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Can novel pest outbreaks drive ecosystem transitions in northern-boreal birch forest?

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Abstract

1. The boreal biome exhibits distinct alternative ecosystem states with high and low levels of tree cover. Insect outbreaks facilitated by climate warming could potentially drive transitions from high to low tree cover states. We investigated whether two key premises for such outbreak-induced transitions – critical thresholds (tipping points) and positive feedbacks that could maintain alternative states – are present in the northern-boreal mountain birch forest of Fennoscandia. Here, climate warming has promoted range expansions of defoliating geometrid moths, resulting in novel, severe multispecies outbreaks, most recently during 2002-2010.
2. We conducted regional-scale field surveys of forest damage and recovery in 280 mountain birch stands in a northeast Norway immediately after the outbreak (2010) and six years later (2016). Satellite-derived time series of the normalized difference vegetation index (NDVI) provided an index of stand defoliation during the outbreak period.
3. The proportion of dead stems per stand displayed a bimodal distribution, with stands generally being either lightly or severely damaged. This was due to a critical threshold in the relationship between defoliation and stem mortality, with mortality rates increasing abruptly in stands experiencing a mean drop in NDVI of more than 4 % during the outbreak. The two key forest regenerative pathways – basal sprouting and sapling production – both displayed positive feedbacks with surviving stems and trees, so that regeneration success declined with increasing damage to the mature tree

layer. These feedbacks imply that stands which have been forced across critical defoliation thresholds and suffered collapses of living tree cover may struggle to recover, especially if the loss of positive regenerative feedbacks is compounded by ungulate browsing on birch recruits.

4. Synthesis. The north Fennoscandian mountain birch forest displays critical thresholds and positive feedbacks that conform to theoretical expectations for a system that could be vulnerable to abrupt and persistent changes of state in the face of novel, climatically facilitated insect outbreaks. These findings deepen the understanding of the persistent losses of tree cover that have occasionally been observed after outbreaks in this system in the past, and add to the list of mechanisms that could help explain the bistability of tree cover across the boreal biome.

Key words: Critical threshold, *Epirrita autumnata*, facilitation, forest regeneration, Global change ecology, *Operophtera brumata*, positive feedback, range expansion

Native language abstract (Norwegian)

1. I det boreale biomet finner vi distinkte alternative økosystemtilstander kjennetegnet av høye og lave nivåer av tredekke. Insektutbrudd som har blitt intensivert av et varmere klima kan potensielt drive transisjoner fra tilstander med høyt til lavt tredekke. Vi undersøkte om to grunnpremisser for slike utbruddsinduserte transisjoner – kritiske terskler (vippepunkter) og positive tilbakekoblinger som kan opprettholde alternative tilstander – er til stede i den nord-boreale fjellbjørkeskogen i Fennoskandia. I dette systemet har et varmere klima tillatt sørlige bjørkemålerarter å

utvide utbredelsesområdet sitt nordover og østover. Dette har resultert i en ny og alvorlig type utbrudd hvor flere målerarter opptrer sammen, senest i 2002-2010.

2. Vi gjennomførte takseringer av skogskade og gjenvekst på regional skala i 280 overvåkningstransekter i fjellbjørkeskog i nordøst-Norge rett etter det seneste utbruddet (2010) og seks år etter (2016). Satellittbaserte tidsserier av vegetasjonsindeksen NDVI (Normalized Difference Vegetation Index) ble brukt for å gi et mål på nedbeiting forårsaket av målere gjennom utbruddsperioden.
3. Andelen døde stammer per transekt viste en bimodal fordeling, hvor de fleste transektene enten hadde lav eller svært høy stammedødelighet. Dette skyldtes en kritisk terskel i sammenhengen mellom nedbeiting og dødelighet, hvor transekter som hadde et gjennomsnittlig fall i NDVI på mer enn 4 % gjennom utbruddsperioden opplevde en brå økning i stammedødelighet. De to viktigste mekanismene for gjenvekst – rotskudd og frøplanter – ble begge positivt påvirket av tilstedeværelse av overlevende trær og stammer, slik at effektiviteten på gjenveksten avtok med økende skade på det voksne tresjiktet. Disse positive tilbakekoblingene innebærer at skog som har blitt presset over en kritisk terskel og opplevd massedød av trær kan komme til å slite med gjenveksten, særlig dersom gjenveksten hemmes ytterligere av at klovdyr beiter på skudd og frøplanter.
4. Syntese. Den nord-Fennoskandiske fjellbjørkeskogen viser kritiske terskler og positive tilbakekoblinger som er i tråd med teoretiske forventninger til et system som kan være sårbart for brå og varige tilstandsendringer i møte med intensiverte insektutbrudd drevet av klimaendringer. Disse funnene bidrar til en bedre forståelse av de varige tapene av tredekke som noen ganger har vært observert etter tidligere målerutbrudd i fjellbjørkeskog, og gir et viktig tilskudd til listen over mekanismer som kan bidra til å forklare bistabiliteten i tredekke i det boreale biomet.

Introduction

Massive outbreaks of pest insects are among the most significant disturbances attributed to climate change in boreal forests. Since the early 2000s, outbreaks of bark beetles and budworms have damaged millions of hectares of coniferous forest in North America (Weed, Ayres & Hicke 2013; Pureswaran *et al.* 2015; Pureswaran, Roques & Battisti 2018), while geometrid moths have defoliated one third of the deciduous forest in northern Fennoscandia (Jepsen *et al.* 2009b). The common denominator for these cases is that climate warming has favorably affected critical stages in the insect lifecycle, thereby facilitating outbreaks of unprecedented scale and severity (Jepsen *et al.* 2008; Jepsen *et al.* 2011; Weed, Ayres & Hicke 2013; Pureswaran *et al.* 2015).

