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# Contrasting Norway spruce disturbance dynamics in managed forests and strict forest reserves in Slovakia

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Forest disturbances are intensifying globally, yet regional drivers of these dynamics remain poorly understood. We investigated recent disturbance intensities in Norway spruce (*Picea abies* L.) forests in Slovakia (Central Europe) with different management objectives in 2000–2017 based on Landsat imagery. We focused on 122 strict reserves without any management, their actively managed surroundings (500 m and 2000 m buffers), and managed production forests beyond the buffer areas. We used generalized additive mixed models to test for differences in temporal trends of disturbance intensity among these management categories. We found that disturbance intensity was increasing in all management categories during the studied period. The increase was more pronounced in the managed forests (compound annual disturbance rate 1.76% year<sup>-1</sup>) and the 2000 m buffer (2.21% year<sup>-1</sup>) than in the strict reserves (0.58% year<sup>-1</sup>). The predicted cumulative disturbance during the 18-year period was 9.9% in the reserves and 30.5% in the 2000 m buffer. We found that forests in nature reserves can be more resistant to disturbances than forests managed for timber production, despite management efforts to control disturbances in managed forests. Our findings can help reconcile the different perceptions of natural disturbances and their management in Central Europe and support climate-adapted management strategies that consider natural disturbances as an indispensable component of ecosystem dynamics.

## Introduction

Forest canopy mortality has doubled over the past 30 years in Central European temperate forests (Senf *et al.*, 2018), mainly due to intensified large-scale droughts, windthrows and bark beetle outbreaks (Schelhaas *et al.*, 2003; Seidl *et al.*, 2011; Senf *et al.*, 2018). The increase in forest disturbances is not constant but is driven by the varying level of climatic stress (Bošela *et al.*, 2020), forest structure and composition, topography (Dobor *et al.*, 2020b), past management practices (Seidl *et al.*, 2011; de Groot *et al.*, 2019) and legacies of previous disturbance events. For example, more diverse tree species compositions and higher topographic complexity might mitigate some disturbance impacts (Senf and Seidl, 2018; Dobor *et al.*, 2020b).

Norway spruce (*Picea abies* L. Karst.) is an economically important European tree species, constituting one-quarter of Europe's growing stock (Hlásny *et al.*, 2021a). Recent years have seen an unprecedented increase in spruce mortality caused by drought, windthrows and bark beetle outbreaks (Senf and Seidl, 2018, 2021). This particularly concerned Norway spruce that was planted outside of its historical climatic range, which exhibited damage 7-fold higher compared to forests within the spruce historical range (Marini *et al.*, 2012). An increasing proportion of spruce mortality is caused by bark beetles, particularly the Eurasian spruce bark beetle, *Ips typographus* L., (Coleoptera, Curculionidae) (Wermelinger, 2004; Økland *et al.*, 2016), which thrives in warmer and drier climates (Marini *et al.*, 2017). The beetles typically attack mature trees with suitable phloem

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thickness (over 50 years old), mechanically damaged by wind, stressed by increased solar radiation in newly created stand edges (Mezei *et al.*, 2012; Kautz *et al.*, 2013), or stressed by drought and heat (White, 2015). Large-scale windthrows and droughts typically trigger the population transition to the epidemic phase. The beetles can then colonize also healthy trees, which support higher brood production and thus initiate strong positive feedbacks in increased tree mortality (Kausrud *et al.*, 2012). The enlarged populations are able to kill trees on a large scale, particularly if a warm weather further boosts the beetles' reproduction (White, 2015).

The measures used to control bark beetle outbreaks include, for example, salvage logging of windthrown trees before their colonizations, and sanitary felling of beetle-infested trees before the emergence of the next generation (Wermelinger, 2004; Stadelmann *et al.*, 2013; Leverkus *et al.*, 2021a). Both operations aim to recoup the value of the damaged wood and prevent future beetle induced damages to trees in the surrounding. An emergent understanding of the role of disturbance legacies in ecosystem functioning and lacking empirical evidence of salvage effectiveness, however, raised concerns about the large-scale use of this practice (Lindenmayer *et al.*, 2017; Leverkus *et al.*, 2018). Salvage logging applied in nature conservation areas often contradicts the objective of conserving biodiversity and natural ecosystems dynamics, which is largely formed by recurrent disturbance impacts (Blicharska and Van Herzele, 2015; Kameniar *et al.*, 2021). Therefore, wide-scale application of sanitary operations have repeatedly triggered social unrest and compromised public perception of forestry operations (Kortmann *et al.*, 2021). This highlights the importance of research aimed at managing forests under intensified disturbance impacts and developing strategies fostering forest resilience, which remain unknown for many ecosystems (Ibáñez *et al.*, 2019; Albrich *et al.*, 2020).

One of the unresolved questions with essential management implications is if and how disturbance intensity differs between forests with different management history and objectives. We note that we use term 'disturbance intensity' (i.e. the cumulative proportion of disturbed forest over time) interchangeably with 'disturbance severity' though some authors use these terms to describe different aspects of disturbance dynamics (Turner, 2010). For example, disturbances in protected areas tend to be smaller and more complex in shape than their surroundings affected by human land use (Senf *et al.*, 2017a; Sommerfeld *et al.*, 2018). At the same time, active disturbance management in production forests is deemed efficient in controlling natural disturbances, while unmanaged nature reserves are thought to act as foci of bark beetle spread (e.g. Montano *et al.*, 2016; Kunca *et al.*, 2019). However, empirical evidence of this process is scarce. For example, Montano *et al.* (2016) found in the Bavarian National Park (Germany) that protected areas attract more beetles from the surrounding managed forests than they export. Moreover, many protected areas harbour structurally highly diverse forests, shaped over centuries by mixed-severity disturbances (Meigs *et al.*, 2017), which often exhibit an enhanced resilience to disturbances (Winter *et al.*, 2015; Janda *et al.*, 2017). The high resistance and resilience of such forests (e.g. Bryant *et al.*, 2019) stem from their high structural and functional diversity and complex autoregulation mechanisms (Doležal *et al.*, 2020), and

were described with established ecological concepts such as the insurance hypothesis (Yachi and Loreau, 1999) and the semiochemical diversity hypothesis (Zhang and Schlyter, 2003). The latter concept suggests that the presence of non-host volatiles from diverse plant communities limits the successful search for host trees and therefore reduces insect herbivory (Schiebe *et al.*, 2011; Bockerhoff *et al.*, 2017). Still, how the actual disturbance level and disturbance trends differ between actively managed forests and unmanaged protected forests remains unknown, hampering the formulation of knowledge-based management strategies.

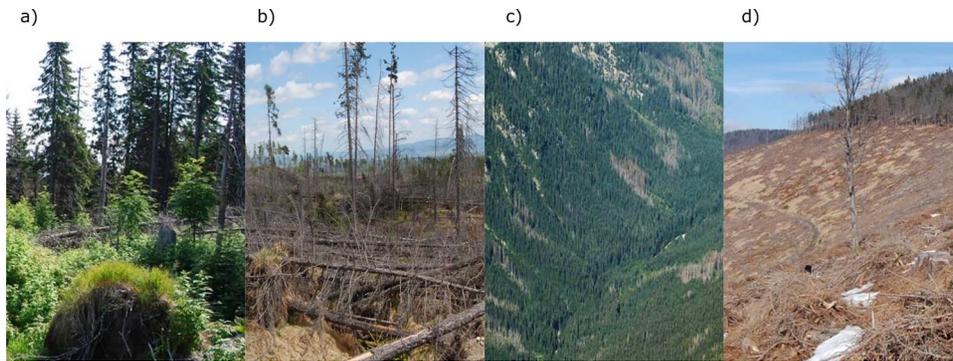
Remotely sensed data and especially freely available Landsat and Sentinel-2 datasets have been used to monitor forest changes (Hansen *et al.*, 2013) and large-scale tree mortality for decades (Meddens and Hicke, 2014; Havašová *et al.*, 2017; Duračiová *et al.*, 2020; Chen *et al.*, 2021; Meng *et al.*, 2022). Stand-replacing disturbances such as logging can be easier to detect than the gradual changes induced by chronic stress or small patches of beetle-induced tree mortality (Senf *et al.*, 2017b; Chen *et al.*, 2021). Applying longer time series and denser stacks of images is one way to more reliably capture standing beetle-infested trees over time, especially during epidemic phases of outbreaks characterized by continuous patches of standing dead trees and regional scale forest dieback (Wulder *et al.*, 2005; Havašová *et al.*, 2015). The use of additional variables such as previous year forest health status (Barka *et al.*, 2018), tree species classification maps (Fernandez-Carrillo *et al.*, 2020) or including climate predictors increased the success rate of early warning systems for bark beetle infestations (Meng *et al.*, 2022).

