

Background insect herbivory increases with local elevation but makes minor contribution to element cycling along natural gradients in the Subarctic

Jeppe Kristensen¹, Anders Michelsen², and Dan Metcalfe¹

¹Lund University

²University of Copenhagen

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Abstract

Herbivores can exert major controls over biogeochemical cycling. As invertebrates are highly sensitive to their environment (ectothermal), the abundances of insects in high-latitude systems, where climate warming is rapid, is expected to increase. In subarctic mountain birch forests research has focussed on geometrid moth outbreaks, while the contribution of background insect herbivory (BIH) to elemental cycling is poorly constrained. In northern Sweden, we estimated BIH along 9 elevational gradients distributed across a gradient in regional elevation, temperature and precipitation to allow evaluation of consistency in local vs. regional variation. We converted foliar loss via BIH to fluxes of C, nitrogen (N), and phosphorus (P) from the birch canopy to the soil to compare with other relevant soil inputs of the same elements, and assessed different abiotic and biotic drivers of the observed variability. We found that leaf area loss due to BIH was ~1.6% on average. This is comparable to estimates from tundra, but considerably lower than ecosystems at lower latitudes. The C, N and P fluxes from canopy to soil associated with BIH were 1-2 orders of magnitude lower than the soil input from senesced litter and external nutrient sources such as biological N fixation, atmospheric deposition of N and P weathering estimated from the literature. Hence, despite the minor contribution to overall elemental cycling in subarctic birch forests, the higher quality and earlier timing of the input of herbivore deposits to soils compared to senesced litter may make this contribution disproportionately important for various ecosystem functions. BIH increased significantly with leaf N-content as well as local elevation along each transect, yet showed no significant relationship with temperature or humidity, nor the commonly used temperature proxy, absolute elevation. The lacking consistency between the local and regional elevational trends calls for caution when using elevation gradients as climate proxies.

Introduction

Herbivores have important effects on elemental cycling in terrestrial ecosystems (Bardgett and Wardle 2003, Schmitz et al. 2018). Most attention has been given to vertebrates, but insect herbivores can exert a similar or even stronger control on ecosystem functioning than mammals (Risch et al. 2018, Kristensen et al. 2020), particularly in forest ecosystems, where their impact is likely to intensify substantially with global change (e.g. Logan et al. 2003).

Studies on insect herbivory in high-latitude forests have hitherto emphasised the importance of outbreaks (e.g. Jepsen et al. 2013, Sandén et al. 2020), especially as some species are increasing their ranges into new areas with climate warming (Jepsen et al. 2008, 2011). However, non-outbreak, low-intensity rates of insect herbivory, termed background insect herbivory (BIH), has attracted increasing attention in recent years (Kozlov and Zvereva 2017). Although BIH at high latitudes is generally low - 1-2 % of the leaf area (Barrio et al. 2017) compared to the global average of ~8% (Kozlov et al. 2015) - the rate will likely increase at high latitudes with global warming (Kozlov et al. 2015), despite the observation that insect predation and

parasitism also increase with temperature (Virtanen and Neuvonen 1999, Roslin et al. 2017). It has been argued that BIH, despite the small annual contribution, may be more important for long-term ecosystem functioning in a wide range of globally important ecosystems, including tropical (Metcalf et al. 2014), boreal (Zvereva et al. 2012, Metcalf et al. 2016), and arctic systems (Barrio et al. 2017).

The fact that most of the global terrestrial soil C is stored at high latitudes (Hugelius et al. 2014), where global warming is most pronounced (ACIA 2004), makes it particularly important to understand perturbations in this region. While low productivity ecosystems dominate at high latitudes (Higgins et al. 2016), subarctic birch forests constitute a relatively productive ecosystem (Sjögersten and Wookey 2009). Therefore, perturbations in birch forests may exert disproportionately large impacts on regional biogeochemical cycling. The end consequences of herbivory, by primarily the geometrid moths *Epirrita autumnata* and *Operophtera brumata*, have been demonstrated in terms of plant traits (Haukioja 2003; Karlsson et al. 2004), plant (Jepsen et al. 2013, Sandén et al. 2020) and soil community composition (Saravesi et al. 2015, Parker et al. 2016, Kristensen et al. 2018), soil nutrient and carbon (C) turnover (Kaukonen et al. 2013, Parker et al. 2016, Kristensen et al. 2018, Sandén et al. 2020), and photosynthetic C-fixation (Heliasz et al. 2011, Bjerke et al. 2014), but quantification of the key mechanism driving these changes - canopy to soil fluxes of C, N and P through insect deposits - is still lacking. Elements channelled through insects are not a novel element input to the ecosystem, but rather an alternative pathway of transferring high quality organic matter from the canopy to the soil in the early growing season rather than the usual transfer of senesced litter by the end of the season. Most studies indicate that N is the main plant growth-limiting nutrient in most forest systems (e.g. LeBauer and Treseder 2008), but an increasing body of literature suggests that P is co-limiting plant growth (Vitousek et al. 2010, Sundqvist et al. 2014). Further, nutrient limitation will become even more widespread in the future due to warming and CO₂-fertilisation, which may weaken the terrestrial ecosystem C-sink (Fisher et al. 2012, Wieder et al. 2015). Therefore, it is relevant to assess the amounts of both N and P channelled through labile insect deposits and recalcitrant litter respectively. Insect deposits contain much larger amounts of nutrients compared to senesced litter (e.g. Kristensen et al. 2018) because insects feed on green leaves before the highly conservative Subarctic birches resorb up to ~70 % of their nutrients during senescence (Nordell and Karlsson 1995). Thus, the balance of elemental transfer between the litter and insect pathways regulate the timing and quality of soil substrate inputs, which can in turn lead to both increased and reduced soil C and nutrient turnover (Parker et al. 2016, Kristensen et al. 2018, Sandén et al. 2020).

