

1 Cascading effects of canopy mortality drive long-term changes in understory diversity
2 in temperate old-growth forests of Europe

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4 Running title: Cascading effects of canopy mortality

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35

36 Abstract

37 **Questions:** We investigated the influence of protracted mortality of a canopy dominant
38 tree (*Abies alba*) on long-term understory dynamics. We ask 1) how tree regeneration
39 and understory species diversity and composition changed over 32 years; and 2)
40 whether the observed changes were mainly driven by mortality of *A. alba*.

41 **Location:** Three old-growth forest reserves dominated by *A. alba* and *Fagus sylvatica*
42 in the Dinaric Mountains of Slovenia.

43 **Methods:** Tree layer and understory regeneration and herbs were surveyed in 147 plots
44 across the three forest reserves in 1983 and 2015. Soils were also sampled in 2015. The
45 study period coincides with a protracted period of increased *A. alba* mortality in the
46 canopy layer associated with anthropogenic emissions.

47 **Results:** Between 1983 and 2015, the decline in canopy layer *A. alba* caused a
48 recruitment pulse of *F. sylvatica* regeneration to the subcanopy tree layer across the
49 three reserves. These changes were accompanied by a significant decline in plot level
50 herb species richness. A model-based analysis of beta-diversity revealed significant
51 community convergence during the study period, mainly caused by loss of rare species.
52 Ellenberg values indicate that these changes were mainly driven by loss of understory
53 light, while an increase in soil pH may have also played a role.

54 **Conclusions:** This observational study suggests that the long-term decline of *A. alba*
55 resulted in a cascade of processes – widespread *F. sylvatica* recruitment that impeded
56 penetration of light to the forest floor, and possibly a change in soil conditions due to
57 the decline of coniferous litter. These changes caused a significant loss of herb diversity
58 and homogenization of the understory community across the three sites. This study
59 sheds light on the potential cascading consequences triggered by episodes of increased
60 tree mortality resulting from global change type drivers.

61

62 **Keywords:** beech, fir decline, forest dieback, forest herbs, foundation species, old-
63 growth, tree mortality, resurveys, semi-permanent plots, understory vegetation

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70 Introduction

71 There is widespread concern that global-change stressors, particularly drought
72 accompanied by warmer temperatures and associated increases in pests and pathogens,
73 may lead to forest die-off, decline, or chronic increases in tree mortality (van Mantgem
74 et al. 2009; Jactel et al. 2012; Allen et al. 2015; Anderegg et al. 2015). Such mortality
75 processes will likely cause cascading effects in forest ecosystems (Wardle et al. 2011;
76 Millar & Stephenson 2015; Shiels et al. 2015), especially when mortality is targeted on
77 tree species that play a foundational role in a given forest community. Loss of
78 foundational tree species have been documented to cause important changes to various
79 properties and processes of forest ecosystems, including forest microclimate, understory
80 herbs and tree regeneration, invertebrate communities, soil and litter properties,
81 decomposition rates, and nutrient cycling (Ellison et al. 2005; Sackett et al. 2011;
82 Lustenhouwer et al. 2012; Orwig et al. 2013; Kendrick et al. 2015).

83 *Abies alba* (silver fir), a conifer species distributed across mountain regions of
84 the European temperate and Mediterranean zones (Mauri et al. 2016), shares many of
85 the characteristics of a foundation tree species (sensu Ellison et al. 2005). It is both
86 locally abundant and widespread over large regions, and has ecological traits that make
87 a unique contribution to its habitat. It primarily occurs in mixed forests with *Fagus*
88 *sylvatica* (beech), where it often represents a large proportion of stand-level basal area.
89 It is one of the tallest and most shade tolerant tree species in Europe, traits which
90 together contribute to the structural heterogeneity and resource use complementarity of
91 mixed species stands (Tinner et al. 2013; Nagel et al. 2014; Forrester 2014). *Abies alba*
92 has a strong influence on understory microclimate and soil properties due to the deep
93 shade and litter cast from the canopy (Augusto et al. 2002; Augusto et al. 2003;
94 Pizzeghello et al. 2006; Paluch & Gruba 2012). Finally, both living and dead trees of *A.*
95 *alba* support a diverse assemblage of flora and fauna (Lagana et al. 2000; Brändle &
96 Brandl 2001; Floren & Gogala 2002; Táborska et al. 2015).

97 Over a large part of its range, many populations of *A. alba* experienced a
98 protracted decline characterized by increased levels of morbidity and mortality during
99 the 1970s-1990s (Diaci et al. 2011), now thought to be largely the result of high levels
100 of atmospheric SO₂ pollution (Elling et al. 2009). For some populations that
101 experienced more severe dieback, this event is analogous to the global-change type
102 dieback that is gaining attention in the literature, and affords a unique glimpse into the

103 long-term effects of such events on forest ecosystem dynamics. Few studies, however,
104 have examined how this episode of increased mortality influenced long-term processes
105 and patterns, such as tree regeneration and understory herb dynamics (e.g. Nagel et al.
106 2015). Changes to the canopy can exert an important influence on understory
107 communities via changes in light, microclimate, and soils (Augusto et al. 2002; Wulf &
108 Naaf 2009; Verheyen et al. 2012; Woods et al. 2012; De Frenne et al. 2013).
109 Understanding these mechanistic links between the canopy and understory, particularly
110 for the herbaceous community that represents most of the plant diversity in temperate
111 forests (Gilliam 2007), will be important for developing effective conservation and
112 forest management strategies under global change.

113 Because canopy mortality and subsequent changes to forest ecosystems may
114 play out over years to decades, understanding the dynamics of such systems requires
115 direct observations over long time scales. We take advantage of long-term (1983-2015)
116 resurveys of forest structure and understory vegetation in three temperate old-growth
117 forest reserves in the Dinaric Mountains of Slovenia. The three forests have similar site
118 conditions and have all experienced a relatively severe decline of *A. alba* during the
119 study period, allowing a unique opportunity to examine how long-term mortality of a
120 canopy dominant influences tree regeneration and understory herbaceous diversity.
121 Another novel aspect of this study is that understory resurvey data are particularly rare
122 in old-growth forest conditions in the temperate zone of Europe. Many of the resurvey
123 studies in Europe have attributed long-term changes in herbaceous communities to
124 forest canopy change resulting from management activities, such as the development of
125 more closed canopy forests due to declines in harvesting intensity or abandonment of
126 traditional management practices (e.g. coppicing) (Brunet et al. 1997; Baeten et al.
127 2009; Hédli et al. 2010; Baeten et al. 2010; Verheyen et al. 2012; De Frenne et al. 2013).
128 Given that forest management is likely to confound the interpretation of understory
129 dynamics, working in old-growth conditions allowed us to focus on the effects of *A.*
130 *alba* dieback on the understory. Specifically, we ask 1) how tree regeneration and
131 understory species diversity and composition changed in the old-growth forests over
132 30+ years; and 2) are the observed changes mainly driven by mortality of *A. alba*?

133

134 Material and Methods

135 Study area

136

137 Sampling was carried out in three old-growth forest reserves, Rajhenavski Rog
138 (hereafter Rajhenav) (51 ha; 45°39'48" N, 15°00'25" E), Pecka (60 ha; 45°45'16" N,
139 14°59'38" E), and Strmec (16 ha; 45°37'19" N, 14°48'53" E). These reserves are located
140 within a large forested region of southeastern Slovenia, situated in the northern Dinaric
141 Mountain range. The temperate climate in the region receives approximately 1600 mm
142 of annual precipitation, which is relatively evenly distributed throughout the year; the
143 mean annual temperature at the nearest meteorological station (Kočevje; 461 m a.s.l.;
144 approx. 4-16 km from the study sites) was 8.4 °C for the period 1961-1990, and 8.8 °C
145 from 1981-2010. These long-term averages at the station would correspond to an annual
146 temperature closer to 6 °C at the elevation of the study locations, which all lie on the
147 upper plateau of the mountain range between 800 – 940 m a.s.l. The sites occur on
148 limestone bedrock and soils are predominantly Eutric Cambisols and Rendzic Leptosols
149 (Grčman et al. 2015), which can vary considerably in depth due to the underlying karst
150 geology, typified by sinkholes and occasional rock outcrops.