Here, we investigate disturbance dynamics in Norway spruce forests in Slovakia (Central Europe) along a management intensity gradient, focusing on strictly protected reserves, their surroundings, and actively managed production forests. We hypothesize that the structurally more diverse forests in strictly protected areas are inherently more resistant to disturbances than the production forests; accordingly, we expect a greater disturbance intensity in the production forests. Further, we hypothesize that disturbance intensity has recently increased both in protected and managed forests. However, we expect lower disturbances in the protected forests due to a buffering effect of their complex structure. Alternatively, we hypothesize that high-intensity management in production forests, which includes disturbance prevention and suppression actions, is efficient in controlling the disturbance dynamics, and—contrary to our previous hypothesis—the disturbances will be lower in the production forests. Our research may contribute to reconciling the different perceptions of disturbance management in Europe and support the formulation of context-dependent and climate-adapted disturbance management strategies.

## Methods

### Forest conditions, disturbance dynamics and management

Forests cover 41% of Slovakia (i.e. 20 128 km<sup>2</sup>), with the main species being European beech (34.2%), Norway spruce (22.1%) and oaks (10.5%), (Anonymous, 2019). The forests are predominantly managed for timber production (72.1%).



**Figure 1** Different management strategies in Norway spruce forests in Slovakia: a) natural unmanaged forest; b) unsalvaged windthrow; c) bark beetle infestation spots in the core zone of the national park and d) salvaged areas after windthrow and bark beetle outbreak. Photo credit: Pavel Mezei, photo from the Muránska planina National Park (a, d) and the High Tatras National Park (b, c).

Remaining forests are managed for erosion prevention, water retention and recreation (25.4%, [Anonymous, 2019](#)). Strictly protected unmanaged areas promoting nature conservation account for 2.5% of the forest area, of which 0.5% are unmanaged old-growth forests ([Mikoláš et al., 2019](#)). The prevalent management type is shelterwood management (72%), followed by clear-cutting (26%, [Anonymous, 2019](#)). Rotation periods differ depending on species and site quality; for example, the rotation period of spruce ranges from 70 to 110 years.

Norway spruce forests in Slovakia have experienced extensive disturbances during the last three decades, such as windthrows ([Gubka et al., 2014](#)), and outbreaks of the European spruce bark beetle *Ips typographus* ([Nikolov et al., 2014](#); [Økland et al., 2016](#)) followed by extensive salvage logging ([Kunca et al., 2019](#)). Therefore, the proportion of Norway spruce forests decreased from 26% in 1970 to the present (22.1%, [Anonymous, 2019](#)). Norway spruce originally grew on 4.9% of forest land and at higher elevation (>900 m a.s.l., ([Kunca et al., 2019](#)). The remaining share of Norway spruce were planted outside the natural range of spruce during the 19th and 20th century ([Kunca et al., 2019](#)).

Extensive disturbances resulted in high rates of salvage harvests in the Norway spruce forests, accounting for 84% of the total harvests in the period 2005–2017 ([Kunca et al., 2019](#), National Forest Centre, Slovakia, [Supplementary Fig. S1](#)). Therefore, planned harvesting operations in spruce stands were minimal over the studied period.

Sanitary operations (salvage logging and sanitary felling) of damaged timber are mandatory over all managed Slovak forests, except for strict reserves. To mitigate the spread of bark beetles between strict reserves and production forests, the strict reserves are surrounded by a designated buffer (usually 100 m). In protection buffers, intensive sanitary felling of infested trees is applied, with financial compensation for protective measures against bark beetles for forest owners. These different management strategies resulted in different structures of disturbed Norway spruce forests, varying from lying windthrown (unsalvaged) trees, standing bark beetle-killed trees, to the completely removed tree cover in salvage logged areas ([Fig. 1](#)).

### Forest management categories

The examined study sites include different management categories: (i) strict reserves and (ii) their buffers (500 and 2000 wide) and (iii) the managed forests with a yield-oriented management. The buffers are under the same management as the managed forests though stress is laid on mitigating the spread of bark beetles from the reserves. Therefore, both buffers can be more intensively managed than the normal managed forests.

From the total of 386 small strictly protected forests reserves in Slovakia (corresponding to the IUCN category Ia, Strict Nature Reserve), we selected 122 reserves with a minimal size of 10 ha and more than 5% of the reserves covered by Norway spruce ([Fig. 1](#)). The reserves cover a large gradient of natural conditions, ranging in size from 11 ha to 5965 ha, and Norway spruce proportion from 6.9% to 97% ([Table 1](#)).

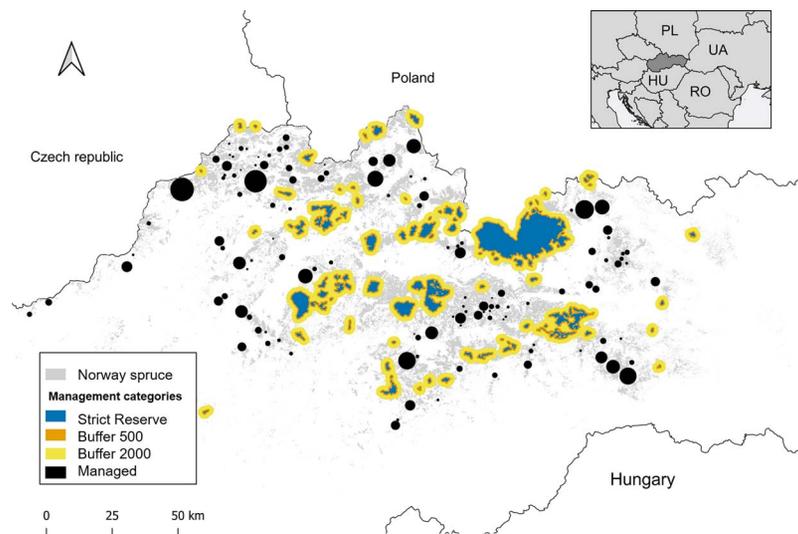
The buffers of 500 m and 2000 m surrounded the strict reserves. The buffer of 500 m encompasses the currently applied 100 m buffer of active bark beetle control and corresponds with the generally recognized dispersal radius of *I. typographus* ([Wermelinger, 2004](#); [Kautz et al., 2014](#)). The buffer of 2000 m encompasses the upper recommended buffer width to prevent the expansion of bark beetles (500 m, [Wermelinger, 2004](#)) applied in some National parks in Central Europe ([Senf et al., 2017a](#)).

Managed forests represent production-oriented Norway spruce forests distant from strict reserves. To identify managed sites, we created a set of random points localized within spruce dominated stands, with a minimal distance from the nearest strict reserve of 4 km. Around each point, we created a buffer with the same size as the randomly selected reserve. We used ArcGIS 10.6 for this analysis ([ESRI, 2021](#)) ([Table 1](#), [Fig. 2](#)).

The mean Norway spruce proportion in all categories ranged from 64% (strict reserves) to 69% (managed forests, [Table 1](#), [Supplementary Fig. S2](#)). The total area and spruce forest cover are relatively equal in strict reserves, buffer 500, and managed site; but it is three times larger in the buffer 2000. The elevation of study sites varied from  $852 \pm 249$  m a.s.l. to  $1057 \pm 235$  m a.s.l. (mean  $\pm$  SD, for managed sites and reserves, respectively). If the reserves are adjacent to each other, the neighbouring reserve was excluded from the buffer of the neighbouring reserve.

**Table 1** Summary statistics of the individual management categories within sites (122): sum of total forest cover (ha), Norway spruce forest cover (ha), share of the Norway spruce from total forest extent, mean  $\pm$  SD of forest and Norway spruce area, age (year), elevation (m a.s.l.) and Shannon index per site.

Management category	Sum total forest (ha)	Sum total Norway spruce (ha)	Forest area (mean $\pm$ SD)	Norway spruce area (mean $\pm$ SD)	Norway spruce share (%)	Age (mean $\pm$ SD)	Elevation (mean $\pm$ SD)	Shannon (mean $\pm$ SD)
Strict Reserve	48 424	33 252	397 $\pm$ 600	273 $\pm$ 456	64.7	102 $\pm$ 22	1057 $\pm$ 236	0.7 $\pm$ 0.4
Buffer 500	49 206	32 672	403 $\pm$ 297	268 $\pm$ 220	65.7	100 $\pm$ 17	1010 $\pm$ 203	0.8 $\pm$ 0.4
Buffer 2000	164 261	104 643	1346 $\pm$ 604	858 $\pm$ 491	64.5	95 $\pm$ 12	950 $\pm$ 198	0.8 $\pm$ 0.4
Managed	50 850	31 221	417 $\pm$ 714	256 $\pm$ 408	69.7	85 $\pm$ 15	852 $\pm$ 249	0.7 $\pm$ 0.5



**Figure 2** Location of selected strict reserves (blue), adjacent buffers (orange and yellow) and managed forests (black) in the Slovakia's Norway spruce forests. Inset map: Position of Slovakia in Europe.