It has been theorized that novel climate-driven insect outbreaks will increasingly exceed the resilience of boreal forests, thereby causing these systems to undergo transitions to alternative ecosystem states with greatly reduced tree cover (Chapin *et al.* 2004; Weed, Ayres & Hicke 2013; Pureswaran *et al.* 2015; Buotte *et al.* 2016). Indeed, sparse woodlands or treeless areas appear to co-exist as persistent alternative states along with densely tree covered forest across the boreal biome, and insect outbreaks have been suggested as one mechanism that may induce transitions between these states (Scheffer *et al.* 2012). At present, however, empirical evidence for such outbreak-induced transitions is scant.

General theory postulates that systems which are prone to state transitions will exhibit two key dynamical properties, namely critical thresholds (tipping points) and positive feedbacks (Scheffer *et al.* 2001; Folke *et al.* 2004; Scheffer 2009; Scheffer *et al.* 2015). Threshold behavior implies that ecosystem state is initially largely unresponsive to forcing, but starts to exhibit rapid change once a critical threshold in forcing has been exceeded. This can cause a

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system to undergo abrupt and unexpected changes of state. Threshold behavior has received relatively little attention in forest systems, including boreal forests (Reyer *et al.* 2015). However, the apparent bistability of tree cover in the boreal biome hints at underlying tipping points, and calls for empirical tests of threshold behavior in response to key forcing factors, like insect outbreaks (Scheffer *et al.* 2012).

Positive feedbacks are mechanisms that cause different ecosystem states to be self-facilitating, thereby allowing alternative states to be stable under the same set of environmental conditions (Kéfi *et al.* 2016; Muthukrishnan *et al.* 2016). This can allow a new state to persist indefinitely once a transition has occurred. There is evidence for such feedbacks in a number of terrestrial and aquatic systems (Suding & Hobbs 2009), but the feedbacks that stabilize alternative tree cover states in the boreal biome are poorly understood. However, recent syntheses have highlighted that post-disturbance regenerative processes often play a key part in state transitions in vegetation communities (Martínez-Vilalta & Lloret 2016; Seidl *et al.* 2016). Moreover, there is increasing evidence that recruitment processes in forests are shaped by facilitative interactions, where tree recruits benefit from the presence of mature conspecifics (Dickie *et al.* 2005; Eränen & Kozlov 2008; Teste & Simard 2008; Booth & Hoeksema 2010; Karst *et al.* 2015). This is a potential source of positive feedbacks, since the maintenance of facilitative interactions may act to stabilize a densely forested state, while loss of facilitation may impede recovery after severe stand-killing disturbances.

The goal of the current study is to evaluate if the two described premises for state transitions – thresholds and positive feedbacks – are present in a system that has recently suffered severely under climatically facilitated insect outbreaks, namely the northern-boreal mountain

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birch (*Betula pubescens* var. *pumila* L.) forest (MBF) of Fennoscandia. In this system, milder winters and springs have allowed southern species of geometrid moths (Lepidoptera: Geometridae) to expand their outbreak ranges northwards and eastwards into areas formerly occupied only by the native autumnal moth (*Epirrita autumnata* Bkh.), resulting in novel and highly severe multispecies outbreaks in many areas (Jepsen *et al.* 2008; Jepsen *et al.* 2011). During the first decade of this century, moths defoliated one million hectares of MBF (Jepsen *et al.* 2009a). These outbreaks caused widespread mass-mortality of birch (Jepsen *et al.* 2009b; Jepsen *et al.* 2013), and arguably represent the largest terrestrial biotic disturbance attributable to climate change on the European continent.

Cyclic outbreaks by the autumnal moth have historically dominated the natural disturbance regime of the MBF (Tenow 1972), and several authors have suggested that outbreaks could trigger transitions between forested and non-forested ecosystems states (Chapin *et al.* 2004; Scheffer *et al.* 2012). In support of this idea, stands that have been killed by outbreaks have sometimes been observed to fail to recover. The most notable example stems from the Utsjoki municipality in northern Finland, where an autumnal moth outbreak during the 1960s caused extensive mortality of MBF over an area of more than one hundred thousand hectares (Kallio & Lehtonen 1973). Forest recovery after this outbreak has been poor, and much of the area has now devolved to treeless secondary tundra (Neuvonen & Viiri 2017). Such regenerative failures have usually been attributed to browsing by semi-domestic reindeer (*Rangifer tarandus* L.) (Käyhkö & Horstkotte 2017), which are abundant in northern Fennoscandia, and have negative impacts on the growth and survival of birch sprouts and saplings (den Herder & Niemela 2003; Kumpula, Stark & Holand 2011; Biuw *et al.* 2014). This explanation has been widely accepted, and the possibility that regenerative failures could also reflect the loss of endogenous positive feedbacks, like facilitation, has received

little attention. However, with ongoing geometrid range expansions now leading to the emergence of novel, multispecies outbreaks in many areas, there is need to deepen the understanding of the mechanisms that could drive outbreak-induced ecosystem transitions in the MBF.

