

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

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21

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24 substantial input and editorial contributions from all co-authors.

25

26

27 **Abstract**

- 28 1. The boreal biome exhibits distinct alternative ecosystem states with high and low levels
29 of tree-cover. Insect outbreaks facilitated by climate warming could potentially drive
30 transitions from high to low tree-cover states. We investigated whether two key
31 premises for such outbreak-induced transitions – critical thresholds (tipping points) and
32 positive feedbacks that could maintain alternative states – are present in the northern-
33 boreal mountain birch forest of Fennoscandia. Here, climate warming has promoted
34 range expansions of defoliating geometrid moths, resulting in novel, severe multispecies
35 outbreaks, most recently during 2002-2010.
- 36 2. We conducted regional-scale field surveys of forest damage and recovery in 280
37 mountain birch stands in a northeast Norway immediately after the outbreak (2010) and
38 six years later (2016). Satellite-derived time series of the normalized difference
39 vegetation index (NDVI) provided an index of stand defoliation during the outbreak
40 period.
- 41 3. The proportion of dead stems per stand displayed a bimodal distribution, with stands
42 generally being either lightly or severely damaged. This was due to a critical threshold
43 in the relationship between defoliation and stem mortality, with mortality rates
44 increasing abruptly in stands experiencing a mean drop in NDVI of more than 4 during
45 the outbreak period. The two key forest regenerative pathways – basal sprouting and
46 sapling production – both displayed positive feedbacks with surviving stems and trees,
47 so that regeneration efficiency declined with increasing damage to the mature tree layer.
48 These feedbacks imply that stands which have been forced across critical defoliation
49 thresholds and suffered collapses of living tree cover may struggle to recover, especially
50 if the loss of positive regenerative feedbacks is compounded by ungulate browsing on
51 birch recruits.

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

59

60 **Introduction**

61 Massive outbreaks of pest insects are among the most significant disturbances attributed to
62 climate change in boreal forests. Since the early 2000s, outbreaks of bark beetles and budworms
63 have damaged millions of hectares of coniferous forest in North America (Weed, Ayres &
64 Hicke 2013; Pureswaran *et al.* 2015; Pureswaran, Roques & Battisti 2018), while geometrid
65 moths have defoliated one third of the deciduous forest in northern Fennoscandia (Jepsen *et al.*
66 2009b). The common denominator for these cases is that climate warming has favorably
67 affected critical stages in the insect lifecycle, thereby facilitating outbreaks of unprecedented
68 scale and severity (Jepsen *et al.* 2008; Jepsen *et al.* 2011; Weed, Ayres & Hicke 2013;
69 Pureswaran *et al.* 2015).

70

71 It has been theorized that novel climate-driven insect outbreaks will increasingly exceed the
72 resilience of boreal forests, thereby causing these systems to undergo transitions to alternative
73 ecosystem states with greatly reduced tree-cover (Chapin *et al.* 2004; Weed, Ayres & Hicke
74 2013; Pureswaran *et al.* 2015; Buotte *et al.* 2016). Indeed, sparse woodlands or treeless areas
75 appear to co-exist as persistent alternative states along with densely tree-covered forest across
76 the boreal biome, and insect outbreaks have been suggested as one mechanism that may induce

77 transitions between these states (Scheffer *et al.* 2012). At present, however, empirical evidence
78 for such outbreak-induced transitions is scant.

79

80 General theory postulates that systems which are prone to state transitions will exhibit two key
81 dynamical properties, namely critical thresholds (tipping points) and positive feedbacks
82 (Scheffer *et al.* 2001; Folke *et al.* 2004; Scheffer 2009; Scheffer *et al.* 2015). Threshold
83 behavior implies that ecosystem state is initially largely unresponsive to forcing, but starts to
84 exhibit rapid change once a critical threshold in forcing has been exceeded. This can cause a
85 system to undergo abrupt and unexpected changes of state. Threshold behavior has received
86 relatively little attention in forest systems, including boreal forests (Reyer *et al.* 2015).
87 However, the apparent bistability of tree-cover in the boreal biome hints at underlying tipping
88 points, and calls for empirical tests of threshold behavior in response to key forcing factors, like
89 insect outbreaks (Scheffer *et al.* 2012).

90

91 Positive feedbacks are mechanisms that cause different ecosystem states to be self-facilitating,
92 thereby allowing alternative states to be stable under the same set of environmental conditions
93 (Kéfi *et al.* 2016; Muthukrishnan *et al.* 2016). This can allow a new state to persist indefinitely
94 once a transition has occurred. There is evidence for such feedbacks in a number of terrestrial
95 and aquatic systems (Suding & Hobbs 2009), but the feedbacks that stabilize alternative tree-
96 cover states in the boreal biome are poorly understood. However, recent syntheses have
97 highlighted that post-disturbance regenerative processes often play a key part in state transitions
98 in vegetation communities (Martínez-Vilalta & Lloret 2016; Seidl *et al.* 2016). Moreover, there
99 is increasing evidence that recruitment processes in forests are shaped by facilitative
100 interactions, where tree recruits benefit from the presence of mature conspecifics (Dickie *et al.*
101 2005; Eränen & Kozlov 2008; Teste & Simard 2008; Booth & Hoeksema 2010; Karst *et al.*

102 2015). This is a potential source of positive feedbacks, since the maintenance of facilitative
103 interactions may act to stabilize a densely forested state, while loss of facilitation may impede
104 recovery after severe stand-killing disturbances.

