



# Are uneven-aged forests in Central Europe less affected by natural disturbances than even-aged forests?

Johannes Mohr<sup>a,\*</sup>, Dominik Thom<sup>a,b</sup>, Hubert Hasenauer<sup>c</sup>, Rupert Seidl<sup>a,d</sup>

<sup>a</sup> Ecosystem Dynamics and Forest Management Group, School of Life Sciences, Technical University of Munich (TUM), Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

<sup>b</sup> Gund Institute for Environment, University of Vermont, 617 Main Street, Burlington, Vermont 05405, USA

<sup>c</sup> Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences (BOKU), Peter Jordan Strasse 82, A-1190 Vienna, Austria

<sup>d</sup> Berchtesgaden National Park, Doktorberg 6, 83471 Berchtesgaden, Germany

## ARTICLE INFO

### Keywords:

Bark beetles  
Plenter forests  
Selection forest  
Silviculture  
Structural complexity  
Wind

## ABSTRACT

Natural disturbances from wind and bark beetles have increased strongly in recent decades across Central Europe. As climate change will likely amplify disturbance activity further, disturbances are increasingly threatening the sustainable supply of ecosystem services to society. Management strategies to mitigate disturbances are thus urgently needed. In Central Europe, managing for complex, uneven-aged forests has been suggested as a measure to reduce disturbance risk. However, the scientific evidence for a dampening effect of uneven-aged management on disturbances remains weak and inconclusive. Here, our objective was to assess differences in the disturbance regimes of uneven-aged and even-aged conifer forests during the years 1986 to 2020. We used remote sensing to quantify wind and bark beetle disturbances across four study sites in Austria. The sites span a large environmental gradient and have been under uneven-aged management for many decades. Here, we contrast them with surrounding even-aged forests with similar environmental conditions (uneven-aged forests: 13,440 ha, even-aged forests: 27,910 ha). Specifically, we used a paired-landscape approach, matching uneven-aged with even-aged forests at the level of sublandscapes and controlling for differences in elevation, slope, exposition, topography and the proportion of coniferous species. For each pair of sublandscapes (n= 5000) we quantified differences in disturbance rate, frequency, size and severity between uneven-aged and even-aged forests. Our findings revealed that in uneven-aged forests, disturbance rates were on average 31.3% lower, disturbances returned with a 36.3% lower frequency, and maximum patch sizes were 15.7% smaller than in surrounding even-aged forests. The proportion of high severity disturbance patches was only marginally influenced, being 3.8% lower in uneven-aged versus even-aged forests. Topography strongly modulated the effect of management on disturbance regimes. While disturbance rate was lower in uneven-aged forests overall, it exceeded the rate of surrounding even-aged forests on steep slopes >20° and elevations >1500 m asl. In conclusion, our results suggest that uneven-aged management may partly counteract increases in natural disturbances in Central European forests. However, we also caution that uneven-aged management is not a silver bullet solution for managing forest change, and highlight that adapted forest management approaches should be tailored to local needs and conditions.

## 1. Introduction

In past decades natural disturbances, i.e. pulses of tree mortality caused by abiotic and biotic agents such as wind and bark beetles, have substantially increased in Europe's forests (Senf et al., 2020; Patacca et al., 2023). Climate change is expected to further amplify disturbance

activity (Lindner et al. 2010; Seidl et al. 2017), threatening the supply of forest ecosystem services to society (Thom and Seidl, 2016; Strith et al. 2021; Bastit et al. 2023). Thus, a key challenge for foresters is developing management approaches to better cope with forest disturbances. This entails both increasing resistance (i.e. the ability of ecosystems to withstand disturbance) and resilience (i.e. the capacity of ecosystems to

\* Corresponding author.

E-mail address: [johannes.mohr@tum.de](mailto:johannes.mohr@tum.de) (J. Mohr).

<https://doi.org/10.1016/j.foreco.2024.121816>

Received 28 November 2023; Received in revised form 26 February 2024; Accepted 28 February 2024

Available online 11 March 2024

0378-1127/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

recover their processes and functions after disturbance) of forest ecosystems to disturbance.

