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Ecosystem Impacts of a Range Expanding Forest Defoliator at the Forest-Tundra Ecotone

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ABSTRACT

Insect outbreaks in northern-boreal forests are expected to intensify owing to climate warming, but our understanding of direct and cascading impacts of insect outbreaks on forest ecosystem functioning is deficient. The duration and severity of outbreaks by geometrid moths in northern Fennoscandian mountain birch forests have been shown to be accentuated by a recent climate-mediated range expansion, in particular of winter moth (*Operophtera brumata*). Here, we assess the effect of moth outbreak severity, quantified from satellite-based defoliation maps, on the state of understory vegetation and the abundance of key vertebrate herbivores in mountain birch forest in northern Norway. We show that the most recent moth outbreak caused a regional-scale state change to the understory vegetation, mainly due to a shift in dominance from the allelopathic and unpalatable dwarf-shrub *Empetrum nigrum* to the productive and palatable grass *Avenella flexuosa*. Both these central understory plant species responded significantly and nonlinearly to increasing outbreak severity. We further provide evidence that the effects of the outbreak on understory vegetation cascaded to cause strong but opposite impacts on the abundance of the two most common herbivore groups. Rodents increased with defoliation, largely mirroring the increase in *A. flexuosa*, whereas ungulate abundance instead showed a decreasing trend. Our analyses also suggest that the response of understory vegetation to defoliation may depend on the initial state of the forest, with poorer forest types potentially allowing stronger responses to defoliation.

Key words: insect outbreak; sub-arctic birch forest; *Operophtera brumata*; *Epirrita autumnata*; geometrids; vegetation state transitions; *Empetrum nigrum*; *Avenella flexuosa*; reindeer; Tundra vole.

INTRODUCTION

Insect pest outbreaks are, along with wildfire and pathogens, the most important disturbance agents in northern-boreal forests (McCullough and others 1998; Malmstrom and Raffa 2000; Logan and others 2003; Callaghan and others 2004). The prevalence and severity of these disturbance agents are

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subject to climatic forcing, and long-established disturbance-recovery regimes are hence likely to change, in some cases abruptly, following climate change (Chapin and others 2004). This will affect ecosystem functioning (for example, primary productivity and carbon cycling), and hence the feedbacks from forest vegetation to regional and global climate (Kurz and others 1995; Williams and Liebhold 1995; Volney and Fleming 2000; Seidl and others 2011). There are large gaps in our understanding of how insect outbreaks affect ecosystem functioning, particularly for forest defoliating insect species (Hicke and others 2012). In contrast to tree-killing species, such as bark beetles (Scolytidae), defoliating species usually do not immediately kill their host trees, but inflict damage that accumulated over several years may result in elevated tree mortality (Tenow 1972), often in interaction with other stressors.

Impacts of defoliating insects in northern-boreal forests are usually studied by recording the growth and survival of the affected host trees (for example, loss of stand volume). In comparison, the assumed limited impacts of defoliation on the understory layer have received little attention (Roberts 2004). This is surprising, because the primary productivity of the tree and understory layers are comparable in northern-boreal forests (Nilsson and Wardle 2005). Understory plants, in particular dwarf shrubs, are important for the integrity and productivity of northern forest ecosystems (Nilsson and Wardle 2005; Nordin and others 2009; Jonsson and Wardle 2010; Manninen and others 2011). Moreover, climate-mediated changes in insect outbreak dynamics may have large implications for local and regional carbon dynamics (Clark and others 2010; Heliasz and others 2011; Hicke and others 2012). This has sparked an interest in unraveling the multi-component effects of insect outbreaks for northern-boreal forest ecosystems, beyond mere tree layer productivity.

In the northern-boreal birch forests of Fennoscandia, outbreaks by defoliating geometrid moths have severe and large-scale impacts on both the tree and the understory layer (Tenow 1972; Kallio and Lehtonen 1973; Lehtonen 1987; Tenow and Bylund 2000). Several geometrid species show approximately decadal population cycles (Tenow 1972), leading to local or regional defoliation of mountain birch (*Betula pubescens* ssp. *tortuosa*). The impact of these outbreaks may cascade through other food web compartments and, occasionally, extend into neighboring tundra ecosystems (Post and others 2009). The geographical extent can be substantial; an estimated 10,000 km^2 or 1/3 of the entire birch forest belt in northern Fennoscandia was severely defoliated during the latest (2002–2008) outbreak cycle (Jepsen and others 2009a). Such mass outbreaks, with densities of several hundred larvae per branch (Hogstad 2005; Klemola and others 2008; Jepsen and others 2009a; Vindstad and others 2011), influence light conditions (as canopy is reduced) and add labile nutrients (from larval droppings and decomposing larval carcasses), and can thus be expected to influence forest floor nutrient cycling and productivity.

Recent results from a re-visitation of permanent 1 m^2 vegetation plots located in forest affected by this massive outbreak of geometrids show that the understory vegetation in oligotrophic birch forest plots shifted completely from ericaceous dwarf shrub to graminoid dominance (Karlsen and others, unpublished). The impact on the understory layer in eutrophic forest plots was minimal in comparison, and plots located outside the outbreak range showed no change whatsoever during the study. The Karlsen study did not take into account the impact of defoliation severity nor did it consider ecosystem components other than the understory vegetation. Nevertheless, the clear contrast between the forest types considered leads us to suggests that the cascading effects of moth outbreaks on the birch forest ecosystem will likely depend on the initial state of the forest.

In this article, we assess the effects of geometrid outbreak severity on the state of the understory vegetation and the abundance of key vertebrate herbivores in northern-boreal birch forest in Fennoscandia on a regional scale. During the most recent moth outbreak in north-eastern Fennoscandia, successive outbreaks of autumnal moth (*Epirrita autumnata*) and thereafter winter moth (*Operophtera brumata*) occurred in close sequence over the period 2002–2008. The areas affected by the two species were partly overlapping, yielding large variation both in outbreak duration and severity. We quantified this variation from yearly defoliation maps based on changes in summer NDVI. The outbreak progressed across a range of birch forest types (''initial states'' of forest in the following), which we expect to affect the outbreak's impact on understory vegetation and herbivores. To control for any modifying effect of initial forest state on the effect of outbreak severity, we quantified forest structure variables, which are not affected by geometrid outbreaks, as a proxy for initial forest state. The spatial design of our study was determined by the spatial characteristics of the regional outbreak. However, to account for any variation caused by the spatial distribution of our sampling sites per se, we specifically include the spatial design of the study in the analysis using an approach based on Spatial Eigenvector Mapping (SEM) (Peres-Neto and Legendre 2010). Thus, our approach exploits a regional-scale opportunity to evaluate (i) the impact of outbreak severity on the understory vegetation, (ii) the potential cascading effects on vertebrate herbivore abundance, and (iii) the contribution of spatial structure and processes not accounted for by the focal predictor variables. We predict that the severity of moth-induced defoliation is a significant contributing factor in structuring post-outbreak plant communities, most noticeably through changes in the abundance of dwarf shrubs and graminoids (Karlsen and others, unpublished), and that defoliation-induced changes in plant communities in turn impact on the abundances of vertebrate herbivores.