N is also the growth-limiting nutrient for the moths in our study system (Metcalf et al. 2019). The foliar content of N is therefore expected to be an important driver of moth success, hence BIH level. In order to conserve nutrients from herbivores, host plants may increase the level of foliar chemical defence compounds (Haukioja 2005, Fürstenberg-Hägg et al. 2013). For example, the leaf content of bioactive specialised compounds, such as condensed tannins (CT), has been found to increase in leaves subjected to herbivory (Fürstenberg-Hägg et al. 2013). Yet, the relationship between herbivory and plant defence compounds is not simple in natural systems. In fact, geometrid moth species in subarctic birch forests are rather tolerant to the birch chemical defence compounds (Haukioja 2003, 2005). Therefore, it is only relevant for the birch to pursue this defence strategy when the growth-limiting nutrient level in the leaves is so low that the insects have to eat large amounts of foliage to compensate for low nutrient concentrations (Haukioja 2003). Thus, a negative relationship between the foliar content of the moth growth-limiting nutrients and foliar defence compounds should be expected at ecosystem scale.

Apart from the links to foliar chemistry, BIH also varies with climate, with an expected increase with warmer temperatures in mid-high latitude systems (Kozlov et al. 2015, Barrio et al. 2017, Galmán et al. 2018). Nonetheless, moth outbreaks most often appear close to the treeline in birch forests across subarctic Scandinavia rather than in valley bottoms, probably due to the higher likelihood of winter temperatures below their egg survival limit (< -35-37 °C) along the valley bottom due to thermal inversion of air masses during winter (Ruohomäki et al. 1997, Hagen et al. 2007), and/or higher parasitism during the summer (Virtanen and Neuvonen 1999). Yet, such decrease in top-down controls on herbivory at higher local elevation may be confounded by decreasing bottom-up controls. For example, the food quality (leaf N content) is also expected

to increase with elevation (Körner 1989, Read et al. 2014). Nonetheless, no systematic increase in BIH with the local elevation above the valley bottom has been found previously (Virtanen and Neuvonen 1999), and such an increase would oppose the overall elevational decrease in herbivory at the global scale (Galmán et al. 2018).

In this study, we quantified BIH on the mountain birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti) along 9 elevation gradients in Subarctic birch forests spanning a considerable portion of the environmental variation in the Fennoscandian mountain birch forests. We estimated the canopy-to-soil fluxes of C, N and P per unit ground area in litter and insect deposits and compared them to other relevant sources of soil input of the same elements. We also evaluated the dependence of BIH and the resulting elemental fluxes on leaf chemistry, climate, elevation and relative position over the valley bottom to identify potential abiotic and biotic drivers. Our setup with multiple gradients spanning a larger regional elevational gradient allowed us to test the universality of relationships between elevation and foliar loss to herbivory. We hypothesised that:

(H₁) *Elemental fluxes* : The BIH levels in subarctic birch forests are minor compared to lower latitude systems, and consequently the annual contribution of nutrients to the soil through this channel is much smaller than other internal (i.e. recycling from litter) and external sources (i.e. fixation, deposition, weathering).

(H₂) *Biotic controls* : The BIH level increases with concentration of leaf N, which is the growth-limiting nutrient in the system. Consequently, we expected no strong relationship with leaf condensed tannin concentration, as this only play a role as a defence compound at low N-levels, where we already expected low foliar loss to herbivory. Moreover, we hypothesised that the importance of insect herbivores for channelling nutrients from the canopy to the soil would increase with stronger foliar nutrient resorption, as this would decrease the transfer of nutrients through senesced litter on annual basis.

(H₃) *Abiotic controls* : We expected a local scale increase in BIH with the relative position above the valley bottom along each transect towards the treeline, due to decreasing likelihood of extreme winter cold and summer parasitism, which are both strongest in the valley bottom. Yet, we also expected an overall BIH level increase with site temperature, as insect herbivory levels are generally higher in warmer mid-latitude systems, but this effect may be substantially weakened by the expected local elevational increase in BIH.