### Forest and disturbance data

Forest species composition map, including Norway spruce distribution, are based on the tree species classification of the Slovak forests based on Landsat imagery (30 m resolution, Bucha, 1998) elaborated in the frame of the national large-scale forest ecosystem biodiversity monitoring. The classification aimed at 15 dominant tree species in Slovakia, using the maximum likelihood classification, a priori knowledge of tree species occurrence in forest regions, and a typical tree species distribution along the elevation gradient (Vladovič, 1994). Stands with a minimal area of 4 ha, Norway spruce proportion  $>$  85%, and stand density  $>$  0.7 were used as a training dataset. The overall classification accuracy varied from 77 to 88%, with the highest accuracy (89–100%) for Norway spruce and European beech. We further evaluated the accuracy of Norway spruce classification against a national forest inventory dataset from 2007 (see Supplementary Table S1 in Supplementary material for Error matrix and Supplementary Fig. S2 for visualization). This test showed high agreement between the two datasets (user's and producer's accuracy  $>$  0.83).

For each site and forest management category, we calculated i) total forest area (ha), ii) proportion of Norway spruce (%) and iii) proportion (%), and total number of tree species to calculate Shannon diversity index (for details for calculation Shannon index from tree species composition map, see Supplementary Fig. S3).

We calculated the mean elevation of each site (i.e. the spatially adjacent group of stands within one management category) based on the Space Shuttle Radar Topography Mission digital elevation model (resolution: 30 m, available online at <http://dwtkns.com/srtm30m/>). We excluded stands younger than 50 years (least disturbance susceptible). Mean age of the site therefore represents the mean age of the Norway spruce dominated stands over 50 years old, e.g. the most susceptible for disturbances. The spruce age estimation per stands originates from the national Forest inventory datasets (2005–2006), extrapolated to stand level by Natural State Conservancy.

To estimate the disturbances extent in the Norway spruce forest over the last two decades, we used data from the Slovak defoliation monitoring system based on the classification of Landsat and Sentinel-2 imagery (Bucha and Barka, 2010;

Barka *et al.*, 2018). The monitoring is based on a two-phase regression sampling. The first phase uses an orthogonal transformation of the red, near-infrared and shortwave infrared bands (sensitive to water content and greenness of vegetation) to pre-classify the level of defoliation. In the second phase, these results are refined by correlating the values with the ground-based defoliation monitoring on 112 permanent monitoring plots within ICP Forests monitoring network <http://icp-forests.net/>. This procedure leads to a high correlation of satellite and ground-truth data (Pearson correlation: 0.86–0.97), with standard error from 2.1 to 10.45. These metrics support the use of this dataset for further studies (see Barka *et al.*, 2018 for more details).

The defoliation maps represent defoliation of every pixel varying from healthy (0% defoliation) to fully defoliated (100% defoliation). The latter category represents stand replacing disturbances, such as harvests or natural disturbances (windthrows, bark beetle outbreaks) (Barka *et al.*, 2018; Bucha and Barka, 2010). The data are available for the period 2000–2017, except for the years 2002, 2003, 2004, 2009 and 2014, when high cloud contamination prevented the assessment (Barka *et al.*, 2018).

We iteratively processed the individual defoliation maps to i) identify the year of first disturbance per pixel, and to ii) assure that disturbed pixels are disturbed only once during the study period (see Supplementary Fig. S4). Starting from the first year (in 2000), we classified the defoliation maps into the binary map, representing ‘undisturbed’ forest [0–60% of defoliation] or ‘disturbed’ [60–100%] forest in particular year. The threshold of 60% (‘heavy defoliation’) follows the recommendations of Bucha and Barka (2010) and previous testing by Havašová *et al.* (2017). The ‘undisturbed’ category was used as a forest mask to filter out disturbed pixels in following years. We continued iteratively over all consecutive defoliation maps. Having created annual disturbance maps, we combined all maps into a cumulative disturbance map for the entire study period (Supplementary Fig. S5, Supplementary material). We used cumulative disturbance values instead of annual values to compensate for missing years in the defoliation maps series. The ‘disturbance’ value [in%] represents the proportion of disturbed pixels relative to the total number of pixels occupied by Norway spruce (state from 1999) from 2000 to 2017 per site. The term ‘disturbance’ includes biotic (bark beetle) and abiotic (wind damage) disturbances, sanitary operations, and planned harvest. However, the proportion of planned harvests in Norway spruce stand was minimal in the study period (on average 16% of the total harvest, National Forest Centre, Supplementary Fig. S1). Therefore, our findings can be interpreted mainly with regard to natural disturbance dynamics.

### Statistical analysis

We summarized cumulative disturbances per management categories using quantiles to capture data central tendency and account for potential skewness. The annual disturbances represent the cumulative disturbances divided by the number of years ( $n = 18$ , from 2000 to 2017).

We used generalized additive mixed models (GAMMs, Wood, 2017) to model the cumulative disturbances (dependent variable) over time by management categories, i.e. each site in the dataset produced one sample point with 18-time steps. We used GAMMs with beta distribution and logit-link function

(Ferrari and Cribari-Neto, 2004) to account for the restriction of the cumulative disturbance values [0–100% interval, from no disturbance to total damage] and to model non-linear temporal trends in cumulative disturbances among categories. In addition, GAMMs allowed us to account for the spatial and temporal dependencies in time series for categories nested within sites. We statistically controlled for the heterogeneity between sites by using local characteristics (spruce proportion, tree diversity, elevation and forest age) to account for the differences between sites in terms of forest structure and conditions and to filter their potential effect.

The fixed parameters of the GAMMs contained a main effect of the category (strict reserve, buffer 500, buffer 2000, and managed sites) and an interaction of the Management category with thin plate regression spline smoother for time to allow for different temporal trends among the categories. Since individual sites varied in spruce proportion, tree diversity (Shannon index), elevation and forest age, we included the fixed effects of those variables to disentangle the influence of management and local environmental characteristics on the forest disturbances. Spruce proportion and tree diversity were treated as linear predictors while elevation and site age were used as smooth terms. Random effect structure of the GAMMs involved factor smooths for time per individual categories within sites. The factor smooth is a non-linear alternative to random intercepts and slopes which may help to reduce temporal autocorrelation in the residuals (Baayen *et al.*, 2017). However, when we used random factor smooths penalized for wiggleness, the autocorrelation function revealed significantly non-independent residuals. We, therefore, used factor smooths in combination with first-order autoregressive errors (Baayen *et al.*, 2018). A small value of the autoregressive parameter ( $\rho = 0.15$ ) was sufficient to eliminate the strong positive autocorrelation structure in the residuals. Residuals of the autoregressive models showed negative autocorrelation at the first and second lags, which can make the tests more conservative but do not invalidate significant results (Yue *et al.*, 2002). Autocorrelation in the lags of higher orders was relatively mild (range of ACF values:  $-0.21$  to  $0.28$ ). No other serious violation of the model assumptions was recorded. The significance of the model terms was assessed using Wald tests, conditional on the smoothing parameter estimates (Wood, 2013).

To evaluate the significance of Management category-by-year interaction, we fitted simpler GAMM without the Management category-specific temporal trends and compared it with the full GAMM involving Management category-specific smoothers using a  $\chi^2$  test on the differences in maximum-likelihood scores (van Rij J *et al.*, 2017). We used the full GAMM model (including all explanatory variables) with the management category-specific temporal trends to analyse the partial effects of forest structural and environmental predictors.

Disturbance intensification over time period was expressed as compound annual disturbance rates from GAMMs predicted values per management category. Compound annual disturbance rates were calculated as the difference between predicted average cumulative disturbances in the last and first year, divided by total number of years ( $n = 18$ ). The analyses were performed in R (R Development Core Team, 2019) using the libraries *itsadug* (van Rij J *et al.*, 2017) and *mgcv* (Wood, 2017) at Finnish IT Centre for Science supercomputing facilities ([www.research.csc.fi](http://www.research.csc.fi)). We

**Table 2** Distribution of cumulative disturbances (% , ha) over management categories (2000–2017). The values are expressed as mean and individual quantiles intervals.