Our study is based on a combination of satellite data and spatially extensive ground survey data from an area of about four hundred thousand hectares at 70°N in northeast Norway (Fig. 1). The MBF of the region was heavily damaged by an outbreak involving the autumnal moth during 2002-2004 and the recently established, range-expanding winter moth (*Operophtera brumata* L.) during 2005-2010 (Jepsen *et al.* 2009b; Jepsen *et al.* 2013). The gradual spread of the winter moth during the outbreak (Jepsen *et al.* 2013) contributed to spatial variability in the cumulative defoliation intensity across the study region. This facilitated tests of whether the premises for outbreak-induced state transitions are present in the MBF system. First, by relating the spatial data on stand-level birch mortality rates (2010) to moth-induced defoliation, we test the premise of threshold behavior in the relationship between defoliation (i.e. forcing) and ecosystem state in the form of living tree cover. Second, to test the premise of positive feedbacks, we quantify the success of forest regeneration almost a decade after the outbreak (2016), and investigate if regenerative pathways exhibit facilitative interactions with living trees/stems.

Materials and methods

Study system

The study was conducted in the Varanger region (70°N, 29°E), which is located in the eastern part of Finnmark County in northeast Norway (Fig. 1). Mean temperatures for January and July are -11.6°C and 12.5°C (1971–2000 normal period for Rustefjelbma meteorological

station 70°23'55'' N, 28°11'36'' E), while annual precipitation is 400-500 mm. The region represents the northern distributional limit of boreal deciduous forest in Europe, and forms a transition zone between the boreal forest biome and the low-arctic tundra. The forests of the region are composed almost exclusively of mountain birch, with rowan (*Sorbus aucuparia* L.) and aspen (*Populus tremula* L.) occurring only sporadically. Aspen is largely unaffected during moth outbreaks (Van Bogaert *et al.* 2009), while rowan can be heavily defoliated (Personal observation by the authors).

The mountain birch may be regarded as a disturbance-adapted species, and can replace lost stems by producing basal sprouts from the root system (Tenow *et al.* 2005). This often results in polycormic (multi-stemmed) trees, which are the dominant growth form in the study region, especially on poor and dry soils (Verwijst 1988). Monocormic (single-stemmed) trees are less common, and mainly occur on favorable soils. In addition to clonal regeneration by sprouting, new birch trees (saplings) can be produced from seeds. Sapling production in the MBF appears to be pulsed on a regional scale, associated with mast seeding and large-scale environmental events (Aune, Hofgaard & Söderström 2011).

Autumnal moth outbreaks occurring at roughly decadal intervals have historically been the principal disturbance factor in the birch forests of the Varanger region (Tenow 1972). This situation changed during the first decade of the 2000s, when the winter moth expanded its outbreak range into the region (Klemola, Andersson & Ruohomaki 2008; Jepsen *et al.* 2013). The range expansion precipitated a massive outbreak involving both moth species, with the autumnal moth outbreaking to the north and west of the Varanger fjord during 2002-2004 and the winter moth outbreaking in the same area during 2005-2006. This was followed by outbreaks of the winter moth to the south and west of the fjord during 2006-2010, with the

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outbreak spreading gradually in a southeast direction during this period [see Jepsen *et al.* (2009b, 2013) for a detailed description of the spatiotemporal development of the outbreak]. The prolonged multiannual defoliation inflicted by the outbreaks caused historically unprecedented damage to mountain birch stands throughout much of the region, and only a few areas were left relatively unaffected.

Study design and sampling

Our survey of forest damage and recovery after the outbreak was based on a system of 40 landscape blocks of 2 × 2 km (Fig. 1). To place the blocks, a large random point sample with a minimum point distance of 2 km was distributed across the entire region to represent the center of potential landscape blocks. A 2 × 2 km quadratic polygon was placed around each point, and the proportion of area covered by forest and open water calculated for each polygon. Polygons containing human infrastructure (settlements, larger roads), <50% forest or >10% open water were excluded. Based on rasterized satellite (MODIS) maps (Jepsen *et al.* 2009a) showing the number of years that each forest pixel had been subject to severe defoliation, the median duration of the outbreak was calculated for each remaining block. Severe defoliation in a given year was defined as a $\geq 15\%$ drop in summer (Day 177 – 225, i.e. late June – mid August) NDVI, relative to reference years without outbreaks. The blocks were grouped into 4 categories based on outbreak duration; no severe defoliation or severe defoliation in 1, 2 or 3+ years. To reduce the sample and ensure equal sample size of all categories, the blocks were sorted based on a random identifier and the 10 blocks at the top of the list were selected within each category. A minimum convex polygon around the 40 selected blocks covers an area of four hundred thousand hectares, of which 44 % is covered by forest.

To facilitate sampling of forest stands within the landscape blocks, each block was divided into 100 quadrates of 200×200 m (Fig. 1). Seven forest-covered quadrates within each block were randomly selected for sampling. Within each quadrate, we laid out a 50 m transect, starting from the center of the quadrate and running due north. If a transect was inaccessible due to steep terrain, or included more than 50 % open mire or boulder fields, the direction of the transect line was progressively shifted 45° clockwise, until a suitable transect was found. The same quadrates were used for sampling in 2010 and 2016, and care was taken to ensure that the transect line was positioned similarly in both years, so that results would be comparable at the transect level. We consider the sample from each transect to represent an individual mountain birch stand, and hereafter refer to transects as “stands”.

