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Perspectives on insect herbivory

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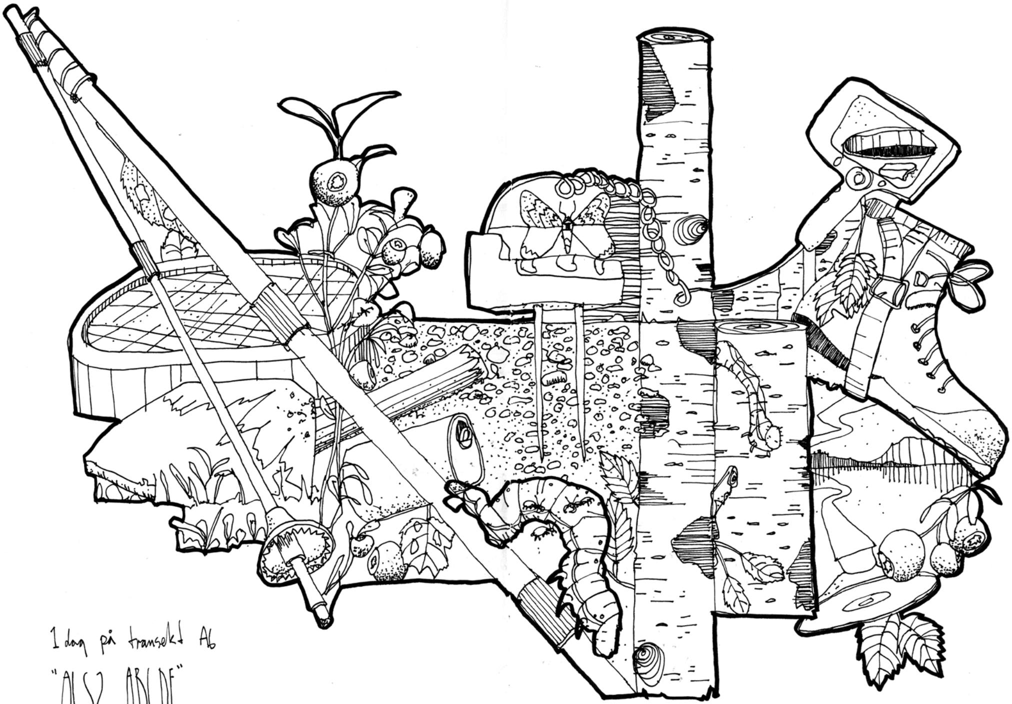

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Biogeochemistry in Subarctic birch forests

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Perspectives on insect herbivory

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Title and subtitle: Biogeochemistry in Subarctic birch forests – perspectives on insect herbivory

Abstract:
Herbivory can influence ecosystem processes, partly through long-term changes of the plant community compositions, but also more rapidly through the herbivores' digestive alteration of the organic matter that is cycled through the soil and back to the primary producers. In the Subarctic mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest (SMBF) in Northern Fennoscandia, outbreaks by the geometrid moths (*Epirrita autumnata* and *Operophtera brumata*) are well-described, widespread, and increasing with global warming. In contrast, the ecosystem effects of background insect herbivory (BIH) in this ecosystem lacks quantification, although belowground responses to aboveground perturbations in high-latitude systems may accelerate global warming due to their storage of large terrestrial organic carbon (C) pools.

We quantified the ecosystem impact of BIH in the SMBF of Northern Sweden. An initial literature review showed that the clear increase in organic matter turnover rates under insect infestations was primarily driven by outbreak conditions. In line with this, our conversion of an average BIH-rate of ~1.6% of the leaf area to annual canopy-to-soil fluxes of nitrogen (~3.5% N) and phosphorus (~2.0% P) showed that the background rates were relatively small compared to internal recycling through litter, and inputs from external sources, such as atmospheric deposition, biological fixation and weathering.
In addition, we showed that the insects themselves efficiently conserve N, as 70-80 % of the ingested N was converted to insect biomass, while respiring 30-50% of the ingested C. When insect excreta (frass) was added to the soil, we showed that another ~30 % of the C was respired by soil organisms. Hence, a total of ~60 % of the C ingested by insect herbivores would be respired during the first growing season, compared to ~10 % of the C added as senesced litter, suggesting a decreased litter C-sink in soils during outbreaks.

In microcosm incubations, frass addition stimulated fungal growth more than bacterial growth while litter addition showed the opposite relationship. In contrast, under non-outbreak conditions along natural environmental gradients in the SMBF, decomposer bacterial growth was strongly correlated with BIH and other indicators of labile organic substrates, while fungal growth showed very little correlation with the potential driver variables. Yet, BIH did not explain a significant portion of the variation in the fraction of microbially assimilated C that was incorporated into soil microbial biomass, i.e. the soil carbon use efficiency (CUE). CUE was strongly controlled by respiration, but when this was controlled for, it increased with both bacterial and fungal growth rates. Further, CUE decreased with increasing soil temperature and the size of the soil microbial biomass pool. This suggests decreased soil C-sequestration with global warming, although an associated decrease in microbial biomass, which is often observed in warming experiments, may moderate this effect. Finally, gross N-mineralisation was also substantially higher after addition of insect frass (~17 % of added N) compared to litter (lower than control), so the availability of mineral N is higher under insect outbreaks increasing the risk of leaching losses.

Finally, we challenged the assumption underlying space-for-time substitution studies, i.e. that variation along natural elevational gradients is scale invariant and universal, by showing that e.g. BIH exhibit contrasting trends with local and regional elevation. Although explorative, these findings merit further considerations of when space-for-time-substitution is a feasible tool for inferring ecosystem responses to environmental change.

Key words: Biogeochemistry; Subarctic; Insect herbivory; Element cycling; Aboveground-belowground interaction; Soil ecology; Carbon use efficiency; Environmental change; Space-for-time substitution

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To my late friend, mentor and inspiration, Henrik Breuning-Madsen, who showed me how amazing life in science can be, while remembering that there is more to life than science.

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Summary

Herbivory can influence ecosystem processes, partly through long-term changes of the plant community compositions, but also more rapidly through the herbivores' digestive alteration of the organic matter that is cycled through the soil decomposer organisms and back to the primary producers. Particularly large vertebrate herbivores have been widely studied, but in some ecosystems, invertebrate herbivores can be equally or more important. One such system is the Subarctic mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest (SMBF) in Northern Fennoscandia, where outbreaks by the geometrid moths (*Epirrita autumnata* and *Operophtera brumata*) are well-described, widespread, and increasing with global warming. In contrast, the ecosystem effects of background insect herbivory (BIH) in this ecosystem lacks quantification. Understanding ecosystem responses to perturbations in high-latitude systems are particularly important, as the climate warms faster in the polar regions, and because these systems may exhibit positive feedback processes due to their storage of large terrestrial organic carbon (C) pools, which could be released as greenhouse gasses.

In this thesis, we quantified the ecosystem impact of BIH in the SMBF of Northern Sweden, after initially reviewing the literature for different patterns in belowground responses to outbreak and background insect densities. The review showed that the clear increase in organic matter turnover rates under insect infestations was primarily driven by outbreak conditions. Our conversion of an average BIH-rate of ~1.6% of the leaf area to annual fluxes of nitrogen (~3.5% N) and phosphorus (~2.0%, P) from canopy to soil confirmed that the background rates were relatively small compared to internal nutrient recycling through litter, and external nutrient inputs from atmospheric deposition, biological fixation and weathering. This is in line with the expectations from the literature.

In addition, we showed that the insects themselves efficiently conserve N, as 70-80 % of the ingested N was converted to insect biomass, while respiring 30-50% of the ingested C, depending on diet. Thus, a large fraction of the C lost from the plants to insect herbivores was respired before it was added to the soil as cadavers or frass (excreta). Nonetheless, when the frass entered the soil, we showed that another ~30 % of the C was respired by soil organisms. Hence, a total of ~60 % of the C ingested by insect herbivores was respired during the first growing season. This compared to ~10 % of the C added as senesced litter, which emphasises the significant potential reduction in soil storage of foliar C during insect outbreaks, where >70% of the leaf area can be consumed.

In microcosm incubations, frass addition stimulated fungal growth more than bacterial growth while litter addition showed the opposite relationship. In contrast, under non-outbreak conditions along natural environmental gradients in the SMBF,

decomposer bacterial growth was strongly correlated with BIH and other indicators of labile organic substrates, while fungal growth showed very little correlation with potential driver variables except a pronounced decrease with elevation. Yet, BIH did not explain a significant portion of the variation in the fraction of microbially assimilated C that was incorporated into soil microbial biomass, i.e. the soil carbon use efficiency (CUE). CUE was strongly controlled by respiration, but when this was controlled for, it increased with both bacterial and fungal growth rates. Further, CUE decreased with increasing soil temperature and the size of the soil microbial biomass pool. This suggests decreased soil C-sequestration with global warming, although an associated decrease in microbial biomass, which is often observed in warming experiments, may moderate this effect. Finally, gross N-mineralisation was also substantially higher after addition of insect frass (~17 % of added N) than litter (lower than control), so the availability of mineral N is higher under insect outbreaks. This may benefit faster growing species like graminoids, but also increase the risk of nutrient loss from the system, as the birch trees have much lower demand due to decreased leaf area. Increased N-leaching in outbreak years was confirmed in the literature.

Our research design allowed us to add perspectives to the ongoing discussion on the application of space-for-time substitution for studying ecosystem responses to environmental change. Our findings challenge the general assumption that variation along natural elevational gradients is scale invariant and universal, by showing that some ecological variables, e.g. BIH, exhibit contrasting trends with local and regional elevation. Further, we present a potential way of accounting for such context dependencies by finding correlations between regional scale abiotic variables and the relationship between ecological variables and elevation at the local scale. Our findings are quite explorative, but they merit further considerations and exploration of when space-for-time-substitution is a feasible tool for inferences about ecosystem responses to environmental change.

In conclusion, this work contributes with some first estimates of the above- and belowground biogeochemical process rates in the SMBF and the relation to BIH. Although the annual cycling of C and nutrients through insect herbivores is modest, the contribution by BIH to overall long-term element cycling may be considerable, due to the long timespans (50-100 years) between each major outbreak. We also explore when inferences from space-for-time substitution studies are feasible, which is particularly important for understanding long-term feedbacks to environmental change, such as climate change responses.

Sammanfattning (SE)

Växtätare kan påverka ekosystemprocesser, dels genom långsiktiga förändringar av växtsamhällets sammansättning, men också på kortare sikt genom deras matspjälkning av organiskt material som cyklas genom markens nedbryderorganismer och tillbaka till de primära producenterna. Särskilt större växtätare har studerats i stor utsträckning, men i vissa ekosystem som skogar kan de mindre ryggradslösa växtätarna vara lika viktiga. Ett sådant ekosystem är de subarktiska fjällbjörkskogerna (*Betula pubescens* ssp. *Czerepanovii*) (SFBS) i norra Skandinavien, där utbrotten av växtätande geometriska malar (*Epirrita autumnata* och *Operophtera brumata*) har studerats noga, och det har gått att konstatera att antal utbrott och deras utbredning ökar med den globala uppvärmningen. Däremot saknas det en kvantifiering av hur befintliga insekters växtätande påverkar ekosystemet (*background insect herbivory*, BIH) i SFBS. Att förstå hur ekosystem påverkas av störningar nära polerna är särskilt viktigt ur ett klimatperspektiv, eftersom temperaturen stiger fortare i dessa regioner, och dessa ekosystem riskerar uppvisa positiva återkopplingsprocesser till klimatet på grund av stora markbundna lager av organisk kol (C), som kan omvandlas till växthusgaser.