Management category	Mean	Quantiles (%)						
		0	1	25	Median (50)	75	99	100
Strict reserve	19.4 (71)	0 (0)	0 (0)	2.9 (1.2)	6.2 (6.9)	24.3 (39.5)	91.1 (785.3)	98.9 (1008.4)
Buffer 500	30.3 (72.7)	2.2 (0.7)	2.5 (1.2)	9.6 (13.1)	18.6 (30.9)	46.8 (102)	96.9 (377.4)	99.7 (496.7)
Buffer 2000	30.9 (205.4)	2.3 (0.8)	3.4 (1.1)	13.2 (56.4)	20.3 (129.5)	40.4 (306.7)	96.6 (934.1)	99.1 (1031.9)
Managed forests	31.4 (79.9)	0 (0)	0 (0)	12.2 (6.2)	23.7 (27.7)	45 (79.8)	95.1 (547.9)	97.1 (812.6)

processed spatial datasets and created maps using ArcGIS 10 software (ESRI, 2021) and QGIS 3.6 (QGIS Development Team, 2020).

## Results

### Cumulative disturbances

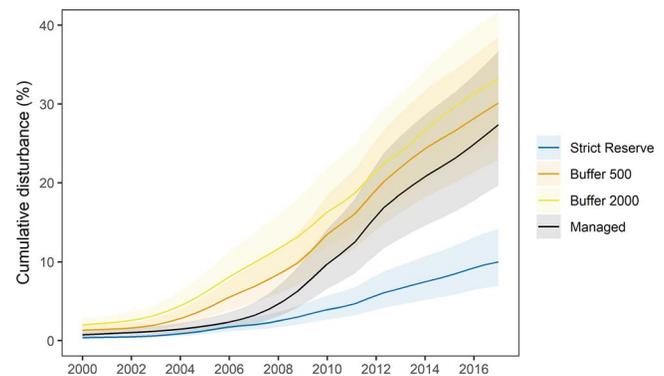
In the period 2000–2017, the cumulative disturbances varied among the categories (Table 2) and were strongly right skewed. Strict reserves experienced lower cumulative disturbances (mean 19.4%, median 6.2%) than production forests (mean 30.3–31.4%, median: 18.6–23.7% for buffer 500 and managed forest, respectively). Mean annual disturbances calculated from cumulative values are in Supplementary material (Supplementary Fig. S7, Supplementary Table S2).

### Temporal trends

Temporal trends of cumulative disturbances differed among the categories as evidenced by the significant effect of management category  $\times$  time interaction in the GAMM ( $\chi^2$ (df = 6) = 32.3,  $P < 0.0001$ ). After the initial stable period, disturbances accelerated from 2005 and began to diverge among the managed forests and strict reserves (Fig. 3). Disturbances sharply increased in the buffers and managed forests over time. The average predicted cumulative disturbance was 9.9% in strict reserve and varying from 27.2% to 33.1% in between control zone to buffer 2000. Compound annual disturbance rates were considerably lower in the strict reserves ( $0.58\% \text{ y}^{-1}$ ) than in production forests. Although the annual disturbance rates were generally comparable among the managed stands, the buffer 2000 had the highest annual disturbance rate ( $2.21\% \text{ y}^{-1}$ ), followed by the buffer 500 ( $1.97\% \text{ y}^{-1}$ ), and managed forests ( $1.76\% \text{ y}^{-1}$ ).

### Disturbance drivers

Among the forest structural characteristics, spruce proportion and average stand age showed a significant positive relationship with cumulative disturbances (Table 3, Fig. 4). Elevation and tree diversity had non-significant effects on the disturbance intensity, and elevation showed non-significant humped relationships. Interestingly, although non-significant, tree diversity represented by Shannon index was positively associated with the disturbance intensity (Fig. 4). The predictors accounted for almost 25% of variability in the dataset (pseudo- $R^2 = 0.249$ ).



**Figure 3** Cumulative disturbances at 122 sites in the Western Carpathians over the period 2000–2017. Expected cumulative disturbance predicted by the beta GAMM (lines) and 95% confidence intervals (bands) are displayed while controlling for the effect of elevation, Shannon tree diversity and Norway spruce cover. Details of the model are given in Table 3.

## Discussion

Our study confirmed an increasing rate of natural disturbances reported from Europe and around the globe (Seidl *et al.*, 2020) as well disturbance intensification varying between differently managed forests (Sommerfeld *et al.*, 2018). We found a striking difference in the total amount of disturbances and average yearly disturbance rates between strictly protected reserves and production forests (Fig. 3). This might suggest the superiority of complex forest structure and natural regulation mechanism, e.g. autoregulation mechanisms due to high structural and functional diversity (Doležal *et al.*, 2020), abundance of natural enemies (Wegensteiner *et al.*, 2015) and reduced insect herbivory in diverse communities (Brockhoff *et al.*, 2017) over active disturbance control exercised in managed forest. We further discuss the potential drivers of this variation and implications of our findings for managing and conserving forests under climate change.

### Ecological background and implications

The increasing disturbance intensity in Europe's Norway spruce forests has been reported for different environments, including mountains and lowlands (Hlásny *et al.*, 2021a) and for differently managed forests (Sommerfeld *et al.*, 2018). In the past, the forests examined here have been predominantly disturbed by

**Table 3** Summary of the beta GAMM fitted to the cumulative disturbances (% from 2000 to 2017). The random-effects structure includes penalized factor smooth of time by management categories within sites ( $f_s(\text{Time}, \text{Management category}(\text{Site}))$ ). Degrees of freedom (for parametric terms) and effective degrees of freedom (for smooth terms) are displayed (DF) along with Wald test statistics ( $F$ ) and associated  $P$ -values. Partial coefficients (std. errors) and their tests are given for parametric terms. Note that strictly protected reserves are the reference level (intercept) of the variable Management category.

Model terms	Coefficients (SE)	DF	$F$	$P$ -value
Parametric terms				
Intercept (Strict Reserve)	-6.29 (0.56)	1	-11.13	<0.0001
Management category		3	20.92	<0.0001
- Buffer 500	1.31 (0.21)	1	6.24	<0.0001
- Buffer 2000	1.60 (0.22)	1	7.41	<0.0001
- Managed	0.96 (0.24)	1	4.02	<0.0001
Spruce proportion	0.03 (0.01)	1	5.34	<0.0001
Shannon (Tree diversity)	0.53 (0.33)	1	1.59	0.1114
Smooth terms				
$s(\text{Time}) \times \text{Strict Reserve}$		15.5	33.71	<0.0001
$s(\text{Time}) \times \text{Buffer 500}$		15.3	34.61	<0.0001
$s(\text{Time}) \times \text{Buffer 2000}$		14.7	26.07	<0.0001
$s(\text{Time}) \times \text{Managed}$		15.0	47.34	<0.0001
$s(\text{Elevation})$		1.6	2.27	0.2224
$s(\text{Age})$		1.5	9.33	0.0028
$f_s(\text{Time}, \text{Management category}(\text{Site}))$		4322.0	866.08	<0.0001

episodic windthrows followed by bark beetle outbreaks, which is a typical disturbance regime of Central European spruce forests (Čada *et al.*, 2016; Janda *et al.*, 2017). In the Western Carpathians, past large-scale disturbances could, to a certain extent, homogenize tree size and age structure and thus increase forest vulnerability to the present-day disturbances (Janda *et al.*, 2017). The observed increase in disturbance intensity was likely related to the transition to drought-driven outbreak dynamics, which has been recently documented in the neighbouring Norway spruce forests in Czechia (Hlásny *et al.*, 2021b). In particular, the recent disturbance increase can be attributed to the extensive drought in 2003 (Rouault *et al.*, 2006), compound effect of devastating windthrow from 2004, the subsequent increase in bark beetle populations (Nikolov *et al.*, 2014; Kunca *et al.*, 2019), and the subsequent period with exceptionally hot and dry years (particularly increasing from 2014, Bošela *et al.*, 2020; Büntgen *et al.*, 2021).

We found that managed forests exhibited a cumulative disturbances three times higher than forests in the strict reserves, and this difference was increasing over time (9.9% of forest disturbed in strict reserves, on average, and 27–33% in the remaining categories). At the same time, the compound annual disturbance rate was 1.76%  $y^{-1}$  in managed forests and 0.58%  $y^{-1}$  in the reserves. Planned harvests in Norway spruce stands (16% of the total harvest during 2005–2017, Supplementary Fig. S1) partly contributed to this difference, however, they did not negate the identified three-fold difference between the categories. Although the underlying mechanisms of this difference are not entirely understood, we suggest that semi-natural unmanaged forests are better buffered from climate change-driven disturbance intensification than managed production forests.