One mechanism through which forest management can influence disturbance regimes is by modulating the structure of forests. Forest structure describes the number, size, age and spatial arrangement of trees in a forest. Particularly the decision to manage stands in an even-aged or uneven-aged fashion has a strong influence on forest structure. Even-aged management systems typically clear a cohort of trees of the same age simultaneously, while uneven-aged management harvests individual trees or small groups of trees based on their respective properties and functions in the system. The two systems differ in their within-stand variation in tree heights and diameters (low under even-aged management, high under uneven-aged management) as well as in the size of canopy openings (large under even-aged management, small under uneven-aged management). Consequently even-aged management is typically associated with low structural complexity within a stand. In contrast, uneven-aged management promotes variability in diameter classes and the number of canopy layers at small spatial scale, resulting in high structural complexity at stand level (McElhinny et al. 2005; Peck et al. 2014; Sharma et al. 2016). However, there is considerable variation even within forest management strategies, as modulated e.g. by topography. Uneven-aged forests are typically managed by single-tree selection (Schall et al. 2018). In steep terrain, however, single-tree selection systems are often not feasible, and group-selection systems are employed because logging frequently requires cable yarding systems to extract harvested trees. Under such conditions, groups of trees are selected in irregular shapes ("slit-shaped gaps") adjacent to cable yarding tracks (Streit et al. 2009) to achieve an uneven age structure within stands.

Uneven-aged forests remain less common in Europe compared to even-aged forests, yet they are widely perceived to have many benefits. Currently, uneven-aged forests account for approximately one quarter of the total forest area of Europe (Forest Europe, 2020), with the highest prevalence in areas where timber production is not the dominant service provided by forests (e.g., in southern Europe). Yet, the proportion of uneven-aged forests is increasing in Europe (Forest Europe, 2020), as they might better fulfil multiple demands of society than even-aged forests (Kuuluvainen et al. 2012; Pukkala and Gadov, 2012; Hanewinkel et al. 2014; Diaci et al. 2017; Schall et al. 2018). Furthermore, high canopy rugosity and variation in rooting depth enable complementary use of resources by trees (Rämö and Tahvonen, 2014; Bohn and Huth, 2017; Gough et al. 2019), potentially yielding higher productivities (Bohn and Huth, 2017; Gough et al. 2019). In addition, uneven-aged forests usually regenerate well naturally (Diaci et al. 2017). High productivity in combination with low regeneration costs may thus provide higher economic revenues in uneven-aged forests compared to even-aged forests (Knoke, 1997, 2012).

The effect of uneven-aged forest management on disturbance regimes remains controversially discussed. With regard to resilience, evidence points towards decreased recovery time after disturbance with increasing canopy complexity (Diaci et al. 2017). This also results in higher economic resilience of uneven-aged stands compared to even-aged stands (Knoke et al. 2023). With regard to resistance, it is frequently hypothesized that uneven-aged forests are less impacted by natural disturbances (O'Hara and Ramage, 2013; Hanewinkel et al. 2014; Diaci et al. 2017; Díaz-Yáñez et al. 2017; Ma et al. 2023). Yet, the quantitative evidence is limited (Nolet et al., 2018; Bauhus et al., 2013), as most studies (e.g., Mohr and Schori, 1999; Hanewinkel et al. 2014) focus on small spatial extent (i.e., tree to stand level), which makes it difficult to assess disturbance characteristics that only emerge at larger spatial scales (e.g., patch size). The mechanisms assumed to be responsible for increased resistance are higher individual-tree stability (e.g., against windthrow, Mason, 2002; Bodin and Wiman, 2007), improved vitality (e.g., tree defenses against insect attacks), and, with regard to drought, less direct solar radiation for subcanopy trees (Ma et al. 2023). However, disturbance susceptibility remains largely

constant over time in uneven-aged forests, while susceptibility of even-aged systems varies with stand development stage (e.g., early stages of stand development characterized by small trees are less prone to windthrow and bark beetle infestation, Schmidt et al. 2010). Resetting stand development in even-aged management might thus lead to periods of low disturbance susceptibility compared to uneven-aged forests (Seidl et al. 2008), and ultimately to lower disturbance rates.

