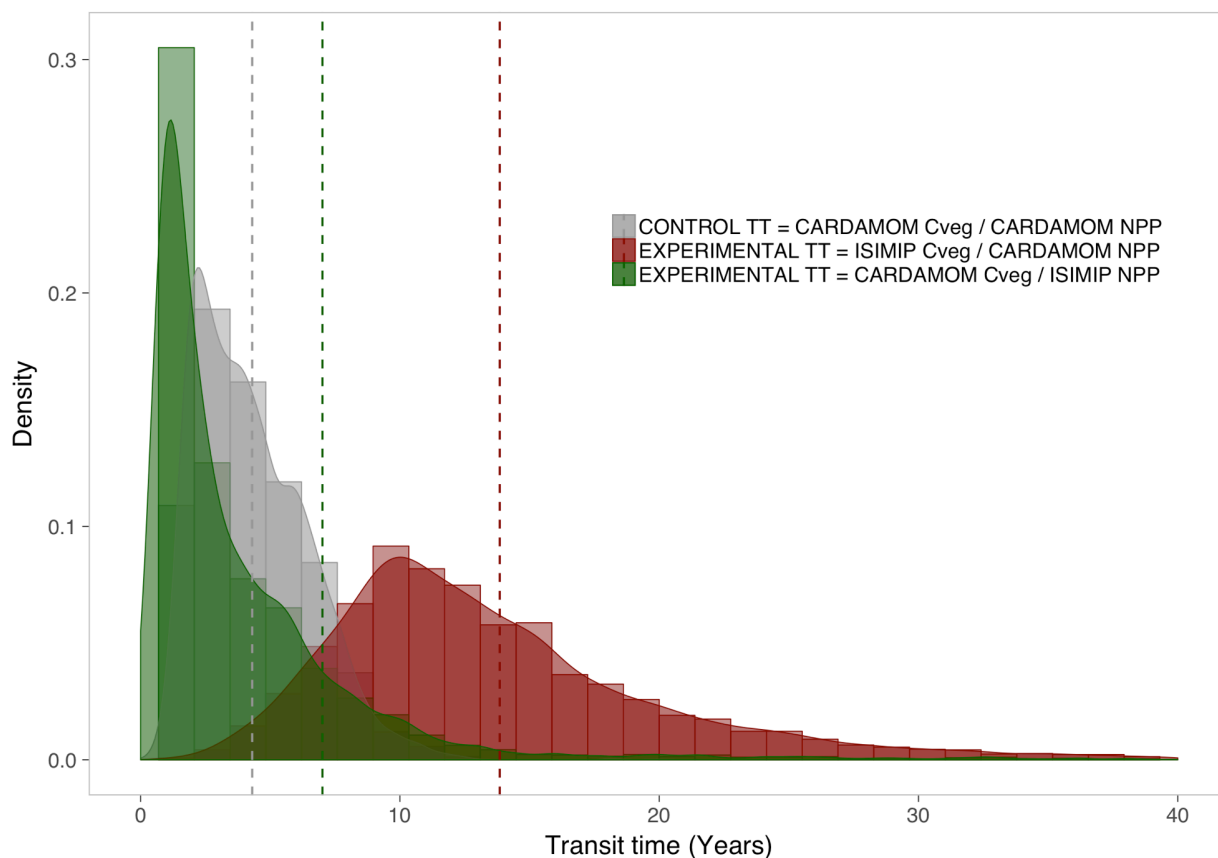


Figure 7. Distribution functions derived from the attribution analysis used to estimate the origin of vegetation transit time (TT_{veg}) bias from ISIMIP models. The control TT includes both biomass (C_{veg}) and net primary production (NPP) estimated by CARDAMOM (grey), while each of the two experimental TTs include C_{veg} (yellow) and NPP (blue) from ISIMIP models. The lower the overlapped area is between control and experimental TT, the larger the contribution for TT biases is. Dashed lines represent the average TT value for each population. For readability purposes, the scale in X-axis is delimited to 40 years.

Table 1. Multi-year (2000-2015) annual average of main ecosystem C fluxes [NEE, GPP, NPP, R_{eco}, R_a, R_h; g C m⁻² yr⁻¹], C pools [C_{photo}, C_{veg}, C_{dom}, C_{tot}; kg C m⁻²] and transit times [TT_{photo}, TT_{veg}, TT_{dom}, TT_{tot}; years] for the pan-Arctic, tundra (non-forested) and taiga (forested), region. The averages contain the estimations between the 5th and 95th percentiles, and the median in bold (50th percentile).

	Pan-Arctic					Tundra					Taiga				
	P05	P25	P50	P75	P95	P05	P25	P50	P75	P95	P05	P25	P50	P75	P95
C fluxes															
NEE	-260.5	-152.0	-55.8	156.9	1158.1	-158.5	-81.1	-13.0	176.6	1107.7	-375.4	-232.0	-104.1	134.7	1215.0
GPP	385.8	456.0	513.1	578.5	681.1	226.9	273.4	315.0	367.2	450.7	564.9	661.9	736.5	816.8	940.9
NPP	177.4	224.6	263.3	307.3	376.6	104.8	133.9	159.9	192.1	243.9	259.3	326.9	379.9	437.1	526.1
R _{eco}	193.2	316.3	449.9	716.6	1792.9	119.3	204.0	300.0	528.1	1515.0	276.6	442.9	619.0	929.1	2106.3
R _a	164.3	207.7	245.3	289.9	364.0	98.4	126.5	152.3	184.9	239.9	238.7	299.2	350.1	408.2	503.9
R _h	28.9	108.6	204.6	426.7	1428.9	21.0	77.5	147.6	343.2	1275.1	37.9	143.7	268.9	520.9	1602.3
C pools															
C _{photo}	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.2	0.3
C _{veg}	0.5	0.9	1.4	2.5	6.0	0.3	0.5	0.8	2.1	7.1	0.7	1.3	2.0	3.0	4.8
C _{dom}	10.3	18.2	24.4	32.2	47.6	10.0	17.3	23.3	30.8	46.0	10.7	19.3	25.7	33.8	49.4
C _{tot}	11.7	19.8	26.2	34.5	51.3	10.8	18.3	24.6	33.0	50.7	12.8	21.5	28.0	36.1	52.0
Transit times															
TT _{photo}	0.9	1.1	1.4	1.7	2.2	1.0	1.3	1.6	2.0	2.8	0.7	0.9	1.1	1.3	1.6
TT _{veg}	1.6	2.7	4.3	7.2	15.3	1.4	2.3	3.5	6.0	13.0	1.9	3.2	5.2	8.6	17.8
TT _{dom}	10.2	54.5	129.3	266.0	891.1	11.3	63.1	157.3	329.9	1096.2	8.9	44.8	97.9	194.1	660.2
TT _{tot}	11.9	59.9	142.5	297.8	1089.4	12.8	68.6	173.1	370.5	1347.4	10.8	50.0	108.1	216.2	800.1

Table 2. Statistics of linear fit between the CARDAMOM framework (independent) and the FLUXNET2015 field observations (dependent) per individual site and per C flux [NEE, Net Ecosystem Exchange; GPP, Gross Primary Production; R_{eco} , ecosystem Respiration]. The units for RMSE and bias are $C\ m^{-2}\ month^{-1}$ in NEE, GPP and R_{eco} .