Materials and Methods

Study Region and Moth Outbreak History

The Varanger fiord region (70°N, 29°E, Figure 1A) in Norway lies in the transition zone between northern-boreal deciduous forest and low arctic tundra. Annual precipitation is 400–500 mm and mean temperatures during the warmest (July) and coldest (January) months are 12.5 and −11.6°C (1971–2000 normal period, Rustefjelbma meteorological station 70°23′55″N, 28°11′36″E). The most common forest type, which occurs on dry to mesic, nutrient-poor to intermediate ground, is characterized by polycormic (''multi-stemmed'') birch and a field layer dominated by the dwarf-shrubs *Empetrum nigrum*, *Vaccinium myrtillus*, and the forb *Chamaepericlymenum suecicum* (Hämet-Ahti 1963; Karlsen and others 2005; Johansen and

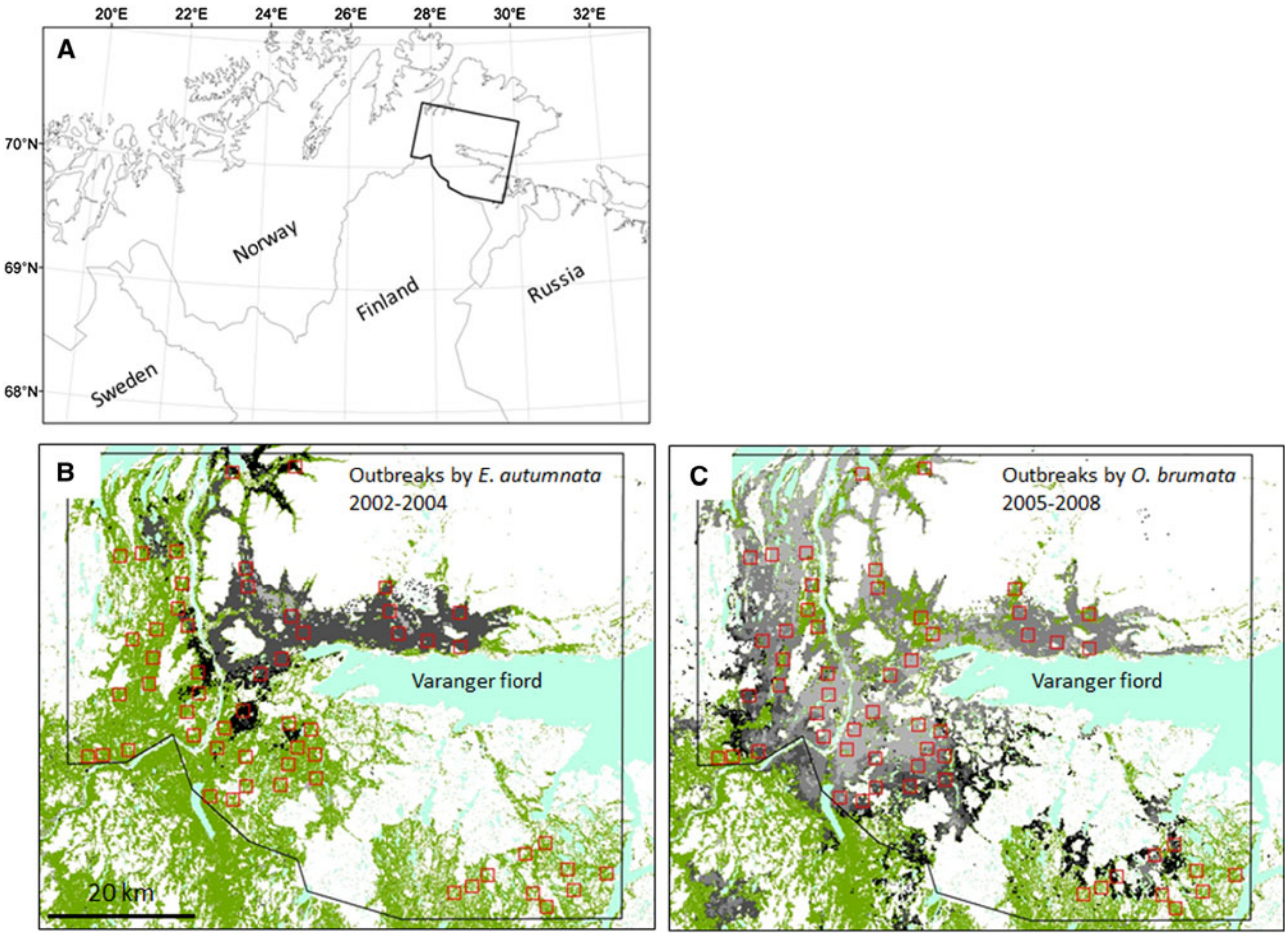

Figure 1. The location of the survey region in northernmost Norway **A** and the progress of the outbreak during the years **B** 2002–2004 (mostly autumnal moth, *E. autumnata*), and **C** 2005–2008 (mostly winter moth, *O. brumata*). *Green areas* in **B** and **C** show the distribution of birch forest. Within each outbreak sequence, the outbreak progressed from *light gray areas* (early, 2002/2005) to *black areas* (late, 2004/2008). The 40 landscape blocks sampled in this study are shown in *red*. Defoliation maps in **B** and **C** are modified from Jepsen and others (2009a) (color in online).

others 2009). Favorable and nutrient-rich locations support smaller patches of monocormic (''single-stemmed'') birch and a field layer dominated by graminoids and tall forbs such as *Geranium sylvaticum*.

Recurring population outbreaks by *E. autumnata* (autumnal moth) and *O. brumata* (winter moth) dominate the natural disturbance regime in the Fennoscandian birch forest in the absence of wild fires. Both moth species have univoltine life cycles. The overwintering eggs hatch in approximate synchrony with birch bud burst (late May–early June in Northern Fennoscandia). The larvae feed for 4–8 weeks, depending on temperature and forage quality (Ruohomäki and others 2000), after which they pupate in the soil. Both moth species exhibit cyclic population outbreaks at approximately 10-year intervals in this region (Tenow 1972; Bylund 1999; Neuvonen and others 1999), documented as far back as the 1860 s (Tenow 1972; Nilssen and others 2007). During outbreaks the forest can be defoliated and occasionally killed over vast areas (Tenow 1972; Lehtonen and Heikkinen 1995; Tenow and Bylund 2000).