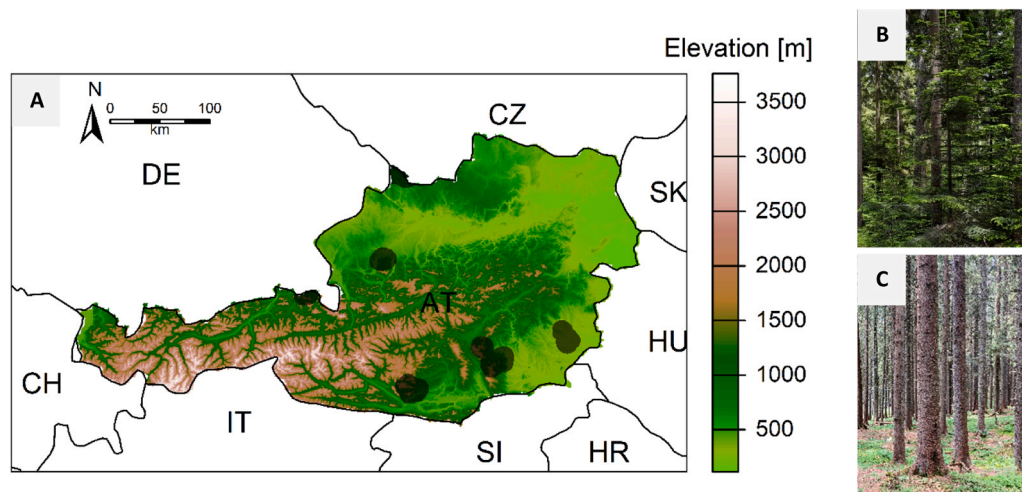
Large-scale datasets on forest disturbance derived from remote sensing offers new opportunities to study the effects of forest management systems on disturbance activity. Remote sensing data, such as the European forest disturbance map (Senf and Seidl 2021a), enable the standardized investigation of management effects across wide environmental gradients and with a larger number of observations compared to previous empirical assessments (e.g., Mohr and Schori, 1999; Dvořák et al. 2001; Hanewinkel et al. 2014; Pukkala et al. 2016). Disturbance characteristics that are difficult to quantify at the plot level can be easily assessed with remote sensing, e.g., the effects of uneven-aged management on the size of disturbed patches (Jin and Sader, 2005; Senf and Seidl 2021a). Yet, to date remotely sensed data remains underutilized in the context of assessing management effects on forest disturbance regimes.

Here, we harnessed remotely sensed information on forest disturbances between 1986 and 2020 to quantify the divergence in disturbance regimes (i.e., the rate, frequency, size, and severity of disturbances) between forests under uneven-aged vs. even-aged management. In particular, we addressed the following research questions: (Q1) Do natural disturbance regimes differ by management system (even-aged versus uneven-aged forests) in Central European forests? (Q2) Does topography modulate the effect of forest management on disturbance regimes? We hypothesized that (H1) uneven-aged forests are less affected by natural disturbances (Mohr and Schori, 1999; Dvořák et al., 2001; Hanewinkel et al., 2014). The alternative hypothesis was that uneven-aged forests experience equal or higher disturbance activity than even-aged forests. Furthermore, we hypothesized (H2) that the mitigating effect of uneven-aged management on disturbances decreases with increasing topographic ruggedness. Our rationale behind this assumption comes from the necessity to do group selection rather than single tree selection in steep terrain, and because of the linear canopy openings (cable yarding tracks) needed for forest operations under such conditions, which are both factors that make uneven-aged forests in rugged terrain less different from even-aged forests.

## 2. Methods and materials

### 2.1. Study area

To study the effect of forest management on disturbances, we focused our analyses on four forestry companies managing uneven-aged forests (henceforth referred to as study sites). All sites are located in Austria, spanning a wide range of conditions representing Central European forests from the colline to the subalpine elevation belt (Fig. 1), with elevations ranging from 280 to 1700 m above sea level. Forest composition is dominated by Norway spruce (*Picea abies* [Karst.]), with silver fir (*Abies alba* [Mill.]) and European beech (*Fagus sylvatica* [L.]) as admixed species (Figure S1). Individual sites range from 1346 ha to 6739 ha in size, covering a total of 13,440 ha of uneven-aged forests (Table 1). Two of the four sites are owned by the church, one by the state, and the fourth is a private forest company. All four sites have a long local tradition of uneven-aged silviculture and have conducted uneven-aged management for at least 35 years, but frequently much longer. The companies aim for multifunctional forest management with timber production as the main management objective. The sites differ in topography, with high (sites A and B) or low (sites C and D) topographic ruggedness as characterized by elevation and slope (Table 1 and Figure S2). Here, the term topographic ruggedness refers to sites dominated by steep slopes, a high elevation range and frequent local