I den här avhandlingen kvantifierades ekosystempåverkan av BIH i SMBF i norra Sverige efter att ha letat i litteraturen efter mönster i hur markprocesser påverkas av densiteten av befintliga insekter och populationsutbrott. Översynen visade att tydliga ökningar i organiska materialomsättningsnivåer under närvaro av insekter främst drivs av utbrottförhållanden. Konvertering av den genomsnittliga BIH-intensitet på ~1,6 % av trädens bladyta till årliga flöden av kväve (~3,5 % N) och fosfor (~2,0 % P) från trädkronorna till marken bekräftade att näringsflöden genom BIH var relativt små jämfört med intern återvinning genom löv, och externa källor såsom atmosfärisk deponering, biologisk fixering och förvittring. Detta överensstämde med förväntningarna från litteraturgenomgången.

Dessutom visade vi att insekter sparade N effektivt, genom att omvandla 70-80 % av det intagna N till insektsbiomassa, medan de respirerade 30-50 % av det intagna C, beroende på diet. Således respirerades en stor andel av C som förlorades från växter till insektsväxtätare innan den tillfördes marken som kadaver eller exkrement. När exkrement tillsattas markan visade vi att ytterligare ~30 % av C respirerades av markens netbrytarbakterier och -svampar. Följaktligen respirerade insekter totalt ~60 % av det intagna C under den första växtsäsongen. Detta ska jämföras med ~10 % av den C som tillsattas marken som löv, vilket betonar den betydande potentialminskningen i jordens lagring af C från löv under insektsutbrott, där >70 % av bladytan kan konsumeras.

I inkubationsförsök stimulerade tillsättning av insektexkrement svamptillväxt mer än bakterietillväxt medan tillskott av löv hade motsatt effekt. Under förhållanden utan utbrott längs naturliga miljögradienter i SMBF korrelerade tillväxten av nedbrytande bakterier däremot positivt med BIH och andra indikatorer på tilgängligt organiskt material, medan svamptillväxt inte visade stärka korrelationer med andra faktorer än höjd (negativ).

BIH förklarade inte en betydande del av variationen i andelen mikrobiellt assimilerat C som integrerades i markens mikrobiella biomassa, dvs. markens effektivitet i användning av kol (*carbon use efficiency*, CUE). CUE kontrollerades av bakteriel aktivitet, och minskades med ökande jordtemperatur och storleken på jordens mikrobiella biomassapool, och risikerer därför uppvisa positiv återkoppling till klimatförändringarna. Slutligen var brutto N-mineralisering också betydligt högre efter tillsats av insektexkrement (~ 17% av tillsatt N) än tillsats av löv (lägre än befintlig), vilket betyder att tillgängligheten av mineraliskt N är högre under insektsutbrott. Detta kan gynna snabbt växande växtarter såsom gräs, men också öka risken för näringsförlust från ekosystemet eftersom björkträden kan ha betydligt lägre behov av kväve på grund av minskad bladyta.

Vår forskningsdesign gjorde det möjligt att tillföra nya perspektiv till den pågående diskussionen om tillämpning av substituering av plats-för-tid (space-for-time) för att studera ekosystemens respons på miljöförändringar. Våra resultat utmanar det allmänna antagandet att variation längs naturliga höjdgradienter är skalbeständig och universell, genom att visa att vissa ekologiska variabler, t.ex. BIH, visar motsägande trender mellan lokal och regional höjd. Vidare presenterar vi ett potentiellt sätt att redovisa sådana kontextberoende genom att hitta korrelationer mellan regionala abiotiska variabler och förhållandet mellan ekologiska variabler och höjd i lokal skala. Våra resultat är utforskande, men de visar på att det behövs ytterligare överväganden om när plats-för-tid-substitution är ett bra verktyg för att dra slutsatser om ekosystemens respons från miljöförändringar.

Sammanfattningsvis bidrar detta arbete med några första uppskattningar av ovan- och underjordiska näringsflöden som BIH bidrar med i SMBF. Även om den årliga genomflödet av C och näringsämnen genom insektsväxtätare är litet, kan bidraget från BIH till övergripande långsiktig näringscykling vara betydande på grund av de långa tidsperioderna (50-100 år) mellan varje större insektutbrott. Vi undersökte också när slutsatser från plats-för-tid substitutionstudier är möjliga, vilket är särskilt viktigt för att förstå långsiktiga återkopplingar till miljöförändringar, t.ex. ekologiska konsekvenser av klimatförändringar.

Sammenfatning (DK)

Planteædere kan have stor indflydelse på økosystemprocesser. Dels gennem deres påvirkning af planternes artssammensætning på lang tidsskala, men også på den korte bane gennem deres omsætning og transformation af organisk stof, som recirkuleres gennem jordens nedbryderorganismer tilbage til planterne. I særdeleshed store planteædere er velstuderede, men i visse økosystemer kan hvirvelløse planteædere spille en tilsvarende eller enddog større rolle. Eksempelvis er de subarktiske fjeldbirkeskove (*Betula pubescens* ssp. *czerepanovii*) (SFBS) i det nordligste Skandinavien kendte for deres udbredte udbrud af målermøllarver (*Epirrita autumnata* og *Operophtera brumata*), som intensiveres med den globale opvarmning. Økosystempåvirkningen af insektplanteædere ved baggrundstætheder, kaldet *background insect herbivory* (BIH), er derimod ikke kvantificeret i SFBS. Forståelsen af polarnære økosystemers respons på forstyrrelser er særlig vigtig, eftersom klimaet opvarmes hurtigere i disse egne. Opvarmningen risikerer at accellerere temperaturstigningen yderligere på grund af de store mængder organisk kulstof (C), som er bundet i disse økosystemer, og kan frigives som drivhusgasser.

I denne afhandling kvantificeres økosystempåvirkningen af BIH i SFBS i det nordlige Sverige efter en gennemgang af literaturen for mønstre i insekters påvirkning af jordbundsprocesser ved udbruds- og baggrundstætheder. Litteraturgennemgangen viste, at den betydelige stigning i omsætningen af organisk stof i jorden ved insekters tilstedeværelse primært drives af udbrud. Vores konvertering af BIH-intensiteter på ~1.6% af bladarealet til årlige fluxe af kvælstof (~3.5% N) og fosfor (~2.0% P) fra trækrone til jord bekræfter, at BIH udgør en relativ lille mængde af den interne recirkulering af stoffer gennem løvfald, og ligeledes en lille del sammenlignet med eksterne næringsstofkilder såsom atmosfærisk deposition, biologisk fiksering og forvitring.

Vores resultater viste også, at insekterne selv konserverer N, da 70-80 % af det indtagede N blev konverteret til insektbiomasse, mens 30-50% af det indtagede C blev respireret afhængigt af diæten. Dermed bliver en betydelig del af det indtagne C tabt til respiration, allerede inden det bliver tilsat jorden som kadavere eller ekskrementer. Ikke desto mindre respirerede jordbundsmikroberne yderligere ~30% af det C, der blev tilført jorden som ekskrementer, så samlet set blev ~60 % af det C, der blev spist af insekterne, respireret tilbage til atmosfæren i løbet af den første vækstsæson. Dette skal sammenholdes med respirationen af blot ~10 % af det C, der tilførtes som nedfaldet løv, hvilket understreger den betydelige reduktion i lagring af kulstof fra blade i jordbunden i udbrudsår, hvor >70 % af bladarealet kan blive spist.

I inkubationsforsøg steg svampevæksten mere end bakterievæksten, når insektekskrementer tilførtes, mens det modsatte var tilfældet ved tilførsel af nedfaldsløv. Derimod viste nedbryderbakterier en positiv sammenhæng med BIH og andre indikatorer på letomsætteligt organisk materiale langs naturlige klimagradienter i SFBS, mens nedbrydersvampenes vækst ikke viste stærke korrelationer med de valgte faktorer, udover et markant fald med stigende elevation.

BIH forklarede ikke en signifikant del af variationen i andelen af den C, der blev assimileret af mikrober, som blev inkorporeret i mikrobiel biomasse, altså effektiviteten, hvormed jordbundsorganismer bruger den optagne kulstof til vækst (*carbon use efficiency*, CUE). Dette på trods af at CUE var tæt koblet til bakteriel aktivitet. CUE faldt med stigende temperatur og mængde af mikroorganismer i jorden, hvilket indikerer en acceleration af klimaforandringerne, hvilket delvist kan modereres af at den mikrobielle biomasse også mindskes ved opvarming. Endeligt var mineraliseringen af N også væsentligt højere, når organisk stof blev tilført jorden i form af insektekskrementer (~17 % af det tilførte N) fremfor som birkeløv (mindre end baggrund), så tilgængeligheden af N i jorden er højere under insektudbrud. Det kan være en fordel for hurtigtvoksende plantearter, men øger også risikoen for tab af kvælstof fra systemet, da birketræernes behov for N er kraftigt nedsat grundet reduktionen i bladareal. Tab af kvælstof i udbrudsår beskræftes i literaturen af forhøjet udvaskning af N i omkringliggende vandløb.

Vores forskningsdesign tillader os at føje perspektiv til diskussionen vedrørende substitution af rum for tid (*space-for-time*) i studier af økosystemers respons på miljømæssige forandringer. Vores resultater udfordrer den generelle antagelse om, at variationer langs naturlige højdegradienter er uafhængige af skala og universielle, ved at vise at visse økologiske variabler, f.eks. BIH, udviser modsatrettede sammenhænge med lokal og regional højdeændring. Vi præsenterer ydermere en mulig fremgangsmåde, der tager højde for en sådan kontekstafhængighed ved at finde korrelationer mellem udviklingen i økologiske variabler med lokal variation (hældningen) og regionale abiotiske faktorer. Selvom vores studier er eksplorative, understreger de behovet for yderligere overvejelser i forhold til, i hvilke sammenhænge *space-for-time*-substitution er et brugbart værktøj til at studere økosystemers respons på miljømæssige forandringer.

Overordnet bidrager denne afhandling med nogle første bud på BIHs bidrag til kulstof- og næringsstofcyklus i SFBS, både over og under jorden. Selvom den årlige cirkulation af kulstof og næringsstoffer gennem insekter er moderat i normalår, er det overordnede bidrag til næringsstofcirkulation i længere tidsperspektiv muligvis væsentligt, da der typisk er 50-100 år mellem hvert markant insektudbrud. Vores perspektivering af, hvornår space-for-time-substitution kan anvendes til at undersøge sammenhænge mellem økosystemrespons og miljømæssige ændringer er særligt væsentlig i forhold til forståelsen af tilpasning til langsigtede forandringer, såsom klimaændringer.

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List of papers

I. **Kristensen JA**, Rousk J, Metcalfe DB. Belowground responses to insect herbivory in forest ecosystems: a global meta-analysis (under consideration for publication in *Journal of Ecology*).

II. Metcalfe DB, Cherif M, Jepsen JU, Vindstad OPL, **Kristensen JA**, Belsing U (2019). Ecological stoichiometry and nutrient partitioning in two insect herbivores responsible for large-scale forest disturbance in the Fennoscandian subarctic. *Ecological Entomology* **44**, 118–128.