State variables describing the damage and recovery status of the tree layer were sampled following the same protocol in August of 2010 and 2016. Sampling was conducted in 2-m wide corridors, centered on the 50-m transect lines (i.e. corridor area= 100m^2). Within a corridor, we conducted separate measurements for each individual birch stem taller than 1.3 m (here defined as the lower height limit of the tree layer). Stems were classified as dead (foliage absent) or living (foliage present), and scored as being less or more than 2 m tall. Stems in the range of 1.3-2m tall could be regarded as recruits into the tree layer, as new sprouts can grow into this height range within a few years (Vindstad *et al.* 2017). For practical reasons, we measured a maximum of 50 stems per transect, and recorded the position on the transect where this limit was reached to correct stem counts for transect length in the analysis. We also recorded which stems belonged to the same tree. The distinction between trees can be unclear in dense stands of polycormic mountain birch, and we therefore defined a tree as a cluster of trunks with no detectable root connection to neighboring clusters. This definition identifies a tree as a ‘functional’ individual, which is not necessarily

equivalent to a genetic individual. When a tree had been identified, we recorded whether living basal sprouts (stems <1.3 m) were present or absent. Finally, we recorded the number of birch saplings within the sampling corridor. A sapling was defined as a living birch that was less than 1.3 m tall and not associated with an existing established root system.

Statistical analysis

The first step of the analysis was to test for the presence critical thresholds (tipping points) in the relationship between outbreak-induced defoliation and ecosystem state in the form of living tree cover. Our proxy for dead tree cover was the proportion of dead birch stems per stand shortly after the outbreak in 2010 (hereafter referred to as “stem mortality rate”). The mortality rates were arcsine square root transformed to normalize their distribution prior to analysis. We expected that a critical threshold in the defoliation-mortality relationship would manifest itself as a bimodal distribution of stem mortality rates, with the majority of stands showing either light or heavy mortality. To test this prediction, we constructed a histogram of the distribution of mortality rates and applied Hartigan's dip test to formally test for the presence of more than one mode in this distribution. Subsequently, we applied optimal K-means clustering to identify the number of groups (i.e. modes) in the mortality data. The clustering was implemented with the `ckmeans.1d.dp` function in the similarly named library in R.

To determine the shape of the relationship between defoliation and mortality rate, we applied discontinuous regression, as implemented in the `rddtools` library in R. This technique accommodates breakpoints, where the relationship between a predictor and a response becomes discontinuous. Such discontinuity may be expected if the predictor induces an abrupt change in the response when a critical threshold is crossed (Andersen *et al.* 2008). The

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defoliation predictor was defined as the mean drop in summer NDVI from MODIS-based defoliation maps across 2001-2010, thereby producing a measure of cumulative defoliation intensity across the entire duration of the outbreak. To identify the best supported breakpoint in the defoliation-mortality relationship, we fitted models for breakpoints at NDVI drops ranging from 0 to 10 % (where 0 is equivalent to a standard continuous regression). The relationships on either side of the breakpoints were tested as linear, second-order or third-order polynomials, to accommodate additional non-linearity apart from the breakpoints. Model selection was performed based on adjusted R^2 and the small-sample Akaike Information Criterion (AICc.)

The second step of the analysis was to quantify short-term forest regeneration after the outbreak. To do this, we estimated the change in selected regenerative parameters between 2010 and 2016. The estimation was conditioned on the level of damage sustained by the tree layer, as represented by the clusters identified by the K-means clustering of stem mortality rates (see above). Thus, the predictor variables for this analysis were year (2010 or 2016), damage cluster and their interaction. The response variables were the total number of living stems, the number of living stems <2 m tall (which could have emerged from sprouts between 2010 and 2016) and the number of saplings, all per stand. These variables were taken as count responses in generalized mixed effects models, using a negative binomial error distribution to account for the highly aggregated distributions of the counts. Random intercepts were modelled for the 40 landscape blocks. The response ratio comparing 2016 to 2010, within forest damage clusters, was used as a measure of temporal change. For the tree- and stem counts, the log-transformed length of the sampling transect was included as an offset variable, to account for stands where the maximum count of 50 stems was reached before 50 m/100m² had been covered.

The final step of the analysis was to test if regenerative pathways exhibit positive feedbacks with the surviving mature tree layer. For basal sprouting, we modelled the probability of sprouting in individual trees as a function of tree vitality. The presence of sprouts was taken as a binomial (presence/absence) response variable in a logistic mixed effects model, taking landscape blocks and transects nested within blocks as random intercepts. Tree vitality was defined as the proportion of surviving stems in a tree. For polycormic trees, vitality was taken as a four-level categorical predictor with the following levels: No living stems (D), $<1/3$ living stems (L1), $1/3-2/3$ living stems (L2) and $>2/3$ living stems (L3). For monocormic trees, the predictor distinguished between trees with a living and dead main stem. The vitality predictor was allowed to interact with year (2010 or 2016) to account for temporal developments in the probability of sprouting. In addition, to estimate the proportion of trees that had lost all of their stems and were failing to regenerate (i.e. trees permanently removed from the population), we fitted a mixed effects logistic model taking the proportion of dead and nonsprouting trees per stand as the response variable and year (2010 or 2016), forest damage cluster and their interaction as categorical predictors. Random intercepts were modelled for the 40 landscape blocks.

