



# Dynamics and drivers of post-windthrow recovery in managed mixed mountain forests of Slovenia

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## Abstract

Large and severe disturbances may erode the resilience of temperate forest ecosystems and alter their recovery dynamics, especially under global change. We investigated mid-term recovery in mixed mountain forests in Slovenia after three independent severe windstorms in 2008 created large disturbed patches. Across a network of 102 permanent plots and three inventories over the 11-year post-disturbance period, we monitored trends in density, composition, and structure of regeneration, which are key indicators of forest resilience. Ecological drivers of regeneration, including topography, microsites, and biotic interactions, were analysed using linear mixed models. We quantitatively assessed physiognomic recovery by comparing regeneration densities with the restocking target used in forest practice, and compositional recovery by comparison with pre-disturbance stand composition. Regeneration densities and structure tended to converge among post-disturbance treatments (planting vs. natural regeneration) 11 years post-disturbance, as density of natural regeneration substantially dropped between the second and third inventory. Some drivers of recovery (i.e. ground vegetation and distance to the forest edge) varied over time, while the effect of elevation on regeneration density was consistently negative. The results indicate that the forest sites generally show adequate resilience to large-scale wind disturbances, in terms of physiognomic recovery, but not in terms of rapid compositional recovery, as pioneer and light-demanding tree species increased in share compared to the pre-disturbance stands.

**Keywords** Forest resilience · Forest succession · Stand-replacing disturbances · *Fagus sylvatica* · *Picea abies* · Browsing

## Introduction

Mixed temperate forests dominated by *Fagus sylvatica* L. (hereafter beech), *Abies alba* Mill. (fir), *Picea abies* (L.) H. Karst. (spruce), and a variety of noble broadleaf species make up much of the forest landscape across mountain regions of Europe (Brus et al. 2012). As such, they are essential for provisioning of various ecosystem services and wood products (Pretzsch et al. 2015; Mina et al. 2017; Hilmers et al. 2018, 2019). Because these mixed mountain forests often have high structural and compositional heterogeneity at small scales (Keren et al. 2020), features which

are thought to promote resilience to disturbances (O'Hara and Ramage 2013) and drought (Pardos et al. 2021), there is increasing interest in the resilience of mixed mountain forests to global change drivers (Hilmers et al. 2019; Taerou et al. 2019).

In the absence of management, the structure and composition of mixed mountain forests is maintained by relatively continuous formation of small canopy gaps resulting from background mortality of canopy trees (e.g. gap dynamics), as well as periodic intermediate severity disturbances from a variety of agents that create larger canopy openings at stand scales (Kucbel et al. 2010; Nagel et al. 2014, 2021; Frankovič et al. 2021). Because the dominant species in mixed mountain forests are shade tolerant, particularly beech and fir, and often present as advance regeneration in the forest understory, they typically capture and access the canopy in gaps of various size (100 s to 1000 s m<sup>2</sup>) (Nagel et al. 2010), such that forest composition is relatively stable even after intermediate severity disturbances (Splechtna et al. 2005; Nagel et al. 2006).

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While the regeneration process in these forests is well suited to a range of small to moderate sized canopy openings, it is less clear how they may respond to large and severe disturbances. Although there is much uncertainty how climate change will alter future disturbance regimes, there is strong evidence that regimes are changing, including increases in the size and intensity of some agents (Seidl et al. 2017). Future large and severe disturbance events in mixed mountain forests (e.g. events that kill most of the canopy over 10s of ha), combined with heat and drought stress, may push forest regeneration beyond a threshold to which these forests are well adapted, and erode their ability to recover from disturbance (Anderson-Teixeira et al. 2013; Stevens-Rumann and Morgan 2019). To date, the few studies of post-disturbance recovery that have been done in mixed mountain forests of Europe suggest that these ecosystems are resilient to large and severe disturbances (Kramer et al. 2014; Jaloviar et al. 2017; Tsvetanov et al. 2018; Senf and Seidl 2021).

As a major component of forest resilience to disturbances, recovery is important to restore functionality of the ecosystem, both in terms of physiognomic recovery (i.e. in density / cover / biomass of trees) and compositional recovery of the pre-disturbance tree community (Andrus et al. (2020); akin to stand replacement and species maintenance, respectively, in Vickers et al. (2019)). The recovery process is a function of a variety of different, often interacting, abiotic and biotic factors that have been well documented in the literature. For example, these include pre-disturbance structure and composition, disturbance characteristics, legacies remaining after disturbance, seed production and dispersal, suitable (micro)-environmental conditions for germination, competition/facilitation with herb and shrub vegetation, browsing pressure, and post-disturbance management interventions (e.g. salvage logging and planting) (Diaci et al. 2017; Dey et al. 2019; Taerøe et al. 2019).

The present study takes advantage of a unique dataset of permanent plots that monitor forest recovery after three independent large and severe windthrow events that occurred in summer 2008 in mixed mountain forests of Slovenia. While empirical studies of forest recovery often rely upon one inventory in time (Kramer et al. 2014; Michalová et al. 2017; Szwagrzyk et al. 2018a; Tsvetanov et al. 2018) or case studies of individual events over time (Vodde et al. 2015; Jaloviar et al. 2017; Szwagrzyk et al. 2018b; Konôpka et al. 2019), both of which provide valuable information on forest recovery, the present study takes advantage of multiple disturbance sites with the same time since disturbance, as well as multiple inventory years, allowing unique insight into mid-term forest recovery trajectories, which might be poorly predictable from short-term dynamics (Gill et al. 2017). A previous study evaluated the efficacy of naturally regenerated versus planting treatments on short-term

recovery (Fidej et al. 2018). Our study extends the monitoring of recovery from this previous work, with the main goal of assessing physiognomic and compositional recovery, which together provide insight into the resilience of these forests to severe disturbance. We compared the density of tree regeneration to target densities set by the forestry profession and regeneration densities reported in the literature for similar forest types to assess physiognomic recovery. Compositional recovery was assessed by comparing the tree species composition of regenerating vegetation to that of the pre-disturbance stand. We also examined the influence of various drivers on post-disturbance regeneration density and diversity, and assessed how these drivers varied over time.