Flux	Site	Country	Intercept	Slope	R ²	RMSE	Bias
NEE	Hakasia	[RU]	0.89	1.40	0.85	0.67	0.49
	Kobbefjord	[GL]	-0.11	0.35	0.58	0.21	0.08
	Manitoba	[CA]	0.10	0.66	0.70	0.55	0.41
	Poker Flat	[US]	0.15	0.83	0.81	0.37	0.25
	Samoylov	[RU]	0.06	0.45	0.87	0.05	0.14
	Tiksi	[RU]	0.00	0.38	0.41	0.26	0.02
	UCI-1998	[CA]	-0.26	0.59	0.65	0.50	-0.15
	Zackenberg	[GL]	0.03	0.37	0.54	0.07	0.04
GPP	Hakasia	[RU]	-0.24	1.80	0.98	0.57	1.21
	Kobbefjord	[GL]	0.31	0.62	0.80	0.35	-0.07
	Manitoba	[CA]	0.63	1.30	0.93	0.73	1.15
	Poker Flat	[US]	0.06	1.20	0.93	0.51	0.30
	Samoylov	[RU]	0.01	0.70	0.98	0.06	-0.14
	Tiksi	[RU]	0.14	0.78	0.87	0.36	-0.05
	UCI-1998	[CA]	1.00	1.30	0.82	0.95	1.32
	Zackenberg	[GL]	0.22	0.57	0.84	0.14	-0.01
Reco	Hakasia	[RU]	0.59	1.20	0.98	0.30	0.87
	Kobbefjord	[GL]	0.12	0.65	0.86	0.17	-0.22
	Manitoba	[CA]	0.96	0.91	0.80	0.81	0.81
	Poker Flat	[US]	0.21	1.20	0.89	0.35	0.34
	Samoylov	[RU]	0.06	0.87	0.89	0.11	0.01
	Tiksi	[RU]	0.20	0.64	0.76	0.35	-0.15
	UCI-1998	[CA]	0.57	1.20	0.83	0.59	0.81
	Zackenberg	[GL]	0.24	0.66	0.86	0.09	0.10

Table 3. Statistics of linear fit between the CARDAMOM framework (independent) and the ISIMIP models (dependent) per individual model and per NPP [Net Primary Production; kg C m⁻² yr⁻¹], C_{veg} [Vegetation C pool; kg C m⁻²] and TT_{veg} [Vegetation transit time; years]. The units for RMSE and bias are kg C m⁻² yr⁻¹ in NPP, kg C m⁻² yr⁻¹ in C_{veg} and years in TT_{veg}.

	Panarctic					Tundra					Taiga				
	Slope	Intercept	R ²	RMSE	Bias	Slope	Intercept	R ²	RMSE	Bias	Slope	Intercept	R ²	RMSE	Bias
HYBRID	0.80	0.30	0.03	0.30	0.61	0.66	1.00	0.09	0.30	0.66	-0.21	0.01	0.28	0.55	
JEDI	0.17	0.44	0.48	0.08	0.02	0.13	0.59	0.29	0.09	0.06	0.26	0.25	0.05	-0.03	
JULES	0.25	0.36	0.29	0.10	0.07	0.19	0.68	0.33	0.09	0.13	0.17	0.09	0.09	0.00	
LPJ	0.22	0.48	0.41	0.10	0.08	0.15	0.78	0.31	0.11	0.11	0.20	0.21	0.06	0.03	
SDGVM	0.21	0.41	0.52	0.07	0.05	0.17	0.60	0.35	0.08	0.11	0.26	0.47	0.04	-0.01	
VISIT	0.18	0.43	0.28	0.12	0.02	0.11	0.80	0.28	0.12	0.07	0.17	0.07	0.10	-0.03	
HYBRID	5.90	0.13	0.00	2.90	4.61	5.60	-0.05	0.00	2.40	4.60	-0.01	0.00	3.20	4.62	
JEDI	1.40	0.32	0.24	0.84	0.41	1.30	0.00	0.00	0.80	0.45	1.80	0.32	0.40	0.37	
JULES	1.80	0.55	0.08	2.80	1.07	1.60	0.15	0.01	2.40	0.85	2.20	0.57	3.00	1.30	
LPJ	2.40	0.88	0.15	3.10	2.26	1.90	0.06	0.00	2.40	0.92	4.20	0.79	2.80	3.77	
SDGVM	1.60	0.91	0.31	2.00	1.45	1.10	0.07	0.01	1.10	0.21	3.10	0.86	1.30	2.81	
VISIT	1.70	0.17	0.03	1.40	0.45	1.50	-0.06	0.00	1.20	0.45	2.40	0.10	1.30	0.44	
HYBRID	8.70	-0.07	0.00	13.00	4.14	8.80	-0.01	0.00	15.00	5.25	8.10	-0.01	10.00	2.91	
JEDI	4.80	0.29	0.18	1.30	1.80	5.00	0.07	0.01	1.30	1.93	5.40	0.29	0.19	0.97	
JULES	4.00	0.46	0.03	5.30	1.76	4.40	0.07	0.00	4.70	1.19	5.20	0.46	5.50	2.36	
LPJ	4.80	0.97	0.10	6.40	4.70	5.10	0.03	0.00	5.20	1.63	9.00	0.84	5.50	8.16	
SDGVM	2.70	1.30	0.24	4.80	3.81	3.20	0.18	0.02	2.70	0.34	6.60	1.20	3.00	7.64	
VISIT	3.00	1.40	0.01	31.00	4.85	-0.20	3.20	0.03	43.00	7.60	7.20	-0.05	2.30	1.80	

Evaluation of terrestrial pan-Arctic carbon cycling using a data-assimilation system

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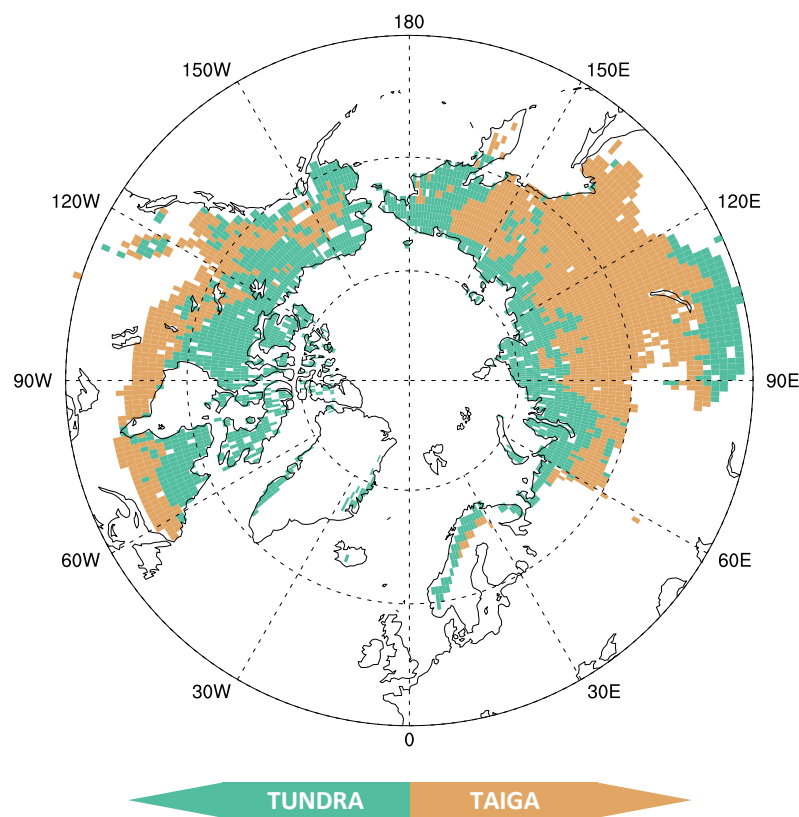


Figure S1. Spatial domain defined by the Northern Circumpolar Soil Carbon Database version 2 (NCSCDv2) region. The tundra- taiga regions were separated based on the presence-absence of forested areas using the GlobCover map (http://due.esrin.esa.int/page_globcover.php). Forested areas included: closed to open broadleaved evergreen or semi-deciduous forest (>5m), closed (>40%) broadleaved deciduous forest (>5m), open (15-40%) broadleaved deciduous forest/woodland (>5m), closed (>40%) needleleaved evergreen forest (>5m), open (15-40%) needleleaved deciduous or evergreen forest (>5m) and closed to open (>15%) mixed broadleaved and needleleaved forest (>5m).