Materials and methods

Study site and design

The study sites were in subarctic mountain birch forests near the Abisko Scientific Research Station, northern Sweden (68.35°N 18.82°E). All samples were taken in 2017. The layout was designed to capture as much of the regional climatic variation as possible within a relatively constrained geographic area (<50 km from Abisko) by taking advantage of the considerable climatic gradients created by the mountainous landscape between Abisko and the Kebnekaise complex (Figure 1). We established 9 elevation transects, each with a site near the valley bottom, one near the treeline, and one in the middle, making a total of 27 sites. Further, 8 of the transects were paired as a north- and a south-facing transect at 4 locations to control for the influence of aspect/solar radiation. According to a digital elevation model (DEM) from Lantmäteriet (50 m resolution), regional variation in elevation across the 27 sites is approximately 500 m (minimum 351 and maximum 845 m above sea level), while the minimum and maximum elevational difference along a single transect is 82 and 233 m respectively. To control for aspect, we used the DEM to estimate the total annual solar radiation of 2017 for each site using the “Area Solar Radiation” function in ArcGIS 10.3 (ESRI, Redlands, CA, US). Sites were preferentially established in dry locations with heath-dominated ground vegetation, however, this was not possible in all instances, as some of the wetter transects were dominated by herbaceous ground vegetation (7 out of 27 sites with >50% herbs). The bedrock geology was dominated by granites and other acidic bedrocks, and there was weak-moderate podzolisation at all sites. According to the Swedish Meteorological and Hydrological Institute Luftwebb record (4x4 km resolution) from the last normal period (1961–1990, isolines in Figure 1), the mean annual air temperature across our sites ranged between -2.5±1.03 and -1.4±1.03 °C (mean ± SE), and the mean annual precipitation ranged from 404±75 to 1250±158 mm. For

the analyses below, we have used the average of the more recent period of 2000-2014 to derive meteorological variables more comparable to the study period.

The rationale behind the design was to assess the assumption underlying the use of elevation as a climate proxy: If there is a universal relationship between elevation and an ecological variable, the slope of the trendline in an X-Y plot would be similar at regional and local scale. To check the design, we included a plot of a commonly measured ecological variable, foliar N content, against elevation, as we expected this to show a clear and consistent increasing trend with elevation across scales (Körner 1989), although potentially weaker at regional scale (Read et al 2014).

Fieldwork and sampling

Measurements were taken from a 20x20 m area at each site. After the tree leaves had fully expanded (late June), the *B. pubescens* leaf area index (m^2 leaf m^{-2} ground, LAI) was estimated with the Hemisfer software, version 2.2 (Schleppi et al. 2007; Thimonier et al. 2010) based on ~10 hemispherical images per site (camera: Nikon Coolpix 4500; lens: Nikon Fisheye converter fc-e8 0.21x). In addition, we used ground slope correction (Schleppi et al. 2007), and the most recent algorithm for LAI estimation following manual thresholding (Gonsamo et al. 2018). We randomly selected ~30-50 fully expanded leaves from the lower canopy (~1.5-2.5 m above the ground) from a minimum of seven *B. pubescens* trees per site to estimate specific leaf area ($\text{m}^2 \text{g}^{-1}$ dry mass, SLA) by scanning the fresh leaves to obtain the area, and then drying (40°C for 48h) and weighing. Annual *B. pubescens* leaf production ($\text{g dry mass m}^{-2} \text{yr}^{-1}$, LP) per site was assumed to be equivalent to fully expanded canopy biomass in this deciduous species, which was estimated by dividing the LAI with the SLA ($\text{LP} = \text{LAI} / \text{SLA}$). After scanning and drying, the leaves were chemically analysed (see below). In the late growing season (late August), ~30-50 freshly fallen or senesced yellow leaves still on the branches were collected from a minimum of 7 trees per site in order to determine leaf chemistry at senescence (see below). All leaves were dried (40°C for 48h) and ground before chemical analyses. In the late growing season, 4 large organic horizon samples (soil from ~1 m^2 each sieved through 6 mm mesh) from each site were collected for a range of chemical analyses as indicators of site fertility (see below). Subsoil samples were collected in sampling rings (3 x 100 cm^3 per site) and composited before analyses.

The insect herbivory level was estimated using a modified version of the method described by Crutsinger *et al.* (2008). At each site, we randomly selected 7 trees in the late growing season (August/September), after the vast majority of insect herbivory had terminated. Trees were selected from a distance (~15 m) where insect herbivory could not be detected, to minimize sampling bias (Zvereva and Kozlov 2019). On each tree, 3 branches were randomly selected on which we visually estimated the percentage of leaf area lost to herbivory (0%, 1-5%, 5-10%, 10-20%, 20-30% ... 90-100%) in the lower canopy (~1.5-2.5 m above the ground). Ten leaves were surveyed per branch, starting from the first full-sized leaf and down the branch surveying every other leaf. When calculating the average herbivory level for each site, each observation was assigned the median value of its interval, e.g. 10-20% = 15%.

For site characterisation, the ground vegetation cover was visually estimated in the early growing season (late June/early July) as the average coverage (%) within 3 randomly selected squares of 3x3 m per site. Dwarf shrubs were determined to the species level, while mosses, lichens, graminoids and forbs were identified to functional group level.