## Methods

### Research sites

Three summer thunderstorm events in 2008 caused severe windthrow patches in forests of western, north-central, and eastern Slovenia, respectively, in Trnovski gozd, Črničev, and Bohor (Fig. S1; Klopčič et al. 2013). The size of the damaged patches ranged from 1.5 to 87 ha among the three sites (Table 1). The three forest stands also differed in species composition and degree of naturalness, ranging from a semi-pure spruce forest planted on a site otherwise dominated by a mixture of beech, fir, and spruce, to a montane beech–fir forest, and a submontane beech-dominated forest mixed with other broadleaf species. Prior to the windthrow events, both private and state-owned forest stands were managed with an irregular shelterwood system. After the disturbances, the sites were salvage logged, followed by patchy planting of spruce and *Acer pseudoplatanus* L. (hereafter sycamore maple), seedlings in 2009 and 2010, mainly in privately-owned parcels. The planting density was 1600–2800 saplings ha<sup>-1</sup> with regular spacing. For more information on site characteristics and details on planting procedures, see Fidej et al. (2018).

### Field methods

In 2012, we placed sample plots using a systematic grid at each site that was proportional to the size of each windthrow patch to ensure sufficient coverage of each patch. At each grid intersection, we placed a 10 × 10 m sample plot and noted whether the plot was located in an area with post-disturbance planting. If planting was present, this plot was designated as a planting plot (hereafter PP). We then found the closest area following the slope contour without planting, and designated this as a natural regeneration plot (hereafter NP). If the grid location first landed in a NP, we then found the nearest PP following the same procedure. Areas

**Table 1** Site, forest, and disturbance characteristics at the three locations damaged by summer windthrow events in 2008 ( adapted from Fidej et al. (2018))

	Bohor	Črnivec	Trnovski gozd
Total annual precipitation (mm)	1000–1150	1700	2200
Mean annual temperature (° C)	8–11	6–7	6–7
Elevation (m a.s.l.)	300–830	900–1260	930–1260
Rockiness (%)	2	2	10
Parent material	Mixed (carbonate and silicate)	Clay shale and tuff	Dolomite and limestone
Tree species composition of pre-disturbance stand and surrounding stands (%)	Beech (50–95), spruce (0–50), noble broadleaves (0–20)	Spruce (95), fir and beech (5)	Beech (50–80), fir (0–40), spruce (10–20), noble broadleaves (0–10)
Number of plots	14	58	30
Size (ha) and [number] of patches	1.5–3 [4]	16–87 [2]	7–16 [3]
Estimated disturbance severity (% of growing stock lost)	80	90	90

with large amounts of pre-disturbance regeneration, logging debris, skidding trails, or large rock outcrops were avoided. In total, we established 52 PPs and 50 NPs. The positions of the plots were georeferenced and their corners marked with iron stakes.

Vegetation was inventoried in each plot in 2012, 2014, and 2019. In the first two inventories, tree seedlings older than one year were counted by species in two 1×3 m subplots systematically placed to the left and right of the plot centre. In 2012, vegetation cover was estimated visually from above by individual plant species, while in 2014 this was done individually for tree species and aggregated for shrub and herbaceous species. Other parameters included the percent cover of coarse woody debris (CWD), litter, and rocks, site characteristics (elevation, slope, and aspect), and plot centre distance from the forest edge. In 2019, we modified the approach to better capture the more developed forest structure; all woody individuals (both shrub and tree species) older than one year were recorded within the 10×10 m plots by species, size class (height < 50 cm; 50 - 149 cm; 150 - 299 cm;  $h \geq 300$  cm and DBH < 5 cm; DBH  $\geq 5$  cm), and browsing class (undamaged: less than 10% of the lateral shoots browsed; moderately to severely browsed: more than 10% of the lateral shoots browsed and/or terminal shoot browsed). We recorded the species and DBH for all individuals  $\geq 5$  cm DBH. In case multiple asexually-regenerated stems of the same individual were present, only the largest stem was recorded. Ground vegetation cover (herbaceous species + *Rubus* spp.) was estimated in 5×5 m subplots in the lower right quadrant of the plot. In 2014, 11 plots (6 NP and 5 PP) were skipped in Trnovski Gozd because the exact position of the subplots could not be located. For these plots, regeneration densities were interpolated assuming a linear relationship between 2012 and 2019. During the last inventory, the height of the three tallest individuals for each species with at least three individuals taller than 300 cm

was measured in order to provide information on dominant saplings that was comparable to previous inventories.

## Data analyses

Data were analysed in R Version 4.0.3 (R Core Team 2020). Data exploration was carried out following the protocol described in Zuur et al. (2010). For the purpose of analyses, aspect and slope were recoded to a variable with three levels: northerly exposed sites (slope > 10° and aspect from NW to E), flat sites (slope  $\leq 10^\circ$ ), and southerly exposed sites (slope > 10° and aspect from SE to W). Woody species were grouped into (1) pioneer tree species (sensu Davidson (1993)), (2) light-demanding tree species, (3) shade-tolerant tree species (sensu Landolt et al. (2010)) and shrubs (Table S1). To account for different survival rates of individuals in different size classes (and thus the greater contribution of larger individuals to forest recovery), we assigned them weights following the approach of Vickers et al. (2019) (Table 2). A lower and upper height boundary were calculated for trees with DBH  $\geq 5$  cm based on the observed heights of dominant saplings from the whole dataset; the lower height boundary was also considered as the upper one for the height class > 300 cm (and DBH < 5 cm). The height midpoint of the largest size class

**Table 2** Weighting factors for all woody species by size class

Height (cm)	DBH (cm)	Height midpoint (cm)	Weighting Factor
<50	–	25	0.0427
50 – 149	–	99.5	0.1699
150 – 299	–	224.5	0.3834
$\geq 300$	<5	409	0.6985
$\geq 300$	$\geq 5$	585.5	1.00

(trees with  $DBH \geq 5$  cm) was arbitrarily weighted by 1, while the other classes were given a weight according to the ratio of their respective height midpoint to that of the largest class. This approach is based on the idea from Fei et al. (2006) that aggregate height (i.e. sum of the heights of a species/group of species) leads to a better estimate of the relative dominance of species and their ability to persist in later developmental stages than the number of seedlings alone, since it combines regeneration density with size. Species diversity was measured using Simpson's and Shannon's diversity index. All indices were calculated using the R package "vegan" (Oksanen et al. 2020).

