



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

Thomas A. Nagel¹  | Giovanni Iacopetti² | Jernej Javornik¹ | Andrej Rozman¹ | Pieter De Frenne³ | Federico Selvi² | Kris Verheyen³ 

¹ Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia

² Department of Agriculture, Food, Environment and Forest Sciences, University of Florence, Firenze, Italy

³ Forest and Nature Lab, Department of Environment, Ghent University, Ghent, Belgium

Correspondence

Thomas A. Nagel, Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia.
Email: tom.nagel@bf.uni-lj.si

Funding information

T.A.N. and J.J. received funding from the Pahernik Foundation and the Slovene Science Foundation (Program financing). K.V. benefited from an ERC Consolidator Grant (PASTFORWARD; grant no. 614839). P.D.F. received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833). F.S. and G.I. benefited from grants by the Italian Ministry of University and Research (M.I.U.R.).

Co-ordinating Editor: Monika Wulf

Abstract

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

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

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

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

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

KEYWORDS

beech, fir decline, forest dieback, forest herbs, foundation species, old-growth, resurveys, semi-permanent plots, tree mortality, understorey vegetation

1 | INTRODUCTION

There is widespread concern that global-change stressors, particularly drought accompanied by warmer temperatures and associated increases in pests and pathogens, may lead to forest die-off, decline, or chronic increases in tree mortality (Allen, Breshears, & McDowell, 2015; Anderegg et al., 2015; Jactel et al., 2012; van Mantgem et al., 2009). Such mortality processes will likely cause cascading effects in forest ecosystems (Millar & Stephenson, 2015; Shiels, Gonzalez, Lodge, Willig, & Zimmerman, 2015; Wardle, Bardgett, Callaway, & Van der Putten, 2011), especially when mortality hits tree species that play a foundational role in a given forest community. Loss of foundational tree species has been documented to cause important changes to various properties and processes of forest ecosystems, including forest microclimate, understorey herbs and tree regeneration, invertebrate communities, soil and litter properties, decomposition rates, and nutrient cycling (Ellison et al., 2005; Kendrick, Ribbons, Classen, & Ellison, 2015; Lustenhouwer, Nicoll, & Ellison, 2012; Orwig et al., 2013; Sackett et al., 2011).

Abies alba (silver fir), a conifer species distributed across mountain regions of the European temperate and Mediterranean zones (Mauri, de Rigo, & Caudullo, 2016), shares many of the characteristics of a foundation tree species (sensu Ellison et al., 2005). It is both locally abundant and widespread over large regions, and has ecological traits that make a unique contribution to its habitat. It primarily occurs in mixed forests with *Fagus sylvatica* (beech), where it often represents a large proportion of stand-level basal area. It is one of the tallest and most shade-tolerant tree species in Europe, traits which together contribute to the structural heterogeneity and resource use complementarity of mixed species stands (Forrester, 2014; Nagel, Svoboda, & Kopal, 2014; Tinner et al., 2013). *Abies alba* has a strong influence on understorey microclimate and soil properties due to the deep shade and litter cast from the canopy (Augusto, Dupouey, & Ranger, 2003; Augusto, Ranger, Binkley, & Rothe, 2002; Paluch & Gruba, 2012; Pizzeghello, Zanella, Carletti, & Nardi, 2006). Finally, both living and dead trees of *A. alba* support a diverse assemblage of flora and fauna (Brändle & Brandl, 2001; Floren & Gogala, 2002; Lagana, Salerni, Barluzzi, Perini, & De Dominicis, 2000; Táborska, Privetity, Vrska, & Ódor, 2015).

Over a large part of its range, many populations of *A. alba* experienced a protracted decline characterized by increased levels of morbidity and mortality during the 1970s–1990s (Diaci et al., 2011), now thought to be largely the result of high levels of atmospheric SO₂ pollution (Elling, Dittmar, Pfaffelmoser, & Rotzer, 2009). For some populations that experienced more severe dieback, this event is analogous to the global change-type dieback that is gaining attention in the literature, and affords a unique glimpse into the long-term effects of such events on forest ecosystem dynamics. Few studies, however, have examined how this episode of increased mortality influenced long-term processes and patterns, such as tree regeneration and understorey herb dynamics (Nagel, Diaci, Jerina, Kopal, & Rozenbergar, 2015). Changes to the canopy can exert an important

influence on understorey communities via changes in light, microclimate, and soils (Augusto et al., 2002; De Frenne et al., 2013; Verheyen et al., 2012; Woods, Hicks, & Schultz, 2012; Wulf & Naaf, 2009). Understanding these mechanistic links between the canopy and understorey, particularly for the herbaceous community that represents most of the plant diversity in temperate forests (Gilliam, 2007), will be important for developing effective conservation and forest management strategies under global change.

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

2 | MATERIALS AND METHODS

2.1 | Study area

Sampling was carried out in three old-growth forest reserves, Rajhenavski Rog (hereafter Rajhenav; 51 ha; 45°39'48" N, 15°00'25" E), Pecka (60 ha; 45°45'16" N, 14°59'38" E), and Strmec (16 ha; 45°37'19" N, 14°48'53" E). These reserves are located within a large forested region of southeastern Slovenia, situated in the northern Dinaric Mountain range. The temperate climate in the region receives ~1,600 mm of annual precipitation, which is relatively evenly distributed throughout the year; the mean annual temperature at the nearest meteorological station (Kočevje; 461 m a.s.l.; ~4–16 km from the study sites) was 8.4°C for the period 1961–1990, and 8.8°C from 1981 to 2010. These long-term averages at the station would correspond to an annual temperature closer to 6°C at the elevation

of the study locations, which all lie on the upper plateau of the mountain range between 800 and 940 m a.s.l. The sites occur on limestone bedrock and soils are predominantly Eutric Cambisols and Rendzic Leptosols (Grčman et al., 2015), which can vary considerably in depth due to the underlying karst geology, typified by sinkholes and occasional rock outcrops.