151 Forests in the three reserves are dominated by *A. alba* and *F. sylvatica*. A
152 number of other less shade tolerant tree species are sporadically present, including *Acer*
153 *pseudoplatanus*, *Ulmus glabra*, *Fraxinus excelsior*, and *Picea abies*. These sites have
154 stand structural features typical of temperate old-growth forests, including complex
155 structure, canopy trees that often exceed 80 cm in diameter and 40 m in height, and
156 large amounts of standing and lying deadwood (Nagel et al. 2017). While there is no
157 historical evidence that these stands have ever been managed, they have all been
158 indirectly influenced by anthropogenic drivers, including air pollution that presumably
159 played an important role in the dieback of *A. alba*, climate change, and high population
160 densities of red deer. The latter has resulted in chronic browsing of palatable tree
161 species, particularly *A. alba*, causing a pronounced recruitment failure across the region
162 (Nagel et al. 2015). Both of these processes have been well documented during the time
163 period of the study. Population densities of red deer, reconstructed from archival
164 hunting data, indicate that densities are high but have remained relatively stable over the
165 past three decades (i.e. approximately 12-15 deer / km²) (Nagel et al. 2015). To
166 document the dieback of *A. alba*, we draw upon archival data of the Slovenian Forest
167 Service, which surveys each reserve approximately every decade, whereby all live trees
168 within entire reserves are tallied in 5 cm diameter classes. A comparison of recent and
169 past inventories (the closest inventory years to those of the vegetation surveys) shows a
170 clear decline in the density of *A. alba* trees across nearly all diameter classes, and a

171 marked decline of canopy sized trees (i.e. trees > 30 cm DBH) across the three reserves
172 based on multiple inventories during the past 40 years (Figure 1).

173

174 Field measurements

175

176 Vegetation surveys were carried out in each of the study sites in 1983 as part of
177 a larger national level inventory of old-growth forests reserves in Slovenia (Hočevár et
178 al. 1995). Across the entire area of each reserve, 7 x 7 m plots were placed on a
179 systematic 1-ha grid, for a total of 62 plots in Rajhenav, 64 plots in Pecka, and 21 plots
180 in Strmec. Within each plot, all vascular plants were recorded in herb, shrub, and tree
181 layers. The herb layer consisted of all herbaceous and woody species, while the shrub
182 layer only included woody species. The tree layer in 1983 was split into bottom, middle,
183 and upper stratum height classes and was recorded within a larger circular plot with a
184 radius of 20 m extending from the center of each vegetation plot (see Appendix S1 for
185 details). The abundance of each species was estimated using the following scale: 1– 5
186 specimens; 6 – 10 specimens; > 11 specimens and < 10 % cover; 11 – 20 % cover; 21 –
187 40%; 41 – 60 %; 61 – 80%; and 81 – 100%.

188 In 2015, we resurveyed all plots in each reserve from May to July, when both
189 spring ephemerals were still visible and late summer species were sufficiently
190 developed. Species abundance was estimated using the same scale as in the original
191 survey. Plots were not permanently located in the original survey, but were drawn on
192 detailed maps. These maps were georeferenced to obtain coordinates of plot centers,
193 which were used in combination with field notes taken during the original inventories
194 (information on topography, sink holes, rock outcrops, etc.) to relocate plots in the field.
195 Plot locations were also double checked to ensure that the distance and bearing between
196 plots matched the original grid. Plot size and vegetation sampling matched the original
197 approach and cover estimation followed the same scale described above. We
198 nevertheless keep in mind that relocation and observer errors can be significant
199 (Verheyen et al. 2018), such that interpretation should be done with care.

200 Soils were also sampled in 2015 to characterize plot level site conditions.
201 Sampling was carried out on a subset of 5 locations within each plot (i.e. corners and
202 center). The depth of the ectorganic horizon was recorded and then removed; a 10 cm
203 deep sample of mineral soil was then sampled using a 3 cm diameter auger. These
204 subsamples were combined, dried to constant weight at 40°C for 48h, ground, and

205 sieved over a 2 mm mesh. Samples were analysed for pH-KCl by shaking a 1:5 ratio
206 soil/KCl (1M) mixture for 5 min. at 300 rpm and measured with a pH meter (Orion
207 920A with pH electrode, model Ross Sure-flow 8172 BNWP, Thermo Scientific Orion,
208 USA). For total N and C, the samples were combusted at 1200°C and gases were
209 measured with a thermal conductivity detector in a CNS elemental analyzer (vario
210 Macro Cube, Elementar, Germany).

211 To augment our data on understory changes during the study period, we also
212 compiled published and original archival data on regeneration densities of *F. sylvatica*
213 (by height class) surveyed at different times during the period covered by the study.
214 These regeneration inventories were carried out with a relatively large number of plots
215 systematically distributed across reserves, and provide a good indication of reserve wide
216 changes in regeneration structure over time. For a detailed description of these
217 inventories, refer to Appendix S2.

218

219 Data analyses

220

221 We first examined variation in soil characteristics among the three reserves
222 because this could confound our interpretation of understory dynamics. Although plot
223 level soil pH and C/N ratio varied widely within individual reserves, there was broad
224 overlap among the three reserves (Appendix S3). Soils were therefore sufficiently
225 similar to allow for further examination of how changes to the canopy across the
226 reserves influenced understory dynamics.

227 The second step in the analysis focused on characterizing the changes in the tree
228 canopy and regeneration layers over the 32-year study period. To prepare the data for
229 this step, cover estimates for each species were transformed from the scale used in the
230 field surveys to cover values (Appendix S1). We also combined several of the
231 vegetation layers within each survey year to make the data more comparable between
232 surveys; the final layer structure used in the analyses consisted of the herb (all herb
233 species; woody species less than 30 cm in height), regeneration (30 cm - 5 m in height),
234 subcanopy (5 - 20 m), and canopy layers (> 20 m) (Appendix S1). Changes in the cover
235 of each layer were examined with paired t-tests, taking into account the dependence of
236 the old and new surveys.

237 The third part of the analysis focused on changes in the understory herb layer
238 across the sample period, and included several measures of α , β , and γ diversity. Alpha

239 (α) diversity was calculated as species richness and Shannon's Index for every plot
240 using the vegan package in R (Oksanen et al. 2017). Beta (β) diversity was estimated as
241 model-based beta diversity using the approach of Baeten et al. (2014), which quantifies
242 changes in community heterogeneity over time using presence/absence data, providing a
243 general indication of community convergence or divergence. Gamma (γ) diversity was
244 based on reserve-scale species richness and total species richness across all three
245 reserves. We also performed an indicator species analysis to assess the strength and
246 statistical significance of the change in herb species occurrence between the two
247 surveys. This analysis was done with the "indicspecies" R package (Cáceres &
248 Legendre 2009).

249 The fourth part of the analyses examined potential mechanisms of observed
250 changes based on proxies for environmental conditions. We calculated plot level
251 Ellenberg indicator values for light, temperature, soil moisture, soil reaction/pH, and
252 soil nitrogen for each survey year; these indicator values allow inference into the
253 underlying drivers of understory dynamics during the survey period (Diekmann 2003).
254 Indicator values were calculated according to Pignatti (2005), who revised Ellenberg's
255 values for the flora of Italy (the northeastern region of Italy has a similar flora to
256 Slovenia). Note that the calculations presented here were weighted with species cover;
257 calculations based only on the presence/absence data gave comparable results.
258 Wilcoxon signed rank tests for paired samples were used to compare measures of
259 diversity and indicator values between the two survey years for individual reserves.
260 Additionally, we performed a linear mixed effects analysis to examine changes across
261 the three reserves for the same measures of diversity and indicator values, with reserve
262 as a random effect and survey year as a fixed effect; this analysis was carried out with
263 *lme4* (Bates et al. 2015). All analyses were performed in R (R Core Team 2018).