III. **Kristensen JA**, Michelsen A, Metcalfe DB. Background insect herbivory along natural gradients in Subarctic birch forests: contributions to carbon and nutrient fluxes from canopy to soil (under consideration for publication in *Ecosystems*).

IV. **Kristensen JA**, Metcalfe DB, Rousk J (2018). The biogeochemical consequences of litter transformation by insect herbivory in the Subarctic: a microcosm simulation experiment. *Biogeochemistry* **138**, 323–336.

V. **Kristensen JA**, Metcalfe DB, Rousk J. The environmental controls of soil fungal and bacterial carbon-use along elevational gradients in Subarctic birch forests (unpublished manuscript).

Author contributions

Paper I: JAK and DBM conceptualised the meta-analysis. **JAK** designed the methodology (review table), performed the formal analysis and investigations as well as the visualisations. **JAK** wrote the first draft of the manuscript; DBM and JR made substantial contributions during revisions and approved the final version for publication. DBM acquired the funding.

Paper II: DBM, UB and JUJ conceived the work. UB, JUJ and OPLV conducted the field and rearing laboratory work, while **JAK** facilitated the chemical analyses. DBM, MC and **JAK** did the data analysis. DBM wrote the first draft of the manuscript and MC, JUJ, OPLV, **JAK** and UB made substantial contributions during revisions. DBM and JUJ acquired the funding.

Paper III: JAK and DBM conceived the ideas and designed the research. **JAK** performed the fieldwork, while **JAK** and AM conducted the laboratory analyses. **JAK** analysed the data and wrote the first draft of the manuscript. DBM and AM made substantial contributions during revisions and approved the final version for publication. DBM acquired the funding.

Paper IV: JAK, JR and DBM conceived the work. **JAK** did the fieldwork, the laboratory analyses, the data analyses and wrote the first draft of the manuscript. JR and DBM made substantial contributions during revisions. DBM and **JAK** acquired the funding.

Paper V: JAK, JR and DBM conceived the ideas and designed the research. **JAK** did the fieldwork, while JAK conducted the laboratory analyses. **JAK** did the data analyses and wrote the first draft of the manuscript. DBM and JR made substantial contributions during revisions. DBM acquired the funding.

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Aims and objectives

Most of the current knowledge on the ecosystem consequences of herbivory is from studies of vertebrate herbivores in grassland and tundra ecosystems. Particularly high-latitude ecosystems have attracted attention in the last couple of decades due to their rapid and potentially accelerating response to global warming. However, insect herbivores can also impact ecosystems quite dramatically, as they can exhibit very dynamic population peaks causing large scale outbreaks. Such outbreaks are particularly well-described in the Subarctic mountain birch forests in northern Scandinavia, yet little attempt has been made to study the biogeochemical consequences of low-intensity background herbivory in non-outbreak years.

In this thesis, we used a combination of review techniques, laboratory work and field investigations to fill in knowledge gaps particularly on background insect herbivory and consequences for soil processes.

We asked:

- Does background insect herbivory influence ecosystem biogeochemistry similarly to outbreak conditions?
- How does the elemental canopy-to-soil fluxes through insects at background insect densities compare to other relevant soil inputs in Subarctic birch forests?
- How does the soil elemental turnover and microbial growth vary in Subarctic birch forests, and can background insect herbivory influence this?
- Can we infer drivers of these patterns from the variation along natural environmental gradients that are valid at the ecosystem scale in Subarctic birch forests?

In *Paper I* we conducted a global meta-analysis of the available literature on belowground responses to aboveground insect herbivory and distinguished between outbreak and background conditions. *Paper II and III* dealt with the elemental partitioning of the most common geometrid moths in the Subarctic birch forests, in a controlled laboratory rearing experiment (*Paper II*), and the flux of carbon and nutrients from canopy to soil through insect herbivores at background densities studied along natural elevational gradients in Subarctic Sweden (*Paper III*). In *Paper IV and V* we studied the soil decomposer responses to insect herbivory, in a controlled microcosm experiment with addition of mixes of litter and insect deposits (*Paper IV*), and through quantification of the soil microbial carbon use (*Paper V*) along the same environmental gradients as in Paper III. Figure 1 provides a schematic overview of how the papers are linked by highlighting the processes addressed by each paper with a coloured, dashed frame.

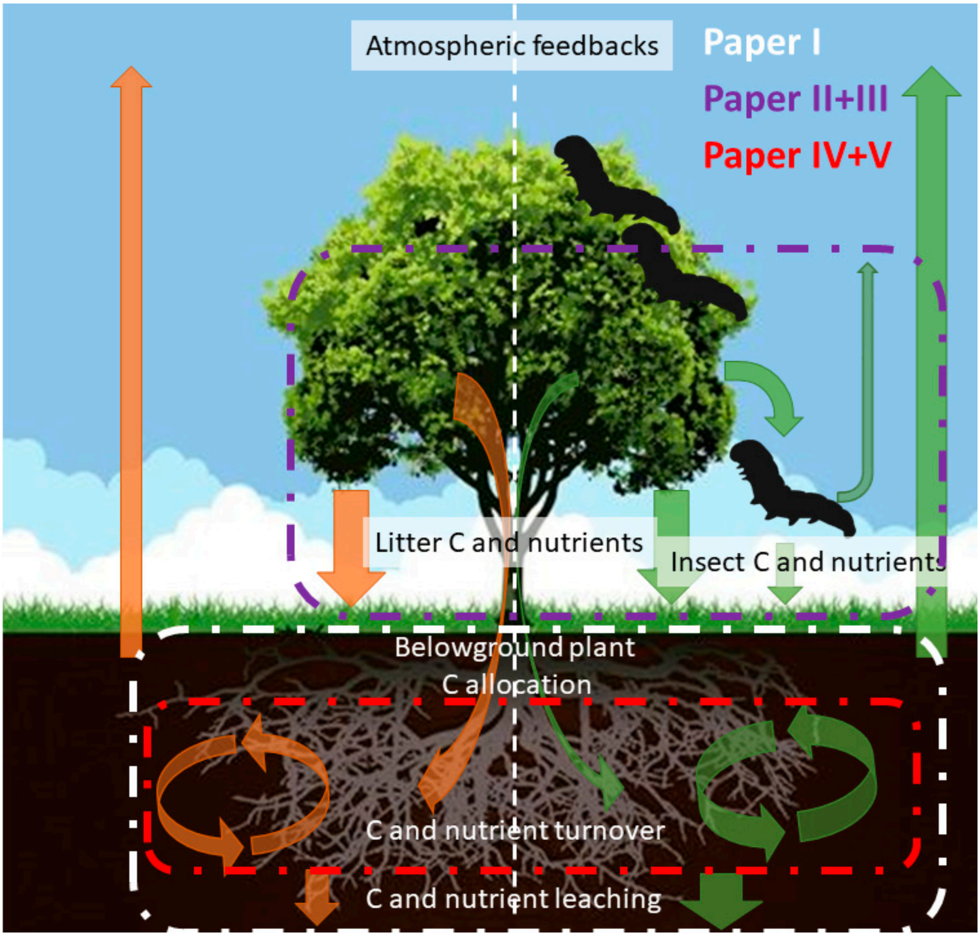

Figure 1. Overview of the papers in this thesis. The right hand side indicates a system with insect herbivory, while the left hand side indicates a system without herbivory. Paper I reviews the corrent knowledge on the belowground consequences of aboveground insect herbivory. Paper II and III investigates the partitioning of elements through insects, and how it affects the overall elemental fluxes from canopy to soil at background insect densities. Paper IV and V examines the belowground responses to insect herbivory in terms of biogeochemical cycling through soil decomposers.

Introduction

The ecosystem consequences of global environmental change have been studied intensively in the last decades. Particularly global warming and the consequent biogeochemical alterations and redistribution of plants and animals in high latitude systems have received a lot of research attention (Post et al. 2009; Wookey et al. 2009), as this is where the warming is most rapid, and where potential positive feedback mechanisms are most severe (ACIA 2004; IPCC 2014). In terrestrial ecosystems, particularly the transformation of the large carbon (C) pools sequestered in high-latitude soils (Hugelius et al. 2014) is immensely important for the long-term feedbacks between the Earth's surface and the atmosphere (Bradford et al. 2016; Schuur et al. 2015).

Animals can be important mediators of ecosystem processes, both in terms of the abundance and distribution of other organisms, but also in terms of redistribution of elements like C and essential plant nutrients, such as nitrogen (N) and phosphorus (P) (Schmitz et al. 2018). A common example is the ability of reindeers to counteract the invasion of shrubs into the Arctic tundra (Bernes et al. 2015; Vowles et al. 2017). Further, vertebrate herbivores tend to speed up belowground elemental cycling (Andriuzzi and Wall 2017), favouring plants adapted to resource competition (van der Wal 2006). Yet, most research has focussed on the consequences of vertebrate herbivores in grassland and tundra ecosystems, while much less attention has been given to herbivory in less fertile ecosystems, such as forests, particularly when it comes to the smallest herbivores, invertebrates. These can be the dominant herbivore in some systems, despite their limited body size (Weisser and Siemann 2008). Insect herbivores can consume substantial portions of the plant biomass (e.g. Metcalfe et al. 2014; 2016), pursuing a large range of life and feeding strategies. Common examples are insects that lay their eggs inside the plant leaves or stems (galling) to let their offspring eat their way out when they hatch, insects that suck sugar-rich sap straight from the xylem, and insects that eat fresh leaves directly from the plants (Weisser and Siemann 2008). Invertebrate herbivory will be discussed in the section *Aboveground insect herbivory*.

All the above-mentioned feeding strategies influence the plant allocation of energy at the individual level. This may induce compensatory measures (Belovsky and Slade 2000; Hamilton et al. 2008) or defence strategies (induced or constitutive) (Fürstenberg-Hägg et al. 2013), which can alter both leaf chemistry and also the allocation of plant resources to belowground symbionts (Ayres et al. 2004; Parker et al. 2017; Saikkonen et al. 1999). On longer time-scales, herbivory may also change the plant community structure, which will in turn alter the belowground faunal and microbial communities (Bardgett and van der Putten 2014; Bardgett and Wardle 2010). Hence, the herbivores aboveground can alter belowground communities and processes and vice versa. Such aboveground-belowground interactions have gained increasing attention the last two decades (Bardgett and Wardle 2010). Their importance for ecosystem responses to abiotic environmental change, for instance climate warming, has become very evident. For instance, plant communities have shown different robustness to biotic and abiotic stress, when growing with their native soil organisms compared to when they are growing in soils conditioned by other plant communities (Mariotte et al. 2018). Moreover, sequential exclusion of aboveground herbivores has shown that belowground functions respond differently to the presence of different assemblages of herbivores (Risch et al. 2018). The role of herbivores in aboveground-belowground interactions will be discussed in the section *Herbivory and* a*boveground-belowground interactions.*

Nonetheless, the ecosystem models we currently use to inform climate models, represent herbivore-plant interactions quite poorly (Dangal et al. 2017). One of the major challenges is to find good ways of inferring realistic relationships between environmental factors and ecological response variables at the right timescales (Dunne et al. 2004; Elmendorf et al. 2015). Observations made along natural environmental gradients are a common way of studying such relationships between ecological response variables and environmental driver variables. The spatial variation in environmental driver variables (e.g. temperature) and ecological response variables (e.g. plant community composition) are used to predict future developments in the same response variable under a future scenario, where the driver variable has changed by a similar magnitude due to temporal rather than spatial change. Hence, space is substituted for time. Despite its wide application, the approach has also been criticized in recent years (Damgaard 2019; Körner 2007; Wogan and Wang 2018). A common type of natural gradient used to make inferences about long-term global warming responses is an elevational gradient. Despite its many merits and valuable contributions to the field of global change ecology (Elmendorf et al. 2015; Sundqvist et al. 2013), it has its limitations, particularly if the elevational trend interacts with other abiotic factors. This is discussed in *Perspectives on space-for-time-substitution*.