105

106 The goal of the current study is to evaluate if the two described premises for state transitions –
107 thresholds and positive feedbacks – are present in a system that has recently suffered severely
108 under climatically facilitated insect outbreaks, namely the northern-boreal mountain birch
109 (*Betula pubescens* var. *pumila* L.) forest (MBF) of Fennoscandia. In this system, milder winters
110 and springs have allowed southern species of geometrid moths to expand their outbreak ranges
111 northwards and eastwards into areas formerly occupied only by the native autumnal moth
112 (*Epirrita autumnata* Bkh.), resulting in novel and highly severe multispecies outbreaks in many
113 areas (Jepsen *et al.* 2008; Jepsen *et al.* 2011). During the first decade of this century, moths
114 defoliated one million hectares of MBF (Jepsen *et al.* 2009a). These outbreaks caused
115 widespread mass-mortality of birch (Jepsen *et al.* 2009b; Jepsen *et al.* 2013), and arguably
116 represent the largest terrestrial disturbance attributable to climate change on the European
117 continent.

118

119 Cyclic outbreaks by the autumnal moth have historically dominated the natural disturbance
120 regime of the MBF (Tenow 1972), and several authors have suggested that outbreaks could
121 trigger transitions between forested and non-forested ecosystems states (Chapin *et al.* 2004;
122 Scheffer *et al.* 2012). In support of this idea, stands that have been killed by outbreaks have
123 sometimes been observed to fail to recover. The most notable example stems from the Utsjoki
124 municipality in northern Finland, where an autumnal moth outbreak during the 1960s caused
125 extensive mortality of MBF over an area of more than one hundred thousand hectares (Kallio
126 & Lehtonen 1973). Forest recovery after this outbreak has been poor, and much of the area has

127 now devolved to treeless secondary tundra (Neuvonen & Viiri 2017). Such regenerative failures
128 have usually been attributed to browsing by semi-domestic reindeer (Käyhkö & Horstkotte
129 2017), which are abundant in northern Fennoscandia, and have negative impacts on the growth
130 and survival of birch sprouts and saplings (den Herder & Niemela 2003; Kumpula, Stark &
131 Holand 2011; Biuw *et al.* 2014). This explanation has been widely accepted, and the possibility
132 that regenerative failures could also reflect the loss of endogenous positive feedbacks, like
133 facilitation, has received little attention. However, with ongoing geometrid range expansions
134 now leading to the emergence of novel, multispecies outbreaks in many areas, there is need to
135 deepen the understanding of the mechanisms that could drive outbreak-induced ecosystem
136 transitions in the MBF.

137

138 Our study is based on a combination of satellite data and spatially extensive ground survey data
139 from an area of about four hundred thousand hectares at 70°N in northeast Norway (Fig. 1).
140 The MBF of the region was heavily damaged by an outbreak involving the autumnal moth
141 during 2002-2004 and the recently established, range-expanding winter moth (*Operophtera*
142 *brumata* L.) during 2005-2010 (Jepsen *et al.* 2009b; Jepsen *et al.* 2013). The gradual spread of
143 the winter moth during the outbreak (Jepsen *et al.* 2013) contributed to spatial variability in the
144 cumulative defoliation intensity across the study region. This facilitated tests of whether the
145 premises for outbreak-induced state transitions are present in the MBF system. First, by relating
146 the spatial data on stand-level birch mortality rates (2010) to moth-induced defoliation, we test
147 the premise of threshold behavior in the relationship between defoliation (i.e. forcing) and
148 ecosystem state in the form of living tree-cover. Second, to test the premise of positive
149 feedbacks, we quantify the efficiency of forest regeneration almost a decade after the outbreak
150 (2016) and investigate if regenerative pathways exhibit facilitative interactions with living
151 trees/stems.

152

153 **Materials and methods**

154 *Study system*

155 The study was conducted in the Varanger region (70°N, 29°E), which is located in the eastern
156 part of Finnmark County in northeast Norway. Mean temperatures for January and July are -
157 11.6°C and 12.5°C (1971–2000 normal period for Rustefjellbma meteorological station
158 70°23′55″ N, 28°11′36″E), while annual precipitation is 400-500 mm. The region represents
159 the northern distributional limit of boreal deciduous forest in Europe, and forms a transition
160 zone between the boreal forest biome and the low-arctic tundra. The forests of the region are
161 composed almost exclusively of mountain birch, with rowan (*Sorbus aucuparia* L.) and aspen
162 (*Populus tremuloides* Michx.) occurring only sporadically.

163

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

172

173 Autumnal moth outbreaks occurring at roughly decadal intervals have historically been the
174 principal disturbance factor in the birch forests of the Varanger region (Tenow 1972). This
175 situation changed during the first decade of the 2000s, when the winter moth expanded its
176 outbreak range into the region (Klemola, Andersson & Ruohomaki 2008; Jepsen *et al.* 2013).

177 The range expansion precipitated a massive outbreak involving both moth species, with the
178 autumnal moth outbreaking to the north and west of the Varanger fjord during 2002-2004 and
179 the winter moth outbreaking in the same area during 2005-2006. This was followed by
180 outbreaks of the winter moth to the south and west of the fjord during 2006-2010 (Jepsen *et al.*
181 2009b; Jepsen *et al.* 2013). The prolonged multiannual defoliation inflicted by the outbreaks
182 caused historically unprecedented damage to mountain birch stands throughout much of the
183 region, and only a few areas were left relatively unaffected.