264

265 Results

266

267 *Tree cover and regeneration dynamics*

268

269 Across the three reserves, there were consistent changes in the tree layers
270 between 1983 and 2015. Canopy layer cover declined in all three reserves, although the
271 change was only significant in Pecka and Rajhenav (Fig 2a). These changes in canopy

272 cover are consistent with the decline of *A. alba* across the reserves during the past four
273 decades (Fig 1). The decline in tree canopy cover was accompanied by a consistent
274 increase in cover of the subcanopy and regeneration layers during the study period
275 across the reserves (Fig 2b,c). Both of these layers were dominated by *F. sylvatica* in all
276 three reserves. These changes were significant for Pecka and Rajhenav, and were
277 particularly pronounced in the subcanopy layer for each reserve.

278 Changes in cover of the different canopy layers are consistent with available
279 archival data on regeneration densities (Table 1). In both Rajhenav and Pecka, from
280 which we have sufficient archival data of repeated inventories, seedlings (10 - 50 cm in
281 height) of *F. sylvatica* decreased from approx. 15000 ha⁻¹ in the early 1980s to approx.
282 5000 ha⁻¹ in the 2000s. In contrast, the density of large saplings and pole sized trees
283 (200 cm in height to 10 cm diameter at breast height) increased from several hundred
284 per hectare in the 1980s to over 3000 ha⁻¹ in the 2000s. Although these inventories are
285 only snapshots in time, they indicate a clear recruitment pulse of *F. sylvatica* from small
286 seedlings to taller layers of the understory and subcanopy during the past four decades.
287 Only one inventory was available for Strmec in the year 2000, when there was a high
288 density of *F. sylvatica* saplings; many of these individuals recruited to the pole stage
289 during the course of the study period, but we lack recent data on densities.

290

291 *Herb-layer response*

292

293 There were marked decreases in Gamma-diversity for each reserve and the
294 whole study region; across all three reserves, there was a decrease from 159 different
295 species in the 1983 inventory to 127 species in 2015 (Table 2). There was also a
296 significant decline in plot level species richness and Shannon diversity from 1983 to
297 2015 within each reserve (Fig 3, Table 2). Changes in species evenness were not
298 consistent across the three reserves (Table 2).

299 The model-based analysis of beta-diversity highlighted significant community
300 convergence between 1983 and 2015 for each reserve and for the pooled dataset ($\Delta D = -$
301 3554; $P < 0.001$) (Appendix S4), indicating a pronounced process of floristic
302 homogenization in the study region. This process was almost exclusively driven by
303 initially rare species (i.e. those present in < 10% of plots in 1983 inventories) that
304 became rarer or entirely absent over time, such that they contributed less to
305 heterogeneity among plots (Fig 4). Only a few species were significantly community-

306 divergent in the pooled dataset; these primarily included species that were initially very
307 common that decreased over time, such as *Oxalis acetosella*, *Daphne mezereum*, and
308 *Festuca altissima*. The indicator species analysis revealed a large number of species that
309 were significantly associated with the old survey, while there were no species that were
310 associated with the recent survey (Appendix S5). Many of the species that were
311 associated with the old survey and showed strong declines included a number of “gap”
312 species that require higher understory light levels, such as *Rubus* species, *Salvia*
313 *glutinosa*, *Fragaria vesca*, *Bromopsis ramosa*, and *Lonicera* species. Across all the
314 sites, only a few herb species consistently increased in frequency and cover, such as the
315 spring ephemerals *Anemone nemorosa*, *Arum maculatum*, and *Cardamine enneaphyllos*.

316 Changes in mean Ellenberg values between the surveys varied among the
317 different indicators and reserves (Table 2, Fig 5). The mean index for light significantly
318 decreased for all three reserves and the pooled dataset (Appendix S6). The only other
319 indicator that showed a significant change on the pooled dataset was soil reaction/pH,
320 which increased between the surveys (Appendix S6). Changes in other indicators,
321 including soil moisture, temperature, and nitrogen, were either non-significant or were
322 inconsistent among sites.

323

324 Discussion

325

326 We observed significant biodiversity losses and homogenization of the
327 herbaceous understory plant community over three decades in the three old-growth
328 forests sites. The dynamics of both the tree and herbaceous community indicate a
329 cascading influence of *A. alba* mortality. The long-term decline of *A. alba* in the canopy
330 layer resulted in a protracted recruitment pulse of *F. sylvatica*. This subcanopy layer of
331 large *F. sylvatica* saplings and pole-sized trees that developed over the past few decades
332 currently covers relatively large areas of the reserves. When *F. sylvatica* is leafed out,
333 the amount of light that reaches the forest floor beneath this subcanopy layer is very
334 low. Although our observational data cannot provide a rigorous mechanistic
335 explanation, we suspect that the decline in understory light was the main mechanism
336 that caused the loss in herb diversity and homogenization of the understory community
337 over time across the sites.

338 The only Ellenberg values that showed significant changes in the pooled dataset
339 included a decrease in light and an increase in soil reaction/pH, both of which are

340 consistent with the cascading effects triggered by the loss of *A. alba* in the canopy.
341 Minimum levels of diffuse light beneath dense patches of *F. sylvatica* saplings and
342 pole-sized trees measured at the study sites were as low as 1.10% (Adamič 2016). This
343 likely explains the decline of light demanding species that typically occur in forest gaps,
344 such as *Salvia glutinosa*, *Fragaria vesca*, and *Rhamnus fallax* (Fig 6). Moreover, these
345 low light levels (e.g. < 2%) likely fall short of the requirements of even the most shade
346 tolerant herb species (Leuschner & Ellenberg 2017). For example, *O. acetosella* and
347 *Galium odoratum*, two of the most shade tolerant and abundant species in the study
348 showed a marked loss of cover during the study period (Fig 6). Likewise, species that
349 maintain green foliage throughout the summer, such as *Brachypodium sylvaticum*, *G.*
350 *odoratum*, *Hordelymus europaeus*, and *Omphalodes verna*, may be particularly prone to
351 the deep shade cast by *F. sylvatica* (Fig 6) (Schmidt 2009). The marked decline in light
352 was likely the main driver for the pronounced decline or complete loss of many of the
353 rare species, especially those with moderately higher light requirements, which
354 contributed to the strong pattern of community convergence for most species. Some of
355 the few species that increased in frequency and cover during the study interval were
356 spring ephemerals, including *A. nemorosa*, *A. maculatum*, and *C. enneaphyllos* (Fig 6).
357 These species have likely benefited from increased light early in the growing season
358 (prior to leaf-out of *F. sylvatica*, which has relatively late leaf out phenology) due to the
359 loss of *A. alba* in the canopy. This is consistent with the loss of spring ephemerals that
360 has been documented when conifers are planted on broadleaf forest sites (Pigott 1990).
361 It is also possible that spring ephemerals may have additionally benefited due to the
362 decline in cover of other dominant competitors in the herb layer, such as *O. acetosella*
363 or *G. odoratum* (Fig 6) (Eber 1972).

364 In addition to the loss of light, a secondary mechanism contributing to the
365 understory changes observed here could be associated with changes in litter
366 characteristics. *Fagus sylvatica* produces leaf litter that differs in physical and chemical
367 properties compared to the coniferous litter and humus of *A. alba*. The decrease in soil
368 acidity indicated by the change in the herb community is also consistent with the
369 decline of *A. alba* and replacement by *F. sylvatica*. Working in mixed *Fagus-Abies*
370 stands, Paluch and Gruba (2012) found increased organic matter accumulation, lower
371 pH, and lower soil moisture when the local density of *A. alba* increased. Augusto et al
372 (2003) reported thicker litter with higher C/N ratios and lower pH for soils under *A.*
373 *alba* compared to those under *F. sylvatica*, although these differences were moderate;

374 likewise, they reported that herb species beneath *A. alba* were typical of moderately
375 more acidic and nutrient poor conditions compared to herbs growing under *F. sylvatica*.
376 Woziwoda and Kopec (2015) reported similar changes in the herb layer in stands that
377 experienced a long-term loss of *A. alba* and replacement by broadleaf species; they
378 documented an increase in nitrophilous species and a decline in species that tolerate
379 more nutrient poor and acidic conditions, presumably due to the decline in conifer litter
380 and the increase in easily decomposable broad leaf litter. According to
381 phytosociological literature, herb species that are typically associated with moderately
382 acidic conditions or a larger component of *A. alba* include species such as *Dryopteris*
383 *filix-mas*, *Oxalis acetosella*, and *F. altissima* (Pignatti & Pignatti 2013; Leuschner &
384 Ellenberg 2017), all of which significantly declined across the study sites. However,
385 because we do not have data on soil chemistry from the initial inventory, this
386 interpretation should be treated with caution.