For saplings, the assessment of positive feedbacks was based on the empirically founded assumption that mountain birch saplings are facilitated by mature conspecifics (Eränen & Kozlov 2008). Thus, we hypothesized that the establishment success of saplings after outbreaks is improved in areas that retain a sufficient density of surviving trees. To test this hypothesis, we derived the density of living trees (trees/100 m²) in our stands and subsequently took this variable as a continuous predictor of sapling count in 2016 in a mixed effects negative binomial model, employing random intercepts for landscape blocks. We suspected that sapling count would decline at both high and low tree densities, owing to

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competition and lack of facilitation, respectively. Tree density was therefore taken as a second-order polynomial term, to allow for a parabolic relationship between saplings and trees. We defined a living tree as an individual with at least one living main stem and/or living basal sprouts. The definition thereby captured all trees with living root systems, since trees with living basal sprouts will have living roots even if all main stems are lost. We were interested in surviving root systems because facilitation could occur via both above- and belowground pathways (see discussion). Importantly, an effect of surviving trees on sapling density could simply reflect the initial (pre-outbreak) structure of the forest, with more saplings being produced in initially denser stands with better growing conditions or a larger seedbank. To control for this, an estimate of initial tree density was also included as a polynomial predictor in the model. Initial tree density was taken as the sum of living and dead trees observed shortly after the outbreak in 2010. Initial tree density and living tree density in 2016 were only weakly correlated ($r=0.31$), meaning that they could be included in the same model without major collinearity issues. Two outlying observations, with living and total tree densities twice as high as any other stands had to be excluded from this analysis to achieve adequate model fit. Thus, the results may not generalize to extremely dense stands. This is of little concern for the present study, since rare stands of this type (2 out of 280 stands in our dataset) will have little influence on the regional-scale patterns that our study concerns. Note that sapling counts in 2010 were too low to be meaningfully modelled as a function of tree density.

All statistical analyzes were conducted in R version 3.4.0 (R Development Core Team 2017), using the `glmer` and `glmer.nb` functions in version 1.1-14 of the `lme4` library (Bates *et al.* 2015) for mixed effects models. Parameter estimates for the fixed effects in the

mixed models are provided in the tables S3-S6 in the supplementary information. A summary of sample sizes for all statistical models is provided in table S7.

Results

Forest mortality and its relationship with defoliation

The stand-level frequency distribution of birch stem mortality rates in 2010 was clearly bimodal (Hartigan's dip test: $P < 0.001$) and thus in support of two distinct ecosystem states in terms of forest damage (or equivalently: living tree cover) just after the moth outbreak (Fig. 2A). In accordance with this, K means clustering identified two clusters in terms of mortality rate; one “healthy state” with a mean mortality rate of 0.11 (range: 0-0.43) and one “damaged state” with a mean of 0.80 (range: 0.44-1) (Table S1 and S2).

The discontinuous regression indicated that the bimodal distribution of mortality rates resulted from the crossing of a critical threshold in the defoliation-mortality relationship. Both linear and polynomial models provided substantial support for a breakpoint at an NDVI drop of 4 % ($\Delta AICc > 10$ compared to alternative breakpoints in all cases. Table S8), with the globally best model (adjusted $R^2 = 0.61$) employing second-order polynomials for the defoliation-mortality relationship at either side of the breakpoint. The estimated change in the arcsine square root transformed mortality rate when crossing the breakpoint was 0.54 [0.34-0.74], corresponding to a change in predicted (back-transformed) mortality rate from 0.18 [0.08-0.30] to 0.71 [0.59-0.81] (Fig. 2B). Due to the abrupt change in mortality when crossing the breakpoint, stands with low and high mortality rates were common, while stands in intermediate states were rare, resulting in the bimodal distribution in Fig. 2A.

Regeneration from basal sprouts and saplings

Judging from the change in regenerative parameters between 2010 and 2016, forest recovery after the outbreak has progressed slowly. Although the density of stems < 2 m in damaged forest had shown an increase that was narrowly statistically significant (Fig. 3A), the predicted increase only amounted to a change from 0.76 [0.52-1.11] to 1.14 [0.79-1.64] stems per 100 m² (Fig. 3C). This recruitment in the tree layer is small compared to the estimated total density of living stems in healthy forest in 2016 (22.20 [16.06-30.69] stems per 100 m²), and did not lead to any increase in the total density of living stems in damaged forest (Fig. 3D).

The low stem recruitment rate appears to be linked to a positive feedback mechanism in basal sprout production, since the probability of sprouting for individual trees depended strongly on the presence of surviving stems. When a polycormic tree had lost all its stems, the probability of producing basal sprouts dropped dramatically (Fig. 4A). This effect was less apparent for trees that (initially) had only one stem (monocormic), although the probability of sprout production for such trees was also somewhat higher for trees retaining a living main stem in 2016 (Fig. 4B). These results indicate a positive feedback, where increased stem survival rate also implies increased regeneration success, while the loss of all stems typically results in regenerative failure. As of 2010, around 45% of the trees in damaged forest lacked living stems and were not sprouting (Fig. 4C), suggesting that the outbreak forced nearly half of the tree population in the outbreak area out of the positive feedback loop where stem survival promotes sprouting.