Aboveground insect herbivory

Insect herbivores constitute only about 2% of the animal biomass on the planet (Weisser and Siemann 2008). Despite the relatively small contribution to biomass, their opportunistic reproduction strategy allows them to increase population densities to extreme levels, when conditions are favourable (Weisser and Siemann 2008). This can cause large-scale infestations with tremendous short-term consequences for biogeochemical cycling (Heliasz et al. 2011; Kaukonen et al. 2013; Parker et al. 2017; Paper Í), but also long term consequences like altered plant community compositions or even rejuvenation of certain ecosystems (Jepsen et al. 2013; Tenow and Bylund 2000).

Insect outbreaks have been widely studied. Particularly in the Subarctic birch forests constituting the northern margin of the canopy-forming vegetation, population peaks of the autumnal moth (*Eprrita autumnata*) and more recently also the winter moth (*Operophtera brumata*), have reoccurred every ~10 years as an integrated part of the natural system (Bylund 1999; Jepsen et al. 2008; Tenow 1972). Yet, the really severe outbreaks, which can defoliate more than 70 % of the leaf area at the landscape scale and locally >95% (Heliasz et al. 2011; Olsson et al. 2017) only re-occur every 50-100 years (Tenow and Bylund 2000), but have shown a tendency to expand in range and increase in frequency due to recent climate warming (Jepsen et al. 2008; 2011). This may change the ecosystem, as it takes decades to recover from severe outbreaks (Tenow and Bylund 2000), and several accounts of changes to the plant community structure have been reported (Jepsen et al. 2013). But what about all the years between the outbreaks, when insect densities are low but not completely absent?

A relatively recent global review of background insect herbivory (BIH) showed that the average leaf area lost to insects in a non-outbreak year was roughly 8 % (Kozlov et al. 2015). Further, they showed that the area lost to herbivory decreased from mid-latitudes towards the polar regions. Thus, insect herbivory in high-latitude systems may increase with climate warming, despite the fact that insect predation is also expected to increase (Roslin et al. 2017). In Paper III in this thesis we quantify the leaf area lost to BIH in the SMBF. We found an average background insect herbivory rate in these forests of ~1.6 % of leaf area, while ~10% of the leaves received some degree of insect damage (Table 1). These numbers compare well to rates found in the dwarf shrub tundra (Barrio et al. 2017), but were substantially lower than at lower latitudes (Kozlov et al. 2015).

Table 1. Selected site characteristics from the 27 sites in the Subarctic mountain birch forest. MAT: mean annual temperature; MAP: mean annual precipitation. Modified from Paper III.

VARIABLE		UNIT	MEAN	MIN	MAX
Air climate	MAT	°C	**-0.3±0.2**	-1.1±0.2	0.3±0.2
	MAP	mm year^{-1}	**887±84**	447±17	1366±34
Soil climate (5-10 cm depth)	MAT	°C	**2.5±0.01**	1.7±0.06	4.5±0.2
	Moisture	%vol	**19.3±0.5**	11±1.1	38±2.5
Dissolved inorganic soil nutrients	Total inorganic N	µg capsule^{-1}	**10.5±2.2**	1.07±0.55	77.3±28.8
	P	µg capsule^{-1}	**10.4±0.92**	1.68±0.7	26.7±10.3
Forest floor (organic soil)	C:N		**25±0.7**	19±0.7	31±1.4
	C:P		**253±20**	97±40	439±68
	pH		**4.6±0.06**	4.1±0.1	5.3±0.31
Green leaves	Leaf production	g dw m^{-2} ground	**47±5**	2.9±1.07	104±13.8
	C	%dw	**43±0.2**	41±3	46±3
	N	%dw	**3.0±0.11**	2.1±0.3	4.5±0.6
	P	%dw	**0.29±0.01**	0.17±0.03	0.43±0.07
Senesced leaves	C	%dw	**44±0.3**	43±1	47±1
	N	%dw	**1.2±0.06**	0.8±0.1	1.9±0.3
	P	%dw	**0.18±0.008**	0.1±0.02	0.25±0.06
Hebivory rate	prop. of leaf area	%	**1.6±0.33**	0.01±0.012	7±0.82
	prop. of leaves damaged	%	**10±1.6**	0.48±0.476	42±5.34
Insect herbivory losses	prop. of annual C	%	**1.5±0.3**	0.01±0.012	6.3±3.7
	prop. of annual N	%	**3.6±0.7**	0.03±0.028	14.1±7.3
	prop. of annual P	%	**2.4±0.5**	0.03±0.031	9±5.9

Herbivory and aboveground-belowground interactions

Herbivory and other ecosystem perturbations happening aboveground also have consequences belowground (Bardgett and Wardle 2010; van der Putten et al. 2013; Wardle et al. 2004). Traditional ecology studies patterns and distribution of organisms, and their associated energy and nutrient fluxes. This has typically been done mostly aboveground but the emergence of more advanced techniques for studying soil processes (reviewed by Kirchman 2018) has unlocked the field of soil ecology and how aboveground-belowground processes are linked. Yet, while recent development in Earth observation and ecosystem modelling techniques have become powerful tools for quantifying patterns in large scale landscape ecology and biogeochemistry (Schmitz et al. 2018), aboveground-belowground interactions are still quite poorly represented in such models (Dangal et al. 2017).

A first step towards model representation can be to conduct literature reviews and meta-analyses. A recent review of the effects of animals on landscape scale biogeochemistry demonstrated the importance of accounting for the presence of animals to get a more complete ecosystem representation in ecosystem models informing climate models (Schmitz et al. 2018). A review of the belowground consequences of large vertebrate herbivores showed that overall belowground process rates were surprisingly unresponsive to the presence of large herbivores (Andriuzzi and Wall 2017). There were, however, important differences between biomes, with stronger positive responses to herbivore presence in warmer and more productive systems and stronger negative responses in cold and unproductive systems, such as many Arctic ecosystems. Moreover, the authors found a similar gradient towards stronger negative responses by belowground fauna to herbivore presence with increasing herbivore body size, most likely due to physical disturbance of the soil due to trampling (Andriuzzi and Wall 2017). Finally, they pinpoint the vast overrepresentation of studies from grassland and tundra ecosystems, which has also been emphasised previously (Bardgett and Wardle 2010).

To supplement these findings and to form the basis for the rest of our work on insect herbivory in Subarctic birch forests, we conducted a global meta-analysis of the belowground consequences of insect herbivory in forest ecosystems (Paper I). Hence, we attempted to address two knowledge gaps; the underrepresentation in the herbivory literature of invertebrate herbivores, and the underrepresentation of infertile systems like forests. We found that insect herbivores increased soil C and N turnover rates (Figure 2), which is similar to the effect of vertebrate herbivores (Andriuzzi and Wall 2017). Yet, while the results by Andriuzzi and Wall (2017) were only divided into whether herbivores were present or not (exclusion studies), we also considered whether herbivore densities were at outbreak levels or background levels. Regarding soil biogeochemical responses, we found that only during outbreaks do the insect herbivores cause substantial loss of carbon and nutrients from the system (Figure 2), which is in line with previous reviews of insect herbivory (Hunter 2002; Lovett et al. 2002). These outbreak responses of element cycling were similar to what was found for vertebrate herbivores (Andrizzi and Wall 2017), and in fact we saw the same tendency to a gradient in responses from stronger positive in warm/wet environments and stronger negative in cold/dry environments (Paper I).

Accounts of insect herbivory responses by soil biota were fewer, hence should be a focus of future research (Paper I). The abundance of ectomycorrhizal fungi decreased significantly as a response to herbivory, likely as a direct consequence of less belowground C-allocation by their host-plants. Further, the mycorrhizal communities tended to shift from species with high energy requirements towards species with lower requirements, possibly as a coping strategy (Parker et al. 2017; Saikkonen et al. 1999; Saravesi et al. 2015). Further, we found a positive effect of insect herbivory on soil fauna (Paper I). This is in contrast to the response to vertebrates, where soil fauna were the only group of belowground organisms that were significantly negatively influenced by herbivore presence (Andriuzzi and Wall 2017). This difference is sensible, as the most likely explanation for the negative response to vertebrate herbivory proposed by Andriuzzi and Wall (2017) was physical soil disturbance, which can probably be assumed negligible for insect herbivores. Free living soil microbial abundances tended to show little response to both vertebrate (Andriuzzi and Wall 2017) and invertebrate herbivory (Paper I), although there were very few observations from invertebrate studies.