Forests in the three reserves are dominated by *A. alba* and *F. sylvatica*. A number of other less shade-tolerant tree species are sporadically present, including *Acer pseudoplatanus*, *Ulmus glabra*, *Fraxinus excelsior*, and *Picea abies*. These sites have stand structural features typical of temperate old-growth forests, including complex structure, canopy trees that often exceed 80 cm in diameter and 40 m in height, and large amounts of standing and lying deadwood (Nagel, Firm et al., 2017; Nagel, Mikac et al., 2017). While there is no historical evidence that these stands have ever been managed, they have all been indirectly influenced by anthropogenic drivers, including air pollution that presumably played an important role in the dieback of *A. alba*, climate change, and high population densities of red deer. The latter has resulted in chronic browsing of palatable tree species, particularly *A. alba*, causing a pronounced recruitment failure across the region (Nagel et al., 2015). Both of these processes have been well documented during the time period of the study. Population densities of red deer, reconstructed from archival hunting data, indicate that densities are high but have remained relatively stable over the past three decades (i.e. ~12–15 deer/km²; Nagel et al., 2015). To document the dieback of *A. alba*, we draw upon archival data of the Slovenian Forest Service, which surveys each reserve approximately every decade, whereby all live trees within entire reserves are tallied in 5 cm diameter classes. A comparison of recent and past inventories (the closest inventory years to those of the vegetation surveys) shows a clear decline in the density of *A. alba* trees across nearly all diameter classes, and a marked decline of canopy-sized trees (i.e. trees >30 cm DBH) across the three reserves based on multiple inventories during the past 40 years (Figure 1).

2.2 | Field measurements

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

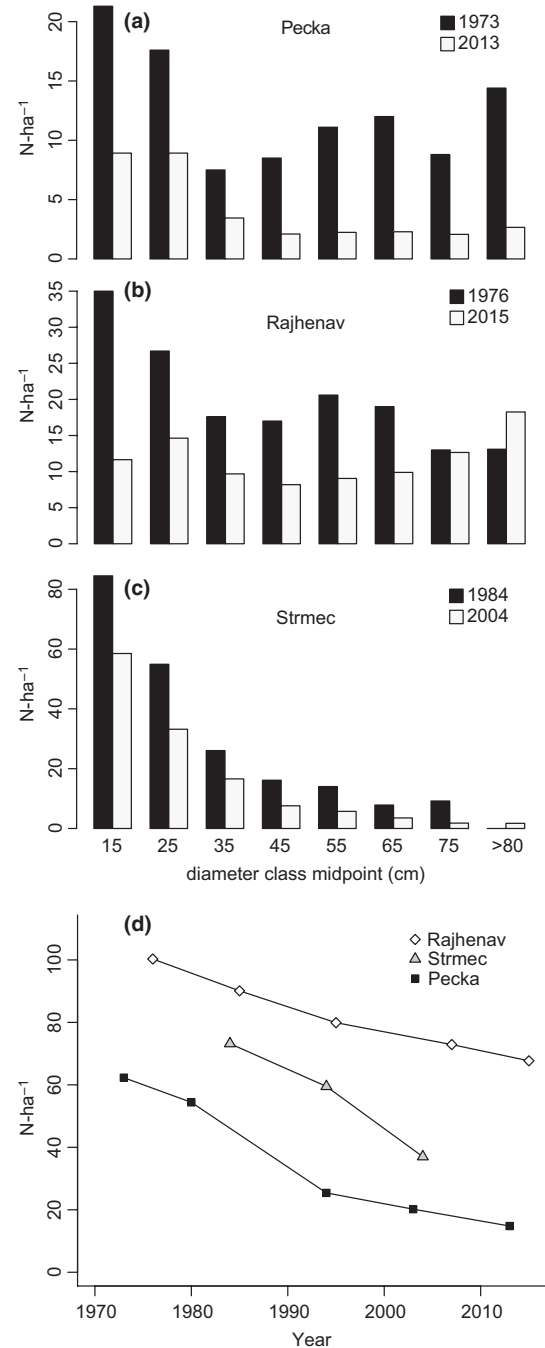


FIGURE 1 Decline of *Abies alba* across the three old-growth forest reserves during the past four decades. Diameter distributions (at 1.37 m) in 10 cm size classes from available inventory years closest to the understory surveys in this study for the (a) Pecka, (b) Rajhenav, and (c) Strmec study sites,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

In 2015, we resurveyed all plots in each reserve from May to July, when both spring ephemerals were still visible and late summer species were sufficiently developed. Species abundance was estimated

using the same scale as in the original survey. Plots were not permanently located in the original survey, but were drawn on detailed maps. These maps were georeferenced to obtain coordinates of plot centers, which were used in combination with field notes taken during the original inventories (information on topography, sink holes, rock outcrops, etc.) to relocate plots in the field. Plot locations were also double checked to ensure that the distance and bearing between plots matched the original grid. Plot size and vegetation sampling matched the original approach and cover estimation followed the same scale described above. We nevertheless keep in mind that relocation and observer errors can be significant (Verheyen et al., 2018), such that interpretation should be done with care.

Soils were also sampled in 2015 to characterize plot level site conditions. Sampling was carried out on a subset of five locations within each plot (i.e., corners and center). The depth of the ectorganic horizon was recorded and then removed; a 10 cm deep sample of mineral soil was then sampled using a 3 cm diameter auger. These subsamples were combined, dried to constant weight at 40°C for 48 hr, ground, and sieved over a 2 mm mesh. Samples were analysed for pH-KCl by shaking a 1:5 ratio soil/KCl (1 M) mixture for 5 min at 300 rpm and measured with a pH meter (Orion 920A with pH electrode, model Ross Sure-flow 8172 BNWP, Thermo Scientific Orion, Waltham, MA, USA). For total N and C, the samples were combusted at 1,200°C and gases were measured with a thermal conductivity detector in a CNS elemental analyzer (vario Macro Cube; Elementar Analysensysteme GmbH, Langensfeld, Germany).

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

2.3 | Data analyses

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

The second step in the analysis focused on characterizing the changes in the tree canopy and regeneration layers over the 32-year study period. To prepare the data for this step, cover estimates for each species were transformed from the scale used in the field surveys to cover values (Appendix S1). We also combined several of the vegetation layers within each survey year to make the data more comparable between surveys; the final layer structure used in the analyses consisted of the herb (all herb species; woody species

<30 cm in height), regeneration (30 cm–5 m in height), subcanopy (5–20 m), and canopy layers (>20 m; Appendix S1). Changes in the cover of each layer were examined with paired *t* tests, taking into account the dependence of the old and new surveys.

The third part of the analysis focused on changes in the understorey herb layer across the sample period and included several measures of α , β , and γ diversity. Alpha (α) diversity was calculated as species richness and Shannon's Index for every plot using the vegan package in R (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). Beta (β) diversity was estimated as model-based beta diversity using the approach of Baeten et al. (2014), which quantifies changes in community heterogeneity over time using presence/absence data, providing a general indication of community convergence or divergence. Gamma (γ) diversity was based on reserve-scale species richness and total species richness across all three reserves. We also performed an indicator species analysis to assess the strength and statistical significance of the change in herb species occurrence between the two surveys. This analysis was done with the "indicspecies" R package (Cáceres & Legendre, 2009).