184

185 *Study design and sampling*

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

202

203 To facilitate sampling of forest stands within the landscape blocks, each block was divided into
204 100 quadrates of 200×200 m (Fig. 1). Seven forest-covered quadrates within each block were
205 randomly selected for sampling. Within each quadrate, we laid out a 50 m transect, starting
206 from the center of the quadrate and running due north. If a transect was inaccessible due to steep
207 terrain, or included more than 50 % open mire or boulder fields, the direction of the transect
208 line was progressively shifted 45° clockwise, until a suitable transect was found. The same
209 quadrates were used for sampling in 2010 and 2016, and care was taken to ensure that the
210 transect line was positioned similarly in both years, so that results would be comparable at the
211 transect level. We consider the sample from each transect to represent an individual mountain
212 birch stand, and hereafter refer to transects as “stands”.

213

214 State variables describing the damage and recovery status of the tree layer were sampled
215 following the same protocol in August of 2010 and 2016. Sampling was conducted in 2-m wide
216 corridors, centered on the 50-m transect lines (i.e. corridor area= 100m^2). Within a corridor, we
217 conducted separate measurements for each individual birch stem taller than 1.3 m (here defined
218 as the lower height limit of the tree layer). Stems were classified as dead (foliage absent) or
219 living (foliage present), and scored as being less or more than 2 m tall. Stems in the range of
220 1.3-2m tall could be regarded as recruits into the tree layer, as new sprouts can grow into this
221 height range within a few years (Vindstad *et al.* 2017). For practical reasons, we measured a
222 maximum of 50 stems per transect, and recorded the position on the transect where this limit
223 was reached to correct stem counts for transect length in the analysis. We also recorded which
224 stems belonged to the same tree. The distinction between trees can be unclear in dense stands
225 of polycormic mountain birch, and we therefore defined a tree as a cluster of trunks with no
226 detectable root connection to neighboring clusters. This definition identifies a tree as a

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

232

233 *Statistical analysis*

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

246

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

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

260

261 The second step of the analysis was to quantify short-term forest regeneration after the outbreak.
262 To do this, we estimated the change in selected regenerative parameters between 2010 and
263 2016. The estimation was conditioned on the level of damage sustained by the tree layer, as
264 represented by the clusters identified by the K-means clustering of stem mortality rates (see
265 above). Thus, the predictor variables for this analysis were year (2010 or 2016), damage cluster
266 and their interaction. The response variables were the total number of living stems, the number
267 of living stems <2 m tall (which could have emerged from sprouts between 2010 and 2016) and
268 the number of saplings, all per stand. These variables were taken as count responses in
269 generalized mixed effects models, using a negative binomial error distribution to account for
270 the highly aggregated distributions of the counts. Random intercepts were modelled for the 40
271 landscape blocks. The response ratio comparing 2016 to 2010, within forest damage clusters,
272 was used as a measure of temporal change. For the tree- and stem counts, the log-transformed
273 length of the sampling transect was included as an offset variable, to account for stands where
274 the maximum count of 50 stems was reached before 50 m/100m² had been covered.

275

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

292

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

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

320

321 All statistical analyzes were conducted in R version 3.4.0 (R Development Core Team 2017),
322 using the `glmer` and `glmer.nb` functions in version 1.1-14 of the `lme4` library (Bates *et al.*
323 2015) for mixed effects models. Parameter estimates for the fixed effects in the mixed models
324 are provided in the tables S3-S6 in the supplementary information. A summary of sample sizes
325 for all statistical models is provided in table S7.

326

327 **Results**

328 *Forest mortality and its relationship with defoliation*

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

335

336 The discontinuous regression indicated that the bimodal distribution of mortality rates resulted
337 from the crossing of a critical threshold in the defoliation-mortality relationship. Both linear
338 and polynomial models provided substantial support for a breakpoint at an NDVI drop of 4
339 ($\Delta AICc > 10$ compared to alternative breakpoints in all cases. Table S8), with the globally best
340 model (adjusted $R^2 = 0.61$) employing second-order polynomials for the defoliation-mortality
341 relationship at either side of the breakpoint. The estimated change in the arcsine square root
342 transformed mortality rate when crossing the breakpoint was 0.54 [0.34-0.74], corresponding
343 to a change in predicted (back-transformed) mortality rate from 0.18 [0.08-0.30] to 0.71 [0.59-
344 0.81] (Fig. 2B). Due to the abrupt change in mortality when crossing the breakpoint, transects
345 with low and high mortality rates were common, while transects in intermediate states were
346 rare, resulting in the bimodal distribution in Fig. 2A.

347

348 *Regeneration from basal sprouts and saplings*

349 Judging from the change in regenerative parameters between 2010 and 2016, forest recovery
350 after the outbreak has progressed slowly. Although the density of stems < 2 m in damaged forest

351 had shown an increase that was narrowly statistically significant (Fig. 3A), the predicted
352 increase only amounted to a change from 0.76 [0.52-1.11] to 1.14 [0.79-1.64] stems per 100 m²
353 (Fig. 3C). This recruitment in the tree layer is small compared to the estimated total density of
354 living stems in healthy forest in 2016 (22.20 [16.06-30.69] stems per 100 m²), and did not lead
355 to any increase in the total density of living stems in damaged forest (Fig. 3D).