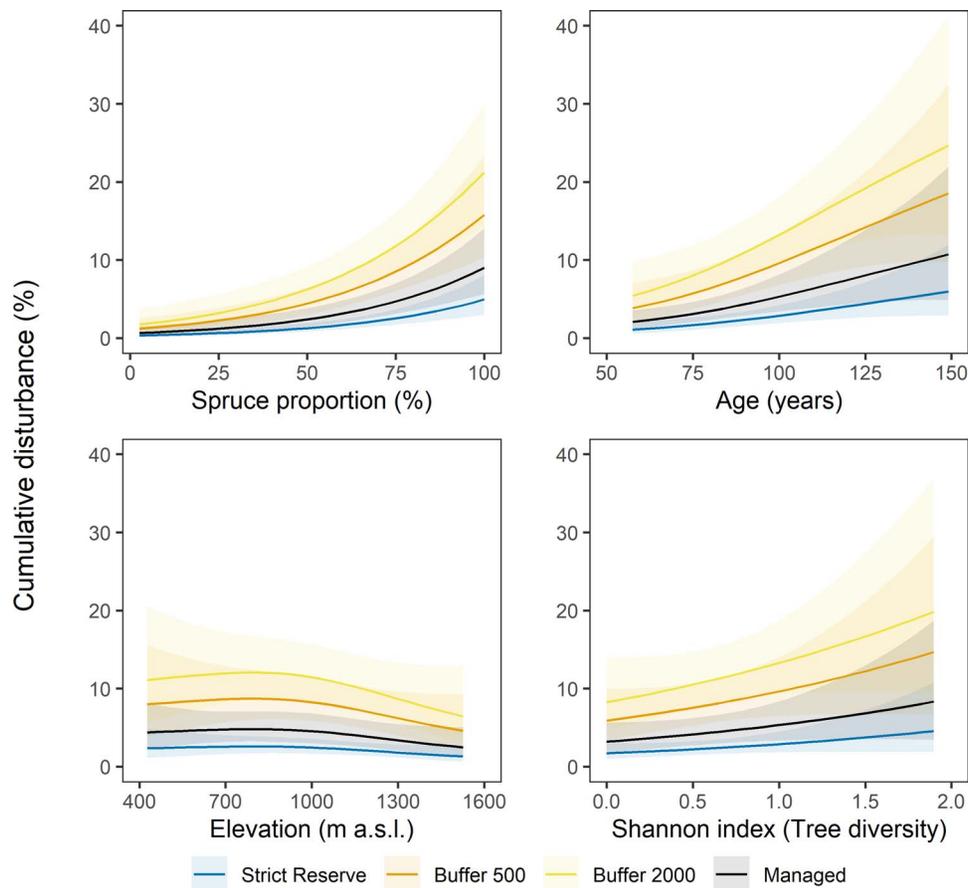
The forests in strict reserves were generally older, occurred in higher elevations, had lower tree species diversity, and a lower Norway spruce proportion than the managed forests

(Supplementary Fig. S6). While higher age and lower species diversity are likely to increase forest propensity to wind and bark beetles, these effects may have been overwhelmed by the thermal limitation constraining beetles' development and a smaller abundance of vulnerable spruce. Although lower species diversity in the strict reserves can be surprising, some of the investigated forests represent subalpine Norway spruce ecosystems formed by a limited number of species and with a monotonous age structure (Mikoláš *et al.*, 2019). However, such forests can show a high ecological resilience to disturbances (Janda *et al.*, 2017).

All national parks in Slovakia, which represent a substantial proportion of here investigated strict reserves, were established after 1949, and these forests had been managed with varying intensity in the prior period. Therefore, the legacies of the previous management remain in these forests, and they may differ in their structure and functioning from old-growth natural forests. Our findings indirectly suggest that resilient forest structures can evolve within decades after the management has ceased. This agrees with Albrich *et al.* (2021), who suggested that a number of important forest attributes can recover quickly after disturbance and therefore even formerly managed forests may contribute to enriched landscapes, although a full return to old-growth conditions can take centuries. These observations highlight the importance of conserving natural forests, which allows comparing their dynamics with the dynamics of forests modified by humans, serving as natural laboratories (Smit *et al.*, 2017; Sterner *et al.*, 2019).

### Implications for forest management

Forest management in Central Europe has strived historically to foster forest productivity by promoting profitable tree species such as Norway spruce, applying rotation forestry, and different



**Figure 4** Partial effect of Norway spruce proportion (%), elevation (m a.s.l.), stand age (years) and tree diversity (Shannon index) on cumulative disturbance at 122 sites in the Western Carpathians for different management categories. The model details are in Table 3.

tending strategies. This approach led to high forest cover in many European countries and the overall increase in afforested areas on the continent during the 20th century. However, focusing excessively on productivity has eroded ecosystem resilience and increased the forest's vulnerability to wind and insect outbreaks. Therefore, additional measures were introduced to improve tree static stability by thinning and shortening of rotation length (Roberge *et al.*, 2016), and keeping pest populations low by sanitation removal of infested trees, beetle trapping, and using insecticides and semiochemicals (Hlásny *et al.*, 2021a; Wermeinger, 2004). However, the success of efforts aimed to replace the natural regulation mechanisms emerging from species, structural and functional diversity (Mori *et al.*, 2017), remains unclear. Therefore, comparing disturbance dynamics in natural and managed forests does not only advance our understanding of system resilience and vulnerability but also reveals possible limitations of cultural practices for disturbance control. Although our findings are not conclusive in this regard, they question a broadly held belief that salvage logging and sanitary felling practiced in production forests will prevent disturbance impacts, while protected areas serve as foci of disturbance spread. The decreasing efficiency of removing windthrown spruce trees on bark beetle populations under a warmer climate has been suggested, for example, by

Zimová *et al.* (2020), Dobor *et al.* (2020a) and Leverkus *et al.* (2021b). Our findings suggest that forests containing old-growth conditions can be more resilient to climate change, including intensified disturbance impacts. This may require reconsidering current management practices and promote strategies such as Natural Dynamics Silviculture, which aims to emulate natural disturbance dynamics at several scales through silviculture manipulations (Drever *et al.*, 2006; Kuuluvainen *et al.*, 2021; Aszalós *et al.*, 2022).

A lower disturbance intensity in strictly protected forests is remarkable in the perspective of a relatively short period (<70 years) since the management has been ceased. Moreover, salvage logging after extreme disturbance events have only been banned from 2002 (Anonymous, 2002). Although this is not the only difference between the investigated managed and strictly protected forests (for example, elevation and topographic complexity were, on average, higher in the reserves), it highlights the potential for reaching resilient forest structures within relatively short periods (Sabatini *et al.*, 2020; Albrich *et al.*, 2021) and benefiting from natural dynamics in selected parts of the landscape (Aszalós *et al.*, 2022). However, this requires shifting from the narrow historical focus of conservation on the iconic landscapes and wildlife towards creating large multifunctional landscapes helping to reach conservation

objectives and securing human well-being (Watson *et al.*, 2014). This is critically important at the era of increasing demand for forest-based products in an effort to reduce our dependence on fossil-fuels.

### Methodological aspects and limitations

The main limitation of the current study is a possible confusion of natural and anthropogenic disturbance (e.g. planned and sanitary harvests). Although we included only strict reserves under a no-management regime, some harvests may have occurred in old-growth forests, although to a limited extent (Mikoláš *et al.*, 2019), for example, in relation to sanitation removal of trees infested by bark beetles that are permitted under some circumstances. Another issue is a problematic differentiation of planned harvest and natural disturbance in production forests, where they concur. This was to a large extent resolved by focusing on spruce forests only, where >84% of harvests were related to the salvaging of dead trees in the studied period (Supplementary Fig. S1). We, therefore, argue that the effect of planned harvests does not undermine our conclusions, yet it needs to be considered.

Further limitations relate to the resolution of used satellite imagery, the accuracy of forest tree species classification and tree defoliation monitoring. These data obviously underestimated single tree mortality (e.g. until 2005, Havašová *et al.*, 2015, 2017), and tree species diversity have been evaluated only at the beta-level. Future studies should therefore exploit ground-based forest inventory data to compare mortality rates between managed and protected forests, and thus extend the here presented coarse-resolution assessment. Such research could also extend the set of here used predictors, and consider, for example, indices describing the complexity of vertical structure, functional forest diversity, the abundance of beetles' antagonists, and other factors associated with forest resistance and resilience (Erfanifard *et al.*, 2019). Further extension of the current study should contrast changing disturbance dynamics in the period before 1990 and after 2000 to unravel the speed of forest decline under rapidly changing climate. Still, the investigated period 2000–2017 covers a dramatic increase in disturbance intensity, displaying a clear temporal signal.