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

3 | RESULTS

3.1 | Tree cover and regeneration dynamics

Across the three reserves, there were consistent changes in the tree layers between 1983 and 2015. Canopy layer cover declined in all three reserves, although the change was only significant in Pecka and Rajhenav (Figure 2a). These changes in canopy cover are consistent with the decline of *A. alba* across the reserves during the past four decades (Figure 1). The decline in tree canopy cover was accompanied by a consistent increase in cover of the subcanopy and regeneration layers during the study period across the reserves

(Figure 2b, c). Both of these layers were dominated by *F. sylvatica* in all three reserves. These changes were significant for Pecka and Rajhenav, and were particularly pronounced in the subcanopy layer for each reserve.

Changes in cover of the different canopy layers are consistent with available archival data on regeneration densities (Table 1). In both Rajhenav and Pecka, from which we have sufficient archival

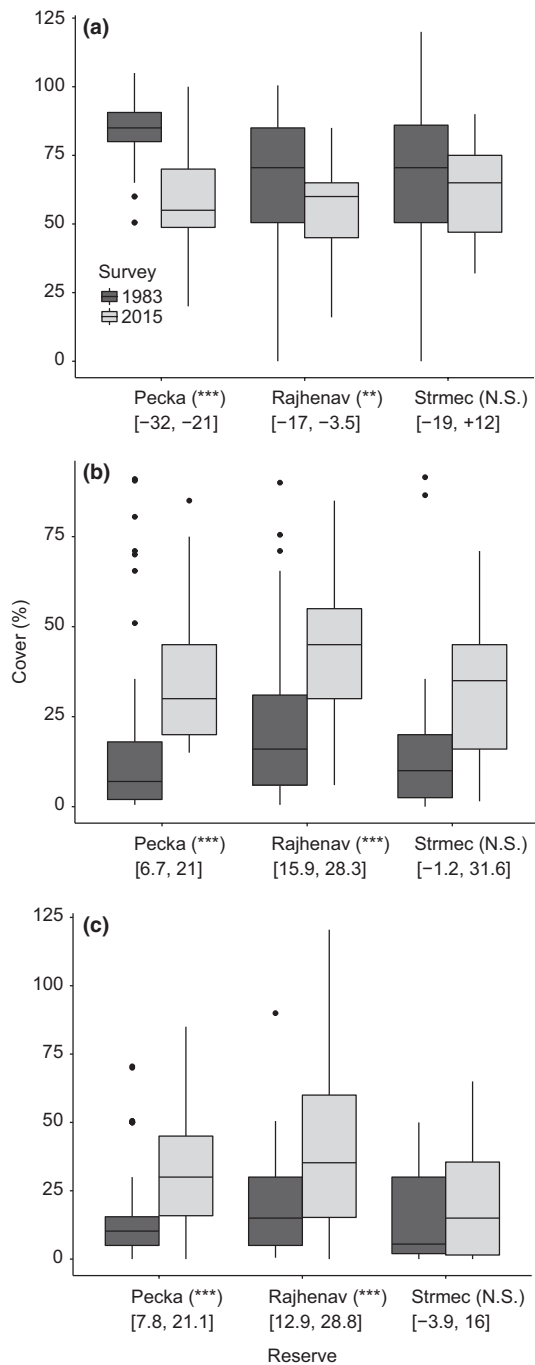


FIGURE 2 Box plots showing plot-level changes in cover of (a) canopy, (b) subcanopy, and (c) regeneration layers between 1983 and 2015 across the three old-growth forest reserves. Statistical differences in cover between the two survey years and 95% confidence intervals of the difference are indicated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

data of repeated inventories, seedlings (10–50 cm in height) of *F. sylvatica* decreased from $\sim 15,000 \text{ ha}^{-1}$ in the early 1980s to $\sim 5,000 \text{ ha}^{-1}$ in the 2000s. In contrast, the density of large saplings and pole sized trees (200 cm in height to 10 cm diameter at breast height) increased from several hundred per hectare in the 1980s to over $3,000 \text{ ha}^{-1}$ in the 2000s. Although these inventories are only snapshots in time, they indicate a clear recruitment pulse of *F. sylvatica* from small seedlings to taller layers of the understorey and subcanopy during the past four decades. Only one inventory was available for Strmec in the year 2000, when there was a high density of *F. sylvatica* saplings; many of these individuals recruited to the pole stage during the course of the study period, but we lack recent data on densities.

3.2 | Herb-layer response

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

The model-based analysis of beta-diversity highlighted significant community convergence between 1983 and 2015 for each reserve and for the pooled dataset ($\Delta D = -3,554$; $p < 0.001$; Appendix S4), indicating a pronounced process of floristic homogenization in the study region. This process was almost exclusively driven by initially rare species (i.e., those present in $<10\%$ of plots in 1983 inventories) that became rarer or entirely absent over time, such that they contributed less to heterogeneity among plots (Figure 4). Only a few species were significantly community-divergent in the pooled dataset; these primarily included species that were initially very common that decreased over time, such as *Oxalis acetosella*, *Daphne mezereum*, and *Festuca altissima*. The indicator species analysis revealed a large number of species that were significantly associated with the old survey, while there were no species that were associated with the recent survey (Appendix S5). Many of the species that were associated with the old survey and showed strong declines included a number of “gap” species that require higher understorey light levels, such as *Rubus* species, *Salvia glutinosa*, *Fragaria vesca*, *Bromopsis ramosa*, and *Lonicera* species. Across all the sites, only a few herb species consistently increased in frequency and cover, such as the spring ephemerals *Anemone nemorosa*, *Arum maculatum*, and *Cardamine enneaphyllos*.

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

Size class	Height/size range	Rajhenav		Pecka		Strmec
		1984	2010	1980	2007	2000
Seedlings	10–50 cm	15,981	5,012	14,500	5,640	15,911
Saplings	50–200 cm	4,508	6,175	4,786	4,726	13,778
Poles	200–10 cm dbh	161	3,024	534	3,569	376

Note: Only one inventory of *Fagus* regeneration was available for the Strmec reserve.