We used a series of linear mixed-effects models (LMMs) to examine the influence of various drivers (i.e. elevation, aspect, distance to forest edge, post-disturbance treatment, ground vegetation cover in the 2019 inventory, cover of rock, CWD, litter, herbs, shrubs, and trees in the 2012 inventory) on weighted density of regeneration (overall and for each of the tree species groups) and diversity (all woody species, including shrubs, and tree species only) from the most recent inventory (see Table S2 for further details). Because we sampled multiple plots from the same study sites, the three sites were included as random intercepts in the models. Based on inspection of the diagnostic plots and analysis using the `symbox` function (Fox and Weisberg 2011), the above response variables were transformed using the square root or common logarithm function to meet the assumptions of normality and homogeneity of variance, while the explanatory variables were transformed using the common logarithm or arcsin function to prevent the presence of outliers. The linear mixed-effects models were computed using the package "nlme" (Pinheiro et al. 2021).

All final models were selected using a top-down approach following the methodology proposed by Zuur et al. (2009). First, different models were built with combinations of ecologically meaningful fixed effects (Table S2). These maximally complex models were then compared with simpler nested models based on the Akaike Information Criterion. Explanatory variables were dropped until the difference in AIC between the simpler model and the one with the variable ( $\Delta AIC$ ) was  $> 2$  (Burnham and Anderson 2004). Model assumptions were verified by plotting the residuals against the fitted values, against each covariate in the model, and against each covariate not included in the model, following the protocol described in Zuur & Ieno (2016). Complementary to the formal analysis, we calculated descriptive statistics on regeneration density, composition, structure, and their temporal trends. Unlike the results of the models, which can be generalized beyond our study sites, caution must be taken in drawing conclusions from the descriptive results, which only summarize the three case studies investigated.

Recovery was evaluated in terms of tree regeneration ability to restore forest density, i.e. physiognomic recovery, and to restore the species composition of the forest type prior to disturbance, i.e. compositional recovery (sensu Andrus et al. (2020)). For the first objective, 2019 regeneration was quantitatively compared to a threshold density of 2500 seedlings per hectare, which was derived from common practice in Central European forestry and expert knowledge about restoration of forest protective functions (Burschel and Huss 1987; Bühler 2005). Furthermore, we contextualised the recorded regeneration densities by qualitatively comparing them to those reported in the literature from managed (including different silvicultural systems) and unmanaged (either old-growth or near-natural forests) stands of beech-dominated and mixed forests in temperate mountain regions of Europe. Differences in the definition of regeneration reported in the literature (minimum and maximum size) were neglected; only the number of individuals older than one year are reported. For the second objective, species-specific density targets were set for each site as a proportion of the threshold density for physiognomic recovery, based on the share of dominant species (beech, spruce, and fir) in the forest prior to disturbance (Table 1; when a range was given, the midpoint value was used in the analysis). The objective was considered met if the 2019 plot-level density of a given species was at least equal to the corresponding target value.