A regional recruitment pulse of saplings appears to have taken place during the study period, as there was a substantial increase in sapling density between 2010 and 2016 in both damaged and healthy forest (Fig. 5A, B). However, there was large spatial heterogeneity in

sapling recruitment between the forest stands. The model relating sapling density in 2016 to the density of living trees in the same year suggested that some of this variation could be attributed to positive feedbacks with surviving mature conspecifics. The model produced a highly significant parabolic relationship, with the density of saplings peaking at an intermediate tree density of 9.5 trees per 100 m² (Fig. 5C). At this point, the predicted density of saplings was more than twice as high as it was at tree densities of zero and 19 trees per 100 m², holding initial tree density (see below) constant in the model. This suggests that saplings also benefit from a positive feedback with the mature tree layer, where the survival of some mature trees increases the probability of sapling establishment and hence promotes the production of new trees. Notably, sapling density also showed a fairly linear (non-significant second order polynomial term) positive relationship with initial tree density (Table S5), suggesting that factors like growing conditions and seedbank also affected sapling production. However, this effect of initial tree density was independent from the effect of living tree density in 2016, as both predictors were partially significant in the model.

Discussion

The theory of ecological state transitions (regime shifts) has alerted ecologists to the possibility that ecosystems may respond to climate change by abrupt state transitions rather than gradual change. However, good empirical case studies – which exemplify this type of non-linear response to climatic forcing in the field – have so far been few and mostly limited to aquatic systems (Smol *et al.* 2005; Kortsch *et al.* 2012; Clark *et al.* 2013). The case of tree cover in the boreal biome is a good example of this. Here, the discovery of alternative tree cover states has led to the suggestion that boreal forests will undergo abrupt state transitions under climate change (Scheffer *et al.* 2012). However, little empirical evidence has emerged to support this, and field studies that identify non-linear responses to climatic forcing in

boreal forests have repeatedly been called for (Post *et al.* 2009; Reyer *et al.* 2015; Kuuluvainen *et al.* 2017). Our present case study in the northernmost boreal forest (MBF) in Europe answers these calls, by empirically demonstrating that two key premises for state transitions – critical thresholds and positive feedbacks – are fulfilled in this system. First, we show that a climatically determined forcing factor – namely defoliation imposed by outbreaks of range-expanding geometrid moths – exhibits a distinct threshold relationship with ecosystem state in the form of living tree cover. Second, we demonstrate that the post-outbreak recovery rate of the forest is a declining function of the damage sustained by the tree layer, owing to positive feedbacks that make both sprouting and sapling production more successful in the presence of surviving stems or trees. These dynamic features conform to expectations for a system where climatically determined forcing could induce swift and potentially persistent changes of state.

Moth outbreaks are a natural feature of the MBF (Tenow 1972), but there is reason to believe that the pressure imposed by this driver will increase in the future. Milder winters and springs are currently allowing the winter moth and the scarce umber moth (*Agriopsis aurantiaria* Hübner) to expand their ranges into areas that have formerly experienced outbreaks only by the autumnal moth (Jepsen *et al.* 2008; Jepsen *et al.* 2011; Ammunet *et al.* 2012; Jepsen *et al.* 2013). The establishment of multiple outbreaking defoliators leads to outbreaks of the type that we have targeted in the present study, where defoliation can be sustained for 4-5 years, as opposed to the typical 1-2 years with only one defoliator present (Jepsen *et al.* 2009a; Jepsen *et al.* 2009b). This upswing in cumulative defoliation pressure may increasingly drive forested areas beyond their critical threshold (tipping point) of defoliation tolerance. The threshold behavior of the system implies that even small directional changes in

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defoliation pressure may spell the difference between negligible forest damage and collapses in living tree cover.

Stands that lose most of their mature stems due to exceedance of defoliation thresholds will depend on saplings and basal sprouts to recover. These regenerative mechanisms are not always effective, as stands that have been killed by more small-scale outbreaks in the past have sometimes failed to recover, and undergone a transition to secondary tundra. Reindeer browsing on birch recruits has traditionally been invoked to explain these regenerative failures (Käyhkö & Horstkotte 2017; Neuvonen & Viiri 2017). Browsing undoubtedly has negative effects on birch sprouts and saplings (den Herder & Niemela 2003; Kumpula, Stark & Holand 2011; Biuw *et al.* 2014), but our current results suggest that dead stands may also struggle to recover due to the loss of internal positive feedbacks between birch recruits and mature conspecifics. Our data shows that the probability of basal sprouting drops to about 20 % when a tree has lost all of its main stems. This indicates that stands suffering mass mortality of stems will often fail to regenerate by sprouting alone, and will tend to lose many of their established trees. Recovery will then depend mainly on new establishing saplings. However, our results indicate that sapling production also declines in stands that have lost most of their living trees. Thus, in summary, stands that suffer the heaviest damage also appear to be the least capable of regenerating. These results shed new light on post-disturbance recovery processes in the MBF, and align with an increasing body of evidence for the importance of facilitative/positive interactions for recruitment in forest systems (Dickie *et al.* 2005; Teste & Simard 2008; Karst *et al.* 2015). Our findings indicate that persistent regenerative failures are most likely if outbreaks decimate the mature tree cover to the extent that positive recruitment feedbacks start to be lost. The role that such events may play in shaping future ecosystem trajectories in the MBF is difficult to predict. However, if

moth range expansions continue unabated, it is possible that the elevated defoliation pressure imposed by novel, multispecies outbreaks will cause an increasing incidence of very severe forest mortality events that put stands at risk of regenerative failure.