Lastly, the improvement of the remote sensing sensors over time can lead to the false estimation of the magnitude of the agent of forest change (Palahí *et al.*, 2021; Breidenbach *et al.*, 2022). For example, recent improvement of the sensors' capacity led to erroneous estimation of the abrupt increase in forest harvests after 2015 (Palahí *et al.*, 2021). On the other hand, the improvement of sensors also allowed to improve identification of the small-scale disturbances such as thinning (Breidenbach *et al.*, 2022) or early bark beetle infestations (Chen *et al.*, 2021; Meng *et al.*, 2022). Therefore, changes in sensors and classification methods need to be carefully considered when examining long term remotely sensed datasets. Our results show the abrupt increase in disturbances since 2005 (Fig. 3) that agreed with interpretation of aerial imagery (Nikolov *et al.*, 2014) and national forest management statistics (Kunca *et al.*, 2019). Although our datasets suffer from the known artefacts of the remotely sensed data (Breidenbach *et al.*, 2022) and classification errors

(Olofsson *et al.*, 2013, 2014), we suggest that the errors were equally distributed among the management categories and over the years and therefore do not substantially affect our results.

### Conclusion

A body of evidence suggests that forest disturbances intensify globally in response to climate change. We showed that this trend is present also in Central European spruce forests; yet the cumulative disturbance rate differed between differently managed forests. A lower disturbance intensity in strict forest reserves suggests that these forests can be more resistant to disturbance impacts than forests actively managed for timber production. This indirectly questions the efficiency of disturbance control measures, such as sanitary logging, to prevent further tree mortality in managed forests. These findings highlight the importance of protected forests with complex structures which can act as important stabilizing elements in the landscapes exposed to climate change and intensifying disturbance regimes.

### Supplementary data

Supplementary data are available at *Forestry* online.

### Data availability

Tree species classification raster and near-yearly forest defoliation datasets are available upon request at the National Forest Centre, Zvolen, Slovakia on <https://www.nlcsk.org/stale/s/>. The Strict reserves layer is available upon request from State Nature Conservancy of the Slovak Republic <http://www.soprs.sk/>. The code and the summary dataset to reproduce the model and plots are available at <https://github.com/mariapotterf/disturbanceIntensification>.

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### Conflict of interest statement

None declared.

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## References

- Albrich, K., Rammer, W. and Seidl, R. 2020 Climate change causes critical transitions and irreversible alterations of mountain forests. *Glob. Chang. Biol.* **26**, 4013–4027. <https://doi.org/10.1111/gcb.15118>.
- Albrich, K., Thom, D., Rammer, W. and Seidl, R. 2021 The long way back: development of Central European mountain forests towards old-growth conditions after cessation of management. *J. Veg. Sci.* **32**, 1–13. <https://doi.org/10.1111/jvs.13052>.
- Anonymous 2019 *Report on the Forest Sector of the Slovak Republic 2019*. Green Report, Bratislava.
- Anonymous 2002 *Zákon o ochrane prírody a krajiny, 543/2002 [Nature and Landscape Protection Act, 543/2002]*. Národná rada Slovenskej republiky [National Council of the Slovak Republic]. Slovak Republic.
- Aszalós, R., Thom, D., Aakala, T., Angelstam, P., Brūmelis, G., Gálhidy, L., et al. 2022 Natural disturbance regimes as a guide for sustainable forest management in Europe. *Ecol. Appl.* **32**, e2596–e2523. <https://doi.org/10.1002/eap.2596>.
- Barka, I., Lukeš, P., Bucha, T., et al. 2018 Remote sensing-based forest health monitoring systems-case studies from Czechia and Slovakia. *Cent. Eur. For. J.* **64**, 259–275. <https://doi.org/10.1515/forj-2017-0051>.
- Baayen, H., Vasishth, S., Kliegl, R., & Bates, D. (2017) The cave of shadows: Addressing the human factor with generalized additive mixed models. <https://doi.org/10.1016/j.jml.2016.11.006>.
- Baayen, R.H., van Rij, J., de Cat, C. and Wood, S.N. 2018 Autocorrelated Errors in Experimental Data in the Language Sciences: Some Solutions Offered by Generalized Additive Mixed Models. In *Mixed-Effects Regression Models in Linguistics*. D., Speelman, K., Heylen, D., Geeraerts (eds.). Springer, Cham, pp. 49–69.
- Blicharska, M. and Van Herzele, A. 2015 What a forest? Whose forest? Struggles over concepts and meanings in the debate about the conservation of the Białowieża Forest in Poland. *For. Policy Econ.* **57**, 22–30. <https://doi.org/10.1016/j.forpol.2015.04.003>.
- Bošela, M., Tumajer, J., Cienciala, E., et al. 2020 Climate warming induced synchronous growth decline in Norway spruce populations across biogeographical gradients since 2000. *Sci. Total Environ.* **752**, 141794. <https://doi.org/10.1016/j.scitotenv.2020.141794>.
- Breidenbach, J., Ellison, D., Petersson, H., Korhonen, K.T., Henttonen, H.M., Wallerman, J., et al. 2022 Harvested area did not increase abruptly—how advancements in satellite-based mapping led to erroneous conclusions. *Ann. For. Sci.* **79**, 1–9. <https://doi.org/10.1186/s13595-022-01120-4>.
- Brockhoff, E.G., Barbaro, L., Castagnyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., et al. 2017 Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodivers. Conserv.* **26**, 3005–3035. <https://doi.org/10.1007/s10531-017-1453-2>.
- Bryant, T., Waring, K., Sánchez Meador, A. and Bradford, J.B. 2019 A framework for quantifying resilience to forest disturbance. *Front. For. Glob. Chang.* **2**, 1–14. <https://doi.org/10.3389/ffgc.2019.00056>.
- Bucha, T. 1998 Classification of tree species composition in Slovakia from satellite photograph as a part of monitoring of forest ecosystem biodiversity. *Acta Inst. For.* **9**, 65–84.
- Bucha, T. and Barka, I. 2010 Satellite-based regional system for observation of forest response to global environmental changes. In *Advances in Geoinformation Technologies*. J., Horák, L., Halounová, T., Hlásny, et al. (eds.). Technical University of Ostrava, Ostrava, pp. 1–14.
- Büntgen, U., Urban, O., Krusic, P.J., Rybníček, M., Kolář, T., Kyncl, T. et al. 2021 Recent European drought extremes beyond Common Era background variability. *Nat. Geosci.* **14**, 190–196. <https://doi.org/10.1038/s41561-021-00698-0>.
- Čada, V., Morrissey, R.C., Michalová, Z., Bače, R., Janda, P. and Svoboda, M. 2016 Frequent severe natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest in central Europe. *For. Ecol. Manag.* **363**, 169–178. <https://doi.org/10.1016/j.foreco.2015.12.023>.
- Chen, S., Woodcock, C.E., Bullock, E.L., Arévalo, P., Torchinava, P., Peng, S., et al. 2021 Monitoring temperate forest degradation on Google Earth Engine using Landsat time series analysis. *Remote Sens. Environ.* **265**, 112648. <https://doi.org/10.1016/j.rse.2021.112648>.
- de Groot, M., Diaci, J. and Ogris, N. 2019 Forest management history is an important factor in bark beetle outbreaks: lessons for the future. *For. Ecol. Manag.* **433**, 467–474. <https://doi.org/10.1016/j.foreco.2018.11.025>.
- Dobor, L., Hlásny, T., Rammer, W., Zimová, S., Barka, I. and Seidl, R. 2020a Is salvage logging effectively dampening bark beetle outbreaks and preserving forest carbon stocks? *J. Appl. Ecol.* **57**, 67–76. <https://doi.org/10.1111/1365-2664.13518>.
- Dobor, L., Hlásny, T. and Zimová, S. 2020b Contrasting vulnerability of monospecific and species-diverse forests to wind and bark beetle disturbance: the role of management. *Ecol. Evol.* **10**, 12233–12245. <https://doi.org/10.1002/ece3.6854>.
- Doležal, J., Fibich, P., Altman, J., et al. 2020 Determinants of ecosystem stability in a diverse temperate forest. *Oikos* **129**, 1692–1703. <https://doi.org/10.1111/oik.07379>.
- Drever, C.R., Peterson, G., Messier, C., Bergeron, Y. and Flannigan, M. 2006 Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res.* **36**, 2285–2299. <https://doi.org/10.1139/X06-132>.
- Duračiová, R., Muňko, M., Barka, I., Koreň, M., Resnerová, K., Holuša, J., et al. 2020 A bark beetle infestation predictive model based on satellite data in the frame of decision support system Tanabbo. *IForest* **13**, 215–223. <https://doi.org/10.3832/ifor3271-013>.
- Erfanifard, Y., Stereńczak, K. and Miścicki, S. 2019 Management strategies alter competitive interactions and structural properties of Norway spruce in mixed stands of Białowieża Forest, Poland. *For. Ecol. Manag.* **437**, 87–98. <https://doi.org/10.1016/j.foreco.2019.01.035>.
- ESRI 2021. In *ArcGIS Desktop: Release 10*. Environmental Systems Research Institute, Redlands, CA.
- Fernandez-Carrillo, A., Patočka, Z., Dobrovolný, L., Franco-Nieto, A. and Revilla-Romero, B. 2020 Monitoring bark beetle forest damage in central Europe. A remote sensing approach validated with field data. *Remote Sens.* **12**, 1–19. <https://doi.org/10.3390/rs12213634>.
- Ferrari, S., & Cribari-Neto, F. (2004) Beta Regression for Modelling Rates and Proportions. *J Appl Stat* **31**:799–815. <https://doi.org/10.1080/0266476042000214501>.
- Gubka, A., Kunca, A., Longauerová, V., et al. 2014 *Vetrová Kalamita Žofia z 15. 5. 2014 [Wind disturbance Žofia from 15. 5. 2014]*. National Forest Centre, Zvolen, Slovakia, pp. 1–8.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., et al. 2013 High-resolution global maps of 21st-century forest cover change. *Science (80-)* **342**, 850–853. <https://doi.org/10.1126/science.1244693>.
- Havašová, M., Bucha, T., Ferenčík, J. and Jakuš, R. 2015 Applicability of a vegetation indices-based method to map bark beetle outbreaks in the High Tatra Mountains. *Ann. For. Res.* **58**, 295–310. <https://doi.org/10.15287/afr.2015.388>.