The Luftwebb record for 2000-2014 shows a range in mean annual air temperature across our transects between -1.1 ± 0.2 and 0.3 ± 0.2 °C (mean \pm SE), and the mean annual precipitation ranged from 447 ± 17 to 1366 ± 34 mm year^{-1} . The mean growing season temperature ranged between 9.9 ± 0.3 and 11.3 ± 0.3 °C. To capture the smaller scale variation in climate at the site level, the soil temperature was measured with iButtons (Maxim Integrated, San Jose, CA, USA) installed in the topsoil (5-10 cm depth, 1 at the centre of each site) from early September 2015 until late August/early September 2017. We used the mean growing season soil temperature as a predictor (averaged between 15/6-15/9) to get the most relevant temperature for aboveground processes, and to reduce the legacy effects of varying snow-cover between sites. The soil moisture was estimated as an average of ~15 measurements per site with a Campbell Hydrosense II moisture

sensor (~10 cm depth) (Campbell Scientific Inc., Logan, UT, USA) at every site visit. For statistical analyses, we used the early growing season moisture content (late June/early July); as the topsoil was very dry at some sites in the late season, which might make these measurements less representative as a proxy for root zone water availability.

Chemical analyses

Total C and N-concentrations of soils (topsoil: 4 samples; subsoil: 1 composite sample from minimum 3 rings per site) and leaves (composite sample from ~30-50 leaves from minimum 7 trees per site) were measured in solid samples (soils: 7 mg, leaves: 5 mg) by Dumas combustion (1040 °C) on an elemental analyser (Eurovector CN analyser, Redevalle, Italy) after thorough homogenization in a ball-mill. Total P content was determined using a FIAstar 5000 flow injection analyser (FOSS, Hillerød, Denmark) on 25 mg samples, after total dissolution in H₂SO₄ with Se. Condensed tannin content was determined in 100 mg leaf material extracted in 5 ml methanol using the vanillin method with catechin as standard, and a Hitachi U 2010 spectrophotometer (Hitachi, Tokyo, Japan).

Estimation of fluxes and resorption

The site fluxes of C, N and P through insect herbivores (X_{herb} , g m⁻² yr⁻¹) was estimated as the product of the leaf production (LP, g m⁻² yr⁻¹), proportion of the leaf area lost to herbivory (H), and the elemental proportions in the green leaves collected in the early growing season ($[X_{\text{green}}]$):

$$X_{\text{herb}} = \text{LP} \times H \times [X_{\text{green}}]$$

Similarly, the flux of elements through the litter (X_{litter} , g m⁻² yr⁻¹) was estimated as the product of the leaf production (LP, g m⁻² yr⁻¹) corrected for the proportion lost to herbivory (H), and the elemental concentrations in the senesced leaves collected in the late growing season ($[X_{\text{sen}}]$):

$$X_{\text{litter } i} = (1-H_i) \text{LP}_i \times [X_{\text{sen}}]_i$$

Foliar nutrient resorption (X_{resorp} , %) was calculated according to van Heerwaarden *et al.* (2003). Briefly, it was estimated as the difference in nutrient concentrations between the green and the senesced leaves normalised to leaf area, and expressed as a fraction of the green leaf nutrient content. Nutrient resorption needs to be accounted for, when comparing fluxes based partly on green leaves (herbivore deposits), and partly on senesced leaves (leaf litter), as strong resorption amplifies the relative importance of the green-leaf component, i.e. the herbivory-mediated flux.

Statistical analyses

Descriptive statistics were expressed as arithmetic means and standard errors (SE). When feasible, errors were propagated to maintain an estimate of variance. We tested correlations between our predictor variables and herbivory levels as well as the annual proportion of elemental fluxes using linear mixed effect modelling ('lmer' function in 'lme4' package, Bates et al. 2015). Confidence intervals (95%) were constrained with 999 bootstrap simulations. The relative position above the valley bottom was included in the models as Z-scores based on the elevation grouped by transect, i.e. yielding values close to -1 for the lowest site, close to 0 for the middle site, and close to +1 for the highest site. For herbivory levels, we tested volumetric soil water content, mean growing season soil temperature, annual solar radiation, relative position above the valley bottom and absolute site elevation as abiotic predictors, while leaf C:N and CT:C ratios were included as biotic predictors. When testing these as fixed effects, the other variables were classified (4 approximately normally distributed groups per variable) and included as random effects. Further, the transect number was included as a random effect in all models (9 groups). For the annual proportion of elemental fluxes, we tested herbivory level, leaf production, leaf nutrient (N or P) content, and nutrient (N or P) resorption as fixed effects. Nutrient resorption was included, as strong nutrient resorption would decrease the nutrient flux through senesced litter, and result in a larger proportion of the annual nutrient fluxes through insect deposits for a given leaf area loss. Variables were transformed when needed to comply with model assumptions and

assure similar variance for all variables. All statistical analyses were conducted in R version 3.6.2 (R Core Team, Vienna, Austria).