The last outbreak cycle in northernmost Fennoscandia (mainly 2002–2008) reached a historically unprecedented severity; the Varanger fiord was the region most severely affected. An outbreak range expansion of winter moth (Jepsen and others 2008) may be part of the explanation. Although the Varanger fiord region historically has suffered outbreaks by the autumnal moth, the most current outbreak involved both species with a 1–2 year lag between population peaks. Consequently, most areas north and west of the Varanger fiord were first defoliated by the autumnal moth and then by the winter moth. This pattern has been documented in field records of larval densities (Klemola and others 2008) and confirmed from annual defoliation maps based on observed changes in summer MODIS NDVI values since 2000 (Jepsen and others 2009a, b). Together, these studies show that the areas north and to some extent west of the Varanger fiord had outbreaks both in 2002–2004 (primarily autumnal moth, Figure 1B) and again in 2005–2006 (primarily winter moth, Figure 1C), whereas the areas south and west of the fiord had a single outbreak during 2005–2008 (winter moth, Figure 1C). Few areas in the region were left unaffected by the outbreaks.

Field Design and Sampling of State Variables

A campaign-based, large-scale field survey was conducted in August 2010 to quantify impacts of moth outbreaks on understory vegetation and vertebrate herbivores. Assuming a link between outbreak duration and impact on vegetation, we stratified our sampling according to outbreak duration. Using annual defoliation maps (Jepsen and others 2009a), we partitioned the study region into zones subject to outbreaks for a period of 3 years or greater, 2 years, 1 year, or not at all (see definition of what constitutes ''severe'' defoliation in the ''Defoliation'' section). Within each zone, a total of 10 2 × 2 km landscape blocks containing a minimum 50% forest cover and a maximum of 10% open water were randomly selected (40 landscape blocks in total). State variables within each landscape block were recorded as follows (Figure 2): each block was overlaid by a grid with 200 × 200 m quadrates (totally 100 potential quadrates) of which 7 forest covered quadrates were randomly drawn. The center of each quadrate was the starting point of a 50 m sampling transect running due north. If a sampling transect included more than 50% large boulder fields or open mire, or was inaccessible due to steep terrain, the direction was shifted 45° clockwise (for example, NE, E, SE, and so on) until an accessible sampling transect could be established. A total of 280 sampling transects (40 × 7) were established (Figure 2).

State variables consisted of four multivariate and two univariate sets (Table 1; Figure 3) related to (i) vegetation abundance and composition in the understory layer, (ii) herbivore abundance

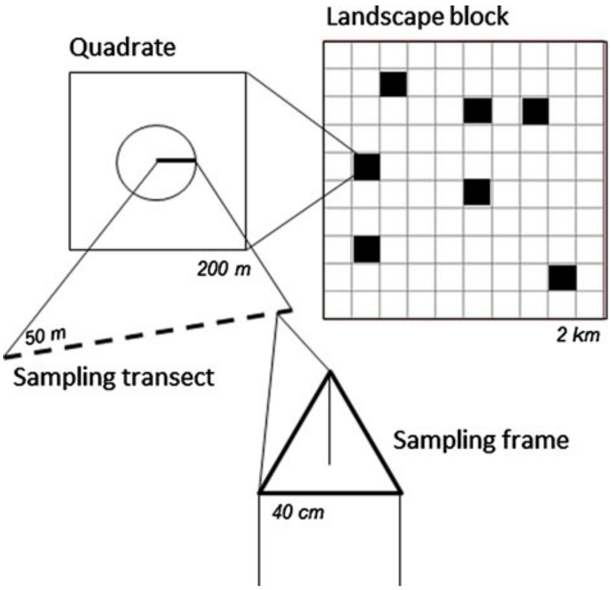

Figure 2. A schematic representation of the survey design used in the study. Modified from Killengreen and others (2007).

Table 1. A List of Response and Predictor Tables, Listing the State Variables Included in Each Table and Explanations of How the Variables were Derived

Table	Type	Variables	Explanation
Vegetation (V)	Response/ predictor	Abundance and heights of plant species/species groups	Mean abundance of individual plant species. Mean of maximum height of growth forms
Herbivores	Response	Reindeer and sheep abundance (Ungulates)	Number of sampling frames with pellets present
		Voles and lemming abundance (Rodents)	Number of sampling frames with pellets or activity signs present
Forest structure (F)	Predictor	Tree density (Treedens)[1]	Number of individual trees recorded per m^2 along transect
		Trunk density (Trunkdens)[1]	Number of trunks recorded per m^2 along transect
		Mean tree height (Height)	Mean height category of all trunks recorded along transect. Categories: 1 = 1.3–2 m; 2 = 2–4 m; 3 => 4 m
		Mean tree diameter (Diam)	Mean diameter 1.3 m above ground of all trunks recorded along transect
		Proportion canopy cover (Canopy)	Number of sampling frames that is under canopy cover
		Tree distance (Dist)	Mean distance from sampling frames to nearest tree
		Monocormic/polycormic ratio (MPratio)	Ratio between the number of trees of the monocormic and the polycormic morph
		Trunks per individual (TrunkN)	Mean number of trunks recorded per individual tree
		Height of tall woody vegetation (Htwo)[2]	Mean of the maximum height of tall woody species in sampling frames
		Lichen cover (Lichen)[2]	Mean abundance of lichens
Defoliation (D)	Predictor	Annual defoliation scores in years 2002–2010	Percentage drop in summer NDVI relative to a reference year (Jepsen and others 2009a)
Space (S)	Predictor	Spatial eigenvectors	Parallel analyses, with broad- or medium-scale spatial patterns (see Appendix C in Supplementary material)

The vegetation table was used both as a response (in the vegetation model) and as a predictor (in the herbivore model). All variables were expressed at the transect level.

[1] *Variable adjusted for actual transect distance recorded.*

[2] *Vegetation variables related to lichen abundance and the height of tall woody vegetation (see Appendix A in Supplementary material) were considered indicative of forest structure and included in the forest structure predictor table rather than the vegetation response table, see text for details).*

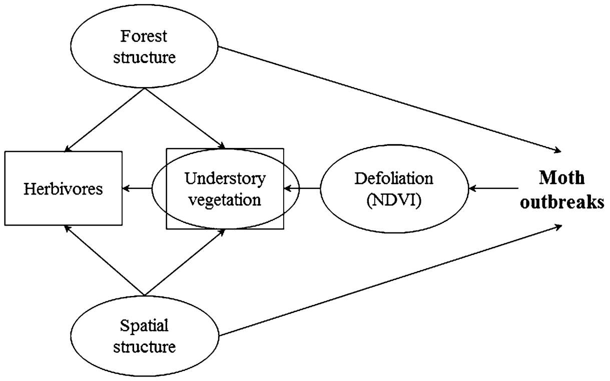

Figure 3. A conceptual diagram depicting the potential inter-relations between key response (*squares*) and predictor (*ovals*) variable sets analyzed in this study. Note that understory vegetation is a response variable and also a predictor in the herbivore models.

(2 univariate sets), (iii) forest structure, (iv) defoliation, and (v) spatial structure. State variable sets related to vegetation, herbivores and forest structure (i–iii) were field sampled variables, whereas defoliation variables (iv) were extracted from annual defoliation maps and spatial structure (v) was quantified using SEM (Dray and others 2006). In the following, we outline the details of how each set of state variables was obtained.