356

357 The low stem recruitment rate appears to be linked to a positive feedback mechanism in basal
358 sprout production, since the probability of sprouting for individual trees depended strongly on
359 the presence of surviving stems. When a polycormic tree had lost all its stems, the probability
360 of producing basal sprouts dropped dramatically (Fig. 4A). This effect was less apparent for
361 trees that (initially) had only one stem (monocormic), although the probability of sprout
362 production for such trees was also somewhat higher for trees retaining a living main stem in
363 2016 (Fig. 4B). These results indicate a positive feedback, where increased stem survival rate
364 also implies increased regeneration efficiency, while the loss of all stems typically results in
365 regenerative failure. As of 2010, around 45% of the trees in damaged forest lacked living stems
366 and were not sprouting (Fig. 4C), suggesting that the outbreak forced nearly half of the tree
367 population in the outbreak area out of the positive feedback loop where stem survival promotes
368 sprouting.

369

370 A regional recruitment pulse of saplings appears to have taken place during the study period,
371 as there was a substantial increase in sapling density between 2010 and 2016 in both damaged
372 and healthy forest (Fig. 5A, B). However, there was large spatial heterogeneity in sapling
373 recruitment between the forest stands. The model relating sapling density in 2016 to the density
374 of living trees in the same year suggested that some of this variation could be attributed to
375 positive feedbacks with surviving mature conspecifics. The model produced a highly significant

376 parabolic relationship, with the density of saplings peaking at an intermediate tree density of
377 9.5 trees per 100 m² (Fig. 5C). At this point, the predicted density of saplings was more than
378 twice as high as it was at tree densities of zero and 19 trees per 100 m², holding initial tree
379 density (see below) constant in the model. This suggests that saplings are also subject to a
380 positive feedback, where the survival of some mature trees makes the production of new trees
381 more efficient. Notably, sapling density also showed a fairly linear (non-significant second
382 order polynomial term) positive relationship with initial tree density (Table S5), suggesting that
383 factors like growing conditions and seedbank also affected sapling production. However, this
384 effect of initial tree density was independent from the effect of living tree density in 2016, as
385 both predictors were partially significant in the model.

386

387 **Discussion**

388 The theory of ecological state transitions (regime shifts) has alerted ecologists to the possibility
389 that ecosystems may respond to climate change by abrupt state transitions rather than gradual
390 change. However, good empirical case studies – which exemplify this type of non-linear
391 response to climatic forcing in the field – have so far been few and mostly limited to aquatic
392 systems (Smol *et al.* 2005; Kortsch *et al.* 2012; Clark *et al.* 2013). The case of tree-cover in the
393 boreal biome is a good example of this. Here, the discovery of alternative tree-cover states has
394 led to the suggestion that boreal forests will undergo abrupt state transitions under climate
395 change (Scheffer *et al.* 2012). However, little empirical evidence has emerged to support this,
396 and field studies that identify non-linear responses to climatic forcing in boreal forests have
397 repeatedly been called for (Post *et al.* 2009; Reyer *et al.* 2015; Kuuluvainen *et al.* 2017). Our
398 present case study in the northernmost boreal forest (MBF) in Europe answers these calls, by
399 empirically demonstrating that two key premises for state transitions – critical thresholds and
400 positive feedbacks – are fulfilled in this system. First, we show that a climatically determined
401 forcing factor – namely defoliation imposed by outbreaks of range-expanding geometrid moths

402 – exhibits a distinct threshold relationship with ecosystem state in the form of living tree-cover.
403 Second, we demonstrate that the post-outbreak recovery rate of the forest is a declining function
404 of the damage sustained by the tree layer, owing to positive feedbacks that make both sprouting
405 and sapling production more efficient in the presence of surviving stems or trees. These
406 dynamic features conform to expectations for a system where climatically determined forcing
407 could induce swift and potentially persistent changes of state.

408

409 Moth outbreaks are a natural feature of the MBF (Tenow 1972), but there is reason to believe
410 that the pressure imposed by this driver will increase in the future. Milder winters and springs
411 are currently allowing the winter moth and the scarce umber moth (*Agriopsis aurantiaria*
412 Hübner) to expand their ranges into areas that have formerly experienced outbreaks only by the
413 autumnal moth (Jepsen *et al.* 2008; Jepsen *et al.* 2011; Ammunet *et al.* 2012; Jepsen *et al.*
414 2013). The establishment of multiple outbreaking defoliators leads to outbreaks of the type that
415 we have targeted in the present study, where defoliation can be sustained for 4-5 years, as
416 opposed to the typical 1-2 years with only one defoliator present (Jepsen *et al.* 2009a; Jepsen *et*
417 *al.* 2009b). This upswing in cumulative defoliation pressure may increasingly drive forested
418 areas beyond their critical threshold (tipping point) of defoliation tolerance. The threshold
419 behavior of the system implies that even small directional changes in defoliation pressure may
420 spell the difference between negligible forest damage and collapses in living tree cover.