4 | DISCUSSION

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

The only Ellenberg values that showed significant changes in the pooled dataset included a decrease in light and an increase in soil reaction/pH, both of which are consistent with the cascading effects triggered by the loss of *A. alba* in the canopy. Minimum levels of diffuse light beneath dense patches of *F. sylvatica* saplings and pole-sized trees measured at the study sites were as low as 1.10% (Adamič, 2016). This likely explains the decline of light-demanding species that typically occur in forest gaps, such as *Salvia glutinosa*, *Fragaria vesca*, and *Rhamnus fallax* (Figure 6). Moreover, these low light levels (e.g. <2%) likely fall short of the requirements of even the most shade tolerant herb species (Leuschner & Ellenberg, 2017). For example, *O. acetosella* and *Galium odoratum*, two of the most shade tolerant and abundant species in the study showed a marked loss of cover during the study period (Figure 6). Likewise, species that maintain green foliage throughout the summer, such as *Brachypodium sylvaticum*, *Galium odoratum*, *Hordelymus europaeus*, and *Omphalodes verna*, may be particularly prone to the deep shade cast by *F. sylvatica* (Figure 6; Schmidt, 2009). The marked decline in light was likely the main driver for the pronounced decline or complete loss of many of the rare species, especially those with moderately higher light requirements, which contributed to the strong pattern of community convergence for most species. Some of the few species that increased in frequency and cover during the study interval were spring ephemerals, including *Anemone nemorosa*, *Arum maculatum*, and *Cardamine enneaphyllos* (Figure 6). These species have likely benefited from increased light early in the growing season (prior to leaf-out of *F. sylvatica*, which has relatively late leaf-out phenology)

TABLE 1 Density of *Fagus sylvatica* regeneration ($N\ ha^{-1}$) by size class sampled at different time periods during the course of the study

due to the loss of *A. alba* in the canopy. This is consistent with the loss of spring ephemerals that has been documented when conifers are planted on broadleaf forest sites (Pigott, 1990). It is also possible that spring ephemerals may have additionally benefited due to the decline in cover of other dominant competitors in the herb layer, such as *Oxalis acetosella* or *Galium odoratum* (Figure 6; Eber, 1972).

In addition to the loss of light, a secondary mechanism contributing to the understorey changes observed here could be associated with changes in litter characteristics. *Fagus sylvatica* produces leaf litter that differs in physical and chemical properties compared to the coniferous litter and humus of *A. alba*. The decrease in soil acidity indicated by the change in the herb community is also consistent with the decline of *A. alba* and replacement by *F. sylvatica*. Working in mixed *Fagus-Abies* stands, Paluch and Gruba (2012) found increased organic matter accumulation, lower pH, and lower soil moisture when the local density of *A. alba* increased. Augusto et al. (2003) reported thicker litter with higher C/N ratios and lower pH for soils under *A. alba* compared to those under *F. sylvatica*, although these differences were moderate; likewise, they reported that herb species beneath *A. alba* were typical of moderately more acidic and nutrient-poor conditions compared to herbs growing under *F. sylvatica*. Woziwoda and Kopeć (2015) reported similar changes in the herb layer in stands that experienced a long-term loss of *A. alba* and replacement by broadleaf species; they documented an increase in nitrophilous species and a decline in species that tolerate more nutrient-poor and acidic conditions, presumably due to the decline in conifer litter and the increase in easily decomposable broad leaf litter. According to phytosociological literature, herb species that are typically associated with moderately acidic conditions or a larger component of *A. alba* include species such as *Dryopteris filix-mas*, *Oxalis acetosella*, and *Festuca altissima* (Leuschner & Ellenberg, 2017; Pignatti & Pignatti, 2013), all of which significantly declined across the study sites. However, because we do not have data on soil chemistry from the initial inventory, this interpretation should be treated with caution.

Indeed, a number of other drivers, including deer browsing, climate change, and nitrogen deposition, may have played some role in the understorey dynamics observed in our dataset. The density of red deer is high in the study area and has remained high throughout the past three decades, at about 15 deer km^{-2} (Nagel et al., 2015). Most species, regardless of palatability, declined during the study period, while *Anemone nemorosa*, documented as a preferred browse species (Pellerin et al., 2010), increased in cover. These patterns suggest that deer browsing was unlikely a primary driver of

TABLE 2 Changes in species diversity metrics and Ellenberg indicator values between 1983 and 2015 for the three old-growth forest reserves

	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}

Abbreviations: n.s., not significant; SD, standard deviation; z, z-value test statistic based on a Wilcoxon signed rank tests. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

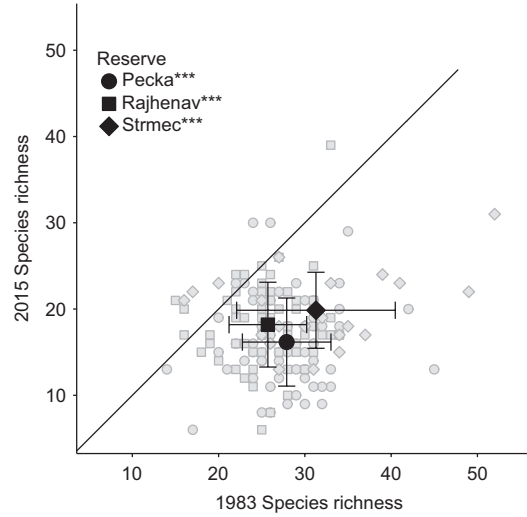


FIGURE 3 Plot-level changes in species richness between 1983 and 2015 across the three old-growth forest reserves. The line indicates a 1:1 relationship of no change. The grey symbols denote individual plots, while the black symbols show the mean change for each reserve. Statistical differences between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

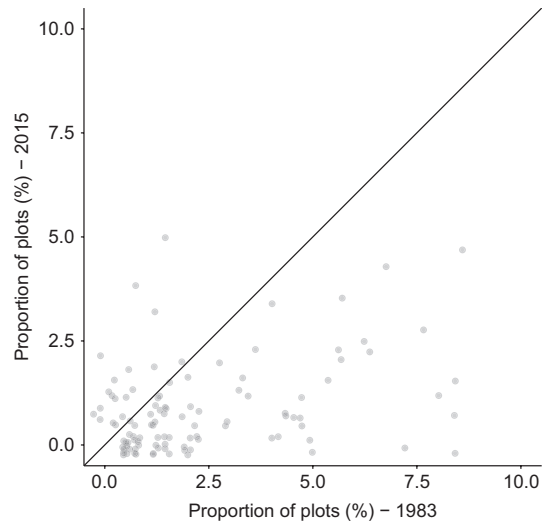


FIGURE 4 Changes in the frequency of rare species between 1983 and 2015 across the pooled dataset from the three old-growth forest reserves. Rare species were defined as those present in <10% of plots in 1983 inventories. The line indicates a 1:1 relationship of no change. Note that a dispersion function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

the understorey herb dynamics observed here. However, herbivory has likely had an indirect effect on herb communities via its influence on tree regeneration. Preferential browsing has resulted in a long-term recruitment failure of *A. alba*, thereby facilitating the contemporary dominance of *F. sylvatica* in the understorey (Nagel et al.,