Vegetation Abundance and Composition

Abundance of vascular plants species, mosses, and lichens was estimated using the point intercept method following Killengreen and others (2007; Figure 2). Every 5 m along the 50 m transects, a 40-cm triangular sampling frame with 3 pins (Bråthen and Hagberg 2004) was lowered through the vegetation with one side parallel to the transect (11 frames per transect). For each plant species all intercepts between plant parts and each of the 3 pins were recorded as a measure of plant abundance. Mosses and lichens, which were not identified to species, were recorded with a maximum of one intercept per pin. A total of 29 different plant species or functional groups, representing 7 major growth forms, were recorded. In addition, we recorded the maximum height of each growth form within the sampling frame. A full list of plant species is given in Appendix A in the Supplementary material.

Herbivore Abundance

The community of herbivores in the study region is dominated by semi-domestic reindeer (*Rangifer tarandus*) and small rodents with multi-annual population cycles. The two main herding districts in the region contain altogether approximately 14,000 reindeer (Anonymous 2011), but grazing pressure varies seasonally. Domestic sheep (*Ovis aries*) are locally abundant. Abundances of reindeer, domestic sheep, moose (*Alces alces*), hare (*Lepus timidus*), small rodents (Arvicolidae), and ptarmigans (*Lagopus* spp.) were indexed for each transect by counting the number of sampling frames (out of 11 per transect) in which fecal pellets from each herbivore species were present (Ims and others 2007). For small rodents, both fecal pellets and conspicuous signs of activity (runways, grazing scars, and burrows) were recorded. Reindeer and sheep were subsequently pooled into one group representing ungulates, as their feces sometimes are difficult to distinguish. Similarly, voles and lemming (*Lemmus lemmus*) were pooled into one group representing rodents as their pellets and activity signs are difficult to distinguish. Live trapping at 5 different localities distributed across the study region indicated that the rodent community at the time of study was strongly dominated by tundra vole, *Microtus oeconomus* (83% of catches, authors' unpublished data). Hare, ptarmigan, and moose were not included in the statistical analysis due to insufficient sample sizes for these species (see Appendix B in the Supplementary material).

Forest Structure

Forest structure is an indicator of soil nutrient status and may also influence herbivore abundance either directly or indirectly through vegetation communities (Figure 3), As a proxy for the initial state of the forest, state variables related to forest structure were recorded within a 2-m-wide strip centered on the 50 m measurement ribbon. Measures were taken at the level of the individual trunks along the sampling transect and subsequently aggregated to the transect level. In a dense polycormic birch forest (that is, with multi-stemmed trees), the distinction between individual trees is often unclear. In such situations, we defined a tree as a ''functional'' individual, consisting of a cluster of trunks with no detectable root connections to neighboring groups of trunks. Only trunks larger than 1.3 m tall and present within the 2-m-wide strip centered on the sampling transect were recorded. Because trunk density was highly variable between transects (from a few to hundreds), a maximum of 50 trunks were recorded per transect. The position along the transect (in meters) where this limit of 50 trunks was reached was recorded to permit a correction of state variables related to tree and trunk density for actual transect length. In addition to these trunk level measures, abundance of lichens and the maximum height of tall woody plants recorded in the vegetation abundance survey [Table 1, (Lichen) and (Htwo)] were included in the set of forest structure indicators. This was done because (i) these variables are not expected to be influenced by moth defoliation and (ii) they can be considered to capture important aspects of the initial forest state. Note that the height of tall woody plants mainly reflects the maximum height of the smaller species in the tall woody plant category (that is, *Betula nana*, *Ledum palustris*, and *Juniperus communis*). This is because the other species in this category rarely entered the sampling frame, owing to their large size. In addition to the forest structural variables included in Table 1, we also recorded the proportion of trunks per transect that were dead (no live foliage or basal shoots) or severely damaged (live trunk, but $<1/3$ of crown foliage intact) to evaluate the relationship between defoliation and tree mortality.

Defoliation

Defoliation estimates on a regional scale are not practically obtained using field-based campaigns. Therefore, annual estimates of defoliation for each field transect were derived from defoliation maps developed from MODIS NDVI (Jepsen and others 2009a, b). Defoliation scores, expressed as the % change in summer NDVI relative to reference years without outbreaks, have shown to be accurate predictors for the prevalence of defoliation and a good proxy for local larval densities measured on the ground (Jepsen and others 2009a). The main outbreak years in the study region were 2002–2008, but because defoliation may have occurred locally also in 2009–2010, all years 2002–2010 were included in the analysis. The defoliation score for each transect in each year was extracted at the transect center point. Defoliation scores were subsequently grouped into 3 categories representing ''no defoliation'' (0–5% change), ''moderate defoliation'' (6–14% change), and ''severe defoliation'' (≥15% change).

Spatial Structure

Spatial structuring of environmental variables represents an analytical challenge: unless properly accounted for, the role of ecological and environmental drivers may be overestimated (Legendre 1993). To control for any variation that could potentially be a result of the spatial distribution of our transects, we used an approach based on SEM to obtain a set of explanatory variables, where each variable essentially represent the spatial clustering of our transects at a different spatial scale. This approach has recently been used extensively in ecological studies where spatial structure was believed to account for at least some of the variation, and it can be used to assess such effects at different spatial scales (Dray and others 2006; Griffith and Peres-Neto 2006; Peres-Neto and Legendre 2010). In our case, spatial eigenvectors were visually divided into three groups representing broad (>12.5 km), medium (3–12.5 km), and small (<3 km) scale spatial clustering patterns. Small-scale eigenvectors were excluded from further analyses, because the spatial range over which they showed correlation did not exceed the maximum spatial extent of a block of transects. Further details and references are given in Appendix C in the Supplementary material.

Partitioning of Environmental and Spatial Variation

Our dataset consisted of several distinct sets of multivariate variables, and we refer to these distinct sets as ''tables.'' One common approach for these kinds of datasets is to use variance partitioning to assess the explanatory power of the different predictor tables. This approach partitions the variation observed in one or several response variables into components which can be attributed either uniquely to each predictor table, or to combinations of predictor tables. In our case, response variables were either herbivore abundance (two separate models: either reindeer/sheep abundance or rodent abundance as univariate response variables) or vegetation community structure (one model with vegetation abundance as a multivariate response table). Candidate predictor variables in the model with vegetation as a response were forest structure, defoliation, and spatial structure. In the herbivore models, defoliation was replaced by vegetation, based on the assumption that defoliation affects herbivore abundance indirectly via defoliation-mediated changes in vegetation abundance and/or community structure (Figure 3).