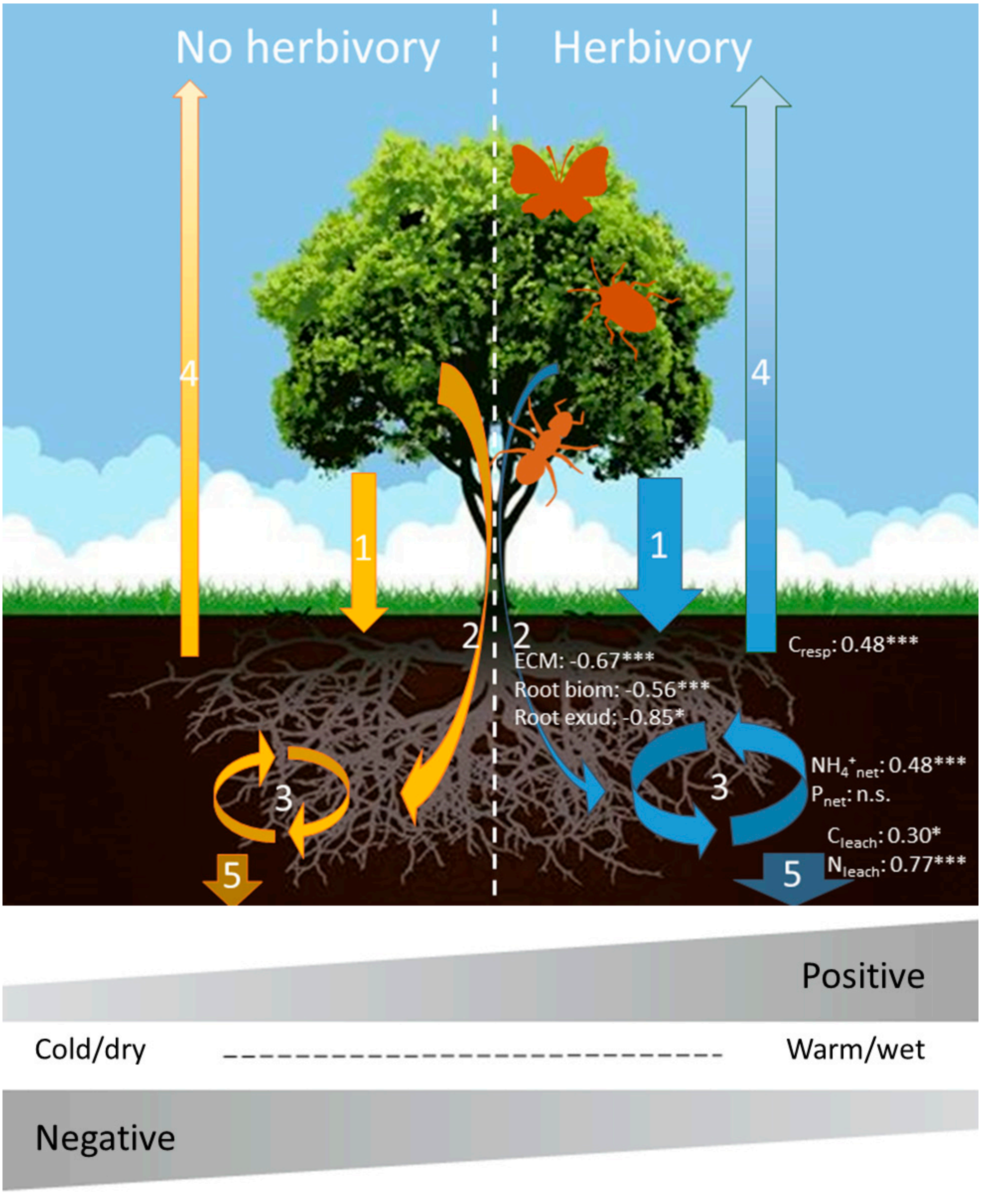

Figure 2. Summary of the main conclusions from the meat-analysis on belowground responses to aboveground insect herbivory in forest ecosystems. Insect herbivory decreased belowground C-allocation by plants (2) with associated shifts in root-associated microbial communities. The increase in labile deposits (1) increased belowground elemental turnover (3) which was reflected in increased atmospheric (4) and leaching losses (5) of elements from the soil system. The aggregated change (Cohen's d) in the main response variables are shown with significance levels (*P<0.05, **0.05>P>0.01, ***P<0.01, n.s. P>0.05). ECM=ectomycorrhizal abundance; Root biom=root biomass; Root exud=root C-exudation; C_{resp}=soil respiration/organic matter turnover; $NH_4^+{}_{net}$= net ammonification; P_{net}= net P mineralisation; C_{leach}= dissolved organic C in leaching water; N_{leach}= N in leaching water. The positive responses tended to become stronger, while the negative responses tended to become weaker along a climate gradient from colder and drier ecosystems towards warmer and wetter systems. Copied from Paper I.

Insect mediated element fluxes from canopy to soil

The canopy herbivory rates are rarely translated into nutrient fluxes. However, in a number of temperate forest studies, elemental fluxes under outbreak conditions have been quantified (e.g. Grüning et al. 2017; 2018; l-M-Arnold et al. 2016). Fewer reports exist for background insect herbivory (BIH) (Metcalfe et al. 2014; 2016; Reynolds et al. 2003; Schowalter et al. 2011; Zvereva et al. 2012). None of these studies are from the SMBF, despite the well-described cyclic population dynamics of the geometrid moths in this system (see *Aboveground insect herbivory*). Paper III in this thesis is the first attempt to quantify the elemental contributions from the canopy-to-soil fluxes through insects relative to leaf litter under background insect densities in Subarctic mountain birch forests. To represent most of the natural variation within the birch forest biome, we sampled along nine elevational gradients distributed along a regional elevational and climatic gradient (Paper III; see also Figure 6). As mentioned above, we estimated the average annual leaf area lost to BIH to ~1.6 % (Table 1), which is little compared to other lower latitude systems and the global average of ~8% (Kozlov et al. 2015). Further, we found that herbivory rates increased with local elevation, yet decreased with regional elevation (Figure 3a; Paper III). Moreover, leaf C:N (Figure 3b) showed a negative relationship with BIH, and the content of potential chemical defence compound (condensed tannins) correlated positively with insect herbivory rate. As the birch trees in this system were efficient at resorbing nutrients before leaf abscission (~55% of N and ~30% of P resorbed, Figure 3c, d), the contribution by insect herbivores to the nutrient fluxes was higher than the leaf area lost. When accounting for the nutrient resorption, the average proportion of the annual flux from canopy to soil through insects at background densities was ~3.5% for N and ~2.0% for P (Table 1; Paper III). Although the average rates were quite modest, the insect mediated fluxes constituted up to 14% of annual canopy-to-soil N-inputs at the sites with the highest BIH rates (Table 1). Nonetheless, the average insect mediated fluxes were 1-2 orders of magnitude lower than both internal cycling through litter, and external inputs from atmospheric deposition, biological fixation and weathering estimated from the literature (Paper III).

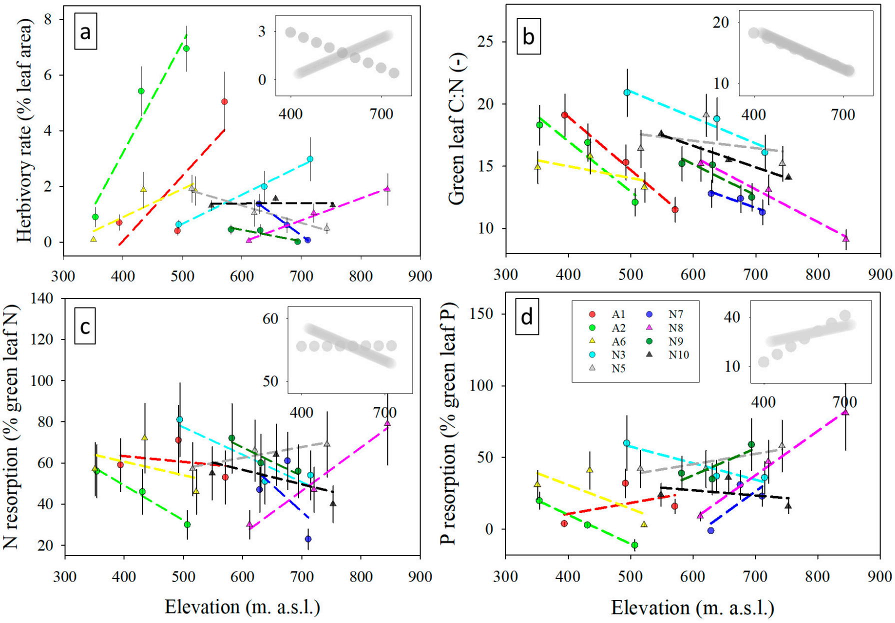

Figure 3. Elevational trends in key aboveground variables. Leaf herbivory (a), Green leaf C:N (b), N-resorption (c), and P-resorption (d). Each colour represents a transect corresponding to Figure 6. In the insets, dotted lines show the average regional trend while solid lines show the average local trend. Modified from Paper III.

All insect deposits except greenfall (pieces of uningested green leaves falling to the ground due to sloppy feeding by herbivores) are processed by the insects to some degree before entering the soil. Different animals have different efficiencies of converting ingested biomass to body biomass, and waste (excreta and respiration), which impacts their transfer of elements from plants to soils, and the availability of elements in their products to decomposers and eventually primary producers (Sterner and Elser 2002). In Paper II, we examined the partitioning of C, N and P into bodies and excreta (frass), and respiration in the case of C, by the two most common geometrid moth species in the SMBF, *E. autumnata* and *O. brumata*. The results suggested that the moths respired 30-50 % of the ingested C and only converted ~20-30 % of it to body mass, dependent on the diet (Figure 4). In contrast, they conserved N quite efficiently, by converting 70-80 % of ingested N to body mass, rather independent of diet (Paper II). The P-use was less efficient, where both moth types converted 45-60 % of the ingested P to body mass (Paper II). The strong nutrient-conservation was in line with the general conception that these high-latitude birch forest ecosystems are strongly nutrient limited (Jonasson et al. 1999; Michelsen et al. 2012). The differences between the two moth types were not substantial, but there was a tendency for the native species, *E. autumnata*, to be slightly better adapted to the environment. This was indicated by lower mortality rates than the invasive species, *O. brumata*, despite the latter being slightly more efficient in assimilating and converting both C, N and P to body mass (Paper II). Nonetheless, there was a strong correlation between the stoichiometric ratios of the diet and the excreta, caused by the strong ability of both species to maintain a constant body stoichiometry independent of diet (homeostasis) (Paper II). Future studies should examine how different deposits (excreta and cadavers) from insects with different partitioning ratios influence the soil turnover.

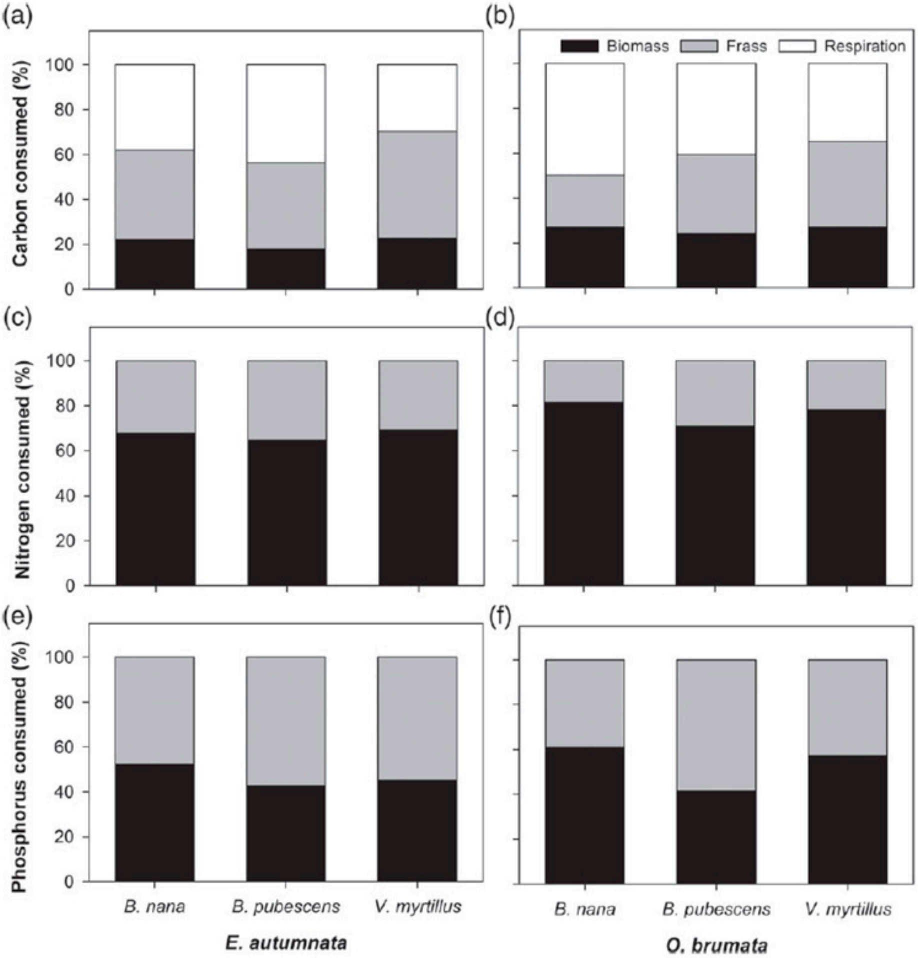

Figure 4. Proportional element partitioning by the two moth species .*E. autumnata* (a, c, e) and *O. brumata* (b, d, f). Carbon (a, b), nitrogen (c, d) and P (e, f) partioning into insect biomass (black), frass (grey) and respiration (white). Copied from Paper II.