Table S1. List of supplementary information detailing all acronyms related to model structure, Global Vegetation Models, General Circulation Models, model intercomparison projects, input data, C flux, stocks and transit times variables and statistical analyses.

Model structure used in this paper	
DALEC2	Data Assimilation Linked Ecosystem Carbon version 2
CARDAMOM	CARbon Data MOdel fraMework
MHMCMC	Metropolis-Hastings Markov Chain Monte Carlo
EDC	Ecological and Dynamic constraints
Global Vegetation Models (GVM)	
HYBRID	-
JEDI	Jena Diversity-Dynamic Global Vegetation Model
JULES	Joint UK Land Environment Simulator
LPJmL	Lund-Postdam-Jena managed Land
SDGVM	Sheffield Dynamic Global Vegetation Model
VISIT	Vegetation Integrative Simulator for Trace Gases
LPJ-WhyMe	Lund-Postdam-Jena - Wetland Hydrology and Methane model
ORCHDEE	ORganizing Carbon and Hydrology In Dynamic Ecosystems Environment
TEM	Terrestrial Ecosystem Model
TCF	Terrestrial Carbon Flux model
CLM4C	Community Land Model for Carbon
CLM4CN	Community Land Model for Carbon and Nitrogen
Hyland	-
LPJ-Guess	Lund-Postdam-Jena - General Ecosystem Simulator
O-CN	ORCHIDEE - Carbon Nitrogen
TRIFFID	Top-down Representation of Interactive Foliage and Flora Including Dynamics
BETHY/DLR	Biosphere Energy-Transfer Hydrology Model
General Circulation Models (GCM)	
HadGEM2-ES	Hadley Global Environment Model 2 - Earth System
IPSLCM5A-LR	Institut Pierre-Simon Laplace Coupled Model - Low Resolution
MIROC-ESM-CHEM	Model for Interdisciplinary Resarch On Climate- Earth System Model - CHEMistry
GFDL-ESM2M	Geophysical Fluid Dynamics Laboratory - Earth System Model
NorESM1-M	Norwegian Earth System Model 1 - Medium resolution
Model Intercomparison projects	
ISIMIP	Inter-Sectoral Impact Model Intercomparison Project
CMIP5	Coupled Model Intercomparison Project (5th phase)
TRENDY	Trends in net land carbon exchange intercomparison project
Input data	
MODIS	Moderate Resolution Imaging Spectroradiometer
LAI	Leaf Area Index
SOC	Soil Organic Carbon
HWSD	Hamonized World Soil Database
NCSCD	Northern Circumpolar Soil Carbon Database
C flux variables	
NEE	Net Ecosystem Exchange
GPP	Gross Primary Production
NPP	Net Primary Production
R _{eco}	Ecosystem Respiration
R _a	Autotrphic Respiration
R _h	Heterotrophic Respiration
C stock variables	
C _{photo}	Photosynthetic C stock [leaf + labile]
C _{veg}	Vegetation C stock [leaf + labile + stem + root]
C _{dom}	Soil C stock [litter + soil organic carbon]
C _{tot}	Total C stock [leaf + labile + litter + soil organic carbon]
Transit times	
TT _{photo}	Photosynthetic transit time [leaf + labile]
TT _{veg}	Vegetation transit time [leaf + labile + stem + root]
TT _{dom}	Soil transit time [litter + soil organic carbon]
TT _{tot}	Total transit time [leaf + labile + litter + soil organic carbon]
Statistical analyses	
R ²	Coefficient of determination
RMSE	Root Mean Square Error
BIAS	Bias error
P05	5 th percetile
P25	25 th percetile
P50	50 th percetile
P75	75 th percetile
P95	95 th percetile

Table S2. DALEC2 model parameter description, and prior ranges based on ecologically viable limits.

Process	Parameter	Prior range	Units
Plant phenology	Leaf onset day	1-365	day
	Leaf fall leaf	1-365	day
	Leaf fall period	20-150	day
	Labile C release period	10-100	day
	Canopy efficiency	5.0-50	
	Leaf mass per area	5-200	g C m ⁻²
Allocation of NPP	Fraction of GPP respired	0.3-0.7	
	Fraction of NPP to foliage C pool	0.01-1	
	Fraction of NPP to labile C pool	0.01-1	
	Fraction of NPP to roots C pool	0.01-1	
C pools	Foliar C pool	20-2000	g C m ⁻² yr
	Labile C pool	20-2000	g C m ⁻² yr
	Woody C pool	100-100000	g C m ⁻² yr
	Fine root C pool	20-2000	g C m ⁻² yr
	Litter C pool	20-2000	g C m ⁻² yr
	Soil organic matter C pool	100-200000	g C m ⁻² yr
Turnover rates	Lifespan	1.001-8	
	Wood turnover	0.000025-0.001	/day
	Root turnover	0.0001-0.01	/day
	Litter mineralization	0.0001-0.01	/day
	Soil organic matter mineralization	0.000001-0.001	/day
	Decomposition rate	0.00001-0.01	/day
	Temperature dependence exponent factor	0.018-0.08	

Table S3. Data set description of the 8 selected sites derived from the FLUXNET2015 database. MAT stands for Mean Annual Temperature while MAP for Mean Annual Precipitation.

Site ID	DK-NuF	DK-ZaH	RU-Ha1	US-Prr	CA-Man	CA-NS7	RU-Sam	RU-Tks
Site Name	Nuuk Fen	Zackenbergh	Heath Hakasia steppe	Poker Flat	Manitoba	UCI-1998 burn site	Samoylov	Tiksi
Latitude	64.1	74.5	54.7	65.1	55.9	56.6	72.4	71.6
Longitude	-51.4	-20.6	90.0	-147.5	-98.5	-99.9	126.5	128.9
MAT (°C)	-1.4	-9.0	-	-2.0	-3.2	-3.5	-	-12.7
MAP (mm)	750.0	211.0	-	275.0	520.0	483.0	-	323.0
Eco-type (IGBP)	Wetland	Heathland	Grasslands	Evergreen Needleleaf	Evergreen Needleleaf	Open shrubland	Grassland	Grasslands
Tundra-Taiga	Tundra	Tundra	Tundra	Taiga	Taiga	Taiga	Tundra	Tundra
Data availability	2008-2015	2000-2014	2002-2004	2010-2014	1994-2008	2002-2005	2002-2014	2010-2014

Table S4. General properties of the global vegetation models used in this study (derived from Nishima et al. 2014 and 2015).

GVM	Vegetation	Number of PFT	Nitrogen	Fire	Permafrost	Soil depth	Soil temperature function	Soil moisture function	Reference
HYBRID4	DGVM	6	Yes	No	No	-	Exponential with optimum	Optimum curve	Friend and White (2000)
JeDi	DGVM	15	No	No	No	> 5 m	Exponential (Q10: 1.4)	-	Pavlick et al. (2013)
JULES	DGVM	5	No	No	Yes	-	Exponential (Q10: 2.0)	Linear with plateau	Clark et al. (2011)
LPJml	DGVM	10	No	Yes	Yes	3 m	Lloyd & Taylor	Linear with plateau	Sitch et al. (2003)
SDGVM	Fixed PFT	7	Yes	Yes	No	1 m	Optimum curve	Optimum curve	Woodward et al. (1995)
VISIT	Fixed PFT	16	No	Yes	No	1 m	Lloyd & Taylor	Optimum curve	Ito and Inatomi (2012)

Table S5. Information about the 4 different scenarios used in the sensitivity analysis, using HWSD soil database with and without biomass, and NCSCD with and without biomass. We report C fluxes [NBE, Net Biome Exchange; NPP, Net Primary Production; R_h, heterorophic Respiration], C pools [C_{photo}, C_{veg}, C_{dom}, C_{tot}] and transit times [TT_{photo}, TT_{veg}, TT_{dom}, TT_{tot}]. The averages contain the estimations between the 5th and 95th percentiles, and the median in bold (50th percentile).