To assess the consistency in the relationship between local and regional elevation and herbivory, we linearly regressed BIH against the local elevation (elevation centred per transect) and the regional elevation (absolute elevation centred). We included green leaf N-content (% of mass) plotted against elevation to check the design, as we expected a more consistent positive relationship between leaf N and elevation (Körner 1989, Read et al. 2014), while the expectation to foliar loss to herbivores was less straight forward (see introduction).

Results

Site characteristics

For full site characteristics, see Table S1. The ground vegetation was dominated by typical Subarctic dry heath dwarf shrubs, particularly *Empetrum hermaphroditum*, *Vaccinium myrtillus* and *Vaccinium vitis-idea*, with higher coverage of graminoids and forbs at the relatively wetter and more fertile sites and mosses and (rarely) lichens at the low fertility end (Table S1). The mean annual soil temperature (averaged from summer 2016 to summer 2017) across all sites ranged between 1.7 ± 0.06 and 3.5 ± 0.1 °C, while the mean annual growing season (averaged from 15/6 to 15/9 2017) soil temperature ranged between 6.7 ± 0.1 and 11.1 ± 0.2 °C. These figures are slightly lower but comparable to the coarse scaled (4x4 km) modelled Luftweb record for the mean growing season air temperature per transect for the period 2000-2014 (mean: 10.7 ± 0.2 °C, Table S1), so we believe the variance in mean growing season soil temperature reflects the site air temperature variance relatively well. Early growing season volumetric soil moisture content ranged from 11 ± 1.1 to 38 ± 2.5 % across sites (Table S1). All sites were characterised by relatively acid (mean pH: 4.5 ± 0.06) and nutrient poor soils. Dissolved inorganic N-content was low, and at the same level as dissolved P, while dissolved base cations (calcium, magnesium, sodium and potassium) were an order of magnitude more abundant than N and P (Table S1), suggesting no scarcity of other macronutrients than N.

Insect herbivory and elemental fluxes

The mean leaf area lost to BIH across all sites was $1.6 \pm 0.33\%$, while $10.0 \pm 1.6\%$ of the leaves sampled across all sites were subjected to some degree of insect herbivory (Table 1). The proportional leaf area lost to herbivory was positively correlated with the relative position above the valley bottom ($p < 0.001$), annual solar radiation ($p = 0.028$), and leaf N-content ($p = 0.028$), yet showed no link to temperature, absolute elevation, or leaf content of condensed tannins (Table 2).

The overall mean elemental canopy loss to herbivores was estimated to 0.25 ± 0.048 g C m⁻² yr⁻¹, 0.017 ± 0.0033 g N m⁻² yr⁻¹, and 0.0017 ± 0.00032 g P m⁻² yr⁻¹ (Table 1). The mean leaf production across sites was 47 ± 5 g dry matter m⁻² yr⁻¹, corresponding to 21 ± 2 g C m⁻² yr⁻¹, 0.6 ± 0.08 g N m⁻² yr⁻¹, and 0.09 ± 0.011 g P m⁻² yr⁻¹ (Table 1). The estimated proportion of nutrients resorbed from the birch leaves towards the end of the season was $56 \pm 2.8\%$ for N and $30 \pm 4.1\%$ for P (Table 1). The resulting proportion of the annual flux from the canopy through insect deposits make up $1.5 \pm 0.3\%$ of the total C flux (litter+herbivore input), while the proportion of N and P were slightly higher ($3.6 \pm 0.7\%$ and $2.4 \pm 0.5\%$, respectively) due to foliar nutrient resorption during senescence. The annual proportion of canopy-to-soil N and P fluxes caused by herbivory were positively correlated with herbivory level (N and P: $p < 0.001$) and resorption (N: $p = 0.002$, P: $p = 0.024$). Moreover, the proportional insect mediated flux of N was negatively correlated with leaf production (N: $p = 0.005$). There was no significant link to leaf N or P concentrations (Table S2).

Consistency between local and regional elevational trends

Our design was setup to examine the consistency between local and regional elevational trends in BIH (inset in Figure 2a). Yet, while the leaf area lost to herbivory tended to increase with local elevation along each transect (solid line, linear regression $P = 0.07$), it showed a neutral-to-negative relationship with regional elevation (dotted line, linear regression $P = 0.45$). In contrast, the green leaf N-content showed a similar increase with elevation along both the regional (linear regression $P = 0.01$) and local (linear regression $P < 0.01$)

gradients (inset in Figure 2b). Hence, as our design captured the expected trend in leaf foliar chemistry, it seems quite robust to test the consistency between local and regional elevation in other ecological variables.