387 Indeed, a number of other drivers, including deer browsing, climate change, and
388 nitrogen deposition, may have played some role in the understory dynamics observed in
389 our dataset. The density of red deer is high in the study area and has remained high
390 throughout the past three decades, at about 15 deer km⁻² (Nagel et al. 2015). Most
391 species, regardless of palatability, declined during the study period, while *A. nemorosa*,
392 documented as a preferred browse species (Pellerin et al. 2010), increased in cover.
393 These patterns suggest that deer browsing was unlikely a primary driver of the
394 understory herb dynamics observed here. However, herbivory has likely had an indirect
395 effect on herb communities via its influence on tree regeneration. Preferential browsing
396 has resulted in a long-term recruitment failure of *A. alba*, thereby facilitating the
397 contemporary dominance of *F. sylvatica* in the understory (Nagel et al. 2015). Long-
398 term nitrogen deposition and ongoing climate change may have also contributed to the
399 diversity declines (Stevens et al. 2004; Scheffers et al. 2016), but there was no clear
400 pattern for these drivers based on the Ellenberg indicator values. Several other studies
401 have documented that loss of light from canopy shading overrides the influence of
402 nitrogen deposition and climate warming on understory communities (Verheyen et al.
403 2012; De Frenne et al. 2013; De Frenne et al. 2015; Verheyen et al. 2017; Helm et al.
404 2017). We suspect that this has likely been the case in this study as well.

405 In addition to the cascading influence of *A. alba* decline, our results highlight the
406 importance of non-equilibrium dynamics in these old-growth forest systems. The
407 traditional view of forest dynamics, particularly in Central Europe, maintains that the

408 forest structure and composition of old-growth systems are stable at stands scales,
409 regulated by a shifting mosaic of small patches created by relatively continuous
410 mortality of old canopy trees. A more contemporary view suggests that old-growth
411 systems are in a continuous state of change in response to historical disturbances
412 (Woods 2000; Woods 2004; Nagel et al. 2014). Given the important influence that tree
413 canopies may exert on understory herbs via changes in light and litter characteristics, it
414 follows that herb communities would also exhibit long-term non-equilibrium dynamics in
415 old-growth forest systems. The results of our study are consistent with another multi-
416 decade study of understory dynamics in temperate old-growth forests of Michigan that
417 documented declines in fine-scale diversity; the authors attributed these changes to
418 long-term competitive filtering following historical disturbances that cause moderate
419 severity damage to forest canopies (Woods 2004; Woods et al. 2012).

420

421 *Conclusions*

422

423 Unlike the typical natural disturbances that cause abrupt changes to forests in the
424 temperate region of Europe, such as strong winds, heavy snow, or icestorms (Nagel et
425 al. 2017), the decline of *A. alba* was a species-specific and protracted episode of
426 increased mortality, a pattern that may be characteristic of the global-change type
427 dieback of forests due to a combination of nonnative insects, pathogens, and drought
428 under an increasingly warmer climate (Allen et al. 2010; Anderegg et al. 2015). In cases
429 when forest die-back targets foundational tree species (*sensu* Ellison et al. 2005), the
430 consequences for various ecosystem properties and functions may be particularly
431 pronounced. The effects of widespread hemlock mortality from the woolly adelgid in
432 the eastern USA is a thoroughly studied example (Ellison et al. 2005; Ellison 2014). In
433 many mixed *Fagus-Abies* type forests in Europe, the past decline of *A. alba* and
434 ongoing recruitment failure due to overbrowsing may result in an analogous situation.
435 We suspect that the continued loss of *A. alba* will likely result in a number of long-term
436 changes to these forest ecosystems, including the homogenization of the understory
437 environment and decreased herb diversity. These changes could have consequences for
438 ecosystem function (Clavel et al. 2011), but would require additional trait based
439 analyses (Baeten et al. 2014). The understory changes documented here may shed light
440 on some of the potential cascading consequences triggered by protracted episodes of
441 widespread tree mortality resulting from global change type drivers. Ongoing examples

442 include the invasive fungal pathogen (*Hymenoscyphus fraxineus*) affecting ash trees
443 across Europe (Pautasso et al. 2013), and numerous nonnative insects and pathogens in
444 North America, such as white pine blister rust, sudden oak death, beech bark disease,
445 and the emerald ash borer (Lovett et al. 2016).

446

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451

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453 T.A.N., K.V., P.D.F, and F.S. conceived of the research idea; J.J., G.I., and A.R.
454 collected data; G.I., J.J., and A.R., with help from P.D.F. and K.V performed statistical
455 analyses; T.A.N., with contributions from all authors, wrote the paper; all authors
456 discussed the results and commented on the manuscript.

457

458 Data Availability Statement: Data are available through forestREplot
459 (www.forestreplot.ugent.be)

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711 Table 1. Density of *Fagus sylvatica* regeneration (N-ha⁻¹) by size class sampled at
 712 different time periods during the course of the study. Only one inventory of *Fagus*
 713 regeneration was available for the Strmec reserve.

Size class	Height / size range	Rajhenav		Pecka		Strmec
		1984	2010	1980	2007	2000
seedlings	10 - 50 cm	15981	5012	14500	5640	15911
saplings	50 - 200 cm	4508	6175	4786	4726	13778
poles	200 cm - 10 cm dbh	161	3024	534	3569	376

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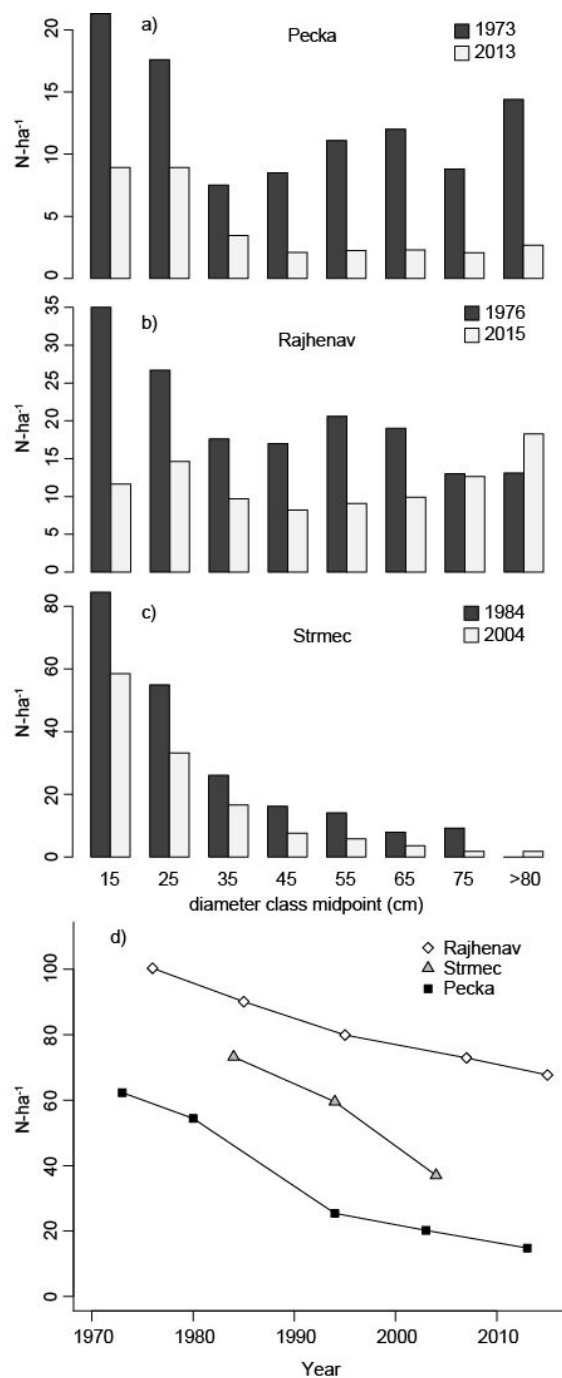
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719 Table 2.Changes in species diversity metrics and Ellenberg indicator values between 1983 and 2015 for the three old-growth forest reserves. SD =
720 standard deviation; z = z-value test statistic based on a Wilcoxon signed rank tests; n.s.: not significant;* P < 0.05; **P < 0.01; ***P < 0.001).