		HWSD						NCSCD					
		With biomass			Without biomass			With biomass			Without biomass		
		P05	P50	P95	P05	P50	P95	P05	P50	P95	P05	P50	P95
C fluxes	NBE	-261	-62	894.6	-267.5	-98.2	924.9	-258.2	-52.2	1158.6	-266.5	-89.9	1165.7
	NPP	176.8	262.3	376.1	158.6	242.3	355.5	177.5	263.5	377.6	159.8	244	357.2
	R _h	26.6	193.9	1162.9	19.3	131.6	1164.4	29	206	1428.4	20.6	141.6	1407.1
C pools	C _{photo}	63.1	118.9	223.1	150.3	562.5	1653	63.4	119.6	224.8	151.2	565.4	1650.5
	C _{veg}	486.6	1353	5296	1031.7	3573.8	43899.1	489.2	1398.3	6006.5	1037.8	3588.3	43949.5
	C _{dom}	7843.5	18749.7	36056.9	9082	20946.8	50601.3	10329.3	24489.4	47506.6	11906	27079.1	60657.6
	C _{tot}	9183.9	20377.7	39553.4	11877.9	26398.7	86233.1	11737.3	26276.1	51209.8	14966.5	33140.4	93666.2
Transit times	TT _{photo}	0.9	1.4	2.4	2.9	10.9	61	0.9	1.4	2.4	2.9	10.7	58.5
	TT _{veg}	1.6	4.2	16.5	3.1	10.3	46	1.6	4.2	16.2	3.1	10.2	45.9
	TT _{dom}	10	106.7	724	12.2	126.4	625.2	10.2	133.9	897.6	12.4	154.8	792.6
	TT _{tot}	12	120	933.5	19.4	212	1692.2	12.1	150.8	1139.7	18.9	243	1878.7

Paper SI

Pirk, N., Mastepanov, M., **López-Blanco, E.**, Christensen, L. H., Christiansen, H. H., Hansen, B. U., Lund, M., Parmentier, F.-J. W., Skov, K., and Christensen, T. R.: **Toward a statistical description of methane emissions from arctic wetlands**, *AMBIO*, 46, 70-80, 10.1007/s13280-016-0893-3, 2017.



Zackenberg site, East Greenland. 2017 field season. Photo by Efrén López-Blanco

Toward a statistical description of methane emissions from arctic wetlands

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Abstract Methane (CH₄) emissions from arctic tundra typically follow relations with soil temperature and water table depth, but these process-based descriptions can be difficult to apply to areas where no measurements exist. We formulated a description of the broader temporal flux pattern in the growing season based on two distinct CH₄ source components from slow and fast-turnover carbon. We used automatic closed chamber flux measurements from NE Greenland (74°N), W Greenland (64°N), and Svalbard (78°N) to identify and discuss these components. The temporal separation was well-suited in NE Greenland, where the hypothesized slow-turnover carbon peaked at a time significantly related to the timing of snowmelt. The temporally wider component from fast-turnover carbon dominated the emissions in W Greenland and Svalbard. Altogether, we found no dependence of the total seasonal CH₄ budget to the timing of snowmelt, and warmer sites and years tended to yield higher CH₄ emissions.

Keywords Emission · Greenland · Methane · Svalbard · Tundra

INTRODUCTION

The small coverage of measurement sites in arctic tundra causes large uncertainties in regional emission budgets of the greenhouse gas methane (CH₄) (McGuire et al. 2012). The process-based upscaling of CH₄ flux measurements requires detailed information about the local ground conditions (Davidson et al. 2016), which typically cannot be obtained with remote sensing techniques. Arctic tundra ecosystems are predicted to warm and change significantly in the near future (Johannessen et al. 2004; Callaghan et al. 2011a; Cohen et al. 2012), so there are pressing questions

about the CH₄ flux response to, e.g., earlier snowmelt and generally warmer growing seasons (Callaghan et al. 2011b). Temperature and water table position are often identified as key controls for the short-term CH₄ fluxes (Turetsky et al. 2008, 2014; Tagesson et al. 2013), but longer-term seasonal patterns could relate more to the decomposability of the different pools of organic substrates and the development of plants (Christensen et al. 2003; Whalen 2005). So would an earlier snowmelt, causing a longer growing season, lead to larger seasonal emissions? If so, the potentially increased CH₄ concentrations in the atmosphere could further amplify climate change effects.

Gas exchange measurements in the Arctic are challenging due to the harsh weather and logistical constraints. The used measurement techniques can also differ tremendously between sites (e.g., Crill et al. 1988; Wagner et al. 2003; Corradi et al. 2005; Parmentier et al. 2011), which complicates inter-site comparisons. The closed chamber technique has proven to be a robust method for CH₄ flux measurements, but it is generally not applied continuously throughout the whole growing season (Olefeldt et al. 2013). In the larger framework of the Greenland Ecosystem Monitoring Program, three arctic sites were therefore equipped with the same automatic closed chamber system to continuously monitor CH₄ fluxes on the same plots over many growing seasons and the subsequent freeze-in periods. The collected dataset gives unique possibilities to analyze the seasonal patterns at these different ecosystems. The first five years from one of the high-arctic sites (Zackenberget) were previously analyzed by Mastepanov et al. (2013). The derived flux pattern led the authors to hypothesize a bi-component origin of growing season CH₄ emissions, driven by two different mechanisms related to slow and fast carbon turnover (Chanton et al. 1995). Accordingly, a first emission peak stems from the slow-

Discussion, future perspective and key conclusions

To be able to comprehend and predict the driving mechanisms of climate change in the Arctic, it is of major importance to understand the contemporary state of the C cycle. Descriptive studies at a local scale are required to achieve a richer understanding of the ecosystems functioning. Observations networks such as FLUXNET (Baldocchi et al., 2001), ICOS or NEON as well as ecosystem monitoring programmes similar to GEM (Christensen and Topp-Jørgensen, 2017; Christensen et al., 2017) have demonstrated to be crucial systems in order to fill C cycle related knowledge gaps. However, reference sites in northern latitudes are difficult to coordinate and hardly incorporate (i) comprehensive spatial coverage in heterogeneous landscapes, (ii) high temporal resolution to sample episodic events, (iii) continuous samples to achieve full annual cycles, and (iv) field measurements with direct line power in remote areas (McGuire et al., 2012). Exclusive data-driven analyses become insufficient to provide a wide-ranging picture of the global Arctic system. Observed patterns at very specific sites may not be applicable in other locations and some sort of complements are needed to consider. Process oriented models and data assimilation systems are suitable tools to understand C dynamics at deeper degree of complexity, but also to quantify the underlying processes that are difficult to measure in the field. McGuire et al. (2012) highlighted the importance of reducing uncertainty from observations, process-based models and data assimilation systems to better understand ecosystem-atmosphere interactions. To be able to reduce uncertainties, McGuire et al. (2012) suggested to improve ground-based observation networks of CO₂ to better understand C exchange in response to disturbance (**Paper I, II**) and to effectively transfer information from enhanced observation networks into process-based models (**Paper III, IV**). These critical recommendations were taken into consideration in this thesis to advance science and knowledge of CO₂ exchange in the Arctic.