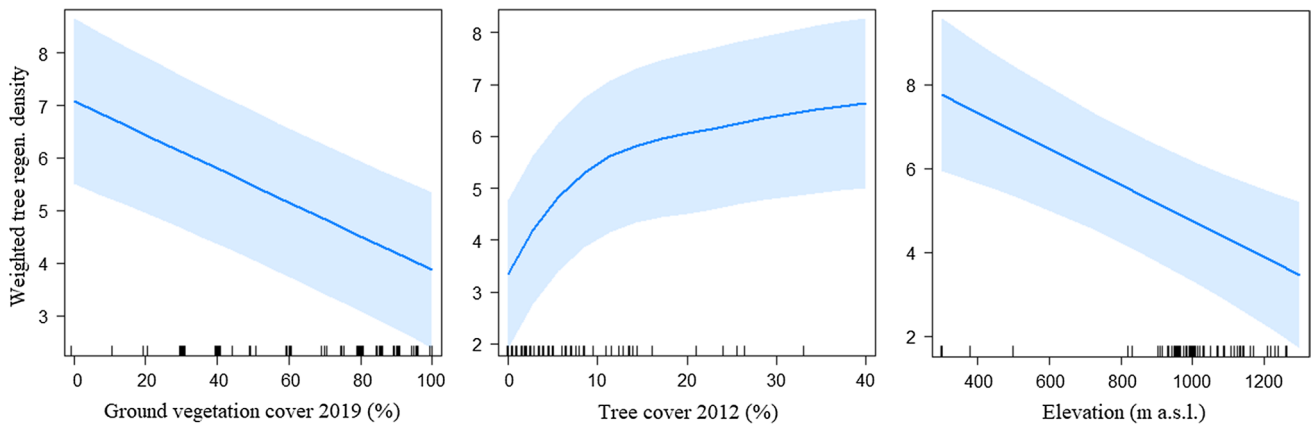
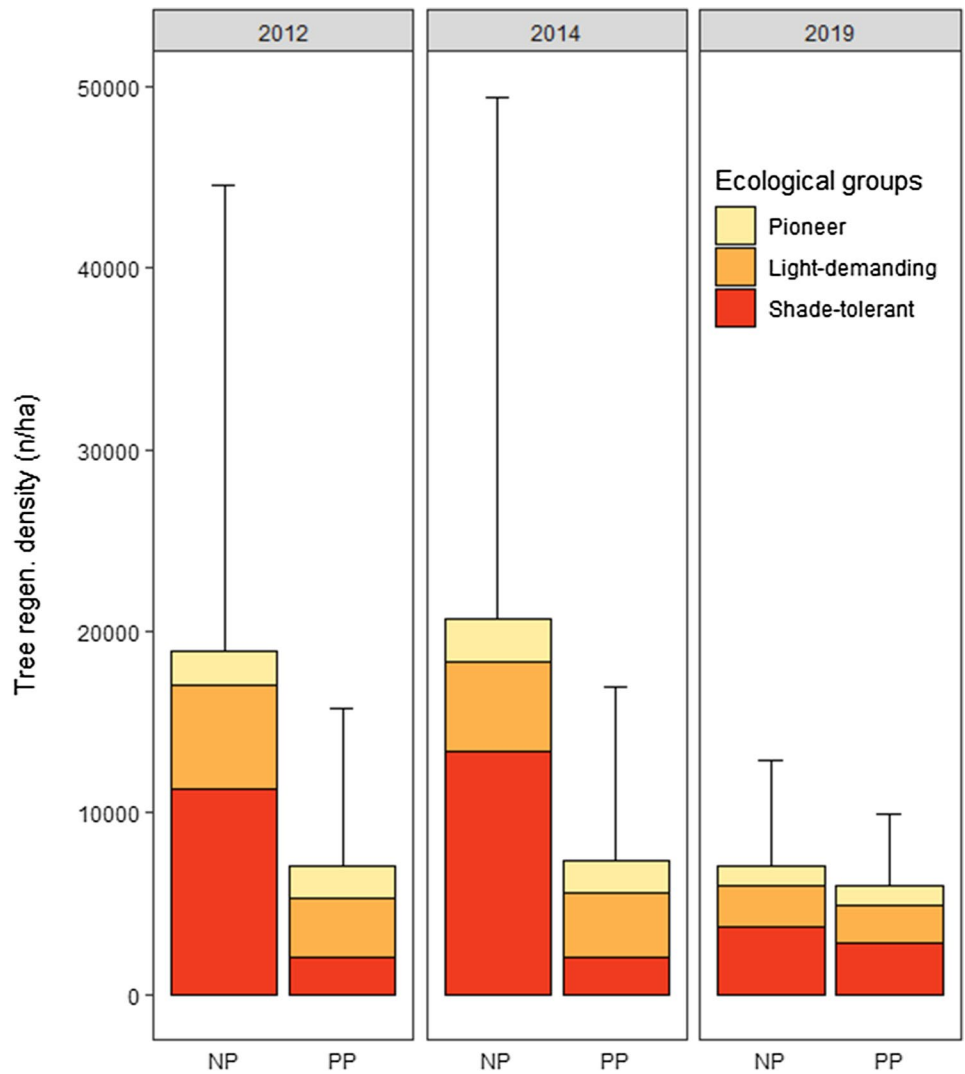
## Results

### Regeneration density and drivers

In 2019, eleven growing seasons after windthrow, the average density of tree regeneration older than one year was  $6500 \pm 4962$  individuals/ha (descriptive values are given as mean  $\pm$  standard deviation), lower than in 2012 and 2014, when it was  $12,876 \pm 19,808$  and  $13,849 \pm 22,220$  individuals/ha, respectively. Furthermore, regeneration density was higher in NP than in PP (on average  $7051 \pm 5835$  and  $5970 \pm 3931$  individuals/ha, respectively), although by a smaller margin than in previous years (Fig. 1). Treatment was not included in the 2019 overall weighted density model, as result of the model selection procedure.

Model analysis (Table S2) showed that the most relevant factors related to the overall weighted regeneration density were 2012 tree species cover, elevation, and 2019 ground vegetation cover ( $\Delta AIC = 0.30$ ;  $\Delta AIC$  is reported as the difference between the final model and the one including the last variable dropped during the selection procedure); the first variable was positively related with overall weighted density, while the latter two showed a negative association (Fig. 2). Topography (i.e. slope, aspect), distance to the forest edge and microsites (i.e. CWD, litter cover) were

**Fig. 1** Average density and variability (error bars represent standard deviation) of regeneration in three ecological groups at natural regeneration (NP) and planting plots (PP) in 2012, 2014 and 2019



**Fig. 2** Effect of recovery drivers (elevation, ground vegetation, and early-stage tree cover) on overall weighted regeneration density in 2019, resulting from the linear mixed model (95% confidence interval

is shown; ticks in x axes represent the observed values of the independent variables; y axes show the square root value of the dependent variable per 100 m<sup>2</sup>)