If the response is a multivariate table variance partitioning is based on redundancy analysis (RDA), whereas in the case of a univariate response it is based on standard multiple linear regression. We used the varpart function in the vegan package for R (Oksanen and others 2011). Plant and herbivore abundance data were Hellinger-transformed to conform with the assumptions of normality (Legendre and Gallagher 2001). Right-skewed positive continuous variables were square root transformed (or cube-root, in the case of heavily skewed variables) to approach normality. Partition results were visualized by area-proportional Venn diagrams using the `venneuler` function in the package by the same name (Wilkinson 2012).

To address the extent to which the initial state of the forest could modify the effects of defoliation on vegetation communities, we looked for a significant interaction between the predictor variable sets forest structure and defoliation (Table 1) in a partial RDA with vegetation as the response and spatial structure as a conditional variable (for example, $V \sim D * F|S$, where V is the vegetation, D is the defoliation, F is the forest structure, and S is the spatial structure). For this, we used the permutation-based ANOVA (function anova.cca with 9999 permutations) in the vegan package (Oksanen and others 2011). A partial biplot was used to examine the scores of individual plant species in relation to the defoliation–forest structure interaction terms for each forest structure variable. This allowed us to (i) identify the subset of plant species most influenced by defoliation while taking into account the possible modifying effect of the initial state of the forest and (ii) interpret the main RDA axis in terms of the initial state of the forest.

Direct and Cascading Effects of Defoliation on Individual Plant and Herbivore Species

Based on the output from the variance partitioning models, we fitted generalized linear models (GLMs with a Poisson error distribution) to further examine the influence of defoliation on key plant species/groups and herbivore groups (ungulates and rodents). For plant species/groups, the GLMs were structured similarly to the vegetation RDA, that is, we assumed an interaction between defoliation and forest structure, and also an additive effect of the main spatial eigenvectors. Rather than running parallel models for broad and medium spatial scales, we included all eigenvectors from these two scales in the same analysis. To facilitate simple prediction of the response to defoliation, we calculated the average response for each transect across all years. To examine the effect of defoliation specifically, we calculated the predicted plant/group occurrence for the three defoliation classes (no, moderate, and severe), while holding all other explanatory variables constant at their mean values. In the herbivore GLMs, only the plant species/groups identified by the RDA as being the most important (ordination scores <-2 or >2 on either axis) were included as explanatory variables. This is based on the assumption that any response of herbivores to defoliation-induced changes in ground vegetation would be largely mediated through changes in these most important plant species/groups. We then predicted the abundance of each herbivore group from these models, using the plant/group occurrences across defoliation scores which were obtained in the prediction stage from the plant GLMs. We assessed the goodness-of-fit of GLMs by testing the significance of their deviances against a χ^2-distribution for the appropriate residual degrees of freedom. We also tested the significance of individual explanatory terms in the models by comparing each model to its respective null (that is, intercept-only) model, again assuming that deviances are approximately χ^2 distributed.

RESULTS

Defoliation History and Tree Mortality

Defoliation scores estimated from MODIS NDVI showed two clear outbreak peaks (2003 and 2006; Figure 4A) corresponding to the outbreak by the autumnal moth (2002–2004) and the winter moth (2005–>), respectively (Figure 1). A high proportion of sampling transects were affected by severe defoliation (defoliation score ≥15) during both outbreak peaks (Figure 4A). Stem mortality observed on the ground increased with increasing defoliation scores (Figure 4B) from less than 10% in the least defoliated transects to greater than 95% in the most defoliated transects (Figure 4B).

Partitioning the Effects of Defoliation, Initial Forest State, and Space

Overall, almost half of the observed variation in vegetation community structure could be attributed to the candidate sets of explanatory variables (see residuals in Figure 5 and Table 2). The initial state of the forest (forest structure) explained the largest proportion of the variation in vegetation community composition at both broad and medium spatial scales, with a total contribution of about 39% and an individual fraction of about 15–18% after controlling for defoliation and spatial structure (Figure 5; Table 2). In comparison, defoliation contributed 25% in total and about 4% uniquely. Spatial structure had a significantly greater total contribution to variation in vegetation at larger spatial scales (~ 28%) than at medium scales (~ 5%), but the unique contribution was low and similar at both scales (2.4% large scale, 3.2% medium scale).

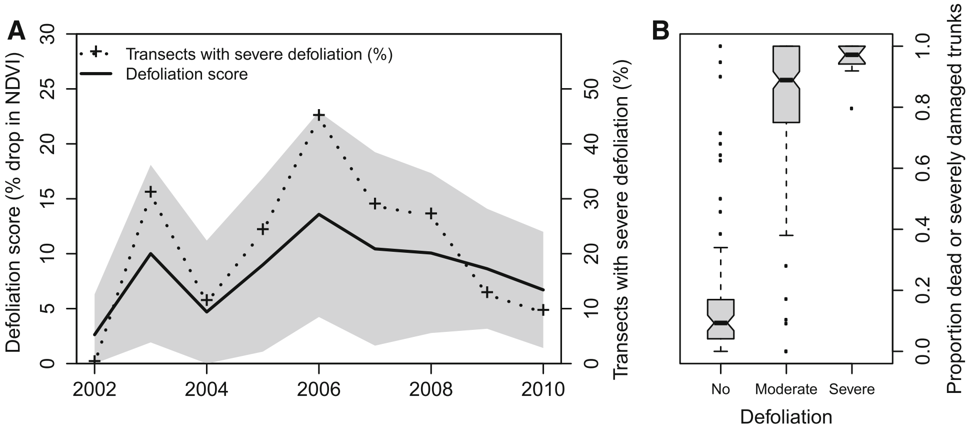

Figure 4. **A** Annual estimates (2002–2010) of the defoliation severity obtained from defoliation maps (Jepsen and others 2009a) of the 280 survey transects. *Full line* The mean defoliation score for all transects (shaded interval corresponds to 1 SD). *Hatched line* the % of transects affected by severe defoliation (corresponding to defoliation score of ≥ 15) in any given year. **B** The transect-wise relationship between the mean defoliation score over all years (grouped into 3 defoliation levels), and the proportion of trunks that were observed to be dead or severely damaged.