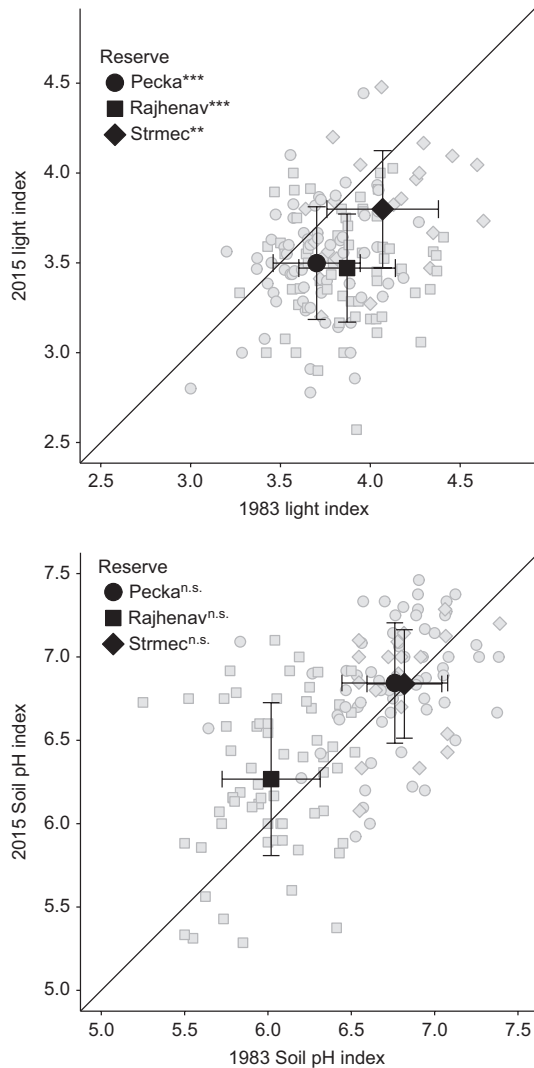


FIGURE 5 Plot-level changes in Ellenberg indicator values for light and soil reaction/pH between 1983 and 2015 across the three old-growth forest reserves. Note that lower values of the light index indicate shade, while higher values correspond to increased light. Lower values for the pH index indicate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

2015). Long-term nitrogen deposition and ongoing climate change may have also contributed to the diversity declines (Scheffers et al., 2016; Stevens, Dise, Mountford, & Gowing, 2004), but there was

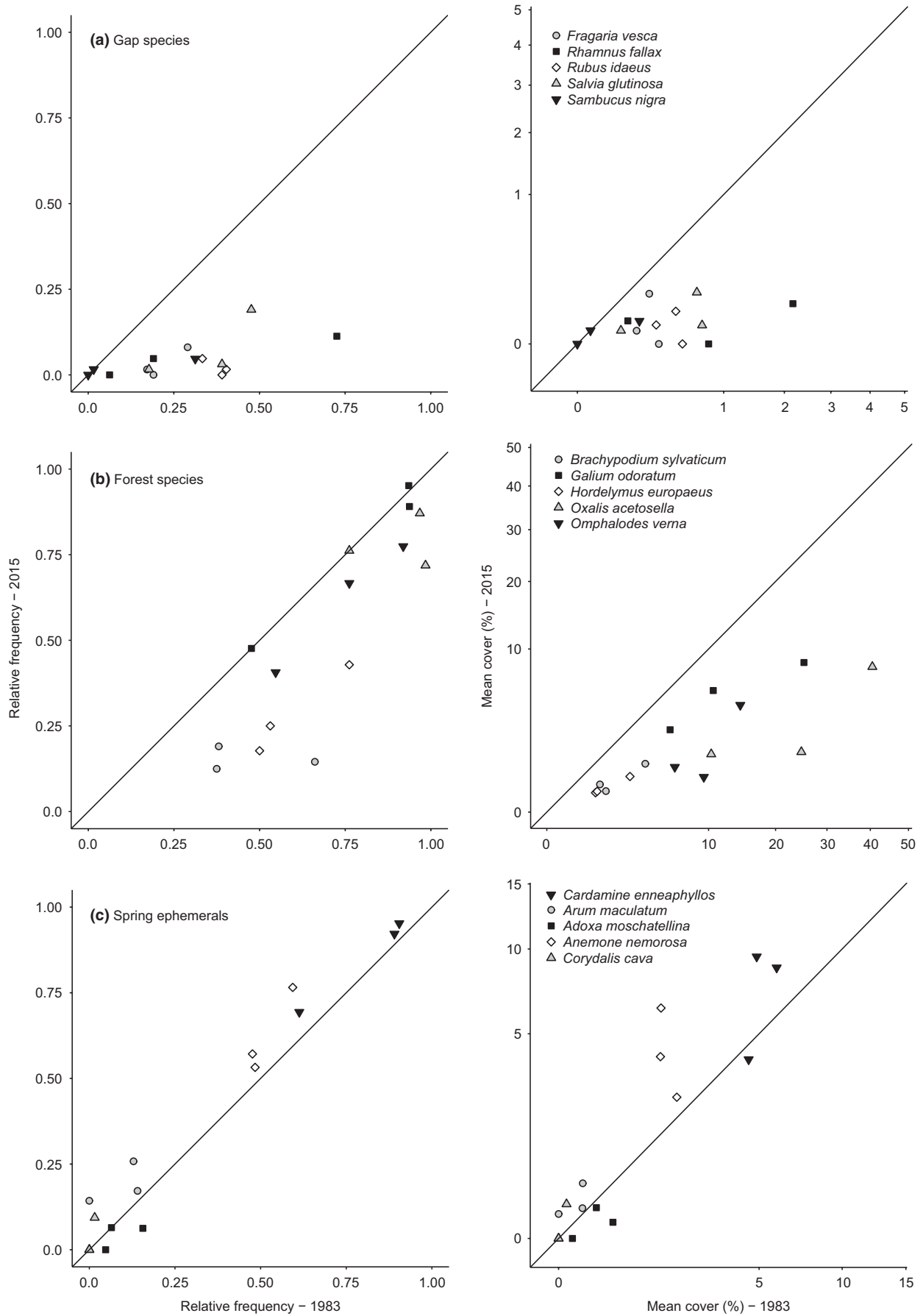
no clear pattern for these drivers based on the Ellenberg indicator values. Several other studies have documented that loss of light from canopy shading overrides the influence of nitrogen deposition and climate warming on understorey communities (De Frenne et al., 2013, 2015; Helm, Essl, Mirtl, & Dirnböck, 2017; Verheyen et al., 2012, 2017). We suspect that this has likely been the case in this study as well.