The overall objective of this thesis is to resolve key uncertainties related to mechanisms driving the net C uptake dynamics and the interplay between photosynthetic inputs, respiratory outputs and changes of C stocks in Arctic ecosystems. This thesis involved field observations (**Paper I, II, III, IV**) and modelling simulations (**Paper III, IV**), both at local (**Paper I, II, III**) and pan-Arctic scale (**Paper IV**). Specifically, the objectives were to:

1. Investigate the impact of the environmental drivers (**Paper I**) and the biological disturbance (**Paper I, II**) over the exchange of CO₂ in Arctic tundra.
2. Investigate the compensatory effect observed and modelled between photosynthesis and respiration losses (**Paper I, III**).
3. Investigate the role of wintertime fluxes over full annual cycles (**Paper III**).
4. Evaluate the terrestrial pan-Arctic C cycle retrievals of the first 15 years of the 21st century and benchmark those retrievals with estimates from extensively used GVMs to pinpoint fixable biases (**Paper IV**).

In this chapter I summarise the key results of each of the four papers, and review their application to the aims of this thesis. Here I also identify key areas for further research emerged from the outcomes of this work.

The impact of environmental drivers and a biological disturbance over the exchange of CO₂ in Arctic tundra

The Nuuk-Kobbefjord Arctic tundra site acted as a consistent sink of CO₂ across the 2008-2015 period except for the anomalous year 2011, which was associated with a major pest outbreak (Paper I, II, III). On the one hand, the flux data suggest that NEE was insensitive to growing season meteorology, despite the large inter-annual variability observed from temperature and precipitation observations. On the other hand, the ranges of annual GPP and R_{eco} were >5 fold larger than NEE, but also more variable, thus gross fluxes were highly sensitive to the meteorological variability, mostly driven by temperature and insolation. In Kobbefjord there was a tendency towards larger GPP and R_{eco} during warmer and wetter years.

The meteorological conditions have markedly shaped the C exchange balance in the Kobbefjord site (Paper I, II, III). Paper I demonstrated that temperature and radiation are the two key environmental controls in the ecosystem, even though their importance oscillate depending on the diurnal, seasonal and annual cycles, but also between different time aggregations. Air temperature dominates the diurnal cycle for NEE (similar to Lindroth et al. (2007)), GPP (except at dawn and dusk) and R_{eco}. In the seasonal and annual cycles, light is found more important than temperature for NEE and GPP, whereas temperature is the key controller of R_{eco}, which is consistently in agreement with literature (Heskel et al., 2016; Lloyd and Taylor, 1994; Tjoelker et al., 2001). Additionally, we found that the variable importance may change depending on how the data is aggregated. For instance, light becomes more important for NEE and GPP at short term scales as reported by Stoy et al. (2014), while temperature is more important in the long term scale for NEE, GPP and R_{eco}. The responses to meteorological sensitivity present, however, discrepancies with some other studies such as Peichl et al. (2014) and Strachan et al. (2015). For example, the temperature-precipitation sensitivity described in Paper I, where warmer and wetter conditions were associated with larger GPP and R_{eco}, and colder and drier conditions were linked to lower GPP and R_{eco}, have not been found by Peichl et al. (2014). Environmental drivers related to water availability (i.e. VPD, precipitation and water table depth) were not found as important as temperature and radiation, in contrast with findings by Strachan et al. (2015). It is particularly interesting that in some sites the C sink strength decreased during dry years (Aurela et al., 2007; Lund et al., 2007; Peichl et al., 2014), while this particular trend occurs in wetter years in other locations (Lafleur et al., 1997). The environmental responses to C dynamics are complex, and these may change depending on factors such as hydrological settings (Strachan et al., 2015), water table changes (Hanis et al., 2015), presence/absence of permafrost (Lund et al., 2015), vegetation shifts and topography (Johansson et al., 2013) or lagged effects after extreme episodes (Zona et al., 2014). Furthermore, some other responses may be counterintuitive. For example, Paper I demonstrated that longer growing seasons do not necessarily increase NEE (i.e. larger C uptake), similar to the findings from Lund et al. (2010) and Parmentier et al. (2011). Therefore, climate change in the Arctic C balance is not straightforward to infer.

The balance between C stocks, C allocation, C turnover, and C fluxes is highly dependent on meteorological variability but, interestingly, this variability can also positively feedback on the biological disturbance occurred in the anomalous year 2011. An useful example of positive feedback loops is represented by the combination of different factors driving the C flux variability observed between 2010 and 2011 (Paper I, II, III). The warmest July-September period in 2010 was followed by a colder than usual October-May period in 2011, featuring the thickest snowpack measured across the 2008-2015 period. These conditions,

together with a colder June, a cloudier July and the larvae feeding on vegetation, have facilitated: 1) optimal conditions for the moth outbreak survival during the winter due to the warmer temperatures created underneath the thick snowpack (Callaghan et al., 2004; Chapin et al., 2004) and 2) minimal conditions for plant growth at the beginning of the growing season. The findings covered in **Paper I, II and III** highlight the importance of shifts in the growing season timing and their direct influence on C exchange balances, but also the lagged effects influencing following years.

Explicitly, the larval outbreak in the anomalous year of 2011 induced a severe impact on vegetation productivity and CO₂ exchange in the Nuuk-Kobbefjord area. Paper I estimates a shift from a sink of -30 g C m⁻² as average for the 2008-2015 period to a source of 41 g C m⁻², even though the moth only affected the surrounding heath. More specifically, Paper II estimates a decrease of C sink strength of 118-143 g C m⁻², corresponding to 1210-1470 tonnes C at the catchment basis, focusing only on manual cambers data in the affected heath. Interestingly, Paper II we observe a counterbalanced increase of C sink strength (i.e. enhanced plant growth) throughout the following 3 years.

To our knowledge, such abrupt shift in C sink strength has not been previously reported in Arctic tundra, excluding other severely disturbed ecosystems like burned areas (Rocha and Shaver, 2011). **Paper I and II** presented a clear impact on vegetation productivity, inducing a 51% and 57% decrease of GPP compared to the previous year respectively. Moreover, the SPA model (**Paper III**) quantified the effect on NEE in 2011 as 45% environmental and 55% moth contributed, suggesting an influence from meteorological-biological drivers of a joint nature. The moth outbreak has clearly played an important role in the C dynamics, not only in 2011, but also in the following years. **Paper I and II** agree on the fact that the ecosystem has shown an ability to efficiently recover from disturbance, suggesting an ecosystem resilience similar to other cases reported before (Hewitt et al., 2013; Peichl et al., 2014; Zona et al., 2014). Specifically, **Paper II** suggests that increased nutrient turnover rates and plant growth were enhanced as a consequence of the outbreak. Higher productivity was likely driven by an increase of nitrogen from decomposed larvae after death and the potential excess of nutrient availability due to the impossibility of usage. As result, the new leaves become greener in following years, a sign of good health and rejuvenation (Tenow et al., 2004). These findings highlight the importance of biological disturbances in the ecosystem productivity and functioning in Arctic ecosystems (Post et al., 2009). Along these lines, ecosystem models are not well prepared for such sporadic events. **Paper II** demonstrated, for the first time in tundra ecosystems, that moth outbreaks can be detected using normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) satellite imagery derived products from the MODIS sensor. Therefore, similar work could be integrated within the CARDAMOM data-assimilation framework (**Paper IV**) to constrain vegetation greenness data and benchmark GVMs. This modelling exercise may provide useful guidance towards model improvements, e.g. evaluating the degree of underestimation in traditional GVM by excluding biological disturbances from their internal structure. Moth outbreaks are expected to occur more often in the coming years (Callaghan et al., 2004) and might affect the future sign of net C uptake from sink to source (Callaghan et al., 2012), thus continued efforts are required to characterize these non-trivial ecosystem processes.