Soil biogeochemistry and responses to insect herbivory

Organic matter is decomposed in the soil and converted to plant nutrients and gases (e.g. CO_2), or incorporated into other C-pools, such as microbial pools or more stable soil organic carbon (SOC) pools (Bradford et al. 2016; Liang et al. 2017). Soil respiration is a typical estimate for organic matter turnover in soils, and particularly the focus on climate change has emphasised the importance of knowing the stability of the SOC stocks representing the largest terrestrial pool of organic C (IPCC 2014). Scientific consensus points to a loss of old SOC with warming (Crowther et al. 2016), yet sequestration of new SOC could potentially counterbalance some of this loss. Recently, a key role for microbial biomass in SOC-storage has been proposed, particularly in high-latitude systems (Clemmensen et al. 2013; Liang et al. 2011; 2017). The ratio between the incorporation of C into microbial biomass and the microbially ingested C is called the soil microbial C use efficiency (CUE). This parameter is important for reliably modelling whether new C entering the soil is respired or stored (Bradford and Crowther 2013; Manzoni et al. 2012; 2017; 2018; Rousk 2016; Sinsabaugh et al. 2016; 2017; Soares and Rousk 2019). Yet, it is often poorly represented in existing ecosystem models (Manzoni et al. 2012; Soares and Rousk 2019). Further, in high latitude systems, N is often the limiting nutrient for plant growth (LeBauer and Treseder 2008), and sometimes microbial growth (Sistla et al. 2012), so the mineralisation of N and its coupling to the C-cycle is also fundamental to understand these systems (Hartley et al. 2010; Jonasson et al. 1999; Michelsen et al. 2012).

In Paper IV, we present a series of laboratory incubations with forest floor soils from the Subarctic birch forests to study the relationship between C and N mineralisation of senesced litter and insect frass under different scenarios, and relate it to the growth of the large microbial decomposer groups, fungi and bacteria (Figure 5; Paper IV). We found that a larger fraction (~30%) of the C added as frass was respired compared to the C added as litter (~10%) (Table 2). The litter decomposition yielded no apparent gross mineralisation of nitrogen, while 17% of the nitrogen added as frass was mineralised (Table 2; Paper IV). Considering also the substantial C-respiration by the insects themselves (~30-50%, see *Insect mediated elemental fluxes from canopy to soil*), this suggests that a substantially larger portion of the foliar C is lost to respiration when eaten by insects (~60%) relative to when C is added to the soil as the less available litter-C. This contrasts the observations from outbreaks in the field, where it is typically found that outbreaks reduce the soil C-turnover (Kaukonen et al. 2013; Parker et al. 2017; Sandén et al. 2019). As we only studied decomposer responses in the microcosms, most of this discrepancy is likely due to the immense reduction in respiration from roots and mycorrhizae during outbreaks when primary productivity, hence their C-source, is dramatically reduced (Heliasz et al. 2011; Olsson et al. 2017; Parker et al. 2017). However, recently Sandén *et al.* (2019) suggested that also heterotrophic respiration decreased even several years after insect defoliation, due to a combination of reduced labile litter input, higher mineral N-availability leading to less N-mining, and N-inhibition of enzyme production by particularly fungi. Our results also suggest that mineral N availability is substantially higher during outbreaks. As the tree demand for N is substantially reduced due to reduced foliage (Kosola et al. 2001), there is a much higher risk of N-loss from the system, which has been observed as peaks in the stream nutrient export during outbreaks in other forest systems (Eshleman et al. 1998; Swank 1988). However, in contrast to the hypothesised reduction in fungal activity due to N-inhibition (Sandén et al. 2019), our results showed that bacterial and not fungal growth was strongly reduced by high mineral N availability (Paper IV), which has also been shown in other recent forest studies (Silva-Sánchez et al. 2019). Although the fungal:bacterial growth ratios did not vary significantly between combinations of frass and litter addition, there was a tendency to higher fungal dominance over bacteria under frass addition compared to litter addition, which was also reflected in the biomass ratios (Paper IV). This is surprising, as the usual expectation is that bacteria are the primary decomposer of labile substrates, and would thrive under higher fertility (proxied by N-availability) while fungi would decompose more recalcitrant compounds like lignin (Rousk 2016). This conception has, however, been challenged recently by accounts of fungi being the primary colonisers of natural substrates in temperate hardwood forests (Rousk and Frey 2015).

Increased insect herbivory expected with climate warming (Jepsen et al. 2008; 2011; Kozlov et al. 2015) might cause generally higher N-concentrations in the soils (Sandén et al. 2019). Our treatment with mineral N and litter addition (Table 2; Paper IV) was supposed to mimic this scenario, and it indicated that only about half (~5%) as much of the added litter-C was respired compared to the pure litter treatment, while a lot more (~35%) of the organic N added as litter was mineralised under high N-availability. Counterintuitively, this indicated that higher N-availability might make the microorganisms target N-rich organic matter compounds (N-mining), which has also been suggested in other (Rousk et al. 2016; Ehtesham and Bengtson 2017), but not all (Wild et al. 2019) Northern systems. Alternatively, it may reflect higher mineralisation of excess N, as the potential N-limitation is relieved (Sistla et al. 2012), although microbes are very efficient in immobilising N in these systems (Michelsen et al. 2012). More surprising, we found that the higher N-mineralisation rate was associated with a shift from bacterial to fungal dominated growth (Figure 6), which was also reflected in the resulting fungal:bacterial biomass ratios (Paper IV). This was in line with other recent studies (Rousk et al. 2016; Ehtesham and Bengtson 2017), but contradicts common theory predicting that high fertility would favour bacteria over fungi, and would be more responsive to relief of limitation (Rousk 2016). Hence, the mechanisms behind these decomposer dynamics remain unclear, but our understanding of bacteria as the primary decomposer of labile substrates and fungi as the primary consumer of more complex organic matter seems incomplete (Rousk and Frey 2015).

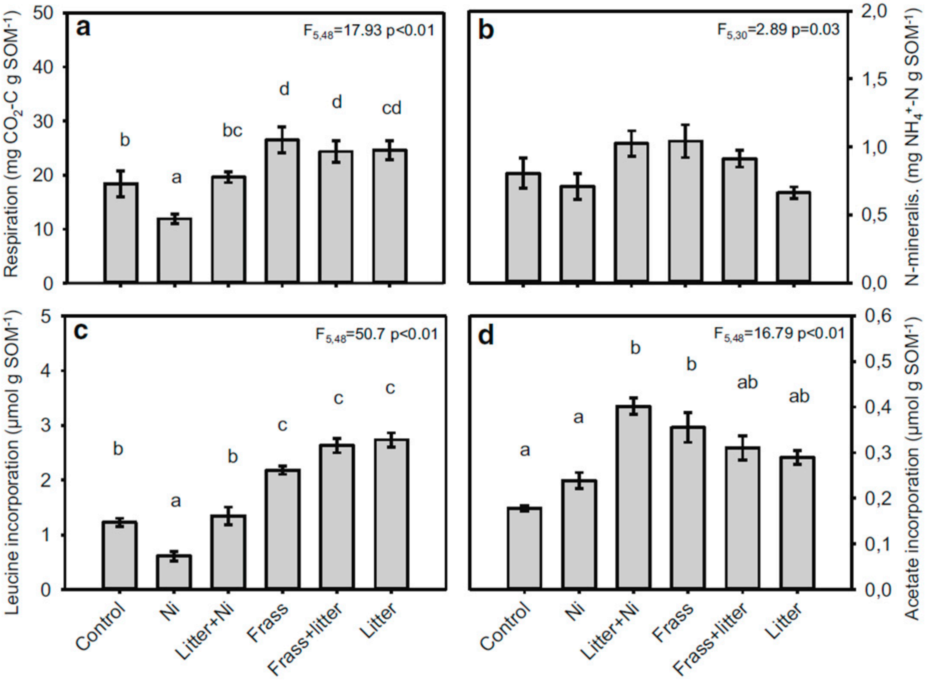

Figure 5. Key soil responses to addition if different combinations of substrate relevant for insect herbivory. Respiration (a), gross N-mineralisation (b), bacterial growth (c) and fungal growth (d) cumulated over 64 days. The amount of added C in substrate increases from left to right due to increasing substrate C:N. The height of the bars shows mean values and the error bars show 1 standard error around the mean (n=9 per treatment in panel a, c, d; n=6 per treatment in panel b). Different letters indicate significantly different values identified by a Tukey's HSD post hoc test. Copied from Paper IV.

Table 2. C and N mineralisation characteristics in soil microcosms. Cumulative amounts of mineralised C and N and as a fraction of added substrate C and organic N after 64 days of incubation (mean ± SE). Different letters indicate significantly differences between treatments (Tukey's HSD post hoc test). Modified from Paper IV.

TREATMENT	**MINERALISATION**						**ADDITION**		**MINERALISATION:ADDITION**			
	C_{min}		N_{min}	$C:N$			C	$N_{organic}$	C^a		N^b	
	mg CO_2-C / g SOM		mg NH_4-N / g SOM	C_{min} / N_{min}			mg C / g SOM	mg N / g SOM	g CO_2-C / g added C		g NH_4-N / g added org. N	
Control	18 ± 2	b	0.81 ± 0.11	23 ± 1.6	abc		0 ± 0	0 ± 0	na ± na		na ± na	
Ni	12 ± 1	a	0.71 ± 0.09	18 ± 1.2	a		0 ± 0	0 ± 0	na ± na		na ± na	
Litter+Ni	20 ± 1	bc	1.02 ± 0.09	20 ± 1.0	ab		29 ± 2	0.69 ± 0.05	5% ± 5%	a	34% ± 15%	b
Frass	26 ± 2	d	1.04 ± 0.12	26 ± 1.4	bc		30 ± 2	1.39 ± 0.09	27% ± 2%	b	17% ± 4%	ab
Frass+litter	24 ± 2	d	0.91 ± 0.06	27 ± 0.8	c		44 ± 3	1.39 ± 0.09	14% ± 2%	a	9% ± 7%	ab
Litter	25 ± 2	cd	0.66 ± 0.04	38 ± 3.0	d		58 ± 4	1.39 ± 0.09	11% ± 2%	a	-8% ± 7%	a

[a] $(C_{mineralised}[treatment] - C_{mineralised}[control])/C_{added}$

[b] $(N_{mineralised}[treatment] - N_{mineralised}[control])/Organic\ N_{added}$

To examine the drivers behind soil fungal and bacterial C-use and organic matter cycling under natural conditions in the Subarctic birch forests, we collected soil samples and estimated herbivory rates along with other potential abiotic and biotic driver variables along the same nine elevational gradients as in Paper III (Paper V). As expected, microbial biomass scaled with process rates, i.e. bacterial (B) growth and respiration, but not fungal (F) growth. In fact, fungal growth showed very limited systematic variation with any of the studied driver variables except elevation, so the patterns were largely due to bacterial responses, which confirm previous findings (e.g. Silva-Sánchez et al. 2019). Bacteria were strongly dominating detrital C-use across all our sites, and although CUE increased with both bacterial and fungal growth when respiration was controlled for, the effect was stronger for bacteria than fungi (Table 3a; Paper V).