In addition to the cascading influence of *A. alba* decline, our results highlight the importance of non-equilibrium dynamics in these old-growth forest systems. The traditional view of forest dynamics, particularly in Central Europe, maintains that the forest structure and composition of old-growth systems are stable at stand scales, regulated by a shifting mosaic of small patches created by relatively continuous mortality of old canopy trees. A more contemporary view suggests that old-growth systems are in a continuous state of change in response to historical disturbances (Nagel et al., 2014; Woods, 2000, 2004). Given the important influence that tree canopies may exert on understorey herbs via changes in light and litter characteristics, it follows that herb communities would also exhibit long-term non-equilibrium dynamics in old-growth forest systems. The results of our study are consistent with another multi-decade study of understorey dynamics in temperate old-growth forests of Michigan that documented declines in fine-scale diversity; the authors attributed these changes to long-term competitive filtering following historical disturbances that cause moderate severity damage to forest canopies (Woods, 2004; Woods et al., 2012).

5 | CONCLUSIONS

Unlike the typical natural disturbances that cause abrupt changes to forests in the temperate region of Europe, such as strong winds, heavy snow, or icestorms (Nagel, Firm et al., 2017; Nagel, Mikac et al., 2017), the decline of *A. alba* was a species-specific and protracted episode of increased mortality, a pattern that may be characteristic of the global-change-type dieback of forests due to a combination of non-native insects, pathogens, and drought under an increasingly warmer climate (Allen et al., 2010; Anderegg et al., 2015). In cases when forest dieback targets foundational tree species (sensu Ellison et al., 2005), the consequences for various ecosystem properties and functions may be particularly pronounced. The effects of widespread hemlock mortality from the woolly adelgid in the eastern USA are a thoroughly studied example (Ellison, 2014; Ellison et al., 2005). In many mixed *Fagus-Abies* type forests in Europe, the past decline of *A. alba* and ongoing recruitment failure due to overbrowsing may result in an analogous situation. We suspect that the continued loss of *A. alba* will likely result in a number of long-term changes to these forest ecosystems, including

FIGURE 6 Changes in relative frequency and mean cover of selected species between 1983 and 2015 across the three old-growth reserves. The species were selected to illustrate different responses to the cascading effects of *Abies alba* decline based on their contrasting life histories. They include (a) light-demanding species that typically occur in forest gaps, (b) common species typical of the forest understorey with characteristics such as high shade tolerance or summer green foliage that were frequent across the study sites, and (c) spring ephemerals. Frequency and cover values are shown for each reserve. Lines indicate a 1:1 relationship of no change. Note the square root transformation of the x-axis for mean cover



the homogenization of the understorey environment and decreased herb diversity. These changes could have consequences for ecosystem function (Clavel, Julliard, & Devictor, 2011), but would require additional trait-based analyses (Baeten et al., 2014). The understorey changes documented here may shed light on some of the potential cascading consequences triggered by protracted episodes of widespread tree mortality resulting from global-change-type drivers. Ongoing examples include the invasive fungal pathogen (*Hymenoscyphus fraxineus*) affecting ash trees across Europe (Pautasso, Aas, Queloz, & Holdenrieder, 2013), and numerous non-native insects and pathogens in North America, such as white pine blister rust, sudden oak death, beech bark disease, and the emerald ash borer (Lovett et al., 2016).

ACKNOWLEDGEMENTS

We thank the undergraduate students from the University of Ljubljana, Luka Šparl, Polona Sušnik, and Tadej Murn, for help with field work, and Igor Dakskobler for help with species identification. The manuscript was improved by the helpful comments of two anonymous reviewers.

AUTHOR CONTRIBUTIONS

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

DATA AVAILABILITY

Data are available through forestREplot (www.forestreplot.ugent.be).

ORCID

Thomas A. Nagel  <https://orcid.org/0000-0002-4207-9218>

Kris Verheyen  <https://orcid.org/0000-0002-2067-9108>

REFERENCES

- Adamič, M. (2016). *Light climate and structural characteristics of Dinaric mixed mountain managed and old-growth forest*. Doctoral Dissertation, Biotechnical Faculty, University of Ljubljana, Slovenia.
- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6, 129. <https://doi.org/10.1890/es15-00203.1>
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Anderegg, W. R. L., Hicke, J. A., Fisher, R. A., Allen, C. D., Aukema, J., Bentz, B., ... Zeppel, M. (2015). Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist*, 208, 674–683. <https://doi.org/10.1111/nph.13477>
- Augusto, L., Dupouey, J.-L., & Ranger, J. (2003). Effects of tree species on understorey vegetation and environmental conditions in temperate forests. *Annals of Forest Science*, 60, 823–831. <https://doi.org/10.1051/forest:2003077>
- Augusto, L., Ranger, J., Binkley, D., & Rothe, A. (2002). Impact of several common tree species of European temperate forests on soil fertility. *Annals of Forest Science*, 59, 233–253. <https://doi.org/10.1051/forest:2002020>
- Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerckhove, K., ... Verheyen, K. (2009). Herb layer changes (1954–2000) related to the conversion of coppice-with-standards forest and soil acidification. *Applied Vegetation Science*, 12, 187–197. <https://doi.org/10.1111/j.1654-109x.2009.01013.x>
- Baeten, L., Hermy, M., Van Daele, S., & Verheyen, K. (2010). Unexpected understorey community development after 30 years in ancient and post-agricultural forests. *Journal of Ecology*, 98, 1447–1453. <https://doi.org/10.1111/j.1365-2745.2010.01711.x>
- Baeten, L., Warton, D. I., Van Calster, H., De Frenne, P., Verstraeten, G., Bonte, D., ... Verheyen, K. (2014). A model-based approach to studying changes in compositional heterogeneity. *Methods in Ecology and Evolution*, 5, 156–164. <https://doi.org/10.1111/2041-210x.12137>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Brändle, M., & Brandl, R. (2001). Species richness of insects and mites on trees: Expanding Southwood. *Journal of Animal Ecology*, 70, 491–504. <https://doi.org/10.1046/j.1365-2656.2001.00506.x>
- Brunet, J., Falkengren-Grerup, U., Rühling, Å., & Tyler, G. (1997). Regional differences in floristic change in South Swedish oak forests as related to soil chemistry and land use. *Journal of Vegetation Science*, 8, 329–336. <https://doi.org/10.2307/3237321>
- Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90, 3566–3574. <https://doi.org/10.1890/08-1823.1>
- Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9, 222–228. <https://doi.org/10.1890/080216>
- De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., ... Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 18561–18565. <https://doi.org/10.1073/pnas.1311190110>
- De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D. A., Hermy, M., Vangansbeke, P., & Verheyen, K. (2015). Light accelerates plant responses to warming. *Nature Plants*, 1, 15110. <https://doi.org/10.1038/nplants.2015.110>
- Diaci, J., Rozenbergar, D., Anic, I., Mikac, S., Saniga, M., Kucbel, S., ... Ballian, D. (2011). Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. *Forestry*, 84, 479–491. <https://doi.org/10.1093/forestry/cpr030>
- Diekmann, M. (2003). Species indicator values as an important tool in applied plant ecology – a review. *Basic and Applied Ecology*, 4, 493–506. <https://doi.org/10.1078/1439-1791-00185>
- Eber, W. (1972). *Über das Lichtklima von wäldern bei Göttingen und seinen einfluß auf die bodenvegetation* (p. 150). Scripta Geobot III. Göttingen: Goltze.
- Elling, W., Dittmar, C., Pfaffelmoser, K., & Rötzer, T. (2009). Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (*Abies alba* Mill.) in Southern Germany. *Forest Ecology and Management*, 257, 1175–1187. <https://doi.org/10.1016/j.foreco.2008.10.014>