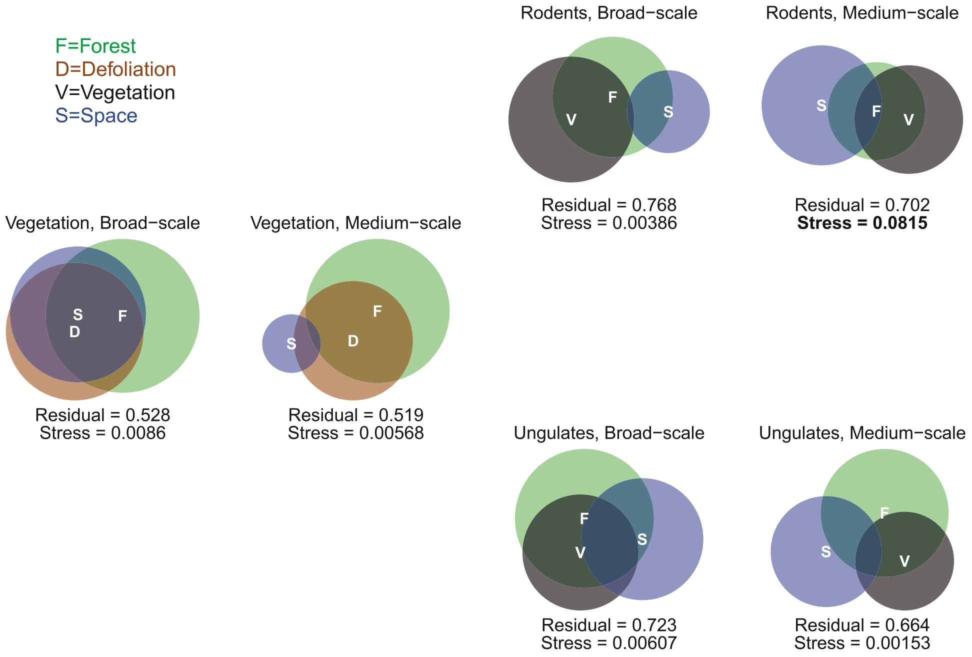

Figure 5. A graphical representation (Venn diagrams) of the contributions of the different explanatory variable sets in explaining the observed variance in vegetation community structure (*left*) and herbivore abundance (*right*; *top row* for rodents and *bottom row* for ungulates) on each spatial scale. The relative size of *circles* indicates the proportion of the variation in the response explained by forest structure (F *green*), defoliation (D *brown*), spatial structure (S *blue*), and vegetation community structure (V *gray*), respectively. Regions of overlap correspond to the variation jointly explained by two or three sets, whereas non-overlapping regions represent the variation uniquely attributed to a specific set of variables. The residual represents the proportion of the total variation that is left unexplained by the three sets of variables. The `venneuler ()` stress statistic (Wilkinson 2012) is a measure of how well the graphical representation matches the actual variation components (given in Table 2). Stress values of all diagrams except for rodents (medium scale) were below the critical 0.01 threshold ($s_{.01} = 0.056$), indicating that the graphical representation fits the data well (color in online).

Table 2. Variance Partitioning Table Showing the Various Effects and Their Contributions to Explaining the Variation in the Three Response Variables: Vegetation Community Structure, Rodent Abundance, and Ungulate Abundance

	Broad scale		Medium scale	
	Df	Adj. R^2	Df	Adj. R^2
Vegetation community structure				
Forest	10	0.394	10	0.394
Defoliation	9	0.247	9	0.247
Space	7	0.278	15	0.047
Forest + defoliation	19	0.449	19	0.449
Forest + space	17	0.434	25	0.438
Defoliation + space	16	0.326	24	0.302
All	26	0.472	34	0.481
Individual fractions				
Forest|defoliation + space	10	0.146	10	0.179
Defoliation|forest + space	9	0.038	9	0.043
Space|forest + defoliation	7	0.024	15	0.032
Residual		0.528		0.519
Rodent abundance				
Forest	10	0.100	10	0.100
Vegetation	28	0.173	28	0.173
Space	7	0.060	15	0.185
Forest + vegetation	38	0.200	38	0.200
Forest + space	17	0.162	25	0.248
Vegetation + space	35	0.204	43	0.300
All	45	0.232	53	0.298
Individual fractions				
Forest|vegetation + space	10	0.028	10	0.000
Vegetation|forest + space	28	0.070	28	0.050
Space|forest + vegetation	7	0.032	15	0.098
Residual		0.768		0.702
Ungulate abundance				
Forest	10	0.153	10	0.153
Vegetation	28	0.157	9	0.153
Space	7	0.130	15	0.136
Forest + vegetation	38	0.200	19	0.237
Forest + space	17	0.252	25	0.285
Vegetation + space	35	0.214	24	0.237
All	45	0.277	34	0.336
Individual fractions				
Forest|vegetation + space	10	0.064	10	0.099
Vegetation|forest + space	28	0.026	9	0.051
Space|forest + vegetation	7	0.077	15	0.099
Residual		0.723		0.664

Overall 25–30% of the observed variation in herbivore abundance could be attributed to the candidate sets of explanatory variables (see residuals in Figure 5 and Table 2). Initial forest state played a less dominant role in structuring herbivore abundance compared to its effect on vegetation, uniquely explaining 6.4–10% of the variation for ungulates and 0–2.8% for rodents (Table 2). In contrast, vegetation community structure accounted for approximately 17% in total and 5–7% uniquely for rodents, and around 15–16% in total and around 2.5–5% uniquely for ungulates. The unique contribution of spatial structure was similar at both spatial scales for ungulates, but differed somewhat for rodents (medium scale 9.8%, broad scale 3.2%). Because the variance partitioning analysis showed the unique contribution of spatial structure being generally similar between scales, all subsequent analyses were performed using a joint table containing all broad- and medium-scale spatial eigenvectors.

Initial forest state modified, at least to some degree, the effects of defoliation on vegetation community, as evident from a significant interaction (permutation-based ANOVA, $p = 0.005$) between forest structure and defoliation in the partial RDA of vegetation versus spatial structure ($V \sim D * F|S$). The effect of defoliation and forest structure on vegetation community is summarized in Figure 6. Both ordination axes were highly significant (permutation-based ANOVA, $p < 0.01$). The first axis represents a gradient from more open forest types characterized by greater distances between predominantly smaller trees and lichen ground cover [variables (Lichens), (Dist)], to a more closed forest type characterized by greater canopy cover and larger trees [variables (Trunkdens), (Canopy), (Height)]. The second axis can be interpreted as representing a gradient from predominantly monocormic (MPratio) to polycormic (TrunkN) forest types. Jointly, these two axes represent a fertility gradient (Figure 6, diagonal gray arrows) from more oligotrophic to more eutrophic conditions. The defoliation years with the highest ordinations scores are, as expected, the main outbreak years 2003–2006, and 2008 when an outbreak occurred south of the Varanger fiord (compare Figure 2). Four plant species/groups in particular were separated by the main ordination axes: *A. flexuosa* showed very strong and positive response to defoliation and was associated with denser, more closed canopy forest; the ericoid dwarf-shrub *E. nigrum* showed a somewhat more moderate, negative response to defoliation and appeared closely associated with the more oligotrophic, polycormic forest types; tall forbs (Forbs) and grasses other than *A. flexuosa* (Grass) both showed a weak to moderate negative response to defoliation and were associated primarily with the monocormic forest type.