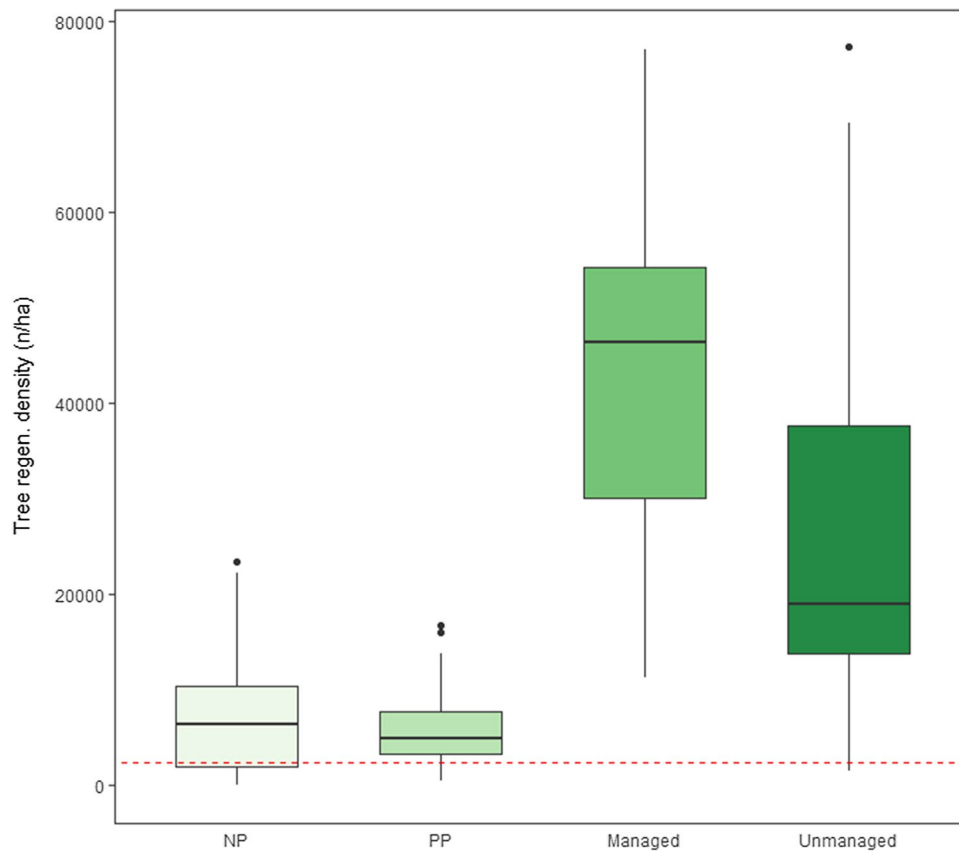
not included in the final model. Browsing was qualitatively assessed to have a mild impact only in Trnovski Gozd, where about 13% of individuals showed moderate to severe damage, whereas it was less important in Črnivec and Bohor (7% and 1%, respectively).

Overall, regeneration was completely absent from only one plot (NP in Bohor) in 2019, where a dense layer of *Rubus idaeus* L. was recorded, whereas it was absent from 24 and 23% of the plots (nearly equally distributed between NP and PP) in 2012 and 2014, respectively. Overall, the percentage of plots with a density above the threshold of 2500 individuals per hectare (i.e. meeting the physiognomic recovery objective) was 76%. PP had a higher share of plots above the threshold, compared to NP, at 83 and 70%, respectively. Regeneration densities extracted from the literature (summarised in Table S3) ranged between 11,245 and 77,012 individuals/ha for managed forests, and between 1578 and 77,292 for unmanaged stands, with most

studies reporting higher densities than found in the three post-windthrow sites studied here, particularly for managed forests (Fig. 3).

### Species composition and diversity

In 2019, a total of 29 tree species and 11 shrub species were observed across the three sites. In the ground vegetation layer *Rubus idaeus* was the most common species, followed by *Pteridium aquilinum* (L.) Kuhn, *Eupatorium cannabinum* L., and *Avenella flexuosa*. Shade-tolerant species represented the majority of regeneration in 2019 at 50.4%, compared to light-demanding and pioneer species at 33.3% and 16.3%, respectively (Fig. 1). These proportions did not change considerably from the first inventory, while there were substantial differences between sites. Shade-tolerant species were dominant at Črnivec, where they accounted for 60.8% of the total regeneration, while light-demanding



**Fig. 3** Comparison of 2019 regeneration densities in natural (NP) and planting plots (PP), and values reported in literature for managed (active or recent management/silvicultural activities at the time of study;  $n=12$ ) and unmanaged (either old-growth or near-natural forests where management stopped > 50 year ago;  $n=29$ ) beech-dominated and mixed mountain forests. The dashed horizontal line indicates our density threshold for physiognomic recovery (2500 individuals/ha). For densities extracted from literature, data from

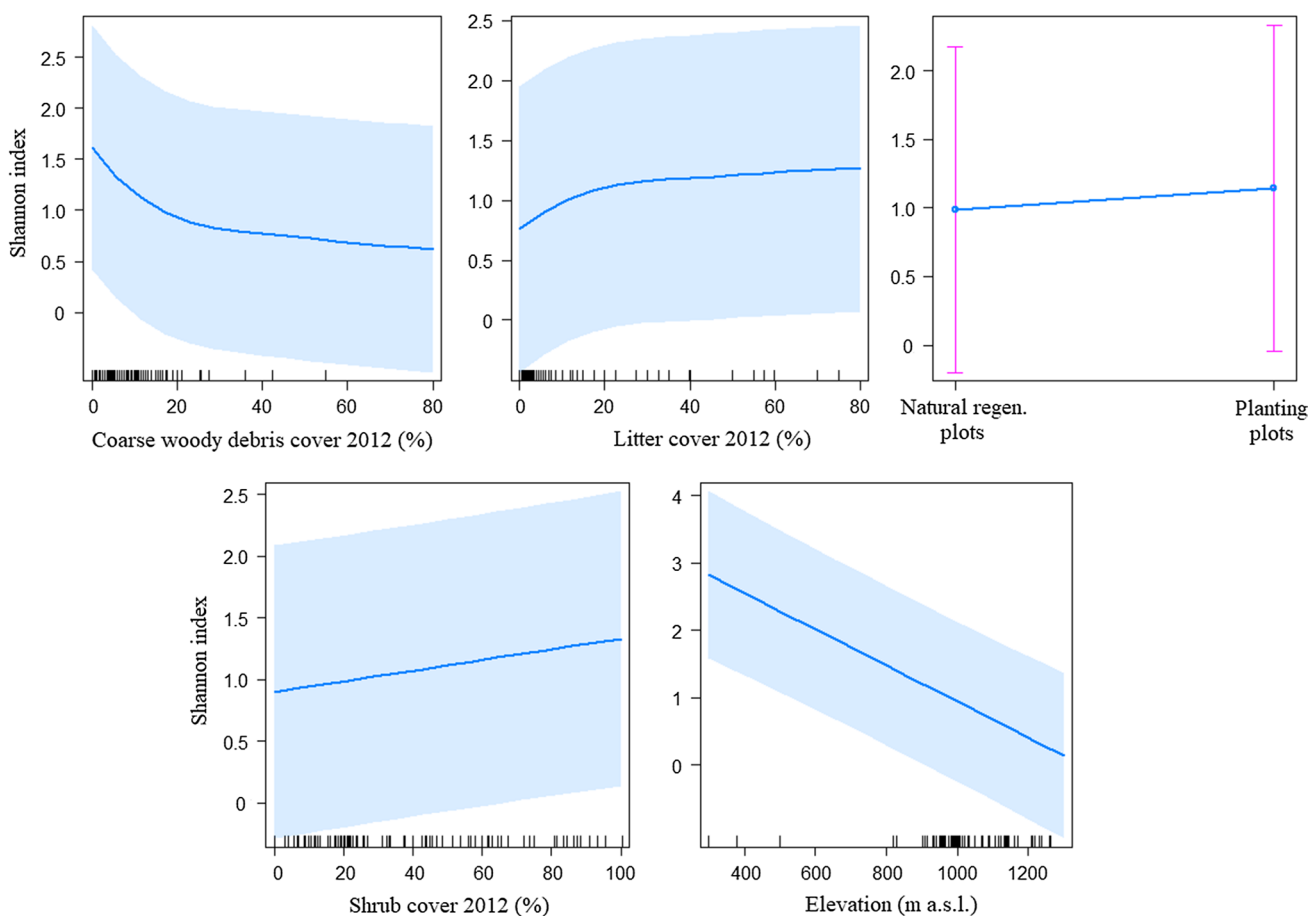
fenced plots or for studies focusing only on a single species (i.e. not including the total density of regeneration) were not included in the figure. If multiple inventories were carried out in the same area, only densities from the most recent one were included in the figure. When a range of values was given only the midpoint value was used. Note that variability in NP and PP is at plot-level, while the “managed” and “unmanaged” categories show site-level variability