- Ellison, A. M. (2014). Experiments are revealing a foundation species: a case study of Eastern Hemlock (*Tsuga canadensis*). *Advances in Ecology*, 2014, 456904. <https://doi.org/10.1155/2014/456904>
- Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., ... Webster, J. R. (2005). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, 3, 479–486. [https://doi.org/10.1890/1540-9295\(2005\)003\[0479:lofscf\]2.0.co;2](https://doi.org/10.1890/1540-9295(2005)003[0479:lofscf]2.0.co;2)
- Floren, A., & Gogala, A. (2002). Heteroptera from beech (*Fagus sylvatica*) and silver fir (*Abies alba*) trees of the primary forest reserve Rajhenavski Rog, Slovenia. *Acta Entomologica Slovenica*, 10, 25–32.
- Forrester, D. I. (2014). The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *Forest Ecology and Management*, 312, 282–292. <https://doi.org/10.1016/j.foreco.2013.10.003>
- Gilliam, F. S. (2007). The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience*, 57, 845–858. <https://doi.org/10.1641/b571007>
- Grčman, H., Vidic, N., Zupan, M., Jones, A., Montanarella, L. & Lobnik, F. (Eds.) (2015). *Soils of Slovenia with soil map 1:250000*. Luxembourg: European Commission Joint Research Centre (JRC). Publications Office of the European Union.
- Hédli, R., Kopecký, M., & Komárek, J. (2010). Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. *Diversity and Distributions*, 16, 267–276. <https://doi.org/10.1111/j.1472-4642.2010.00637.x>
- Helm, N., Essl, F., Mirtl, M., & Dirnböck, T. (2017). Multiple environmental changes drive forest floor vegetation in a temperate mountain forest. *Ecology and Evolution*, 7, 2155–2168. <https://doi.org/10.1002/ece3.2801>
- Hočevar, S., Batič, F., Piskernik, M., & Martinčič, A. (1995). Glive v pragozdovih Slovenije: III. Dinarski gorski pragozdovi na Kočevskem in v Trnovskem gozdu. *Strokovna in znanstvena dela*, 117. Ljubljana, Slovenia: Gozdarski Inštitut Slovenije.
- Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A., & Koricheva, J. (2012). Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*, 18, 267–276. <https://doi.org/10.1111/j.1365-2486.2011.02512.x>
- Kendrick, J. A., Ribbons, R. R., Classen, A. T., & Ellison, A. M. (2015). Changes in canopy structure and ant assemblages affect soil ecosystem variables as a foundation species declines. *Ecosphere*, 6, 77–. <https://doi.org/10.1890/ES14-00447.1>
- Laganà, A., Salerni, E., Barluzzi, C., Perini, C., & De Dominicis, V. (2000). Mycocoenology in *Abies alba* Miller woods of central-southern Tuscany (Italy). *Acta Societatis Botanicorum Poloniae*, 69, 293–298. <https://doi.org/10.5586/asbp.2000.039>
- Leuschner, C., & Ellenberg, H. (2017). *Ecology of Central European Forests: vegetation ecology of Central Europe*. Cham, Switzerland: Springer International Publishing.
- Lovett, G. M., Weiss, M., Liebhold, A. M., Holmes, T. P., Leung, B., Lambert, K. F., ... Weldy, T. (2016). Nonnative forest insects and pathogens in the United States: Impacts and policy options. *Ecological Applications*, 26, 1437–1455.
- Lustenhouwer, M. N., Nicoll, L., & Ellison, A. M. (2012). Microclimatic effects of the loss of a foundation species from New England forests. *Ecosphere*, 3, 26. <https://doi.org/10.1890/es12-00019.1>
- Mauri, A., de Rigo, D., & Caudullo, G. (2016). *Abies alba* in Europe: Distribution, habitat, usage and threats. In J. San Miguel Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant, & A. Mauri (Eds.), *European Atlas of forest tree species* (pp. 48–49). Luxembourg: Publications Office of the European Union.
- Millar, C. I., & Stephenson, N. L. (2015). Temperate forest health in an era of emerging megadisturbance. *Science*, 349, 823–826. <https://doi.org/10.1126/science.aaa9933>
- Nagel, T. A., Diaci, J., Jerina, K., Kobal, M., & Rozenbergar, D. (2015). Simultaneous influence of canopy decline and deer herbivory on regeneration in a conifer–broadleaf forest. *Canadian Journal of Forest Research*, 45, 266–275. <https://doi.org/10.1139/cjfr-2014-0249>
- Nagel, T. A., Firm, D., Pisek, R., Mihelic, T., Hladnik, D., de Groot, M., & Rozenbergar, D. (2017). Evaluating the influence of integrative forest management on old-growth habitat structures in a temperate forest region. *Biological Conservation*, 216, 101–107. <https://doi.org/10.1016/j.biocon.2017.10.008>
- Nagel, T. A., Mikac, S., Dolinar, M., Klopčič, M., Keren, S., Svoboda, M., ... Paulic, V. (2017). The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. *Forest Ecology and Management*, 388, 29–42. <https://doi.org/10.1016/j.foreco.2016.07.047>
- Nagel, T. A., Svoboda, M., & Kobal, M. (2014). Disturbance, life history traits, and dynamics in an old-growth forest landscape of south-eastern Europe. *Ecological Applications*, 24, 663–679. <https://doi.org/10.1890/13-0632.1>
- Orwig, D. A., Barker Plotkin, A. A., Davidson, E. A., Lux, H., Savage, K. E., & Ellison, A. M. (2013). Foundation species loss affects vegetation structure more than ecosystem function in a northeastern USA forest. *PeerJ*, 1, e41. <https://doi.org/10.7717/peerj.41>
- Paluch, J. G., & Gruba, P. (2012). Effect of local species composition on topsoil properties in mixed stands with silver fir (*Abies alba* Mill.). *Forestry: An International Journal of Forest Research*, 85, 413–426. <https://doi.org/10.1093/forestry/cps040>
- Pautasso, M., Aas, G., Quelo, V., & Holdenrieder, O. (2013). European ash (*Fraxinus excelsior*) dieback – A conservation biology challenge. *Biological Conservation*, 158, 37–49. <https://doi.org/10.1016/j.biocon.2012.08.026>
- Pellerin, M., Saïd, S., Richard, E., Hamann, J.-L., Dubois-Coli, C., & Hum, P. (2010). Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. *Forest Ecology and Management*, 260, 429–437. <https://doi.org/10.1016/j.foreco.2010.04.031>
- Pignatti, S. (2005). Valori di Bioindicazione delle piante vascolari della Flora d'Italia. *Braun-Blanquetia*, 39, 1–97.
- Pignatti, E., & Pignatti, S. (2013). *Plant life of the Dolomites: vegetation structure and ecology*. Berlin, Germany: Springer-Verlag. <https://doi.org/10.1007/978-3-642-31043-0>
- Pigott, C. D. (1990). The influence of evergreen coniferous nurse-crops on the field layer in two woodland communities. *Journal of Applied Ecology*, 27, 448–459. <https://doi.org/10.2307/2404293>
- Pizzeghello, D., Zanella, A., Carletti, P., & Nardi, S. (2006). Chemical and biological characterization of dissolved organic matter from silver fir and beech forest soils. *Chemosphere*, 65, 190–200. <https://doi.org/10.1016/j.chemosphere.2006.03.001>
- Sackett, T. E., Record, S., Bewick, S., Baiser, B., Sanders, N. J., & Ellison, A. M. (2011). Response of macroarthropod assemblages to the loss of hemlock (*Tsuga canadensis*), a foundation species. *Ecosphere*, 2, 74. <https://doi.org/10.1890/es11-00155.1>
- Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., ... Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, 354, aaf7671. <https://doi.org/10.1126/science.aaf7671>
- Schmidt, W. (2009). Vegetation. In R. Brumme, & P. K. Khanna (Eds.), *Functioning and management of European beech ecosystems. Ecological Studies*, Vol. 208 (pp. 65–86). Berlin, Germany: Springer.
- Shiels, A. B., Gonzalez, G., Lodge, D. J., Willig, M. R., & Zimmerman, J. K. (2015). Cascading effects of canopy opening and debris deposition from a large-scale hurricane experiment in a tropical rain forest. *BioScience*, 65, 871–881. <https://doi.org/10.1093/biosci/biv111>
- Stevens, C. J., Dise, N. B., Mountford, J. O., & Gowing, D. J. (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science*, 303, 1876–1879. <https://doi.org/10.1126/science.1094678>
- Táborská, M., Přivětivý, T., Vrška, T., & Ódor, P. (2015). Bryophytes associated with two tree species and different stages of decay in a natural fir-beech mixed forest in the Czech Republic. *Preslia*, 87, 387–401.