The compensatory effect between photosynthesis and respiration losses

The marked meteorological insensitivity of NEE during the snow-free period observed from flux data in Paper I was found driven by the correlated response of photosynthesis (GPP) and respiration losses (R_{eco}). However, we could not explain the reasons behind the compensatory responses by just analysing field observations alone. Hence, we constrained and calibrated a process based model to independently calculate respiration losses considering nitrogen (N) related interactions based on formulations described in Reich et al. (2008). The modelling exercise in Paper III validates the NEE buffering in snow-free periods (Paper I), but also demonstrated that the NEE buffering also occurs during year-round cycles. Interestingly, a simple sensitivity analysis revealed that plant traits related to N are likely key determinants of the tight link between photosynthetic inputs and respiratory outputs. Continued exploration of flux time series is required to investigate the robustness of this meteorological buffering.

Richardson et al. (2007) and Wohlfahrt et al. (2008) have found similar ranges of inter-annual variation of ranked cumulative GPP and R_{eco} , but also considerable larger variability compared to NEE, and thus both are in accordance with our results in **Paper I** and **III**. This finding contrasts with previous studies (Goulden et al., 1998; Morgenstern et al., 2004) suggesting that GPP is stable across years, while the R_{eco} variability determines the sign and magnitude of NEE. Oppositely, Barr et al. (2002) found that GPP is more sensitive than R_{eco} , concluding that GPP largely controls the variability in NEE. According to Richardson et al. (2007), the compensatory relationships found between the two gross fluxes may be explained either by an spurious correlation (Brett, 2004; Lasslop et al., 2010) or a genuine physiological relationship. In **Paper III** we independently evaluated and validated the flux data analysis (**Paper I**) with a process-based model specifically modified to account for independent R_{eco} estimations. Our implemented model does not calculate R_{eco} as a fixed ratio of GPP any longer; instead, it calculates maintenance respiration based on N related mechanisms following Reich et al. (2008). Thus, we believe the compensatory effect between GPP and R_{eco} coupling is an authentic physiological relationship rather than a consequence from spurious correlations.

On the one hand, an example of physiological relationship was described by Janssens et al. (2001) where it is claimed that differences in soil respiration are better explained by a variation of plant productivity rather than annual temperature variations. The authors suggested this behaviour could be constrained based on two mechanisms directly related to productivity: (i) root respiration controlled by the amount of photosynthate allocated to roots, and (ii) heterotrophic respiration driven by the availability of readily decomposed substrate such as fresh litter from leaves and fine roots. On the other hand, a variation in R_{eco} may lead to a subsequent variation in GPP. The inter-annual variation of N mineralisation rates might control the variation in foliar N content and, therefore, the photosynthetic capacity at the canopy level (Aber et al., 1996). In our study, field data on leaf mass per area, maximum foliar C stock and average foliar N collected have contributed very positively to constrain the uncertainty of simulated GPP and R_{eco} dynamics (**Paper III**). Regardless of the cause of the compensation, the interplay between productivity and respiration promoted the homeostasis of NEE (Richardson et al., 2017). Finally, four important messages can be extracted from this study: (i) N-related plant traits are the most sensitive parameters in the SPA model, hence (ii) field data on C-N ratios have significantly contributed to the decrease of model uncertainty, (iii) a similar ranked sensitivity of the model parameters have been found both in GPP and R_{eco} , and thus (iv) plant traits are likely key regulators of the gross flux coupling.

Complementary evaluations across the pan-Arctic domain are required to further investigate the strength of the compensatory effect as well as the decoupling impacts triggered by low productivity in episodic biological disturbances. Firstly, in **Paper I** we detected gross flux correlations using flux tower measurements. Secondly, in **Paper III** we verified a comparable performance using a process-oriented modelling technique at the same local scale, expanding the analysis also during full annual cycles. Compensatory effects remain to be tested at coarser spatial resolutions. There are three natural steps to continue in this direction: (i) evaluate more sites similar to **Paper I** using existing datasets across the pan-Arctic region (e.g. FLUXNET2015 sites, **Paper IV**), (ii) perform a sensitivity analysis for each new site to replicate resembling plant trait performance (**Paper III**), and (iii) test whether the compensatory effect emerges globally using the CARDAMOM data assimilation system (**Paper IV**). Hereafter I provide two simple examples with preliminary diagnostics (Figure 4 and 5) utilizing the same model set up as in **Paper IV**. A follow up analysis analogous to Figure 5 in **Paper III** shows very similar contributions of plant productivity (GPP) and respiratory losses (R_a and R_h) to NEE in the Kobbefjord site (Figure 4). This test agrees with **Paper III**, GPP slightly dominates R_{eco} ($R_a + R_h$). Interestingly, the 2008-2015 mean carbon use efficiency (CUE; $GPP - R_a / GPP$) is 0.57 using this simple diagnostic in CARDAMOM, compared to the averaged 0.5 estimated in **Paper III**. There are obvious scaling considerations that must be necessarily taken into account (**Paper IV**), although this approach may allow an interesting exploration of pan-Arctic CUE transects, and ultimately a better understanding of their responses to the environmental change. This is particularly important in a likely future context where warmer scenarios are expected to decrease CUE, this is increasing the overall respiratory losses (Street et al., 2013).

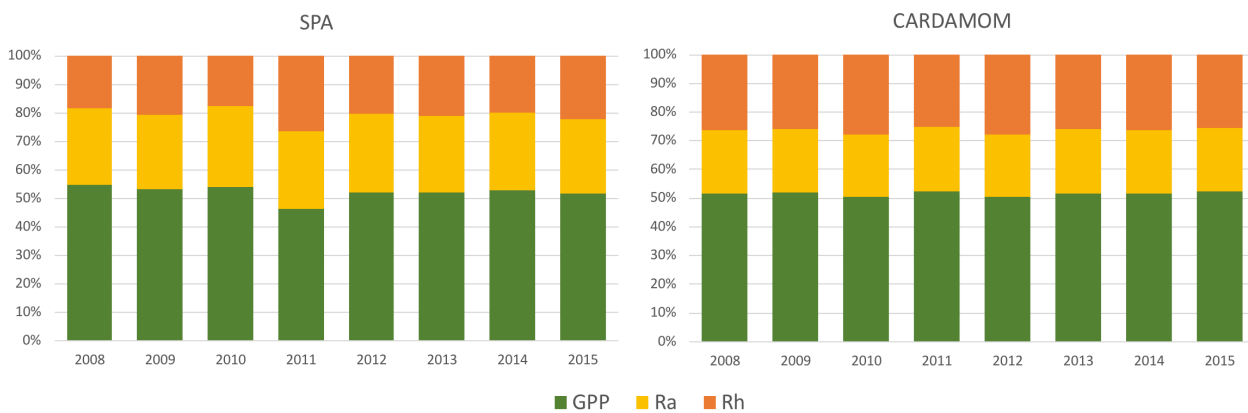


Figure 4. Annual gross fluxes [GPP, Gross Primary Production; R_a , autotrophic respiration; R_h , heterotrophic respiration] modelled by SPA (Paper III) and CARDAMOM (Paper IV) in the $1^\circ \times 1^\circ$ degree pixel where Kobbefjord is located. The y-axis represents the % contributed of gross fluxes to NEE, highlighting the balance between inputs (GPP) and outputs ($R_a + R_h$).