421

422 Stands that lose most of their mature stems due to exceedance of defoliation thresholds will
423 depend on saplings and basal sprouts to recover. These regenerative mechanisms are not always
424 effective, as stands that have been killed by more small-scale outbreaks in the past have
425 sometimes failed to recover and devolved to secondary tundra. Reindeer browsing on birch
426 recruits has traditionally been invoked to explain these regenerative failures (Käyhkö &

427 Horstkotte 2017; Neuvonen & Viiri 2017). Browsing undoubtedly has negative effects on birch
428 sprouts and saplings (den Herder & Niemela 2003; Kumpula, Stark & Holand 2011; Biuw *et*
429 *al.* 2014), but our current results suggest that dead stands may also struggle to recover due to
430 the loss of internal positive feedbacks between birch recruits and mature conspecifics. Our data
431 shows that the probability of basal sprouting drops to only about 20 % when a tree that has lost
432 all of its main stems. This indicates that stands suffering mass mortality of stems will often fail
433 to regenerate by sprouting alone, and will tend to lose many of their established trees. Recovery
434 will then depend mainly on saplings. However, our results indicate that sapling production also
435 declines in stands that have lost most of their living trees. Thus, in summary, stands that suffer
436 the heaviest damage also appear to be the least efficient in terms of regeneration. These results
437 shed new light on post-disturbance recovery processes in the MBF, and aligns with an
438 increasing body of evidence for the importance of facilitative/positive interactions for
439 recruitment in forest systems (Dickie *et al.* 2005; Teste & Simard 2008; Karst *et al.* 2015).
440 Based on these new results, persistent regenerative failures seem most likely if outbreaks
441 decimate the mature tree-cover to the extent that positive recruitment feedbacks start to be lost,
442 and reindeer then browse destructively on the birch recruits that are still produced. The role that
443 such events may play in shaping future ecosystem trajectories in the MBF is difficult to predict.
444 However, if moth range expansions continue unabated, it is possible that the elevated
445 defoliation pressure imposed by novel, multispecies outbreaks will cause an increasing
446 incidence of very severe forest mortality events that put stands at risk of regenerative failure.

447

448 The parabolic relationship between sapling density and the density of surviving trees was
449 surrounded by large scatter in the sapling data (Fig. 5), attesting to the importance of
450 unmeasured influences on sapling production. Factors that may be important in this respect
451 include microtopography, competition from other vegetation and allopathic effects of the

452 abundant dwarf shrub *Empetrum nigrum* L. (Dalen & Hofgaard 2005; González *et al.* 2015). In
453 spite of the noisy data, the effect of surviving trees on saplings emerged as highly statistically
454 significant and predicted that sapling production on average was more than doubled in stands
455 retaining an intermediate density of living trees as opposed to entirely dead stands. This
456 supports positive feedbacks between mature trees and saplings as a mechanism of potential
457 ecological significance in the MBF, and suggests that the biological underpinnings of this
458 mechanism deserve further attention. It is possible that surviving trees enhance sapling
459 production simply by acting as seed trees. However, this assumes that MBF regeneration after
460 outbreaks is seed-limited. This is by no means certain, as dead stands may harbor substantial
461 seed banks deposited before the outbreak, and birch seeds can remain viable in the soil for 5-
462 10 years (Kullman 1993; Tiebel, Huth & Wagner 2018). Moreover, birch seeds can travel over
463 long distances (Molau & Larsson 2000), so that local seed trees may not be essential even in
464 the absence of a viable seed bank.

465

466 Sapling production could also be improved by surviving trees via facilitative interactions. There
467 is evidence that mature birches enhance sapling performance by providing shelter from the
468 elements (Eränen & Kozlov 2008). However, it may also be hypothesized that surviving trees
469 facilitate saplings via underground mycorrhizal networks. Outbreak-induced mass mortality of
470 trees causes strong declines in the abundance and diversity of mycorrhizal networks in forests
471 of both mountain birch (Saravesi *et al.* 2015) and lodgepole pine (*Pinus contorta* Douglas)
472 (Treu *et al.* 2014), but the consequences of this for forest regeneration have been largely
473 overlooked [but see (Karst *et al.* 2015)]. Saplings in many tree species benefit from mycorrhizal
474 networks maintained by mature trees (Dickie *et al.* 2005; Teste & Simard 2008; Booth &
475 Hoeksema 2010), so we may expect that outbreak-induced loss of such networks is detrimental
476 for sapling establishment. Studies of sapling performance and mycorrhizal colonization in areas

477 with contrasting densities of surviving trees will shed light on this topic. In addition to empirical
478 studies of the biological basis for positive feedbacks, our understanding would benefit from
479 more theoretically oriented modelling work (Muthukrishnan *et al.* 2016) of how these
480 feedbacks shape ecosystem trajectories in the MBF. Models can help determine if empirically
481 quantified feedbacks are strong enough to induce bistability in tree-cover, or whether bistability
482 requires additional factors, like browsing. Moreover, such models could help to provide near-
483 term forecast (*sensu* Dietze *et al.* 2018) of the future development of damaged birch stands.

484

485 Our study was limited to the Fennoscandian MBF, and care should be taken in generalizing our
486 results to other boreal forest systems. The MBF is to some extent unique in the boreal context,
487 in the sense that it is formed by a low-statured, sprouting, deciduous tree species (Wielgolaski
488 2005). Thus, the state-transition scenario that we have outlined will not generalize directly to
489 coniferous boreal forests. However, given the emerging evidence for hysteresis in boreal forests
490 (Scheffer *et al.* 2012; Xu *et al.* 2015), and the increasing pressure that these systems now face
491 from climatically determined disturbances (Adams 2013; Weed, Ayres & Hicke 2013), it may
492 be well worth to scrutinize other boreal systems for threshold behavior of the type that we have
493 documented for the MBF.