Discussion

Herbivory mediated canopy-to-soil fluxes and their controls

Our results showed that BIH constitute a minor fraction ($\sim 1.6\%$) of the annual soil input of organic matter from the birch canopies, in line with our hypothesis (H_1). These rates are similar to the estimates of insect herbivory in dwarf shrub tundra (Barrio et al. 2017), but lower than ecosystems at lower latitudes (Kozlov et al. 2015, Galmán et al. 2018). Despite the relatively short recurrence interval of insect population peaks of about 10 years (Jepsen et al. 2008), major outbreaks only return to the same site every ~ 50 -100 year (Tenow and Bylund 2000). Thus, the low contributions to fluxes at low insect densities may cumulatively recycle similar or larger amounts of elements than the major outbreaks, where most of the leaf area is lost, but it is much less disruptive to the ecosystem. Further, as background densities may increase with future climate warming (Kozlov et al. 2015, Galmán et al. 2018), BIH may increase in overall importance for nutrient cycling. The variation in insect herbivory level across our sites was considerable, with leaf area loss at some sites of up to 7%. When the nutrient resorption during leaf senescence ($\sim 55\%$ N, $\sim 30\%$ P) was accounted for, the average herbivore-mediated fraction of the annual soil input was slightly higher than for C ($\sim 3.5\%$ N and $\sim 2.5\%$ P), yet still a relatively small contribution. Nonetheless, at the sites with the highest herbivory levels, this corresponded to $\sim 14\%$ and $\sim 9\%$ of annual N and P fluxes, respectively. These estimates of herbivory mediated fluxes may be in the low end, as our estimated mean N resorption efficiency of 55% was lower than what has previously been found in these forests ($\sim 70\%$, Nordell and Karlsson 1995). This suggests an even larger gap between the substrate quality of litter and insect deposits. The higher substrate quality (availability to soil decomposer microbes) of insect deposits compared to litter (Kristensen et al. 2018) may trigger increased soil N and C-turnover early in the season. Yet, these belowground responses to BIH are most likely within the ranges of what the soil biota can take up and keep within the ecosystem, and so are unlikely to cause nutrient losses, in contrast to outbreaks which can cause substantial nutrient losses from the soil (Lovett et al. 2002, Kristensen et al. 2020).

The positive relationship between herbivory and leaf N-concentration in the green leaves was in line with our expectations (H_2), suggesting that leaves of higher nutritive quality suffer greater herbivore damage, with no apparent effect of foliar condensed tannin concentration. Moreover, the strong negative relationship between leaf N content and condensed tannins (linear regression w. CT:C log-transformed, $p < 0.001$) corroborates the theory of Haukioja (2003) predicting that it is only beneficial for the plants to increase the content of defence compounds when the nutritive quality of the leaves is low. Only under such conditions will the insects eat large enough amounts of the leaves to encounter a negative effect from the tannins. We note that our measurements of leaf condensed tannin content were quite low compared to some other literature observations from similar trees and ecosystems (Paaso et al. 2017; Stark et al. 2007). This may be partly due to large variation between sampling years, genotypes, and responses to other regulators than herbivory, such as soil nutrient content and photochemical conditions (Madritch and Lindroth 2015, Rubert-Nason et al. 2015).

The significant increase in insect herbivory with relative position above the valley bottom, i.e. towards the treeline, was in line with our expectations (H_3) derived from the patterns found for outbreaks (Hagen et al. 2007), and previous indications from studies of non-outbreak conditions in subarctic Finland (Virtanen and Neuvonen 1999). Yet, this is, to our knowledge, the first time a significant effect has been shown for background herbivore densities. Nonetheless, the mechanisms remain unclear. The proposed drivers of the patterns – higher parasitism in valley bottoms during the summer and eggs being killed by extremely cold air masses creeping into valley bottoms during the winter (e.g. Virtanen and Neuvonen 1999) – are confounded by the consistent increase in leaf N content with local elevation. Yet, if foliar chemistry was the paramount driver of BIH across scales, the N concentration should show a neutral-negative trend with elevation at the regional scale. In contrast, the leaf N content also increase with elevation at the regional scale, although the relationship is weaker than at the local scale as should be expected (Read et al. 2014). Thus, abiotic drivers,

e.g. climate, are likely moderating the biotic relationships at the regional scale.

The local increase in herbivory with elevation found here contrasts with the more general decrease with elevation along individual transects across the World's woody species (Galmán et al. 2018). This suggests that the proposed responsible mechanisms in subarctic mountain birch landscapes may only apply to high-latitude systems. Thus, our study serves as a great example of how global generalisations may lead to wrong assumptions in certain ecosystems highly important for the global climate. Interestingly, we found no significant relationship between BIH and the most commonly studied climate variables, temperature and humidity, nor with a commonly used climate proxy, absolute elevation (Table 2). Instead, solar radiation was a marginally significant positive predictor of BIH, which may suggest that this is in fact a better integrator of relevant abiotic conditions, when working in mountainous landscapes. This should be particularly relevant to consider at high latitudes, where sun-angles are low, yielding a particularly marked difference in solar energy input between north- and south-facing slopes in steep-sided valleys (~50 % higher annual solar radiation on south-facing slopes in our dataset, e.g. N8 compared to N7, Figure 1). Hence, our data point to the potential value of including solar radiation as an abiotic predictor of ecological characteristics in other landscapes with complex topography.