The CUE decreased with increasing soil temperature (Table 3c), as our results suggested that respiration was slightly more sensitive to temperature than growth, in line with common theory (Sinsabaugh et al. 2013). This suggests that CUE might decrease with global warming, although some of this effect might be transient (Frey et al. 2013; Melillo et al. 2017), and may in time be balanced by the concomitant decrease in microbial biomass with warming (Allison et al. 2010; Frey et al. 2008).

In contrast, the hypothesised links to soil fertility and substrate availability were not confirmed (Table 3c; Paper V). Laboratory incubations have suggested that high mineral N availabilities selectively inhibit bacteria, which promote fungi due to competitive relief (e.g. Kristensen et al. 2018; Silva-Sánchez et al. 2019), but we found no link between nutrient contents and growth rates nor CUE along our forest gradients. A recent cross-ecosystem field survey did not find this link either, so perhaps the laboratory additions of mineral N induce inhibition of bacterial growth due to a "salt-effect", rather than a physiological response to acidity (Paper V).

The expected positive relationship between CUE and pH was not confirmed either, despite the strong correlation between pH and bacterial (positive) and fungal (negative) growth as well as respiration (positive, Paper V), in line with the literature (Rousk et al. 2009; Silva-Sánchez et al. 2019). We suspect the lack of relationship to CUE was due to the relatively narrow pH-range (~1.2 units) across our sites. However, it may also be due to false expectations based on induction of unintended effects (e.g. release of labile substrates), when pH is artificially manipulated in short-term laboratory incubations (Rousk et al. 2009).

Microbial community structure had no explanatory power for process rates along our gradients (Principal component (PC) 1 and 2 in Table 3b, Paper V) contrary to some previous syntheses (Bardgett and van der Putten 2014; Graham et al. 2016), so our results support the proposal that growth dynamics are superior to community structure in predicting process rates (Blagodatskaya and Kuzyakov 2013; Rousk 2016).

Table 3. Correlates of background soil CUE along natural gradients in the Subarctic mountain birch forest. PERMANOVA models partitioning the CUE variation to the factors in the CUE equation (a), the biotic controls (b), and the abiotic controls (c). Coeff.=coefficient/effect size. See Paper V for details. Modified from Paper V.

a) CUE EQUATION FACTORS			PERMANOVA (R^2=0.86)				
Variables	**Unit**	**Trans.**	**Df**	**F**	**R^2**	**P**	**Coeff.**
Fungal growth	μg C g dry SOM^{-1} h^{-1}	log	1	5.40	**0.03**	**0.022**	2.3E-01
Bacterial growth	μg C g dry SOM^{-1} h^{-1}	log	1	3.27	*0.02*	*0.069*	5.3E-01
Respiration	μg C g dry SOM^{-1} h^{-1}	log	1	135.12	**0.81**	**0.001**	-7.6E-01
Residuals			23		0.14		
Total			26		1.00		

b) BIOTIC CONTROLS			PERMANOVA (R^2=0.52)				
Variables	**Unit**	**Trans.**	**Df**	**F**	**R^2**	**P**	**Coeff.**
Annual birch litter C-input	kg C m^{-2}	log	1	0.27	0.01	0.647	7.3E-02
Birch litter C:N		log	1	0.19	0.01	0.719	1.3E-01
Root biomass C	kg C m^{-2}	log	1	0.53	0.02	0.495	1.3E-01
Root C:N		log	1	0.50	0.02	0.550	-6.5E-01
Herb cover	% of ground cover		1	1.08	0.04	0.347	-4.7E-04
Dwarf shrub cover	% of ground cover		1	1.91	0.07	0.183	1.5E-03
Herbivory rate	% of leaf area	sqrt	1	0.43	0.01	0.573	8.8E-03
Microbial biomass	nmol g SOM^{-1}	log	1	5.73	**0.20**	**0.020**	-7.6E-01
Fungal:Bacterial biomass		log	1	0.24	0.01	0.693	9.3E-02
PLFA PC1			1	0.28	0.01	0.641	1.9E-01
PLFA PC2			1	0.54	0.02	0.485	2.7E-01
Fungal:Bacterial growth		log	1	3.58	*0.12*	*0.070*	-2.4E-01
Residuals			14		0.48		
Total			26		1.00		

Table 3 continued

c) ABIOTIC CONTROLS			PERMANOVA (R^2=0.73)				
Variables	**Unit**	**Trans.**	**Df**	**F**	**R^2**	**P**	**Coeff.**
Transect			1	0.20	0.00	0.680	-2.1E-04
Elevation	m.a.s.l.		1	0.86	0.02	0.387	4.7E-04
Relative position	Z-score (local elev.)		1	1.30	0.03	0.272	-9.7E-02
Annual solar radiation	Wh m^{-2}		1	6.82	**0.15**	**0.022**	2.0E-07
Growing season onset	Julian date		1	5.38	**0.12**	**0.044**	5.5E-03
Mean annual soil temperature	°C	log	1	6.29	**0.14**	**0.021**	-1.3E+00
Mean growing season soil temperature	°C	log	1	0.88	0.02	0.359	1.1E+00
Volumetric water content	%	log	1	3.23	*0.07*	*0.086*	-2.3E-01
Soil pH			1	0.30	0.01	0.593	-4.3E-02
Soil C:N			1	0.25	0.01	0.664	-2.6E-04
Soil C:P			1	2.85	0.06	0.106	4.5E-04
Soil solution N_{inorg}	µg resin capsule^{-1}	log	1	0.54	0.01	0.504	4.1E-02
Soil solution P_{inorg}	µg resin capsule^{-1}	log	1	3.26	0.07	0.102	-1.4E-01
Transect elevationx relative position			1	0.51	0.01	0.520	1.7E-04
Residuals			12		0.27		
Total			26		1.00		

Perspectives on space-for-time-substitution

Substituting space for time is often used to make inferences about ecological responses to long-term environmental alterations, and has made substantial contributions to our understanding of ecosystem responses to climate change (Dunne et al. 2004; Elmendorf et al. 2015). The underlying assumption is that the relationships between environmental driver variables (e.g. temperature) and ecological response variables (e.g. soil respiration) are universal and scale independent (Damgaard 2019). Hence, variation in driver and response variables along spatial gradients are used to make inferences about responses to a similar change in driver variables over time. However, if the assumptions about universality and similar temporal scales of changes in driver and response variables are not met, the inferences are invalid (Damgaard 2019; Wogan and Wang 2018).

One common type of space for time substitution design is studies along elevational gradients. It is typically done under the assumption that the adiabatic lapse rate (~6.5 °C 1000 m^{-1}) cools the air temperature in a predictable manner with elevation, so by studying the variation in response variables with elevation (space), you can predict how these will change as a response to warming over time (Körner 2007). However, the elevational patterns in ecological variables are not always consistent, and more so for some variables than others (Sundqvist et al. 2013), which suggest that the universality assumption is not always met, i.e. the elevational trends can be context dependent. One way of testing the assumptions about universality and scale independence is by studying the same independent-dependent variable relationship along different scales, but within the same ecosystem/context.

In Paper III and V, we studied above- and belowground variables in the Subarctic birch forest along nine elevational transects distributed along a regional elevational and climatic gradient (Figure 6). This allowed us to compare the relationship between driver and response variables along local and regional gradients. If the universality assumption was met, the same elevational trend in the response variable should appear. However, if the local and regional variation with elevation was contrasting, it would be an example of what is referred to as Simpson's paradox (Simpson 1951), occurring when the within and across group independent-dependent variable relationships are inconsistent. Our results showed that some aboveground biotic variables, e.g. herbivory rate, showed contrasting trends with local (increase) and regional (decrease) elevation (Figure 3a). This is troubling in terms of making globally valid inferences about elevational trends in BIH, and subsequently climate warming. Other commonly measured variables, e.g. leaf C:N, showed consistent variation with local and regional elevation (Figure 3b), while some variables, e.g. nutrient resorption, showed little systematic elevational trends (Figure 3c, d; Paper III). We found only little evidence for contrasting local and regional effects in soil processes, despite some clear elevational relationships, e.g.

both fungal biomass and growth were inversely related to elevation (Paper V). Yet, soil temperature correlated poorly with elevation (linear regression $R^2=0.03$, $p=0.42$), so elevation might not be the best proxy for temperature in this system (Paper V).

Our results interestingly showed that annual solar radiation, which is a derivative of topography (elevation and aspect), climate and latitude, was well correlated with a number of both above- (Paper III) and belowground (Paper V) characteristics, independent of elevation and temperature. Solar radiation inevitably varies substantially in mountainous high-latitude systems, where the low sun-angle and many sun-hours during the growing season means that south-facing slopes receive ~50% more annual solar radiation than north-facing slopes in the same steep-sided valley (e.g. N8 vs N7, Figure 6). Hence, solar radiation was a much better predictor of soil temperature (linear regression $R^2=0.25$, $p=0.008$) than elevation in our study system, and might be considered as a temperature proxy instead of elevation. Solar radiation was in fact a better predictor of many above- and belowground ecological processes than temperature, which merits more thorough consideration of variation in solar radiation in future ecosystem evaluations along natural gradients at high latitudes.

Finally, particularly for certain aboveground properties, there seemed to be interactions between regional abiotic variation and the local elevational relationships with biotic response variables (Paper III). This suggests that it may be possible to anticipate the context dependency of local elevational trends. Thus, allowing for dependence on ecosystem context (e.g. mean annual temperature) may allow us to make more solid representations of the expected elevational trends in ecosystem models.

In conclusion, our results highlight three important points for further consideration regarding the use of elevational gradients in ecosystem science:

1) Although contrasting local and regional elevational responses (Simpson's paradox) might be relatively rare, this should be anticipated/assessed when designing the research.
2) Only when the local and regional responses are identical is the universality assumption fulfilled. But even then, the variation in elevation might be a poor proxy for variation in temperature, particularly in mountainous high latitude systems, where solar radiation (integral of topography, climate and latitude) may be a better proxy.
3) In some instances, the local variation with elevation may vary systematically (interact) with regional variation in abiotic variables. This may allow us to anticipate the context dependency of the elevational variation along individual transects.