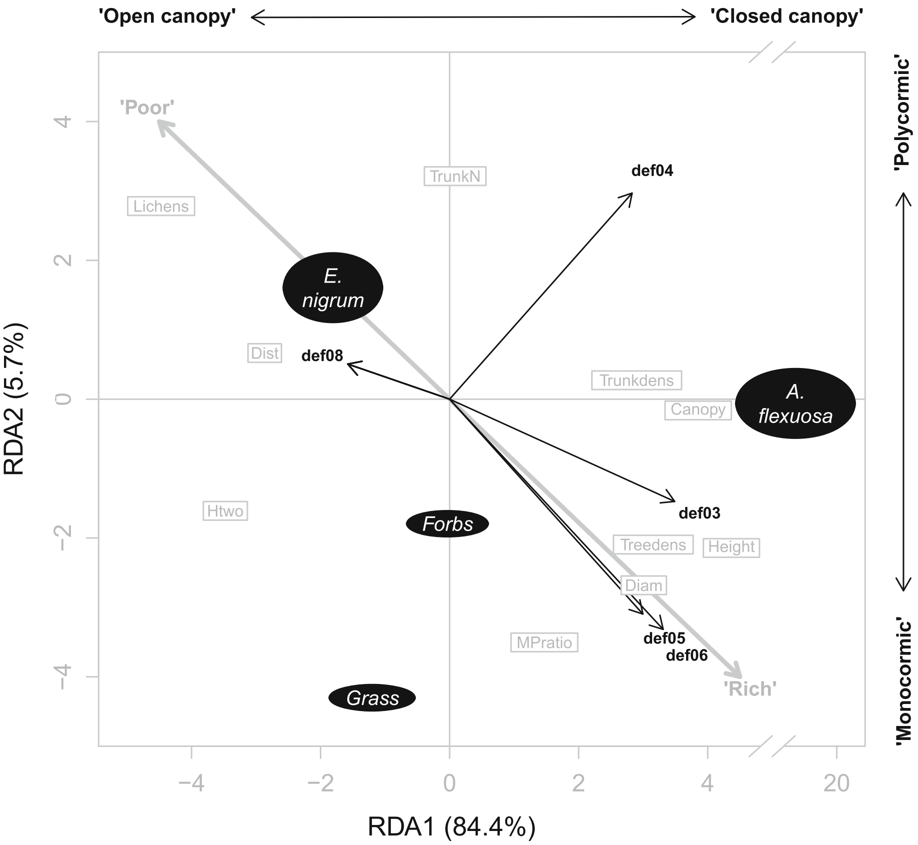

Figure 6. Partial biplot based on the RDA describing the unique effects of defoliation and forest structure variables on the vegetation community ($V \sim D * F|S$, see text for details), and the main interpretation of the axes in terms of initial forest state. Only defoliation years (''def03'' for defoliation in 2003 and so on) and plant species/species groups (*black ovals*) with ordination scores less than −2 or greater than 2 on either axis are shown. The percentage of the total variation explained that can be attributed to each axis are shown in the axis labels.

Direct and Cascading Effects of Defoliation on Individual Plant and Herbivore Species

The abundances of individual plant species/groups based on the GLMs varied significantly in response to varying degree of defoliation when all other variables were held constant (Figure 7A). The abundance of the grass *A. flexuosa* increased sevenfold from the lowest to the highest level of defoliation, with the most notable increase between moderate and severe defoliation levels. Conversely, *E. nigrum* showed a strong decrease in abundance with increasing defoliation. Grasses (other than *A. flexuosa*) increased in abundance in response to moderate defoliation, but decreased at the highest defoliation level. Forbs showed a moderate decrease in abundance with increasing defoliation. The abundances of rodents and ungulates (Figure 7B) indicate significant and opposite impacts of defoliation on the two herbivore groups. Rodent abundance more than doubled in response to defoliation-induced vegetation changes, with a response curve which mirrored that of *A. flexuosa* (Figure 7B); that is, it was influenced positively by the increases in *A. flexuosa* (z-ratio = 4.121, $p = 3.78 \times 10^{-5}$) and Grass (z-ratio = 12.57, $p < 1 \times 10^{-15}$) abundance, and the decreases in occurrence of *E. nigrum* (z-ratio = −4.02, $p = 5.9 < 10^{-5}$) and to a lesser extent Forbs (z-ratio = −2.19, $p = 0.029$). Ungulate abundances on the other hand decreased significantly in response to severe defoliation and the strongest (negative) association was with *A. flexuosa* (z-ratio = −8.25, $p < 1 \times 10^{-15}$).

DISCUSSION

Geometrid moth outbreaks in northern-boreal mountain birch forests may intensify owing to climate warming (Tenow 1996; Neuvonen and others 1999; Callaghan and others 2004). This prediction is supported by the recent northward outbreak range expansion of primarily winter moth in northernmost Fennoscandia (Jepsen and others 2008, 2009b; Post and others 2009). Outbreak severity determines whether birch trees survive defoliation and thus the extent of forest death (Tenow 1972). Although it has been shown that moth outbreaks impact understory vegetation (Tenow 1972; Kallio and Lehtonen 1973; Lehtonen and Yli-Rekola 1979; Lehtonen 1987), and that such impacts can induce gross vegetation state changes (Karlsen and others, unpublished), no

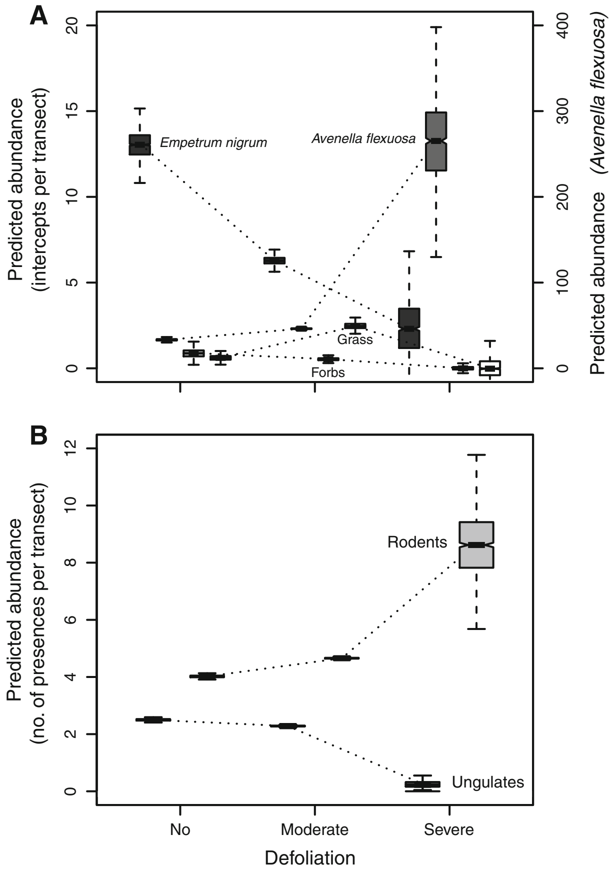

Figure 7. **A** The response to variations in defoliation score of the four plant groups that showed the greatest response in the RDA (see text for further details). *Note* Separate *y* axis for *A. flexuosa.* **B** The response of the two herbivore groups, rodents and ungulates, to defoliation-induced changes in the occurrence of the same four plant species/species groups.

previous study has estimated the extent of such changes as a function of outbreak severity. Moreover, there is virtually no previous knowledge about the potential cascading impacts of moth outbreaks on other components of the ecosystem (that is, beyond that of plants).