Comparison to other ecosystem nutrient inputs

Overall, the contribution by insect herbivores at background densities to internal recycling and external inputs to soils of the key nutrients was relatively small, as we expected (H_1). The annual canopy litter inputs to soils were estimated to ~20 g C, ~0.5 g N and ~0.1 g P m⁻² on average (Table 2). This is comparable to other literature estimates in terms of biomass (e.g. Kjølvik and Kärenlampi 1975), but 1-2 orders of magnitude more than the flux of the same elements through insect herbivores at background densities (Table 1). Relevant external nutrient inputs to the system are atmospheric N deposition, which was estimated to ~0.05-0.1 g N m⁻² yr⁻¹ in the area for the period 2013-2015 (Alpfjord and Andersson 2017), biological N fixation, which has been estimated to be 0.1-0.5 g N m⁻²yr⁻¹ (Jonasson and Michelsen 1996; Rousk et al. 2016; Rousk and Michelsen 2017) and P from mineral weathering, which has been estimated to contribute ~0.01 g P m⁻²yr⁻¹ (Åkesson et al. 2008). This shows that the external inputs of N were comparable to our estimates of what was recycled through the litter, but 1-2 orders of magnitude higher than the contribution by insect herbivores at background densities. The external input of P to the soil via weathering was about an order of magnitude lower than the annual litter input, which reinforces evidence that internal P-recycling from organic matter is crucial for plant production in these high-latitude systems (Sundqvist et al. 2014). Yet, the input of P through weathering was still 1-2 orders of magnitudes higher than the contribution to the canopy-to-soil-flux through insect herbivores. It is, however, important to emphasise that only a small fraction of the nutrients transferred through litter ends up as part of the available pool of soil nutrients in boreal ecosystems (Jonsson and Wardle 2008, Metcalfe et al. 2016). So in terms of relieving nutrient limitations to plant growth, smaller labile inputs from insects may be equally or more important.

Inferences from studies along natural elevational gradients

Despite the contrasting elevational trends along individual transects in our study (increasing) and the general global trend (decreasing) found by Galmán *et al.* (2018), our results confirm that the variation in insect herbivory with elevation along individual transects cannot be explained entirely by traditional climate variables (Galmán et al. 2018). Inconsistent relationships between elevation and ecological characteristics, when comparing multiple individual gradients and regional scale variation, have been shown for a multitude of above- and belowground variables (Sundqvist et al. 2013, Read et al. 2014). While adding ecological context, e.g. field-layer vegetation (Zhao et al. 2018) or grazer presence (Bernes et al. 2015, Vowles et al. 2017), may sometimes be sufficient to explain unexpected trends, the complex geometry of mountainous landscapes poses some challenges to the simplistic, implicit assumption of universality in the relationship between elevation and abiotic variables, such as temperature (Körner 2007). Further, we often implicitly assume that the driver and response variable change at similar rates, i.e. are in a steady state, but this is for instance rarely the case in studies of plant community compositional responses to climate change along natural gradients (Damgaard 2019, Hagedorn et al. 2019). Some of the discrepancies in observed elevation

patterns likely reflect difference in variables, methods and variation in the extent to which confounding factors obscure shifts solely related to temperature change with elevation. Our study provides a useful test of the power of elevation gradients by recording the same suite of variables using the same methods across multiple gradients within the same ecosystem in a rather constrained geographical area. While the relationship with elevation was rather consistent across scales for some variables (leaf N content), we found considerable variation in elevation trends in others (leaf herbivory level). Yet, identifying useful moderator variables (e.g. solar insulation) to account for these scale-dependent differences in trends, might be a way to allow for quick integration of space-for-time substitution data from different geographical contexts into ecosystem models. This could improve understanding of important long-term responses to climate change (Dunne et al. 2004; Elmendorf et al. 2015), until sufficient understanding of the underlying mechanisms emerge. Thus, to understand the effect of elevation at a broader scale, we need both local elevational gradient data and regional moderator variables. For example, the contrasting relationship between elevation and BIH in the Subarctic, shown in our study, and the trend at lower latitudes, may be incorporated into models by using latitude as a moderator variable. This approach needs further confirmation, but we show that setting up multiple elevation gradients in the same biome within a rather constrained area yield useful data for such assessments.

Conclusion

While the biogeochemical consequences of geometrid moth outbreaks in subarctic birch forests have attracted a lot of attention, less consideration has been given to background insect herbivory and its contribution to elemental cycling in this system. We showed that the leaf area loss due to background insect herbivory ($\sim 1.6\%$) was comparable to what was previously found in dwarf shrub tundra, yet lower than ecosystems at lower latitudes, and an increase with climate warming should therefore be anticipated. The nutrient fluxes from canopy to the soil associated with current background herbivore intensities were 1-2 orders of magnitude lower than the fluxes through senesced litter and soil input from external sources. The variation in background insect herbivory rates was substantial, however, and tended to increase with elevation at the local scale, and annual solar radiation, but showed no link to overall elevation, temperature, nor humidity variation. This supports previous reviews suggesting that most commonly recorded abiotic driver variables are not always sufficient to predict variation in insect herbivory and other ecological processes in mountainous landscapes. We speculate that accounting for context dependencies by introducing moderator variables in ecosystem models, e.g. latitude or biome, may be a fast way forward to allow better integration of data from elevational gradients, until we have sufficient understanding of the discrepancies between biotic-abiotic relationships in space-for-time substitution studies at different scales.