In a coarser perspective, pan-Arctic $GPP - R_{eco}$ relationships are also tightly coupled (Figure 5), suggesting a slighter dominance of photosynthetic uptake (20% in tundra, and 30% in taiga) compared to the respiration losses. These preliminary results are in agreement with findings from **Paper I** and **III**, therefore further modelling studies are required to investigate this likelihood and the potential linkages with spatial variability in plant traits.

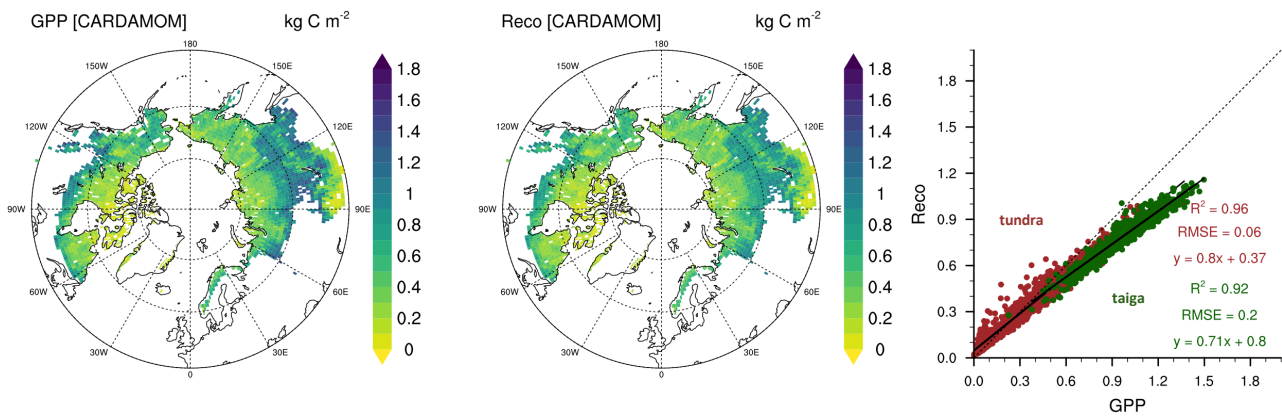


Figure 5. CARDAMOM retrievals from Paper IV characterizing the GPP- R_{eco} relationships across the pan-Arctic domain. In the scatterplot tundra is represented in brown and taiga in dark green.

The role of wintertime fluxes over full annual cycles

Wintertime responses such as low but constant respiration losses underneath the snowpack are usually not considered even though they can significantly affect the total annual C balance (Hobbie et al., 2000; McGuire et al., 2000). The lack of wintertime measurements due to remoteness, hostile meteorology, the difficulty to power-up stations and the occurrence of instrument failure usually complicate this task. The model analysis in Paper III indicated that wintertime periods decrease the C sink strength by 60% and increase up to 25% the annual soil respiration, very similar to the 61-81% and 20% reported by Oechel et al. (1997) and Schimel and Clein (1995) respectively. The R_{eco} partitioning implemented in Paper III also quantified the importance of litter and SOM decomposition processes, suggesting that R_n from litter is the largest contributor with ~20% to the annual budget, 2-fold larger than SOM. The two-characteristic peaks of respiration losses in each shoulder of the growing season were found driven by temperature (spring) and litter decomposition (autumn). These two processes together with the respiration from litter and SOM were identified as the main contributors to the decrease of C sink strength.

Wintertime C fluxes are significant and can even influence the sign and magnitude of the annual net C fluxes (Hobbie et al., 2000). The CO_2 sink/source dynamics without the discussion of non-growing season processes is difficult (Grøndahl et al., 2008). Papers by Zona et al. (2016), Commane et al. (2017) and Aurela et al. (2002) indicate the importance of non-growing season C dynamics. Additionally, delayed effects of wintertime-related variables such as snow depth and cover may induce a positive feedback on the ecosystem dynamics (Paper III). For instance, wintertime periods should be considered to have a more complete picture of the C cycle in Arctic ecosystems. However, little is known about some wintertime related processes. For example, the role of microbial activity is usually lacking in most of the biogeochemical modelling (Xenakis and Williams, 2014), and it is not fully understood whether the microbial activity in winter follows similar mechanisms than in summer (Schimel and Clein, 1996). Moreover, it remains unclear whether litter mass and N loss that usually occur primarily during winter (Hobbie and Chapin, 1996) are associated with biological interactions before snowmelt or with spring leaching (Hobbie et al., 2000). Likewise, it remains uncertain the implications of mosses in relation with CUE and the degree of soil temperature insulation in Arctic topsoils

(Street et al., 2012; Williams et al., 2000). Wintertime R_{eco} , along with litter and SOM turnover rates, need to be further constrained in ecosystem models (Cornelissen et al., 2007; DeMarco et al., 2014; Hobbie et al., 2000). Therefore, we need more field data, although these datasets are scarce and very challenging to measure (**Paper III, IV**).

Alternatively, we can use indirect data constraints to infer the effect of respiratory losses in cold periods. For example, Lund et al. (2012) discussed the insulating effect generated under thick snowpacks, keeping warmer temperatures compared to the surface, and thus increasing heterotrophic respiration rates. Moreover, snowpacks also act as lids avoiding the release of these respiratory outputs until the snowmelt in spring. In **Paper III** we used two different sources of data, snow coverage and soil temperature, as proxy to quantify the effect of snow dynamics in the overall C cycle. The results suggested a substantial improvement once the snow coverage data constrained the soil temperatures, but more interestingly we estimated an increase of 8 % in heterotrophic respiration due to the effect of snow. Following up on this successful implementation, future work on the validation of wintertime processes is needed (Pirk et al., 2016; Zhang et al., 2018). CARDAMOM (**Paper IV**) does not incorporate snow dynamics in the current structure, although such implementations may be pursued in the future. The DALEC model (**Paper III, IV**) embedded in CARDAMOM can be potentially coupled with the Hydrologiska Byråns Vattenbalansavdelning (HBV) snow pack, snow melt and soil moisture approach, broadly described by Seibert (1999) and references from Bergström et al. and Lindström et al. therein. Similar to **Paper III**, presence/absence of snow can be used as a trigger for plant phenology, to potentially influence the turnover of litter, and sublimation as a pathway to satisfy potential evaporation (and thereby adjust GPP). Since CARDAMOM requires to be constrained by 3-5 parameters in the future snow module, a suggested good candidate is the ESA's GlobSnow2 Snow Water Equivalent dataset (Takala et al., 2011).

The current state of the pan-Arctic C cycling modelling and its challenges

To determine the most likely state of the pan-Arctic C cycle we integrated in the same data assimilation system (Paper IV) a range of global gridded data including climate, soil organic C (SOC), leaf area index (LAI) and biomass with a mass balance model (Paper III). The pan-Arctic region was likely a small sink of C for the first 15 years of the 21st century, weaker in tundra and stronger in taiga, but our confidence intervals remain large (and so the region could be a source of C). The largest uncertainty in the net C uptake has been associated with heterotrophic respiration. We also conclude that biomass is the largest contributor to the bias modelled in turnover dynamic from global vegetation models (GVMs) and is a major component of error in their projections. Improved mapping of vegetation C stocks is required for a better understanding of the internal ecosystem C dynamics.