species were the majority at Bohor and Trnovski Gozd, with 63.6% and 43.3%, respectively. Across all sites, spruce was the most common species overall in 2019, adding up to 38.5%, followed by sycamore maple (14.0%), beech (10.6%), *Salix caprea* L., hereafter goat willow (10.1%), and *Sorbus aucuparia* L., hereafter rowan (9.3%). These proportions remained relatively stable over time.

The modelled weighted densities in 2019 of all ecological groups (Table S2;  $\Delta AIC$  equal to 0.99, -1.08, and -0.69 for pioneer, light-demanding, and shade-tolerant models, respectively) were positively related to their respective cover percentage in 2012. Treatment was included only in the model for shade-tolerant species, whose weighted density was positively affected by planting. Nonetheless, the average density of shade-tolerant species remained lower than in NP, although by a much smaller margin than in previous years, when density in NP was about six times higher than in PP. The shade-tolerant weighted density model showed similar results to the overall weighted density model, with elevation, ground vegetation cover in 2019, and shrub cover

in 2012 having a negative association with density. Light-demanding weighted density showed a positive association with weighted shrub density in 2019. Pioneer weighted density in 2019 was negatively associated with rock coverage. Slope or exposition were not selected in any of the final models, nor were densities of other ecological groups. Signs of browsing were present in less than 10% of individuals for each species except sycamore maple and silver fir (30.9 and 43.0% of cases, respectively), while they were almost absent for beech and spruce.

The highest tree and woody species diversity in 2019 by both Shannon and Simpson were found in Bohor. On average, in 2019 PP showed higher diversity values for all the indices than NP, while the opposite was true in 2012 and 2014. In the models for 2019 species diversity, planting had a positive relationship with Shannon index only when all woody species were considered (Fig. 4;  $\Delta AIC = -0.91$ ). Shannon index (both for all woody species, and tree species only) was positively associated with 2012 litter and shrub cover, while it decreased with elevation and CWD cover.



**Fig. 4** Effect of recovery drivers (elevation, treatment, CWD, litter, and shrub cover in 2012) on 2019 Shannon–Wiener diversity index for all woody species, resulting from the linear mixed model (95%

confidence interval is shown; ticks in x axes represent the observed values of the independent variables)

The models for 2019 Simpson diversity showed similar relationships to the ones for the Shannon index (Table S2).

The compositional recovery objective was met in a minority of plots (45%, 38%, and 14% for the pre-disturbance target of beech, spruce, and fir, respectively). The proportion of plots meeting the species restoration objective was similar among treatments for beech and fir, while a larger share of PP than NP met the requirement for spruce (respectively, 46 and 30% of plots for pre-disturbance target).

### Regeneration structure and dominant saplings

The size structure of regeneration during the 2019 inventory was bell shaped with the largest proportion in the middle size class (height between 150 and 300 cm) (Fig. 5). The size distribution of pioneer species was slightly skewed towards larger classes (36% of individuals were in class  $h > 300$  cm,  $DBH < 5$  cm). The size distribution of light-demanding species peaked in the middle size class, but was slightly skewed towards smaller size classes due to the widespread occurrence of sycamore maple with heights between 50 and 150 cm. The size distribution of shade-tolerant species was very similar to the overall distribution. Browsing affected

the smallest size classes more than the largest ones; 17.7% of individuals in the two smallest classes combined showed signs of browsing, while the proportion in the larger classes was negligible.