The parabolic relationship between sapling density and the density of surviving trees was surrounded by large scatter in the sapling data (Fig. 5), attesting to the importance of unmeasured influences on sapling production. Factors that may be important in this respect include microtopography, competition from other vegetation and allelopathic effects of the abundant dwarf shrub *Empetrum nigrum* L. (Dalen & Hofgaard 2005; González *et al.* 2015). Nevertheless, the effect of surviving trees on saplings emerged as highly statistically significant and predicted that sapling production on average was more than doubled in stands retaining an intermediate density of living trees as opposed to entirely dead stands. This supports positive feedbacks between mature trees and saplings as a mechanism of potential ecological significance in the MBF, and suggests that the biological underpinnings of this mechanism deserve further attention. It is possible that surviving trees enhance sapling production simply by acting as seed trees. However, this assumes that MBF regeneration after outbreaks is seed-limited. This is by no means certain, as dead stands may harbor substantial seed banks deposited before the outbreak, and birch seeds can remain viable in the soil for 5-10 years (Kullman 1993; Tiebel, Huth & Wagner 2018). Moreover, birch seeds can travel over long distances (Molau & Larsson 2000), so that local seed trees may not be essential even in the absence of a viable seed bank.

Sapling production could also be improved by surviving trees via facilitative interactions. There is evidence that mature birches enhance sapling performance by providing shelter from harsh environmental conditions, like strong winds (Eränen & Kozlov 2008). It is also

conceivable that the foliage of living trees attracts the attention of herbivores like reindeer and moose (*Alces alces* L.) and thereby protects saplings from browsing. Further, shade created by a living canopy can reduce evapotranspiration rates and thereby ameliorate sapling water stress (Holmgren & Scheffer 2010). However, these effects may be overruled by competition for light and other resources if the canopy becomes too dense. Indeed, such competitive interactions probably explain why we found a decline in sapling counts at high tree densities. Finally, it may be hypothesized that surviving trees facilitate saplings via underground mycorrhizal networks. Outbreak-induced mass mortality of trees causes strong declines in the abundance and diversity of mycorrhizal networks in forests of both mountain birch (Saravesi *et al.* 2015) and lodgepole pine (*Pinus contorta* Douglas) (Treu *et al.* 2014), but the consequences of this for forest regeneration have been largely overlooked [but see (Karst *et al.* 2015)]. Saplings in many tree species benefit from mycorrhizal networks maintained by mature trees (Dickie *et al.* 2005; Teste & Simard 2008; Booth & Hoeksema 2010), so we may expect that outbreak-induced loss of such networks is detrimental for sapling establishment. All of the above mechanisms are compatible with the parabolic relationship between sapling counts and living tree density in our data, and experimental work will be necessary to determine if and how surviving trees facilitate sapling establishment. This is an important challenge for the future, as a mechanistic understanding of the positive feedbacks that operate in the MBF will be needed to predict the future trajectory of this ecosystem under novel outbreak regimes. Ideally, empirical studies of the biological basis for positive feedbacks should be coupled with more theoretically oriented modelling work (Muthukrishnan *et al.* 2016). Models can help determine if empirically quantified feedbacks are strong enough to induce bistability in tree cover, or whether bistability requires additional factors, like browsing. Moreover, such models could help to

provide near-term forecasts (*sensu* Dietze *et al.* 2018) of the future development of damaged birch stands.

Our study was limited to the Fennoscandian MBF, and care should be taken in generalizing our results to other boreal forest systems. The MBF is to some extent unique in the boreal context, in the sense that it is formed by a low-statured, sprouting, deciduous tree species (Wielgolaski 2005). Thus, the state-transition scenario that we have outlined will not generalize directly to coniferous boreal forests. However, given the emerging evidence for hysteresis in boreal forests (Scheffer *et al.* 2012; Xu *et al.* 2015), and the increasing pressure that these systems now face from climatically determined disturbances (Adams 2013; Weed, Ayres & Hicke 2013), it may be well worth to scrutinize other boreal systems for threshold behavior of the type that we have documented for the MBF.

Forest recovery is a multi-decadal process in the north-boreal region (Tenow & Bylund 2000) and we are aware that our current data on short-term recovery rates do not permit definite conclusions about the long-term fate of the MBF in our study region. Nevertheless, our findings demonstrate that targeting the initial stages of recovery can lead to key insights about positive regenerative feedbacks that could potentially shape long-term recovery dynamics. Moreover, with ongoing geometrid range expansions now leading to an increasing incidence of novel, multispecies outbreaks, close monitoring of post-outbreak ecosystem trajectories – including the early phases of recovery – will be essential to understanding the impact of such novel disturbance. Although our assessment indicates that forest recovery rates in our study region have been low a decade after the outbreak, this could merely signify that recovery is delayed, rather than permanently curtailed. On the other hand, the limited recovery rates could also be interpreted as an early warning that lack of reforestation is a

possible outcome for some areas that have been severely affected by novel, multispecies outbreaks. Accordingly, continued monitoring and frequent assessments to ascertain long-term patterns of recovery should be a high priority.

Conclusion

The northern-boreal mountain birch forest displays dynamic features expected from a system that may be vulnerable to abrupt changes of state under climate change. Living tree cover in this system exhibits a distinct threshold relationship with a climatically determined forcing factor in the form of defoliation imposed by moth outbreaks, and the regenerative pathways of the system exhibit positive feedbacks that cause forest recovery rate to decrease with increasing severity of outbreak-induced damage. Thus, in a future where ongoing moth range-expansions are likely to impose increasing defoliation pressure, we predict that there will be an increasing incidence of abrupt and persistent losses of living tree cover in the mountain birch forest, especially if ungulate browsing compounds a loss of positive regenerative feedbacks in dead stands.