- Havašová, M., Ferenčík, J. and Jakuš, R. 2017 Interactions between windthrow, bark beetles and forest management in the Tatra national parks. *For. Ecol. Manag.* **391**, 349–361. <https://doi.org/10.1016/j.foreco.2017.01.009>.
- Hlásny, T., König, L., Krokene, P., Lindner, M., Montagné-Huck, C., Müller, J., et al. 2021a Bark beetle outbreaks in Europe: state of knowledge and ways forward for management. *Curr. For. Rep.* **7**, 138–165. <https://doi.org/10.1007/s40725-021-00142-x>.
- Hlásny, T., Zimová, S., Merganičová, K., Štěpánek, P., Modlinger, R., & Turčáni, M. (2021b) Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications. *For. Ecol. Manag.* **490**. <https://doi.org/10.1016/j.foreco.2021.119075>.
- Ibáñez, I., Acharya, K., Juno, E., Karounos, C., Lee, B.R., McCollum, C., et al. 2019 Forest resilience under global environmental change: do we have the information we need? A systematic review. *PLoS One* **14**, e0222207–e0222217. <https://doi.org/10.1371/journal.pone.0222207>.
- Janda, P., Trotsiuk, V., Mikoláš, M., Bače, R., Nagel, T.A., Seidl, R., et al. 2017 The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. *For. Ecol. Manag.* **388**, 67–78. <https://doi.org/10.1016/j.foreco.2016.08.014>.
- Kameniar, O., Baláž, M., Svitok, M., Reif, J., Mikoláš, M., Pettit, J.L., et al. 2021 Historical natural disturbances shape spruce primary forest structure and indirectly influence bird assemblage composition. *For. Ecol. Manag.* **481**, 118647. <https://doi.org/10.1016/j.foreco.2020.118647>.
- Kausrud, K.L., Økland, B., Skarpaas, O., Grégoire, J.C., Erbilgin, N. and Stenseth, N.C. 2012 Population dynamics in changing environments: the case of an eruptive forest pest species. *Biol. Rev. Camb. Philos. Soc.* **87**, 34–51. <https://doi.org/10.1111/j.1469-185X.2011.00183.x>.
- Kautz, M., Schopf, R. and Imron, M.A. 2014 Individual traits as drivers of spatial dispersal and infestation patterns in a host-bark beetle system. *Ecol. Model.* **273**, 264–276. <https://doi.org/10.1016/j.ecolmodel.2013.11.022>.
- Kautz, M., Schopf, R. and Ohser, J. 2013 The “sun-effect”: microclimatic alterations predispose forest edges to bark beetle infestations. *Eur. J. For. Res.* **132**, 467–467. <https://doi.org/10.1007/s10342-013-0686-1>.
- Kortmann, M., Müller, J.C., Baier, R., Bässler, C., Buse, J., Cholewińska, O., et al. 2021 Ecology versus society: impacts of bark beetle infestations on biodiversity and restorativeness in protected areas of Central Europe. *Biol. Conserv.* **254**, 108931. <https://doi.org/10.1016/j.biocon.2020.108931>.
- Kunca, A., Zúbrik, M., Galko, J., et al. 2019 Salvage felling in the Slovak Republic’ s forests during the last twenty years Salvage felling in the Slovak Republic’ s forests during the last twenty years (1998–2017). **65**, 3–11. <https://doi.org/10.1515/forj-2017-0055>.
- Kuuluvainen, T., Angelstam, P., Frelich, L., Jögiste, K., Koivula, M., Kubota, Y., et al. 2021 Natural disturbance-based forest management: moving beyond retention and continuous-cover forestry. *Front. For. Glob. Chang.* **4**, 1–16. <https://doi.org/10.3389/ffgc.2021.629020>.
- Leverkus, A.B., Benayas, J.M.R., Castro, J., et al. 2018 Salvage logging effects on regulating and supporting ecosystem services — a systematic map. *Can. J. For. Res.* **48**, 983–1000. <https://doi.org/10.1139/cjfr-2018-0114>.
- Leverkus, A.B., Buma, B., Wagenbrenner, J., Burton, P.J., Lingua, E., Marzano, R., et al. 2021a Tamm review: does salvage logging mitigate subsequent forest disturbances? *For. Ecol. Manag.* **481**, 118721. <https://doi.org/10.1016/j.foreco.2020.118721>.
- Leverkus, A.B., Thorn, S., Gustafsson, L., Noss, R., Müller, J., Pausas, J.G., et al. 2021b Environmental policies to cope with novel disturbance regimes—steps to address a world scientists’ warning to humanity. *Environ. Res. Lett.* **16**. <https://doi.org/10.1088/1748-9326/abd5a>.
- Lindenmayer, D., Thorn, S. and Banks, S. 2017 Please do not disturb ecosystems further. *Nat. Ecol. Evol.* **1**, 1–3. <https://doi.org/10.1038/s41559-016-0031>.
- Marini, L., Ayres, M.P., Battisti, A. and Faccoli, M. 2012 Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. *Clim. Chang.* **115**, 327–341. <https://doi.org/10.1007/s10584-012-0463-z>.
- Marini, L., Økland, B., Jönsson, A.M., Bentz, B., Carroll, A., Forster, B., et al. 2017 Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography (Cop)* **40**, 1426–1435. <https://doi.org/10.1111/ecog.02769>.
- Meddens, A.J.H. and Hicke, J.A. 2014 Spatial and temporal patterns of Landsat-based detection of tree mortality caused by a mountain pine beetle outbreak in Colorado, USA. *For. Ecol. Manag.* **322**, 78–88. <https://doi.org/10.1016/j.foreco.2014.02.037>.
- Meigs, G.W., Morrissey, R.C., Bače, R., Chaskovskyy, O., Čada, V., Després, T., et al. 2017 More ways than one: mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. *For. Ecol. Manag.* **406**, 410–426. <https://doi.org/10.1016/j.foreco.2017.07.051>.
- Meng, R., Gao, R., Zhao, F., Huang, C., Sun, R., Lv, Z., et al. 2022 Landsat-based monitoring of southern pine beetle infestation severity and severity change in a temperate mixed forest. *Remote Sens. Environ.* **269**, 112847. <https://doi.org/10.1016/j.rse.2021.112847>.
- Mezei, P., Jakuš, R., Blaženec, M., et al. 2012 The relationship between potential solar radiation and spruce bark beetle catches in pheromone traps. *Ann. For. Res.* **55**, 234–252.
- Mikoláš, M., Ujházy, K., Jasík, M., Wieszik, M., Gallay, I., Polák, P., et al. 2019 Primary forest distribution and representation in a Central European landscape: results of a large-scale field-based census. *For. Ecol. Manag.* **449**, 117466. <https://doi.org/10.1016/j.foreco.2019.117466>.
- Montano, V., Bertheau, C., Doležal, P., et al. 2016 How differential management strategies affect *Ips typographus* L. dispersal. *For. Ecol. Manag.* **360**, 195–204. <https://doi.org/10.1016/j.foreco.2015.10.037>.
- Mori, A.S., Tatsumi, S. and Gustafsson, L. 2017 Landscape properties affect biodiversity response to retention approaches in forestry. *J. Appl. Ecol.* **54**, 1627–1637. <https://doi.org/10.1111/1365-2664.12888>.
- Nikolov, C., Konôpka, B., Kajba, M., Galko, J., Kunca, A. and Janský, L. 2014 Post-disaster forest management and Bark Beetle Outbreak in Tatra National Park, Slovakia. *Mt. Res. Dev.* **34**, 326–335. <https://doi.org/10.1659/MRD-JOURNAL-D-13-00017.1>.
- Økland, B., Nikolov, C., Krokene, P. and Vakula, J. 2016 Transition from windfall- to patch-driven outbreak dynamics of the spruce bark beetle *Ips typographus*. *For. Ecol. Manag.* **363**, 63–73. <https://doi.org/10.1016/j.foreco.2015.12.007>.
- Olofsson, P., Foody, G.M., Herold, M., Stehman, S.V., Woodcock, C.E. and Wulder, M.A. 2014 Good practices for estimating area and assessing accuracy of land change. *Remote Sens. Environ.* **148**, 42–57. <https://doi.org/10.1016/j.rse.2014.02.015>.
- Olofsson, P., Foody, G.M., Stehman, S.V. and Woodcock, C.E. 2013 Making better use of accuracy data in land change studies: estimating accuracy and area and quantifying uncertainty using stratified estimation. *Remote Sens. Environ.* **129**, 122–131. <https://doi.org/10.1016/j.rse.2012.10.031>.
- Palahí, M., Valbuena, R., Senf, C., Acil, N., Pugh, T.A.M., Sadler, J., et al. 2021 Concerns about reported harvests in European forests. *Nature* **592**, E15–E17. <https://doi.org/10.1038/s41586-021-03292-x>.
- R Development Core Team 2019 *R: A language and environment for statistical computing*.
- Roberge, J. M., Laudon, H., Björkman, C., Ranius, T., Sandström, C., Felton, A., Sténs, A., Nordin, A., Granström, A., Widemo, F., Bergh, J., Sonesson, J., Stenlid, J., & Lundmark, T. (2016) Socio-ecological implications of