- Tinner, W., Colombaroli, D., Heiri, O., Henne, P. D., Steinacher, M., Untenecker, J., ... Valsecchi, V. (2013). The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecological Monographs*, 83, 419–439. <https://doi.org/10.1890/12-2231.1>
- van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fulé, P. Z., ... Veblen, T. T. (2009). Widespread increase of tree mortality rates in the western United States. *Science*, 323, 521–524. <https://doi.org/10.1126/science.1165000>
- Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., ... Verstraeten, G. (2012). Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *Journal of Ecology*, 100, 352–365. <https://doi.org/10.1111/j.1365-2745.2011.01928.x>
- Verheyen, K., Bažány, M., Čečko, E., Chudomelová, M., Closset-Kopp, D., Czortek, P., ... Baeten, L. (2018). Observer and relocation errors matter in resurveys of historical vegetation plots. *Journal of Vegetation Science*, 29, 812–823. <https://doi.org/10.1111/jvs.12673>
- Verheyen, K., De Frenne, P., Baeten, L., Waller, D. M., Hédli, R., Perring, M. P., ... Bernhardt-Römermann, M. (2017). Combining biodiversity resurveys across regions to advance global change research. *BioScience*, 67, 73–83. <https://doi.org/10.1093/biosci/biw150>
- Wardle, D. A., Bardgett, R. D., Callaway, R. M., & Van der Putten, W. H. (2011). Terrestrial ecosystem responses to species gains and losses. *Science*, 332, 1273–1277. <https://doi.org/10.1126/science.1197479>
- Woods, K. D. (2000). Dynamics in late-successional hemlock–hardwood forests over three decades. *Ecology*, 81, 110–126. [https://doi.org/10.1890/0012-9658\(2000\)081\[0110:dilshh\]2.0.co;2](https://doi.org/10.1890/0012-9658(2000)081[0110:dilshh]2.0.co;2)
- Woods, K. D. (2004). Intermediate disturbance in a late-successional hemlock–northern hardwood forest. *Journal of Ecology*, 92, 464–476. <https://doi.org/10.1111/j.0022-0477.2004.00881.x>
- Woods, K. D., Hicks, D. J., & Schultz, J. (2012). Losses in understorey diversity over three decades in an old-growth cool-temperate forest in Michigan, USA. *Canadian Journal of Forest Research*, 42, 532–549. <https://doi.org/10.1139/x2012-006>
- Wozniwoda, B., & Kopec, D. (2015). Changes in the silver fir forest vegetation 50 years after cessation of active management. *Acta Societatis Botanicorum Poloniae*, 84, 177–187.
- Wulf, M., & Naaf, T. (2009). Herb layer response to broadleaf tree species with different leaf litter quality and canopy structure in temperate forests. *Journal of Vegetation Science*, 20, 517–526. <https://doi.org/10.1111/j.1654-1103.2009.05713.x>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Vegetation cover and height classes

Appendix S2. Archival surveys of regeneration density

Appendix S3. Soil characteristics

Appendix S4. Beta diversity analysis

Appendix S5. Indicator species analysis

Appendix S6 Linear mixed effects analysis

How to cite this article: Nagel TA, Iacopetti G, Javornik J, et al. Cascading effects of canopy mortality drive long-term changes in understorey diversity in temperate old-growth forests of Europe. *J Veg Sci.* 2019;00:1–12. <https://doi.org/10.1111/jvs.12767>

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main article.



We examined how long-term mortality of a foundation conifer tree influenced understorey 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 understorey community. This study sheds light on the potential cascading consequences triggered by episodes of increased tree mortality resulting from global-change-type drivers.