Ecosystem scale impacts of forest insect outbreaks are typically beyond the realm of planned experiments and observational or quasi-experimental approaches are thus needed to make inferences. In this study, we used an approach that allowed us to target outbreak severity (% drop in summer NDVI) as the key impact predictor in a regional-scale spatial study design. Based on the results from the before–after outbreak comparison of Karlsen and others (unpublished), showing that the impact of the outbreak is dependent on the initial state of the forest vegetation, we also included forest structure as a covariate matrix in the statistical analysis. Interpreting the effect of this covariate in terms of ''initial state dependence'' is, however, complicated for two reasons. First, although forest structural variables (for example, tree height and density) are certainly related to the state of the understory vegetation prior to the outbreak, the specific nature of this relation is not known (as we only assessed the relation after the outbreak). Second, the forest structure variables might have directly influenced the severity of moth outbreak and thus its impact on the understory vegetation. For this reason, some of the variation accounted for by forest structure in our analyses may have been due to the impact of the geometrid outbreak. In either case, the effect of forest structure must be interpreted with caution.

Correcting for spatial autocorrelation and initial forest structure, we found that spatio-temporal variation in outbreak severity was tightly coupled to the proportion of dead and severely damaged trees and had pervasive effects on the understory vegetation and on the cascading impacts of the outbreak on the most abundant vertebrate herbivores in the focal ecosystem. The response of the understory vegetation to increasing outbreak severity was dominated by a dramatic increase in the grass *A. flexuosa* and a similar decrease in the ericoid dwarf-shrub *E. nigrum*. These effects are consistent with findings of Karlsen and others (unpublished) in oligotrophic forest. Here, we have shown that the response of both of these species (but most so for *A. flexuosa*) was nonlinear, in the sense that the effect became much stronger for outbreak severities exceeding ''moderate defoliation.'' *A. flexuosa* and *E. nigrum* are both considered key-stone species in the northern-boreal forest ecosystem. *E. nigrum* is allelopathic and its frequent dominance in late-successional stages of heath and nutrient-poor forest vegetation (Haapaasari 1988; Tybirk and others 2000; Bråthen and others 2010) is associated with retrogressive succession due to accumulation of polyphenolic compounds in the soil. This species is hence an important agent in controlling the productivity of the understory vegetation (Nilsson and Wardle 2005). *E. nigrum* is unpalatable to most herbivores and is not defoliated directly during moth outbreaks. One possible cause of mortality is excess supply of nitrogen. Another possibility is that starving larvae punctuate the leaves, making the plants more susceptible to desiccation or infection by fungal pathogens (Olofsson and others 2011). In contrast to *E. nigrum*, the grass *A. flexuosa* has a high growth potential and presumably responded positively to the moth outbreak owing to *N* enrichment (Manninen and others 2011; Strengbom and Nordin 2012) from larval excreta and increased penetration of light to the understory following the defoliation of the trees and tall shrubs. Light availability has been found to be the main limiting factor for *A. flexuosa* growth in northern-boreal spruce forests (Strengbom and others 2004). Release from the allelopathic effects of *E. nigrum*, which again could be mediated by *N* enrichment (Bråthen and others 2010) may also have contributed to the highly positive response of *A. flexuosa*.

In contrast to the unpalatable *E. nigrum, A. flexuosa* is known to be a preferred food plant for many grazing vertebrate herbivores, in particular for lemmings (Krebs 2011), but also *Microtus* voles (Ericson 1977; Hansson and Larsson 1978; Hansson 1979). Thus, the cascading impact of defoliation on the indexed abundance of small rodents, with a nonlinearly increasing response curve that closely mirrored that of *A. flexuosa* (Figure 7), was according to expectation. More surprising was the negative response of ungulates (that is, mainly reindeer) to the level of defoliation. The reindeer is a mixed feeder (Hofmann 1989) that although known to forage on grasses (Skogland 1984), also show preference for lichens, forbs, and foliage of deciduous woody vegetation in the tall shrub and tree layer (Skjenneberg and Slagsvold 1968). Thus, we suggest that components of the vegetation which were negatively impacted by the outbreak combined may have constituted more important forage for reindeer than *A. flexuosa*. Possible candidates are small trees and tall shrubs that became defoliated in the most impacted areas, and thereby lost their value as browse for reindeer. This effect combined with the reduction of highly preferred forbs (Skogland 1984) may have reduced the overall pasture quality for the reindeer rendering this highly mobile herbivore to select the least impacted forest areas in the region. In particular, the open lichen-rich forest types mainly distributed south of the Varanger fiord appeared to be the least and last defoliated (Figure 7). These forests constitute the main winter pastures for reindeer in the region. Note, however, that the influential effect of initial forest structure (which included the abundance of lichens) was statistically corrected for when estimating the *A. flexuosa* (outbreak intensity) versus reindeer relation (Figure 7). This implies that the geometrid outbreak indeed had a negative cascading impact on reindeer that was partly independent of initial forest structure. Besides the opposite response of reindeer and small rodents, likely due to different forage plant preferences, it is also important to be aware that the response of the two groups of herbivores may also be contingent on their different mobility and demography. Although the response of the relatively little mobile, but r-selected rodents are likely to have resulted from changed population dynamics (that is, a higher amplitude of a population peak; compare Ims and others 2011), the observed response of the mobile, but more K-selected reindeer is more likely to be due to differential range use and habitat selection (Mårell and others 2002). However, even for the reindeer the vast spatial scale of the geometrid outbreak in the Varanger region is also likely to have affected the overall carrying capacity of the pastures in the region and thus the long-term demographic development of the herd.

CONCLUSION

We have demonstrated that the recent geometrid moth outbreak in the birch forest of northern-most Fennoscandia, which included a range expansion of the winter moth, has caused a regional-scale state change of the understory vegetation. This state change was mainly due to a shifted dominance relation between two key-stone plant species of the understory; that is, from the allelopathic and unpalatable dwarf-shrub *E. nigrum* to the productive and palatable grass *A. flexuosa*. By means of satellite image-derived defoliation maps, we quantified the spatio-temporal variation in outbreak severity across the outbreak region/period and showed that this variation predicted the extent of the understory state shift. Our results indicate that the recently observed moth outbreak patterns, presumably induced by climate change, impact the understory much more severely than the more moderate outbreaks of the past. As the state shift of the understory vegetation involved plants with important ecosystem functions, the intensified moth outbreaks are likely to have several cascading impacts through the food web. Here, we have provided evidence that the effects on understory vegetation cascaded to strongly impact the abundance of rodents and ungulates, although with different signs. Future studies ought to unravel the consequences of moth outbreaks for other trophic levels and compartments of the northern-boreal birch forest ecosystem.

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