	Pecka					Rajhenav					Strmec							
	Mean 83	SD 83	Mean 15	SD 15	z	Mean 83	SD 83	Mean 15	SD 15	z	Mean 83	SD 83	Mean 15	SD 15	z			
Species richness	27.89	5.13	16.22	5.17	-6.71	***	25.71	4.50	18.19	4.92	-6.16	***	31.29	9.19	19.95	4.46	-3.60	***
Shannon diversity	2.28	0.28	1.85	0.32	-6.00	***	2.14	0.26	2.02	0.32	-2.33	*	2.63	0.31	2.01	0.39	-4.50	***
Evenness	0.69	0.07	0.67	0.08	-1.35	NS	0.66	0.06	0.70	0.08	-3.12	**	0.77	0.06	0.68	0.12	-2.90	**
Gamma diversity	107		85				99		83				127		90			
Ellenberg Values																		
Light	3.70	0.24	3.50	0.31	-4.10	***	3.87	0.27	3.47	0.30	-5.75	***	4.07	0.31	3.80	0.33	-2.77	**
Temperature	4.99	0.16	4.93	0.17	-2.59	**	4.79	0.10	4.82	0.17	-1.29	NS	4.95	0.17	5.03	0.17	-1.49	NS
Soil moisture	5.28	0.12	5.15	0.18	-5.35	***	5.10	0.14	5.20	0.18	-3.64	***	5.10	0.14	5.09	0.16	-0.58	NS
Soil pH	6.76	0.32	6.84	0.36	-1.73	NS	6.02	0.29	6.27	0.46	-3.74	***	6.82	0.22	6.84	0.33	-0.47	NS
Nitrogen	6.04	0.25	5.94	0.33	-2.48	*	5.64	0.23	5.74	0.33	-1.90	NS	5.57	0.35	5.72	0.46	-1.81	NS

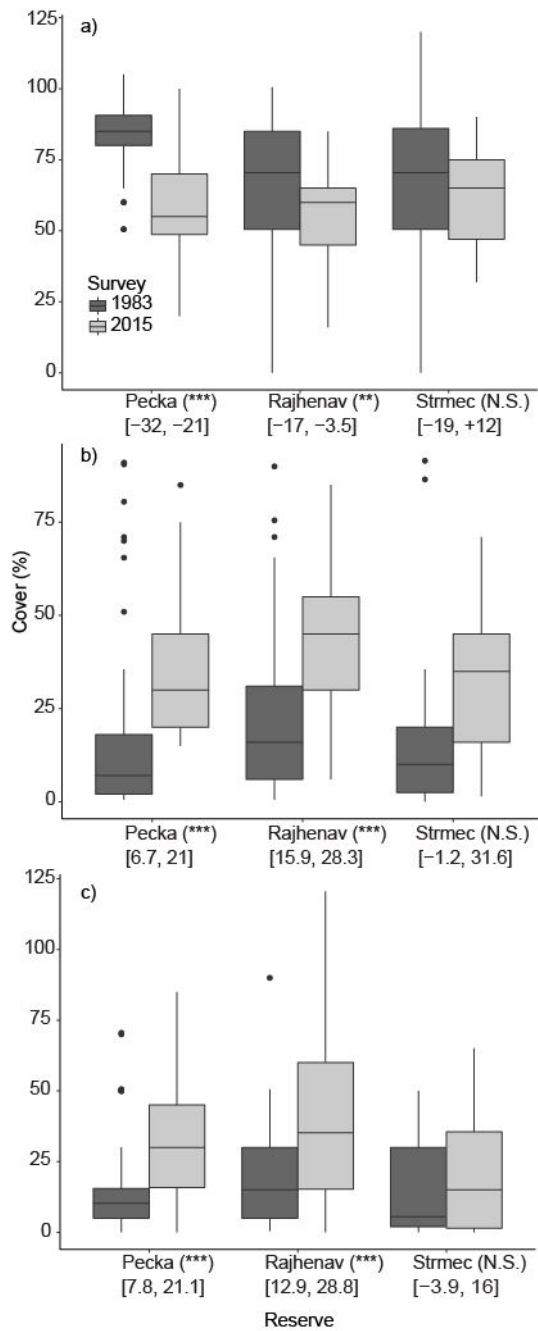
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732 Figure 1. Decline of *Abies alba* across the three old-growth forest reserves during the
 733 past four decades. Diameter distributions (at 1.37 m) in 10 cm size classes from
 734 available inventory years closest to the understory surveys in this study for the (a)
 735 Pecka, (b) Rajhenav, and (c) Strmec study sites, and (d) the density of canopy-sized *A.*
 736 *alba* trees > 30 cm in diameter for all available inventory years during the past four
 737 decades at the three sites. Data were extracted from complete inventories carried out
 738 approximately every decade, in which all live trees were tallied within 5 cm diameter
 739 classes in each reserve.

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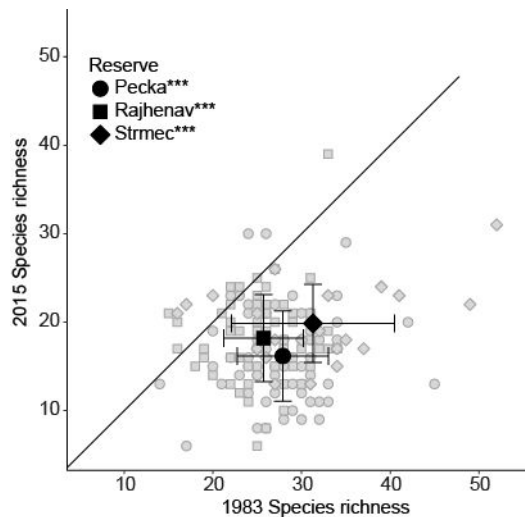
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742 Figure 2. Box plots showing plot-level changes in cover of a) canopy, b) subcanopy,
 743 and c) regeneration layers between 1983 and 2015 across the three old-growth forest
 744 reserves. Statistical differences in cover between the two survey years and 95%
 745 confidence intervals of the difference are indicated on the x-axis (paired t-tests, ** $P <$
 746 0.01 ; *** $P < 0.001$).

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752 Figure 3. Plot-level changes in species richness between 1983 and 2015 across the three
753 old-growth forest reserves. The line indicates a 1:1 relationship of no change. The grey
754 symbols denote individual plots, while the black symbols show the mean change for
755 each reserve. Statistical differences between the survey years are indicated in the legend
756 (Wilcoxon signed rank tests, *** $P < 0.001$). The decline in species richness was also
757 significant ($P < 0.001$) for the pooled dataset based on a linear mixed effects analysis (P
758 < 0.001) (Appendix S6).

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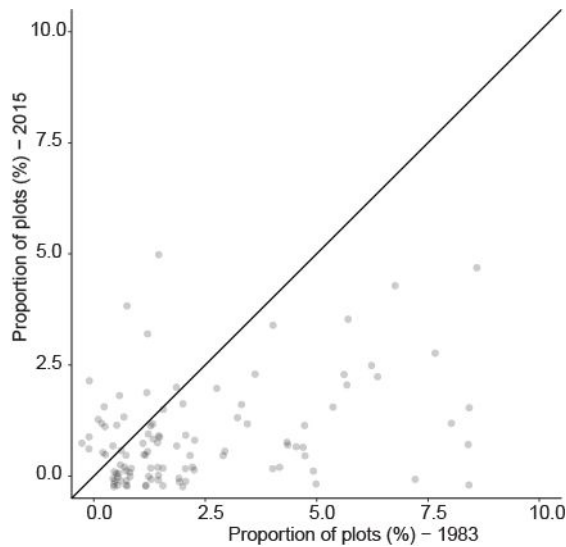
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777 Figure 4. Changes in the frequency of rare species between 1983 and 2015 across the
778 pooled dataset from the three old-growth forest reserves. Rare species were defined by
779 those present in < 10% of plots in 1983 inventories. The line indicates a 1:1 relationship
780 of no change. Note that a dispersion function was used to better illustrate those species
781 that were no longer present in 2015.