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Data Accessibility Statement: All data will be made available at a public repository once the manuscript has been accepted. Until then, it is available upon request from the corresponding author (jeppe.aa.kristensen@gmail.com).

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Author contributions: 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.

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TABLE 1

VARIABLE	VARIABLE	UNIT	MEAN	MIN	MAX
Leaf production	LAI	m ² leaf m ⁻² ground	0.89±0.1	0.05±0.02	1.91±0.25
	SLA	m ² g ⁻¹ dw	0.019±0.0006	0.015±0.0008	0.027±0.001
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
	CT	%dw	0.52±0.13	0.004±0.002	1.9±1.2
	C:N		15±0.5	9±1	21±2
	C:P		160±7.2	95±11	248±27
	CT:C	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
Resorption	P	%dw	0.18±0.008	0.1±0.02	0.25±0.06
	C:N		38±1.8	23±4	58±9.8
Litter input	C:P		254±12	172±41	444±107
	N	%	56±2.8	23±5	81±18
Herbivory level	P	%	30±4.1	-11±4	81±26
	C	g m ⁻²	21±2.2	1.3±0.47	45±6.1
Insect deposits	N	g m ⁻²	0.6±0.08	0.03±0.012	1.6±0.31
	P	g m ⁻²	0.09±0.011	0.006±0.0023	0.24±0.032
Insect deposits	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 deposits	C	mg m ⁻²	250±48	3±3	1030±340
	N	mg m ⁻²	17±3.3	0.3±0.26	60±21
	P	mg m ⁻²	1.7±0.32	0.2±0.023	6.2±2.0
	prop. of annual C	%	1.5±0.3	0.01±0.012	6.3±3.7

VARIABLE	VARIABLE	UNIT	MEAN	MIN	MAX
	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

TABLE 2

Variables	Unit	Coeff.	CI, lo	CI, up	P
Elevation	Z-score (all)	-0.12	-0.48	0.22	0.42
Relative position (local elevation)	Z-score (per transect)	0.48	0.24	0.72	<0.001
Annual solar radiation	MWH m⁻²	3.75	-0.32	7.59	0.028
Mean growing season soil temperature	°C	0.10	-0.15	0.33	0.38
Volumetric soil water content (early GS)	%	0.02	-0.02	0.05	0.33
Green leaf C:N		-0.10	-0.21	-0.00	0.028
Green leaf CT:C _{log}		-0.05	-0.44	0.34	0.76

TABLE AND FIGURE LEGENDS

Table 1. Ecological characteristics . All variables are presented as an overall mean for all sites (MEAN), as well as the minimum (MIN) and maximum (MAX) values to show the variation across sites. Uncertainties show standard errors for all samples (MEAN, n=27), and per site (MIN, MAX, n=3). LAI: leaf area index, SLA: Specific leaf area. CT: Condensed tannins. Note that the insect deposits are in [mg m⁻²] while litter inputs are in [g m⁻²] Insect deposits are also presented in proportion to the total input with leaf litter plus herbivore deposits.

Table 2. Linear mixed effect modelling results for variables explaining variation in herbivory level (% of leaf area, sqrt transformed). Variables with significant predictive power are highlighted in bold. The coefficients (Coeff.) show the direction of change. CI: 95 % confidence intervals after 999 bootstrap simulations. Note that the elevation was transformed to Z-scores, partly to make the units more comparable to local elevation, and partly to make the variance more similar to the other variables.

Figure 1. The study site and design. Mean annual precipitation (a) and temperature (isolines in b) in the study area during the last normal period (1961-1990). The background colour scale in panel b is a digital elevation model of the area. The short black lines in panel a and b show the location and names of the 9 transects. Colours of the transect names correspond to Figure 3. The red dot on the inset in panel b shows the location of the study area in Sweden. Panel c shows a south-facing valley side in Vistasvagge, where transect N8 was located. The approximate relative positions of the three sites along this transect is shown in text. The black arrows in panel b shows the location and direction of where the picture in panel c was taken. The inset in panel c shows a typical site, with a person for scale. Data: SMHI and Lantmäteriet. Photos: Thomas Heister.

Figure 2. Elevational trend in background insect herbivory (a) and green leaf N content (b). Triangles represent gradients along south-facing slopes, while circles represent north-facing gradients. Each colour represents an individual elevational gradient (colours correspond to the transect names in Figure 1). Dashed lines show the trend lines for individual gradients. Note that these are not all significant, but are useful for showing the general trend along each gradient. Error bars show standard errors. In the insets, the dotted line show the approximated linear trend with regional scale elevation, while the solid line show the trend with local scale elevation (n=27).