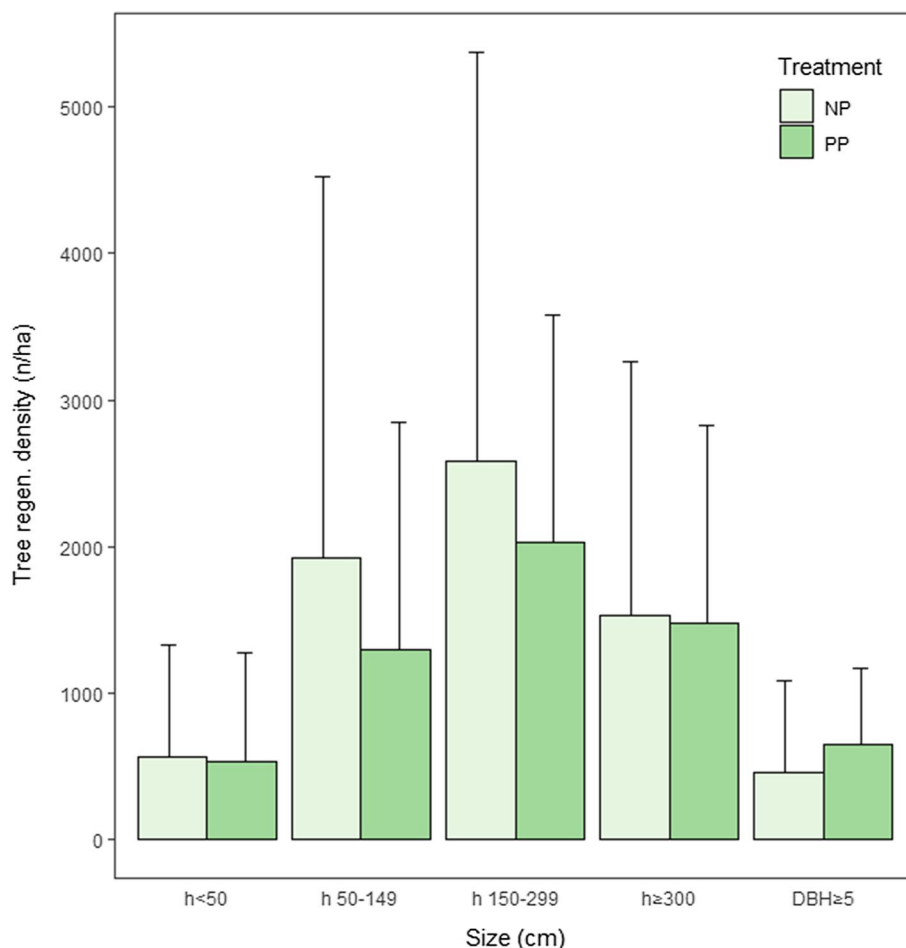
In 2019, 78 of 102 plots had at least three individuals of the same species which were taller than 300 cm. The average height of dominant regeneration, when present, was  $5.2 \pm 1.7$  m. It was, on average, similar between PP and NP, but in the latter it was absent in 19 of 50 plots, while only 5 PPs had no dominant regeneration. The species with the most observations were spruce (135), followed by goat willow (90), rowan (72), *Betula pendula* Roth, hereafter birch (65), sycamore maple (48), and beech (42). The dominant pioneer species birch and goat willow were taller than average at  $6.7 \pm 1.8$  and  $5.6 \pm 1.7$  m, respectively.

## Discussion

### Adequacy of regeneration for forest recovery

Post-disturbance regeneration at the three windthrow sites was adequate for physiognomic recovery when compared

**Fig. 5** Average density and variability (error bars represent standard deviation) of regeneration in 2019 by size class (height and DBH in cm) and treatment (NP = natural regeneration plots; PP = planting plots)





with the threshold density of 2500 individuals/ha, which was derived from expert knowledge (Bühler 2005). A similar share of plots met the same target in mixed forests of the Swiss Alps 20 years after wind disturbance (Wohlgemuth et al. 2017). Areas left to natural regeneration after salvage logging showed slightly worse physiognomic recovery than those aided by planting. Despite reaching site-level restocking densities, average regeneration densities were at the lower end compared to background densities found in similar forest types (Table S3). However, regeneration densities at the sites were well within the range reported for other windthrow studies up to 20 years after the disturbance, both from mountain (Fischer et al. 2002; Wohlgemuth et al. 2002; Ščap et al. 2013; Kramer et al. 2014; Pröll et al. 2015; Fidej et al. 2016; Tsvetanov et al. 2018; Konôpka et al. 2019; Szwagrzyk et al. 2021) and lowland European temperate forests (Dobrowolska 2015; Vodde et al. 2015; Szwagrzyk et al. 2018a), in which densities generally ranged from 1000 to 10,000 individuals/ha, but higher values have also been recorded (Van Couwenberghe et al. 2010; Szwagrzyk et al. 2018b). When considering only sites that were salvaged after the disturbance, our regeneration densities were in the upper end of these studies.

Compositional recovery (i.e. restoring the relative species composition of the pre-disturbance stand) was not met in the majority of plots for any of the dominant species. It was close to half of the plots for beech, while particularly low for fir. Compositional recovery of spruce was close to that of beech, but was favoured by the widespread post-disturbance planting of spruce. Spruce made a large contribution to the prevalence of shade-tolerant species, which tended to show greater densities than light-demanding or pioneer species, overall. Consistent with our findings, other studies have also found that light-demanding and pioneer species (e.g. birch and goat willow) tended to constitute a larger proportion of the overall composition than before the disturbance, both at salvaged (Fischer et al. 2002; Fidej et al. 2016; Jaloviar et al. 2017) and non-salvaged sites (Szwagrzyk et al. 2018b, 2021; Tsvetanov et al. 2018). Moreover, pioneer species were typically the tallest post-disturbance individuals at our sites, which is consistent with other studies (Van Couwenberghe et al. 2010; Szwagrzyk et al. 2018a).

It must be noted that while recovery to the pre-disturbance composition may be desirable from a forestry perspective (although not always the case with regard to spruce monocultures), compositional recovery is not necessarily in-line with other forest functions. Post-disturbance patches dominated by pioneer species represent rare community types in forested landscapes in the temperate region, and may play a critical role for biodiversity and wildlife habitat (Swanson et al. 2011; Donato et al. 2012). Moreover, when pre-disturbance composition is monospecific, non-native, or not projected to be well adapted to future climatic conditions

and disturbance regimes (Seidl et al. 2017), severe disturbances can play an important role in speeding up forest adaptation to climate warming, by favouring the process of thermophilization (Dietz et al. 2020).