At the large scale, CARDAMOM estimates reported in **Paper IV** are found in consistent good agreement with C flux observations, forward and inversions model estimates reported from McGuire et al. (2012), C stocks and transit times described by Carvalhais et al. (2014), and the turnover rates suggested by Thurner et al. (2017). This reasonable performance compared to independently Arctic-specific C cycle retrievals (C fluxes, pools and turnover rates) demonstrates that CARDAMOM is a robust and suitable tool to assess large scale C cycle dynamics in the pan-Arctic domain. CARDAMOM also detected inconsistencies with

independent global datasets. The spatial variability of our analysis suggests that (i) biomass stocks are 28% lower than earth observation (EO) mapping (Carvalhais et al., 2014), (ii) GPP is 50% lower than Multi-Tree Ensemble (MTE) upscaling (Jung et al., 2017), and (iii) R_h is higher in the taiga and lower in the tundra than upscaled estimates (Hashimoto et al., 2015). CARDAMOM confirms that most of the uncertainties found in NEE echoes from the lack of understanding of heterotrophic respiration processes (**Paper III**).

At the local scale, on the one hand, we note that independent tests at EC locations suggest that CARDAMOM's GPP may be 30% overestimated. This mismatch is important in the context of the MTE upscaling, i.e. MTE is 50% lower than CARDAMOM, while CARDAMOM is 30% larger than FLUXNET. On the other hand, the agreement between EO data and EC data is surprisingly good (reproducing both the magnitude and their seasonal cycles) given the enormous scale difference. An increase of the model spatial resolution (i.e. finer grid-cells) may be helpful to closely investigate the agreement with measured flux data, but also to explore intriguing emerging questions that cannot be answered given our current understanding. For example, what controls the spatial variations in C sink/source strength? Since model parameters such as C allocation, turnover or leaf mass per area dynamically change between grid-cells, can we find that these are more linked to NEE variations, or are these mostly controlled by GPP or R_{eco} ?

By moving towards closer data-model integration at different spatio-temporal scales, CARDAMOM would potentially be a suitable candidate to approach new layers of complexity to fill some of the knowledge gaps (Figure 6). This could be achieved either from a bottom-up perspective (i.e. from local to global scale, using for example multi-site data) or a top-down strategy (i.e. from global to local scale, using finer gridded data in CARDAMOM).

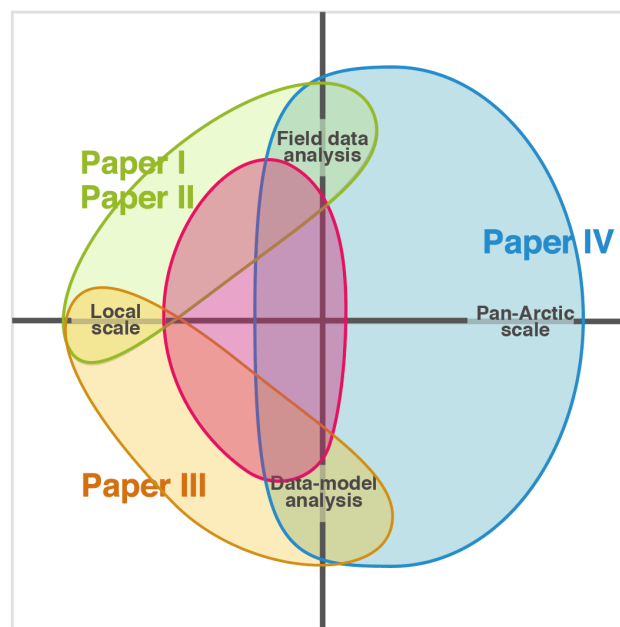


Figure 6. Modified conceptual diagram from **Figure 3** identifying key areas (represented in red) for future research arising from the outcomes of this work.

A key finding in **Paper IV** was the isolation of two important issues. First, the significant and systematic uncertainties regarding (heterotrophic) respiration processes. Interestingly, in **Paper I** we found larger discrepancies in R_{eco} compared to GPP using different partitioning approaches, but also in the data-model comparison in **Paper III**. One potential solution to decrease the uncertainties associated with R_{eco} may be the

use of microbial models rather than first order kinetics (Xenakis and Williams, 2014). Second, biomass is the largest contributor to the bias controlling the turnover rates in GVMs, while productivity processes are more in agreement with CARDAMOM. Recent studies raised strong arguments about the poor representation of C pools dynamics at global scale (Exbrayat et al., 2018; Friend et al., 2014; Nishina et al., 2014; Nishina et al., 2015; Thurner et al., 2017). However, from these studies it remains unclear whether productivity or biomass dominated the biases in transit times. In **Paper IV** we apportion the bias contribution, clearly dominated by GVMs biomass. This finding is especially interesting to benchmark the current process-based understanding of internal C cycle dynamics in the Arctic, but also to pinpoint fixable bias in model performance.

Finally, non-trivial Arctic related processes and responses remain to be tested and implemented in the CARDAMOM framework (**Paper IV**). For example: 1) the biological disturbances integrating remote sensing with modelling (following guidelines from **Paper II**), 2) the compensatory effects between GPP and R_{eco} (addressed in **Paper I, III**), and 3) the impact of snow dynamics in wintertime R_n fluxes (**Paper III**). Additionally, it would be very interesting and highly relevant to validate the performance of the plant trait parameters with independent datasets such as Kattge et al. (2011) and Sloan et al. (2013) to further evaluate the links between C and N, using a different approach to cross-check **Paper III**'s findings. Overall, this work establishes the baseline for more process-based ecological analyses using the CARDAMOM framework (**Paper IV**) as a promising technique to constrain the pan-Arctic C cycle.

Concluding remarks

This thesis illustrated how significant local scale ground-based observations are to the Arctic C balance (**Paper I, II**), but also how modelling techniques at local (**Paper III**) and pan-Arctic scale (**Paper IV**) can benefit and improve using robust field datasets. **Paper I** and **II** addressed the current state of the C exchange balance and how severely C fluxes can be affected by a biological disturbance in West Greenland tundra. Kobbefjord acted as sink of C except for the anomalous year associated with a severe moth outbreak. NEE presented a marked insensitivity to meteorology, while GPP and R_{eco} were highly sensitive and tightly coupled. **Paper III** was built on a couple of knowledge gaps identified in **Paper I**, this is the drivers behind of compensatory effects between gross fluxes and the role of wintertime periods. **Paper III** highlighted that plant traits are key controllers of the tight coupling observed and modelled between GPP and R_{eco} , and that wintertime periods decreased 60% the annual C sink strength. **Paper IV** incorporated a coarser perspective to the C cycling addressing key uncertainties of global productivity and decomposition processes at pan-Arctic scales. We aimed to link this project back with previous work using local scale field observations (**Paper I**) and utilizing the same C cycling modelling core incorporated in **Paper III**. **Paper IV** showed the likely sink of C of the pan-Arctic region although large uncertainties from respiratory losses remain, but also pinpointed the poor performances of GVM's turnover time of vegetation C, a major component of error in their forecasts.

The combination of data-model approaches generates novel outputs, allowing us to explore mechanisms and controls that otherwise would not have been possible to address independently. Moreover, the disagreements between observations and models are very valuable, and these uncertainties help us to recognise specific lacks of understanding and suggest new niches for further investigation such as the biological disturbance in C cycle modelling (**Paper III**), the partition of respiratory losses (**Paper III, IV**) or the

significant bias in vegetation C turnover (**Paper IV**). Considerable efforts are required to implement Arctic ecosystem monitoring programs during full annual cycles (Euskirchen et al., 2012; Grøndahl et al., 2008), and more field measurements on plant phenology, plant and soil structure and C and N stocks are needed to improve ecosystem model constraints. Finally, future work on large scale gross flux compensatory responses, wintertime dynamics and a dedicated focus on episodic biological disturbances are suggested to improve our process-based understanding of the Arctic C cycle in changing environments.

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On the way to the unknown, East Greenland. 2017 field season. Photo by Efrén López-Blanco