- modifying rotation lengths in forestry. *Ambio* **45**:109–123. <https://doi.org/10.1007/s13280-015-0747-4>.
- Sabatini, F.M., Keeton, W.S., Lindner, M., Svoboda, M., Verkerk, P.J., Bauhus, J., et al. 2020 Protection gaps and restoration opportunities for primary forests in Europe. *Divers. Distrib.* **26**, 1646–1662. <https://doi.org/10.1111/ddi.13158>.
- Schelhaas, M.-J., Nabuurs, G.J. and Schuck, A. 2003 Natural disturbances in the European forests in the 19th and 20th centuries. *Glob. Chang. Biol.* **9**, 1620–1633. <https://doi.org/10.1046/j.1529-8817.2003.00684.x>.
- Schiebe, C., Blaženec, M., Jakuš, R., Unelius, C.R. and Schlyter, F. 2011 Semiochemical diversity diverts bark beetle attacks from Norway spruce edges. *J. Appl. Entomol.* **135**, 726–737. <https://doi.org/10.1111/j.1439-0418.2011.01624.x>.
- Seidl, R., Honkaniemi, J., Aakala, T., Aleinikov, A., Angelstam, P., Bouchard, M., et al. 2020 Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. *Ecography (Cop)* **43**, 967–978. <https://doi.org/10.1111/ecog.04995>.
- Seidl, R., Schelhaas, M.-J. and Lexer, M.J. 2011 Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Glob. Chang. Biol.* **17**, 2842–2852. <https://doi.org/10.1111/j.1365-2486.2011.02452.x>.
- Senf, C., Pflugmacher, D., Hostert, P. and Seidl, R. 2017a Using Landsat time series for characterizing forest disturbance dynamics in the coupled human and natural systems of Central Europe. *ISPRS J. Photogramm. Remote Sens.* **130**, 453–463. <https://doi.org/10.1016/j.isprsjprs.2017.07.004>.
- Senf, C., Seidl, R. and Hostert, P. 2017b Remote sensing of forest insect disturbances: current state and future directions. *Int. J. Appl. Earth Obs. Geoinf.* **60**, 49–60. <https://doi.org/10.1016/j.jag.2017.04.004>.
- Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebald, J., Knorn, J., Neumann, M., et al. 2018 Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nat. Commun.* **9**, 4978. <https://doi.org/10.1038/s41467-018-07539-6>.
- Senf, C. and Seidl, R. 2018 Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe. *Glob. Chang. Biol.* **24**, 1201–1211. <https://doi.org/10.1111/gcb.13897>.
- Senf, C. and Seidl, R. 2021 Mapping the forest disturbance regimes of Europe. *Nat. Sustain* **4**, 63–70. <https://doi.org/10.1038/s41893-020-00609-y>.
- Smit, I.P.J., Roux, D.J., Swemmer, L.K., Boshoff, N. and Novellie, P. 2017 Protected areas as outdoor classrooms and global laboratories: intellectual ecosystem services flowing to-and-from a National Park. *Ecosyst. Serv.* **28**, 238–250. <https://doi.org/10.1016/j.ecoser.2017.05.003>.
- Sommerfeld, A., Senf, C., Buma, B., D'Amato, A.W., Després, T., Diaz-Hormazábal, I., et al. 2018 Patterns and drivers of recent disturbances across the temperate forest biome. *Nat. Commun.* **9**, 4355. <https://doi.org/10.1038/s41467-018-06788-9>.
- Stadelmann, G., Bugmann, H., Meier, F., Wermelinger, B. and Bigler, C. 2013 Effects of salvage logging and sanitation felling on bark beetle (*Ips typographus* L.) infestations. *For. Ecol. Manag.* **305**, 273–281. <https://doi.org/10.1016/j.foreco.2013.06.003>.
- Sterner, T., Barbier, E.B., Bateman, I., van den Bijgaart, I., Crépin, A.S., Edenhofer, O., et al. 2019 Policy design for the Anthropocene. *Nat. Sustain.* **2**, 14–21. <https://doi.org/10.1038/s41893-018-0194-x>.
- Turner, M.G. 2010 Disturbance and landscape dynamics in a changing world. *Ecology* **91**, 2833–2849. <https://doi.org/10.1890/10-0097.1>.
- van Rij, J., Wieling, M., Baayen, R. and van Rijn, H. 2017 *itsadug: Interpreting Time Series and Autocorrelated Data Using GAMMs*.
- Vladovič, J. 1994 *Lesné oblasti Slovenska. [Forest regions of Slovakia]*. Zvolen: Lesoprojekt. 500 p.
- Watson, J.E.M., Dudley, N., Segan, D.B. and Hockings, M. 2014 The performance and potential of protected areas. *Nature* **515**, 67–73. <https://doi.org/10.1038/nature13947>.
- Wegensteiner, R., Wermelinger, B. and Herrmann, M. 2015 *Natural Enemies of Bark Beetles: Predators, Parasitoids, Pathogens, and Nematodes*. Elsevier Inc.
- Wermelinger, B. 2004 Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. *For. Ecol. Manag.* **202**, 67–82. <https://doi.org/10.1016/j.foreco.2004.07.018>.
- White, T.C.R. 2015 Are outbreaks of cambium-feeding beetles generated by nutritionally enhanced phloem of drought-stressed trees? *J. Appl. Entomol.* **139**, 567–578. <https://doi.org/10.1111/jen.12195>.
- Winter, M.B., Baier, R. and Ammer, C. 2015 Regeneration dynamics and resilience of unmanaged mountain forests in the Northern Limestone Alps following bark beetle-induced spruce dieback. *Eur. J. For. Res.* **134**, 949–968. <https://doi.org/10.1007/s10342-015-0901-3>.
- Wood, S.N. (2017) *Generalized Additive Models: An Introduction with R* (2nd edition). Chapman and Hall/CRC, New York, NY.
- Wood, S.N. (2013) On p-values for smooth components of an extended generalized additive model. *Biometrika* **100**:221–228. <https://doi.org/10.1093/biomet/ass048>.
- Wulder, M.A., Dymond, C.C. and White, J.C. 2005 *Remote Sensing in the Survey of Mountain Pine Beetle Impacts: Review and Recommendations*. 1st edn. Canadian For. Service, Victoria.
- Yachi, S. and Loreau, M. 1999 Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* **96**, 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>.
- Yue, S., Pilon, P., Phinney, B. and Cavadias, G. 2002 The influence of autocorrelation on the ability to detect trend in hydrological series. *Hydrol. Process.* **16**, 1807–1829. <https://doi.org/10.1002/hyp.1095>.
- Zhang, Q.H. and Schlyter, F. 2003 Redundancy, synergism, and active inhibitory range of non-host volatiles in reducing pheromone attraction in European spruce bark beetle *Ips typographus*. *Oikos* **101**, 299–310. <https://doi.org/10.1034/j.1600-0706.2003.111595.x>.
- Zimová, S., Dobor, L., Hlásny, T., Rammer, W. and Seidl, R. 2020 Reducing rotation age to address increasing disturbances in Central Europe: potential and limitations. *For. Ecol. Manag.* **475**, 118408. <https://doi.org/10.1016/j.foreco.2020.118408>.