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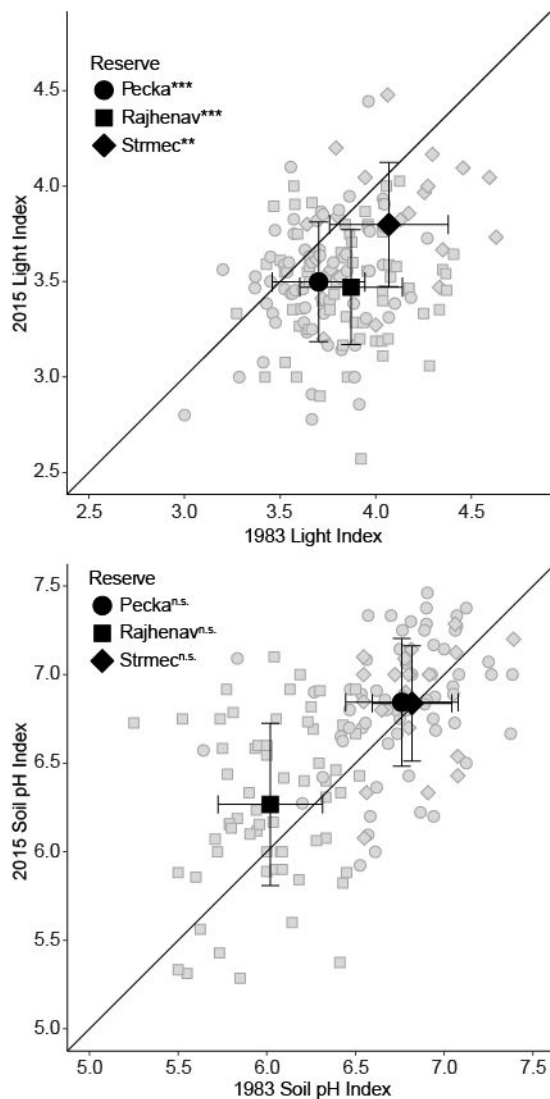
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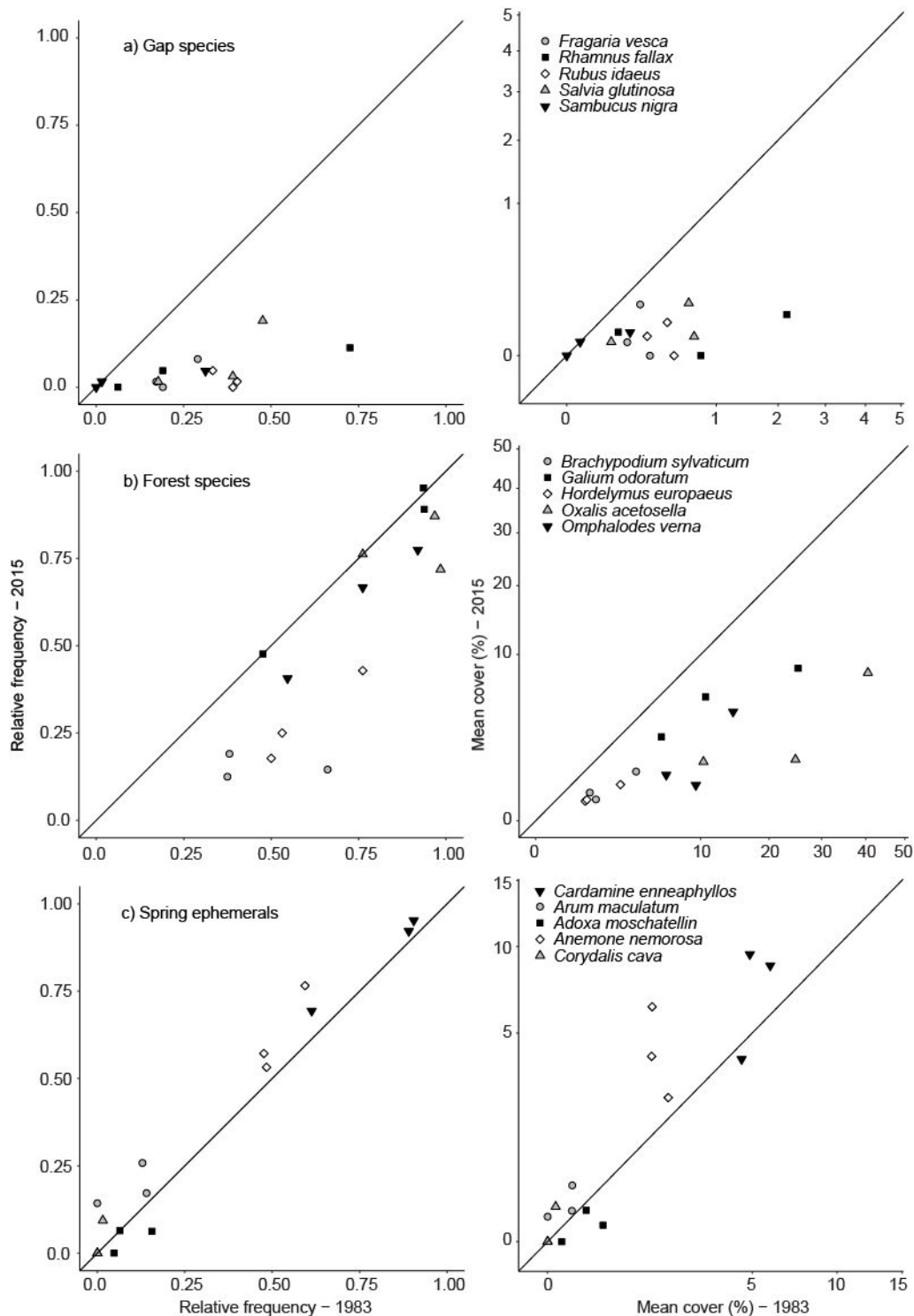
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800 Figure 5. Plot-level changes in Ellenberg indicator values for light and soil reaction/pH
 801 between 1983 and 2015 across the three old-growth forest reserves. Note that lower
 802 values of the light index indicate shade, while higher values correspond to increased
 803 light. Lower values for the pH Index indicate more acidic conditions, while higher
 804 values more alkaline. Lines indicate a 1:1 relationship of no change. The grey symbols
 805 denote individual plots, while black symbols show the mean change for each reserve.
 806 Statistical differences between the survey years are indicated in the legend (Wilcoxon
 807 signed rank tests, n.s.: not significant; ** $P < 0.01$; *** $P < 0.001$). Changes in both the
 808 light and soil reaction/pH index were significant for the pooled dataset based on a linear
 809 mixed effects analysis ($P < 0.001$) (Appendix S6).



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812 Figure 6. Changes in relative frequency and mean cover of selected species between
 813 1983 and 2015 across the three old-growth reserves. The species were selected to
 814 illustrate different responses to the cascading effects of *Abies alba* decline based on
 815 their contrasting life histories. They include (a) light demanding species that typically
 816 occur in forest gaps, (b) common species typical of the forest understory with

817 characteristics such as high shade tolerance or summer green foliage that were frequent
818 across the study sites, and (c) spring ephemerals. Frequency and cover values are shown
819 for each reserve. Lines indicate a 1:1 relationship of no change. Note the square root
820 transformation of the x-axis for mean cover.