494

495 Forest recovery is a multi-decadal process in the north-boreal region (Tenow & Bylund 2000)
496 and we stress that our current data on short-term recovery rates do not permit definite
497 conclusions about long-term fate of the MBF in our study region. However, with ongoing
498 geometrid range expansions now leading to an increasing incidence of novel, multispecies
499 outbreaks, we nevertheless think that it is valuable to make a first assessment of how ecosystem
500 trajectories look after such novel disturbance. Although our assessment indicates that forest
501 recovery rates in our study region have been low a decade after the outbreak, this could merely

502 signify that recovery is delayed, rather than permanently curtailed. On the other hand, the
503 limited recovery rates could also be interpreted as an early warning that lack of reforestation is
504 a possible outcome for some areas that have been severely affected by novel, multispecies
505 outbreaks. Accordingly, continued monitoring and frequent assessments to ascertain long-term
506 patterns of recovery should be a high priority.

507

508 **Conclusion**

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

518

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527

528 **Data availability statement**

529 The data supporting the findings of this study will be uploaded to the Dryad digital repository
530 when the paper has been accepted for publication.

531

532 **Code availability statement**

533 The R script used to produce the statistical analyzes and plots reported in the paper is available
534 as part of the supplementary information for the study.

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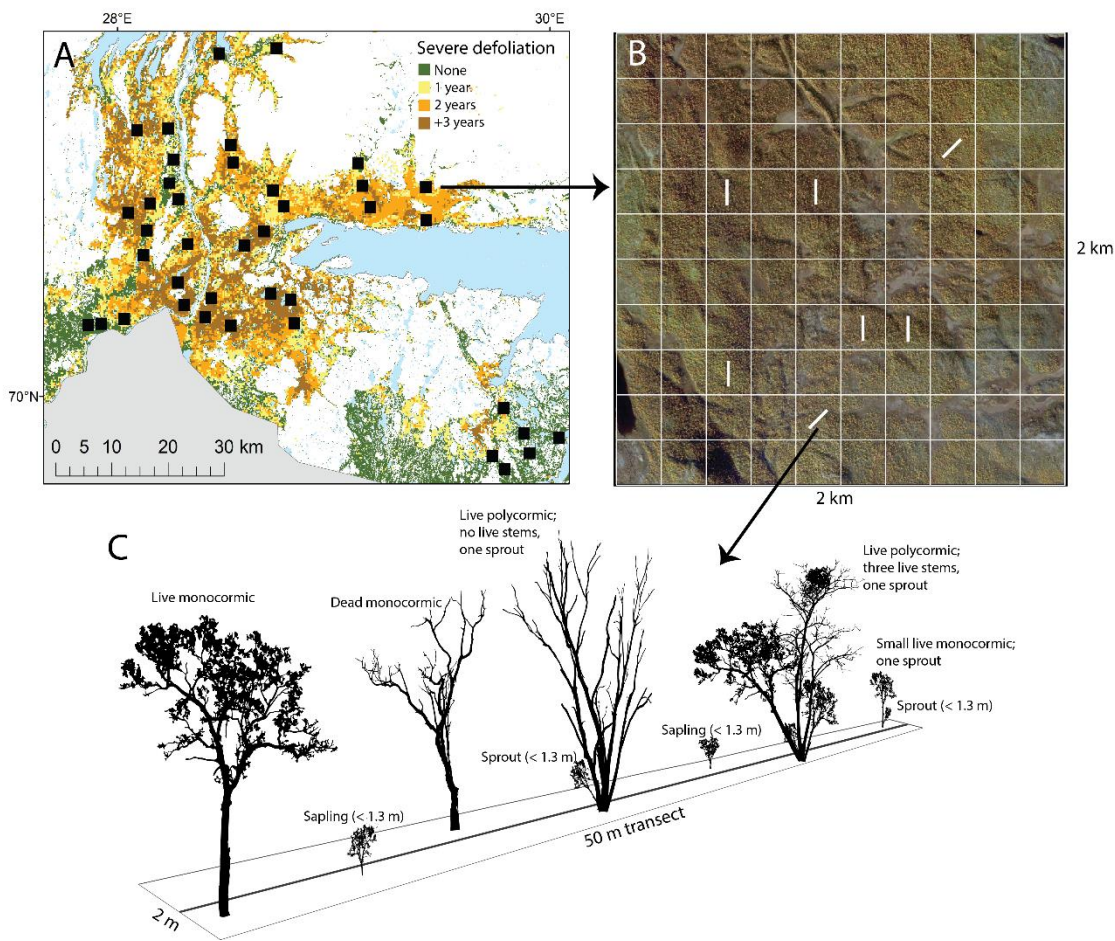
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552 **Figures**



553

554

555 Figure 1. Overview of the study region and the sampling design. (A) Map of the study region
 556 in northeast Norway. Colored areas are covered by forest (almost exclusively mountain birch).
 557 The shading indicates the number of years that the forest experienced severe moth defoliation
 558 (see methods) during the outbreak targeted by the study. Forest state variables were sampled in
 559 40 landscape blocks of 2 × 2 km, that are represented by black squares on the map (squares not
 560 to scale with the map). (B) Aerial photo of a landscape block. Each block was divided into 100
 561 squares of 200 × 200 m, and seven forested squares were randomly selected for sampling.
 562 Sampling within a square was conducted along a 50-m transect (white lines), taken to represent
 563 a sample of the local birch stand (See SI methods for details of transect placement). Aerial
 564 photo: Norwegian Mapping Authority (www.norgebilder.no). (C) Schematic representation of

565 a typical sampling transect. Sampling was conducted in a 2-m wide corridor, centered on the
566 50-m transect line, thus providing a sampling area of 100 m² per stand. Within each corridor,
567 we recorded the number of living and dead birch stems in two height categories (1.3-2 m and >
568 2 m) and noted whether these stems belonged to polycormic (multi-stemmed) or monocormic
569 (single-stemmed) trees. For each tree, we also noted the presence of living basal sprouts (i.e.
570 stems < 1.3 m protruding from the root). Finally, we recorded the number of living birch
571 saplings (i.e. independent birches < 1.3 m tall) in the corridor. Each transect was sampled
572 according to this methodology in August of 2010 and 2016. Tree silhouettes: colourbox.no.