## Drivers and dynamics of recovery

Models results showed that early-stage regeneration cover was a good predictor of mid-term density, both overall and for each of the ecological groups, perhaps indicating that most of the present-day regeneration established shortly after disturbance rather than over a protracted post-disturbance period. The other significant drivers identified in the models were the negative influence of elevation on overall regeneration density and diversity, and of ground vegetation on density. The negative influence of elevation (overall ranging from 300 to 1260 m a.s.l.) on density is likely related to the increasing climatic extremes and shortening of the growing season as elevation increases (Cunningham et al. 2006), while its association with species diversity may be related to the generally lower densities at higher elevations, and consequently to a lower probability of recording a similar amount of species in the same plot area. This pattern is consistent with findings from other post-windthrow recovery studies (Kramer et al. 2014; Fidej et al. 2016, 2018; Szwagrzyk et al. 2021), yet it is worth noting that, contrary to our findings, the influence of elevation may diminish with time since disturbance (Konôpka et al. 2019). The negative influence of ground vegetation, via competition with tree regeneration, has also been reported in a number of windthrow recovery studies (Fischer et al. 2002; Wohlgemuth et al. 2002; Rammig et al. 2007; Kramer et al. 2014; Pröll et al. 2015). Similar to our findings, for example, Dobrowolska (2015) and Michalová et al. (2017) found that *Avenella flexuosa* and *Rubus* spp. (the two dominant competitors found in our study) increased in gaps created by disturbances. It is important to note, however, that the previous study by Fidej et al. (2018) found a positive association between herbaceous cover and total seedling density, suggesting that non-competitive interactions might have been stronger than competition during earlier stages of recovery.

One of the more surprising results of our study was that many of the factors often reported as important drivers of regeneration in previous post-disturbance studies, including topography (Donato et al. 2016; Fidej et al. 2018), distance to seed sources (Van Couwenberghe et al. 2010; Ščap et al. 2013), and microsites, such as litter and CWD (Pröll et al. 2015; Vodde et al. 2015; Tsvetanov et al. 2018), were not selected in our final models. In the previous study by Fidej et al. (2018), south facing aspects tended to have lower seedling densities for some species groups, indicating that aspect may be more important during the initial period of post-disturbance recovery when

seedlings may be more vulnerable to drier conditions. Also in contrast to the previous study by Fidej et al. (2018), we did not find a relationship between regeneration density and distance to the forest edge, which is perhaps related to the marked decline in regeneration density from 2019 to 2014. Finally, we suspect that the deadwood left in our study areas after salvage logging was not sufficiently decayed to function as a regeneration substrate (Zielonka 2006; Bače et al. 2012).

Post-disturbance treatment (i.e. planting of mainly spruce and sycamore maple) turned out not to be a relevant predictor of regeneration densities, except for that of shade-tolerant species, which was positively associated with planting. Despite large differences during the early stage of recovery, densities in naturally regenerated and planted areas tended to converge during the last 2019 inventory, primarily due to the large decline in density in the natural regeneration plots from 2014 to 2019. This decline in density is in accordance with findings from other studies that showed relatively abundant regeneration during early post-disturbance inventories, followed by a decline due to competition induced thinning (Vodde et al. 2015; Szwagrzyk et al. 2018b; Konôpka et al. 2019). Analogously, mean height of dominant individuals was similar among treatments, in contrast with the results from the first two inventories, when planted areas had taller saplings (Fidej et al., 2018). Planting also showed a positive relationship with species diversity, possibly by increasing overall species evenness through the addition of shade-tolerant spruce at sites where they would have been otherwise less abundant.

It is worth noting that deer browsing may have affected the diversity of tree regeneration. Of the two species that were planted, sycamore maple is a highly preferred palatable species, while spruce is generally avoided, and sycamore maple showed clear signs of deer browsing across the study sites. Furthermore, although fir regeneration was rare across the sites, it showed a greater proportion of browsed individuals compared to sycamore maple, which may partly explain the low compositional recovery for fir. Although ungulate browsing was not formally analysed as a recovery driver, a number of studies have demonstrated that it can slow down the post-disturbance recovery process in mixed temperate forests (Rammig et al. 2007; Pröll et al. 2015; Rozman et al. 2015; Szwagrzyk et al. 2018b; Andrus et al. 2020).

## Conclusions

Monitoring 11 years of forest recovery following three independent severe windthrow events in mixed-mountain forests in Slovenia revealed several key findings with regard to mid-term post-disturbance resilience:

- Following an initial establishment pulse of tree regeneration, average regeneration densities tended to converge across treatments, and initial post-disturbance regeneration cover was indicative for mid-term trajectories with regard to density and composition (cf. Gill et al. 2017).
- Post-disturbance regeneration had considerably lower densities compared to those documented in both managed and unmanaged forests (e.g. forests regulated by smaller scale gap dynamics), yet plot level densities were often above the minimum restocking density suggested by forestry guidelines, indicating adequate physiognomic recovery.
- Recovery to the pre-disturbance forest composition was less common than physiognomic recovery, mainly because regeneration was often comprised of more pioneer and light-demanding species compared to the pre-disturbance stands, where beech, fir, and spruce were dominant.
- Drivers of the recovery process varied with time, but few, such as elevation, stayed consistent, suggesting that the ecological factors that influence forest recovery after disturbance vary as succession progresses. Likewise, the early benefits of planting diminished over time, yet areas at higher elevations and with competing ground vegetation still had very little regeneration after 11 years.

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**Availability of data and material** The datasets generated and/or analysed during the study are available from the corresponding author on reasonable request.

**Code availability** The R code generated for the data analysis for the study is available from the corresponding author on reasonable request.

## Declarations

**Conflicts of interest** The authors declare they have no conflict of interest.

**Ethics approval** Not applicable.

**Consent to participate** Not applicable.

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