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823 Supporting Information

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825 Appendix S1: Vegetation cover and height classes

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827 Appendix S2: Archival surveys of regeneration density

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829 Appendix S3: Soil characteristics

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831 Appendix S4: Beta diversity analysis

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833 Appendix S5: Indicator species analysis

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835 Appendix S6: Linear mixed effects analysis

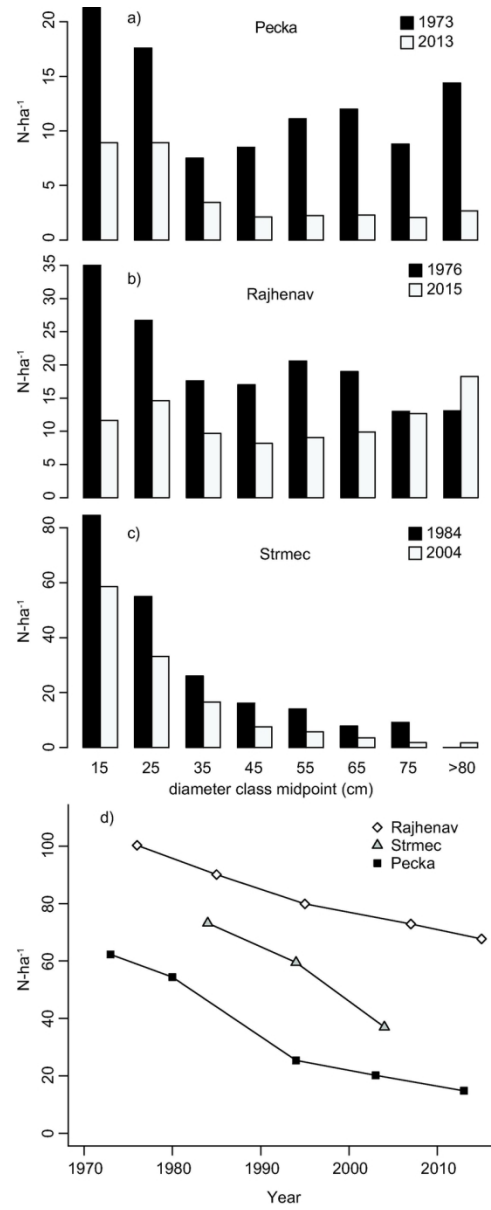


Figure 1

75x184mm (300 x 300 DPI)

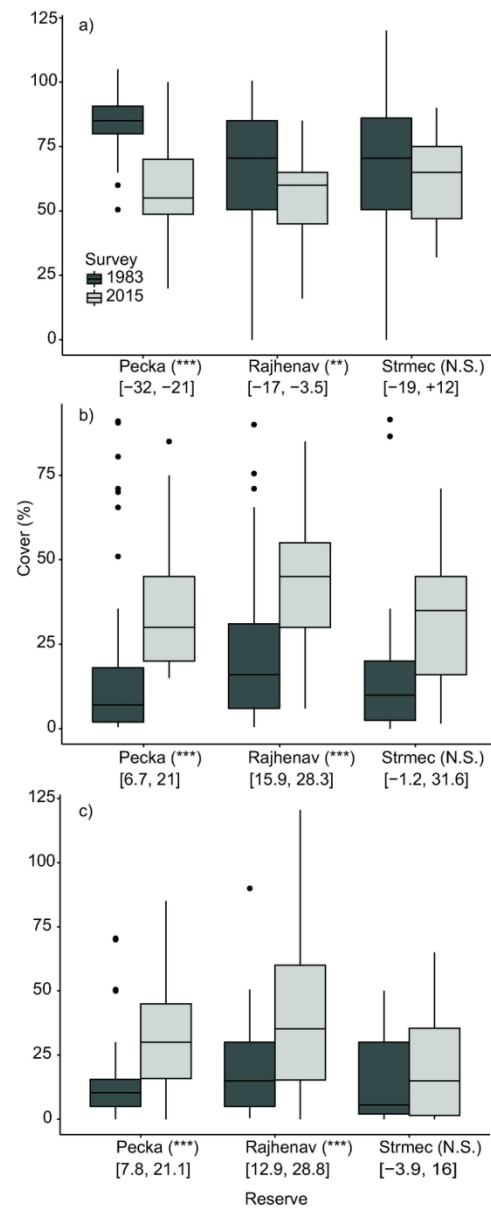


Figure 2

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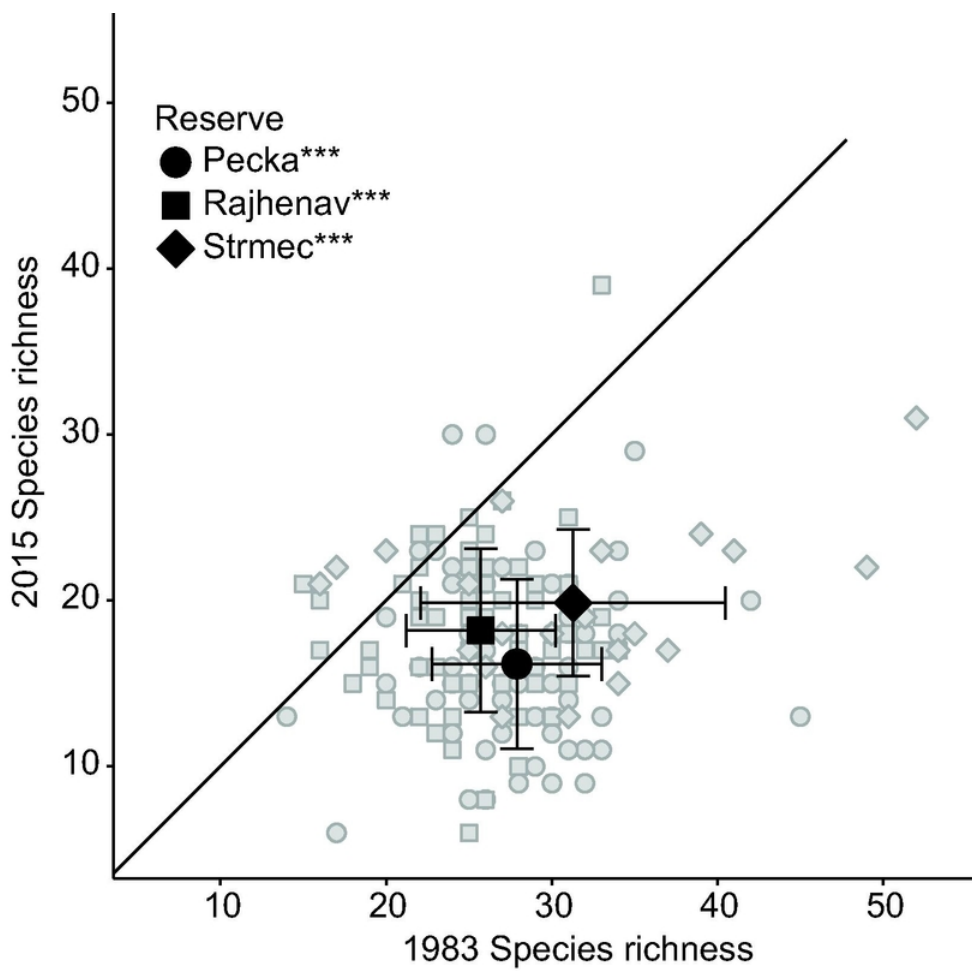