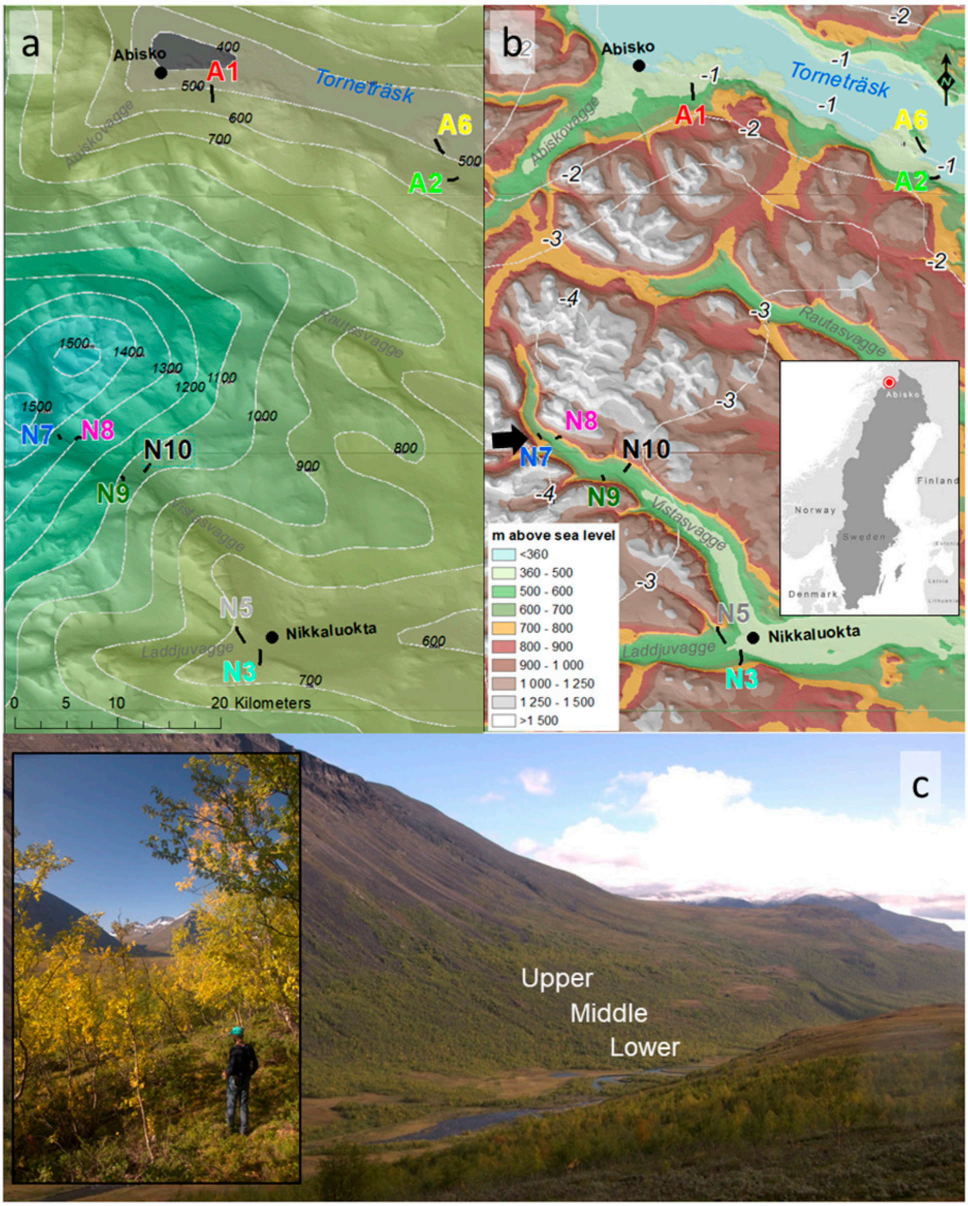

Figure 6. The research design. Nine local elevational gradients were distributed along regional environmental gradients in precipitation (a), temperature (isolines in b), and elevation (colour coding in b). Panel c shows the location of transect N8 taken from the position of the black arrow in panel b. The text shows the approximate positions of the lower (close to the valley bottom), middle (half-way to the treeline) and upper (close to the treeline) sites along this transect. The inset in panel c shows a typical lower site with a person for scale. Photo credit: Thomas Heister.

Conclusions

Insect herbivory can influence ecosystem processes particularly during outbreaks. High latitude ecosystems have received growing attention in recent decades, due to their vulnerability and feedbacks to climate warming. In this thesis, we examined aspects of the insect herbivory influence on biogeochemical cycling, with a primary focus on Subarctic mountain birch forests in Northern Sweden, where the autumnal moth and the winter moth are the dominating herbivorous insects.

The very severe outbreaks defoliating occasionally >70% of the foliage in the Subarctic birch forests have been widely studied, both in terms of above- and belowground consequences. However, we present the first estimate of the leaf area lost to BIH (~1.6%) and the corresponding fluxes of elements from canopy to soils (~3.5% of annual N, ~2.0% of annual P), which is higher than the leaf area lost, due to strong nutrient resorption by the birch trees. BIH contributed only marginally to annual elemental fluxes in Subarctic mountain birch forest compared to internal recycling through litter and external inputs through atmospheric deposition, biological fixation and weathering. The BIH rates were comparable to other Arctic systems, but considerably lower than at lower latitudes.

In line with the small annual contribution to substrate fluxes by insect herbivores at background densities, we showed that insect herbivory increase the turnover of organic matter and mineralisation of N, but much less during non-outbreak than outbreak years. General knowledge on the biological underpinnings is needed, but we add some important first steps for our study system by linking the turnover of substrates of varying availability and nutrient contents to the growth rates and biomass of decomposer fungi and bacteria. Our soil incubation results suggest that fungal growth is stimulated more than bacteria under frass addition, while the opposite was observed for litter decomposition. Along field gradients detrital C-use was strongly controlled by bacterial growth, while fungal growth showed weak correlations with the hypothesised drivers of process rates. Nonetheless, soil CUE was positively correlated with both fungal and bacterial growth when respiration was controlled for. BIH did not influence the background soil CUE, despite the positive relationship with bacterial growth. Background CUE scaled negatively with the microbial biomass pool, and soil temperature, which might suggest weak positive climate warming feedback.

Finally, we contributed to the ongoing discussion about the validity of inferences made along natural gradients, particularly with regard to using spatial variation with elevation as a substitution for temporal variation with temperature. One basic assumption in space for time substitution studies along elevational gradients is that the elevational relationships are universal and scale independent. Our sampling design allowed us to compare local and regional elevational relationships within the same ecosystem. We found that, while the assumption was met for most belowground variables, the local and regional trends with elevation were contrasting for other variables, e.g. BIH rate. This shows that some caution is warranted with respect to the universality of ecosystem scale inferences about processes made along one or few elevational gradients.

Future aims and perspectives

I want to round off with three future aims inspired by the work on this thesis.

First, we should quantify herbivore contribution biogeochemical cycling in normal years in more systems. Particularly invertebrate herbivores can exhibit conspicuous outbreak dynamics, which have attracted most of the scientific attention, but we lack quantitative knowledge on the normal years in between. If the intervals between severe outbreaks are long, the years in between may be equally important for overall elemental cycling, despite not being able to rejuvenate the ecosystems as the outbreaks do (Weisser and Siemann 2008).

Further, a recent review of the role of animals in biogeochemical cycling showed the value and potential for integrating what they term *zoogeochemistry* into ecosystem models (Schmitz et al. 2018). Particularly our knowledge on biological mechanisms driving the belowground organic matter turnover rates (e.g. CUE) represents a missing link between the abiotic driver variables and responses in ecosystem models (Bradford and Crowther 2013; Manzoni et al. 2018; Soares and Rousk 2019). However, as the physical ecosystem disturbance and geographical redistribution of nutrients by large animals can influence soil community compositions and ecological processes more than the chemical transformation of organic matter through digestion (Andriuzzi and Wall 2017; Bardgett and Wardle 2010; Schmitz et al. 2018), substantial differences between the long-term landscape scale effects of vertebrate and invertebrate herbivores might be expected. Recent investigations of the interactions between different types of herbivores, vertebrate and invertebrates (Ritsch et al. 2018), have paved a way for how to approach the complicated interactive roles of different herbivores in shaping ecosystem processes. Such interactions between different types of herbivores may be important for understanding and predicting consequences of the complete role of herbivory in global environmental change, hence should be a focus of future research efforts.

Finally and of broader scientific relevance, our discovery of contrasting elevational trends for some ecological variables needs further attention. A review revealed that inconsistent elevational trends are relatively common within ecology (Sundqvist et al. 2013). While acknowledging the great scientific contributions space-for-time substitution has made for decades and even centuries, we need to carefully consider the timescales of the changes we study. As already mentioned, the ecological response rate to a change in the driver variable should be similar or faster than the rate of change in the driver variable itself (Damgaard 2019), for example the relationship between temperature and plant community structure in climate change studies. In fact, herbivory may further complicate such relationships, if they can change the pace or direction of change relative to the warming induced change. For example, shrub-expansion into Arctic tundra as a response to climate warming has been heavily studied (Vowles and Björk 2018). Yet, herbivory by reindeer can reduce the speed of or even halt this invasion (Bernes et al. 2015; Vowles et al. 2017). Consequently, the apparent rate of change of the response variable (shrub cover) to the driver variable (temperature) in a space-for-time substitution study is different depending on herbivore presence. Our results indicated that certain abiotic factors might influence the relationship between driver and response variables in a similar way, i.e. BIH increase less with local elevation at high regional elevation. Incorporating such abiotic and biotic context dependency on elevational trends may present a way towards more reliable interpretation of space-for-time substitution data.

Popular science summary

Herbivores, or plant eaters, can speed up or slow down the cycling of organic matter and nutrients through ecosystems. The influence of larger animals, such as reindeer in the Arctic and Savannah herbivores in the tropics, have been most intensively studied. They can shape the plant communities and their geographical distributions at the landscape scale, due to their body size and consequently longer digestive times. Yet, smaller animals like insects can also have a marked influence on the cycling of matter and elements, and while each individual cannot consume as much matter as mammal herbivores, they can have profound consequences for ecosystems in patches where conditions are favourable, as they can exhibit very dynamic population increases leading to insect outbreaks.

However, the years in between the outbreaks are many more yet underexplored compared to the more conspicuous outbreak years. While others found that more than 70% of the leaf area can be lost to herbivory during outbreaks in the Subarctic mountain birch forests (SMBF) in Northern Sweden, we show that only about 1.6 % of the leaf area is lost during normal years. This translates to about 3% of the yearly nutrient inputs from canopy to soils, so both the soil inputs from leaf litter by the end of the season and from external sources are 10-100 times higher.

We showed that the belowground consequences of insect herbivory were indeed stronger as a response to outbreaks compared to background insect densities. While only about 10% of the C in litter was respired by soil microbial decomposers during the first growing season, as much as 30% of the C added as insect excreta was turned over and respired. As the insects themselves respire about 40% of the C they eat, a total of about 60 % of the organic matter-C eaten by insects in the SMBF was respired back to the atmosphere during the first growing season. However, as the proportion of leaf area lost to background insect herbivory was relatively low, its influence on soil organic matter cycling was negligible, although the activity of soil decomposer bacteria increased marginally with increased herbivory rates. The partitioning of C taken up by soil microbes into body mass and waste, respectively, is an important estimate of whether organic matter introduced to the soil is stored in the soil or emitted back to the atmosphere as CO_2. Soil temperature and the amount of decomposer microbes present were good predictors of this ratio, suggesting that less organic matter will remain in the soil when it gets warmer or when the abundance of microbes increases. As the amount of decomposer microbes normally decrease with soil warming, that effect may reduce the potential negative climate effect of warming alone.

As global warming is intensifying, it is important to know how ecosystems respond to temperature changes. A common way of investigating relationships between temperature and ecological variables, such as insect herbivory, is by studying variation along a mountain slope, as the air cools when the elevation increases. However, if the ecological variables do not always change in the same way with elevation, we risk making wrong interpretations of its relationship with temperature. This is problematic, if we use this knowledge to make predictions about ecosystem responses to future climatic change. Our study indicated that although it may not be very common, some variables show contrasting responses to elevation increase at the local and regional scales. This implies that some caution is needed in future research designs using variation in space to infer universal relationships between variables changing over time.

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Avhandlingar från Institutionen för naturgeografi och ekosystemanalys (INES), Lunds universitet

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Dissertations from Department of Physical Geography and Ecosystem Science, University of Lund

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