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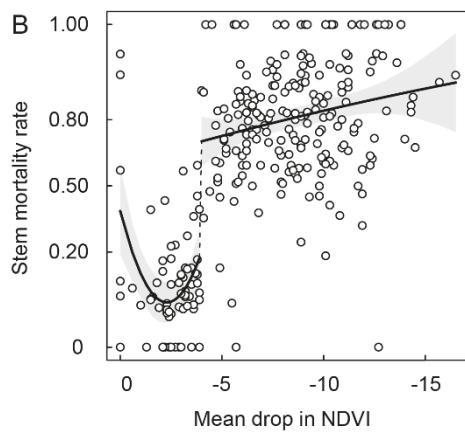
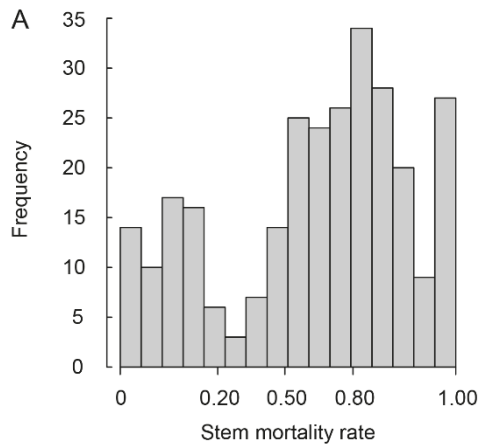
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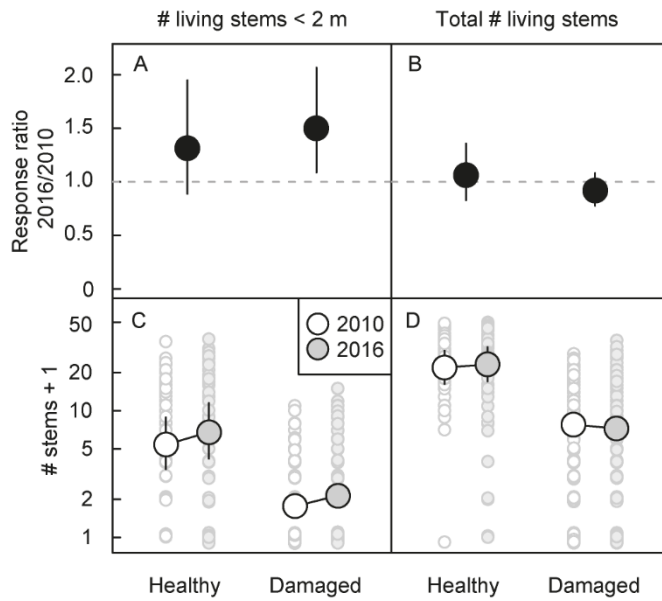


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592 Figure 2. (A) Histogram of arcsine square root transformed stem mortality rates (i.e. proportions
 593 of dead stems) per stand in 2010. (B) Relationship between defoliation pressure, expressed as
 594 the mean drop in NDVI per stand across the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

599



600

601

602 Figure 3. (A, B) Change in the density of living birch stems < 2 m tall (A) and all living birch

603 stems (B), both per stand, from 2010 to 2016, expressed as the response ratio between the two

604 years (2016/2010). The ratios are derived from mixed effects negative binomial models taking

605 the number of stems per stand as the response variable and year (2010 or 2016), forest damage

606 cluster (healthy or damaged) and their interaction as fixed predictors. (See tables S3 and S6 for

607 model parameter estimates and sample sizes). The hatched line represents a response ratio of

608 one, which is equivalent to no change. (C, D) Density of living birch stems < 2 m tall (C) and

609 total density of living birch stems (D) in the tree layer per stand in healthy and damaged forest

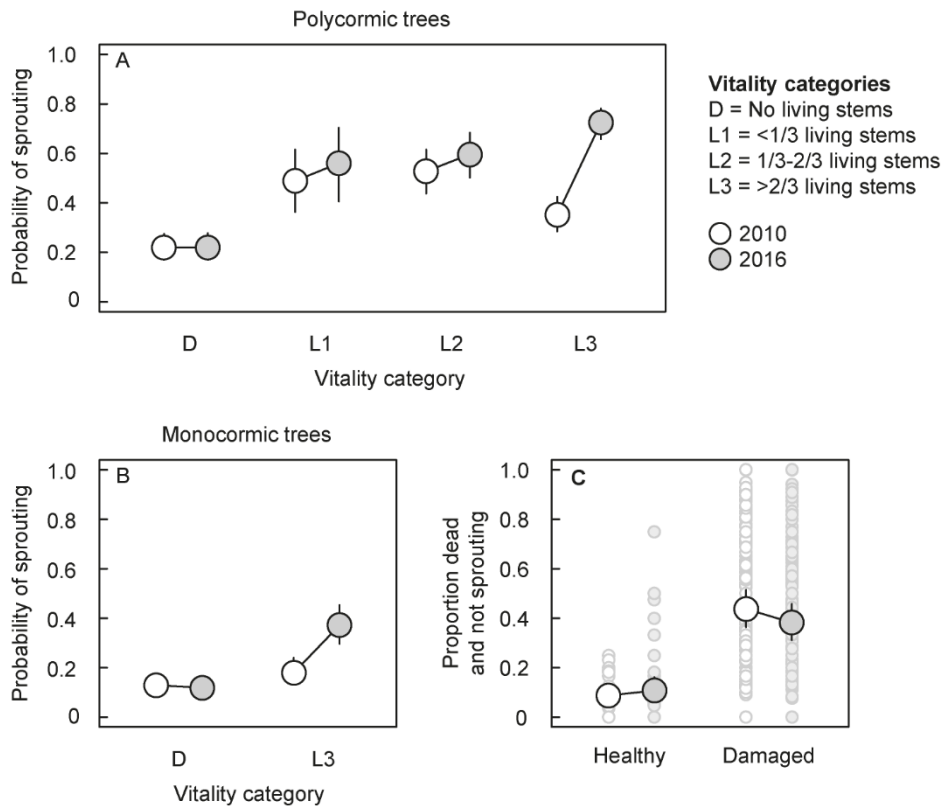
610 in 2010 and 2016. Large symbols represent predictions from the mixed effect models described