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Data availability statement

Data deposited in the Dryad repository: <http://datadryad.org/resource/doi:10.5061/dryad.1nm650h> (Vindstad *et al.* 2018).

Figure legends

Figure 1. Overview of the study region and the sampling design. (A) Overview map showing the location of the study region in northern Fennoscandia. (B) Detailed map of the study region. Colored areas are covered by forest (almost exclusively mountain birch). The shading indicates the number of years that the forest experienced severe moth defoliation (see methods) during the outbreak targeted by the study. Forest state variables were sampled in 40 landscape blocks of 2×2 km, that are represented by black squares on the map (squares not to scale with the map). (C) Aerial photo of a landscape block. Each block was divided into 100 squares of 200×200 m, and seven forested squares were randomly selected for sampling. Sampling within a square was conducted along a 50-m transect (white lines), taken to represent a sample of the local birch stand (see main text for details of transect placement). Aerial photo: Norwegian Mapping Authority (www.norgebilder.no). (D) Schematic representation of a typical sampling transect. Sampling was conducted in a 2-m wide corridor, centered on the 50-m transect line, thus providing a sampling area of 100 m^2 per stand. Within each corridor, we recorded the number of living and dead birch stems in two height categories (1.3-2 m and > 2 m) and noted whether these stems belonged to polycormic (multi-stemmed) or monocormic (single-stemmed) trees. For each tree, we also noted the presence of living basal sprouts (i.e. stems < 1.3 m protruding from the root). Finally, we

recorded the number of living birch saplings (i.e. independent birches < 1.3 m tall) in the corridor. Each transect was sampled according to this methodology in August of 2010 and 2016. Tree silhouettes: colourbox.no.

Figure 2. (A) Histogram of arcsine square root transformed stem mortality rates (i.e. proportions of dead stems) per stand in 2010. (B) Relationship between defoliation pressure, expressed as the mean percentage drop in NDVI per stand across the period 2001-2010, and the arcsine square root transformed stem mortality rate per stand in 2010. The solid lines represent predictions from a discontinuous regression model fitted to the data points, with the shaded polygons representing the 95 % confidence envelopes of the predictions. The hatched line indicates the change in mortality rate at the mean drop in NDVI where the regression becomes discontinuous (see tables S6 and S7 for model parameter estimates and sample sizes).

Figure 3. (A, B) Change in the density of living birch stems < 2 m tall (A) and all living birch stems (B), both per stand, from 2010 to 2016, expressed as the response ratio between the two years (2016/2010). The ratios are derived from mixed effects negative binomial models taking the number of stems per stand as the response variable and year (2010 or 2016), forest damage cluster (healthy or damaged) and their interaction as fixed predictors. (see tables S3 and S7 for model parameter estimates and sample sizes). The hatched line represents a response ratio of one, which is equivalent to no change. (C, D) Density of living birch stems < 2 m tall (C) and total density of living birch stems (D) in the tree layer per stand in healthy and damaged forest in 2010 and 2016. Large symbols represent predictions from the mixed effect models described above. Small symbols represent stem counts for individual stands. Error bars represent 95% confidence intervals in all panels.

Figure 4. (A, B) Predicted probability that a tree will have sprouts in 2010 and 2016 for four categories of tree vitality, expressed as the proportion of living stems in the tree (see legend in figure for explanation of categories). Predictions are derived from mixed effects logistic models taking the presence of sprouts in a tree as the response variable and vitality category, year (2010 or 2016) and their interaction as predictors (see tables S4 and S7 for model parameter estimates and sample sizes). Results are presented separately for polycormic (multi-stemmed) (A) and monocormic (single-stemmed) (B) trees. (C) Proportion of trees that were dead (no living stems and not sprouting) per stand in healthy and damaged forest in 2010 and 2016. Large symbols represent predictions from a logistic mixed effects model taking the proportion of dead and non-sprouting trees per stand as the response variable and year (2010 or 2016), forest damage cluster (healthy or damaged) and their interaction as fixed predictors (see tables S3 and S7 for model parameter estimates and sample sizes). Small symbols represent proportions for individual stands. Error bars represent 95% confidence intervals in all panels.

Figure 5. (A) Change in the density of birch saplings per stand from 2010 to 2016 expressed as the response ratio between the two years (2016/2010). The ratios are derived from a negative binomial mixed effects model taking the number of saplings per stand as the response variable and year (2010 or 2016), forest damage cluster (healthy or damaged) and their interaction as fixed predictors (see tables S3 and S7 for model parameter estimates and sample sizes). The hatched line represents a response ratio of one, which is equivalent to no change. (B) Density of birch saplings per stand in healthy and damaged for 2010 and 2016. Large symbols represent predictions from the mixed effects model described above. Small symbols represent sapling counts for individual stands. Error bars represent 95% confidence

intervals in both A and B. (C) Sapling density per stand in 2016 as a function of the density of trees with living stems and/or basal sprouts. The curve represents predictions from a negative binomial mixed effects model taking tree density as a polynomial predictor of sapling counts (see tables S5 and S7 for model parameter estimates and sample sizes). Predictions were derived while holding the total density of trees in 2010 (which was included in the model as an additional predictor) constant at its mean value. The shaded polygon represents the 95 % confidence envelope of the predictions. Small symbols represent sapling counts for individual stands.

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