Figure 3

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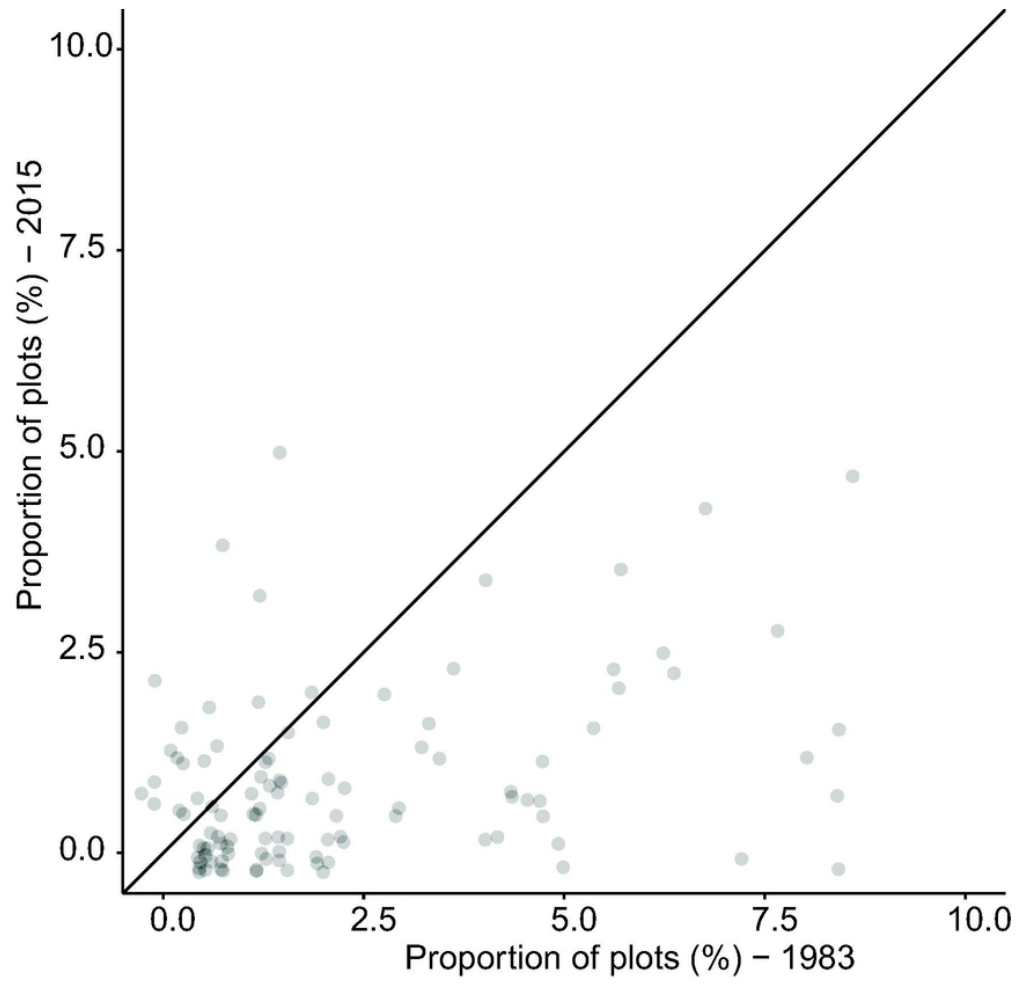


Figure 4

73x70mm (300 x 300 DPI)

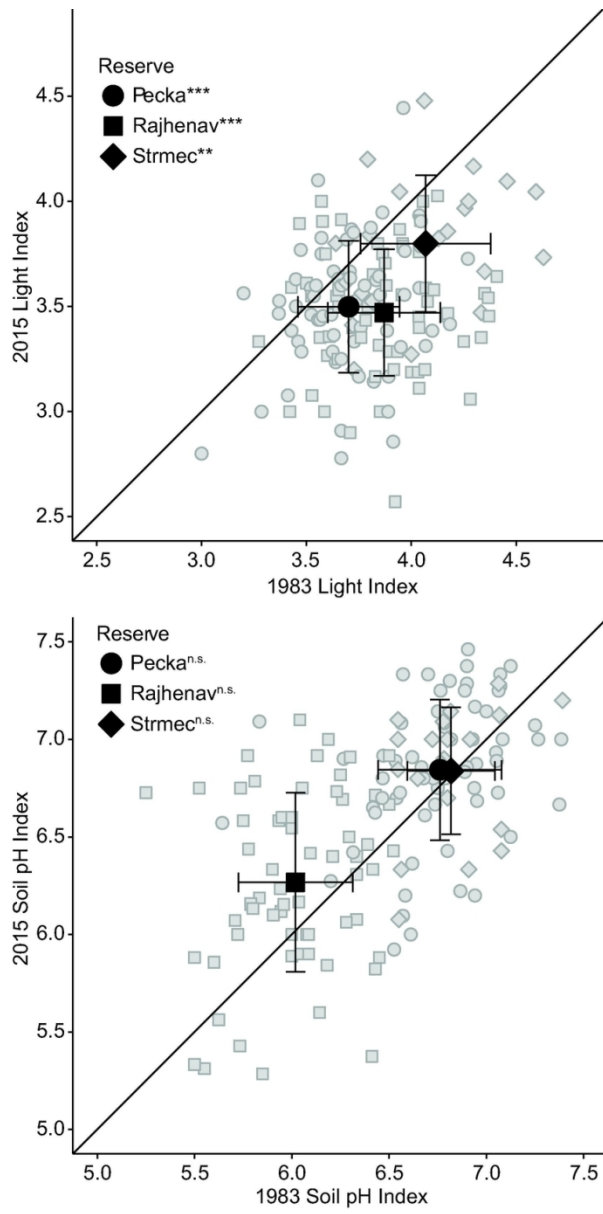


Figure 5

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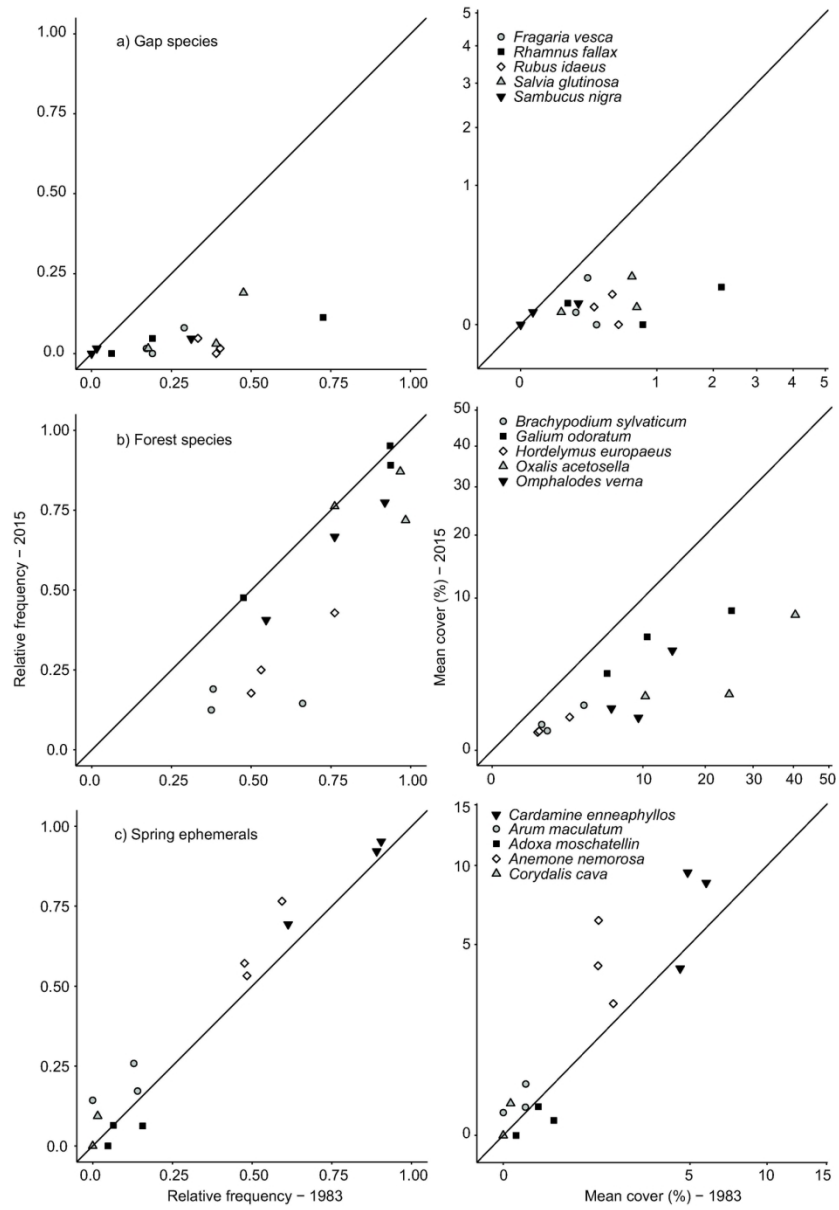


Figure 6

134x196mm (300 x 300 DPI)



119x89mm (300 x 300 DPI)

We examined how long-term mortality of a foundation conifer tree influenced understory vegetation dynamics. Canopy mortality caused a recruitment pulse of broad-leaf regeneration, which resulted in a significant loss of herb diversity and homogenization of the understory community. This study sheds light on the potential cascading consequences triggered by episodes of increased tree mortality resulting from global change type drivers.