611 above. Small symbols represent stem counts for individual stands. Error bars represent 95%

612 confidence intervals in all panels.

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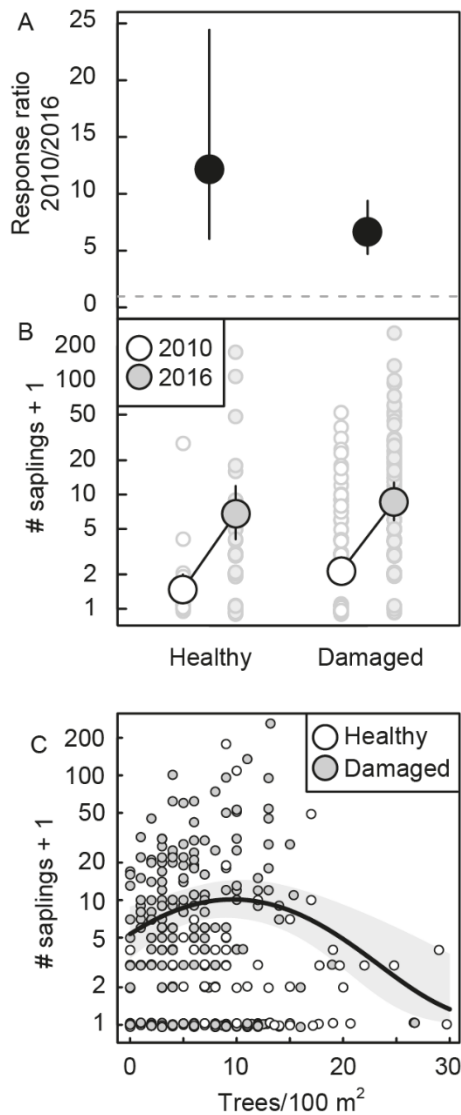
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617 Figure 4. (A, B) Predicted probability that a tree will have sprouts in 2010 and 2016 for four
618 categories of tree vitality, expressed as the proportion of living stems in the tree (see legend in
619 figure for explanation of categories). Predictions are derived from mixed effects logistic models
620 taking the presence of sprouts in a tree as the response variable and vitality category, year (2010
621 or 2016) and their interaction as predictors (See tables S4 and S6 for model parameter estimates
622 and sample sizes). Results are presented separately for polycormic (multi-stemmed) (A) and
623 monocormic (single-stemmed) (B) trees. (C) Proportion of trees that were dead (no living stems
624 and not sprouting) per stand in healthy and damaged forest in 2010 and 2016. Large symbols
625 represent predictions from a logistic mixed effects model taking the proportion of dead and
626 non-sprouting trees per stand as the response variable and year (2010 or 2016), forest damage
627 cluster (healthy or damaged) and their interaction as fixed predictors (See tables S3 and S6 for
628 model parameter estimates and sample sizes). Small symbols represent proportions for
629 individual stands. Error bars represent 95% confidence intervals in all panels.



630

631

632 Figure 5. (A) Change in the density of birch saplings per stand from 2010 to 2016 expressed as
 633 the response ratio between the two years (2016/2010). The ratios are derived from a negative
 634 binomial mixed effects model taking the number of saplings per stand as the response variable
 635 and year (2010 or 2016), forest damage cluster (healthy or damaged) and their interaction as
 636 fixed predictors (See tables S3 and S6 for model parameter estimates and sample sizes). The
 637 hatched line represents a response ratio of one, which is equivalent to no change. (A) Density
 638 of birch saplings per stand in healthy and damaged for 2010 and 2016. Large symbols represent
 639 predictions from the mixed effects model described above. Small symbols represent sapling

640 counts for individual stands. Error bars represent 95% confidence intervals in both A and B.
641 (C) Sapling density per stand in 2016 as a function of the density of trees with living stems
642 and/or basal sprouts. The curve represents predictions from a negative binomial mixed effects
643 model taking tree density as a polynomial predictor of sapling counts (See tables S5 and S6 for
644 model parameter estimates and sample sizes). Predictions were derived while holding the total
645 density of trees in 2010 (which was included in the model as an additional predictor) constant
646 at its mean value. The shaded polygon represents the 95 % confidence envelope of the
647 predictions. Small symbols represent sapling counts for individual stands.

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