**Fig. 1.** : A: Study sites under uneven-aged management and their approximate location in Austria. Examples for typical forest structures under B: uneven-aged management, and C: even-aged management in the study region.

**Table 1**

Characterization of the four study sites of uneven-aged forest management. Average values and ranges (in parentheses) are provided for elevation, slope, and conifer share.

Study sites				
	A	B	C	D
Ownership	Private	State	Church	Church
Size	1917 ha	1346 ha	3432 ha	6739 ha
Geology	Mixed crystalline and calcareous bedrock	Predominately calcareous bedrock	Predominately crystalline bedrock	Predominately crystalline bedrock
Elevation	1373 m (680 m, 1874 m)	1198 m (761 m, 1708 m)	1115 m (256 m, 1780 m)	896 m (520 m, 1368 m)
Slope	20.5° (0.3°, 39.3°)	18.2° (0.2°, 54.9°)	12.6° (0.0°, 38.2°)	10.2° (0.0°, 39.2°)
Conifer share	97.0% (0.0%, 100.0%)	93.4% (0.0%, 100.0%)	95.3% (0.0%, 100.0%)	83.0% (0.0%, 100.0%)
Management	Continuous cover forestry, mixed single-tree selection and group selection	Continuous cover forestry, mixed single-tree selection and group selection	Continuous cover forestry, mainly single-tree selection (Plenter forestry)	Continuous cover forestry, mainly single-tree selection (Plenter forestry)

shifts in aspect and terrain position. All four enterprises apply uneven-aged forest management, yet the implementation differs with terrain. In topographically simple sites, single tree selection is the main silvicultural approach. A large portion of those forests have been managed in a “Plenter” forest system, that is, a specific type of single tree selection system targeting a reverse J-shaped diameter distribution of trees (Schütz 2002b). In rugged terrain and on steep slopes, uneven-aged management often takes the form of a modified group selection system with slit-shaped gaps. Wind and bark beetles are the dominant disturbance agents across all four sites (Thom et al. 2013; Sebald et al. 2021). In particular, the sites have been affected by severe storms in recent years, notably in 2007 (Kyrill), 2008 (Emma and Paula) and 2014 (Yvette), with variable bark beetle activity in the years following storms. Since fires do not play an important role in the natural disturbance regimes of Austria (Müller et al. 2013) and Central Europe (Senf and Seidl 2021b), we didn’t include forest fires in our analysis (cf. Sebald et al. 2021).

We compared uneven-aged study sites to surrounding forests that are almost exclusively even-aged. In Austria the share of Plenter forests (Schütz, 2001) is estimated to be 2% of the total forest area (Röhrig et al., 2006; Schütz 2002a). A very low prevalence of uneven-aged forests in Austria is furthermore supported by the results of the Austrian national forest inventory, which classifies all high forests into distinct age-classes (BFW, 2023). We thus assumed that areas outside of our study sites (which were deliberately selected for their uneven-aged management) are managed as even-aged forests. Surrounding forests

thus serve as the counterfactual for assessing the effect of uneven-aged management in our study sites on forest disturbance regimes. Typical conifer-dominated stands under even-aged management are initiated by planting between 2000 and 2500 stems per hectare, although stem densities can also be considerably higher when natural regeneration is utilized (Weinfurter, 2013). The thinning regime typically consists of one pre-commercial thinning and several commercial thinnings, conducted as selective thinnings from above and aimed at fostering the growth and stability of between 300 and 400 crop trees. Final harvesting is done either in small (~0.5 ha) clear cuts (e.g., small strip cuts), or using gap cut or shelterwood cut systems with subsequent clearing if natural regeneration is desired (Weinfurter, 2013). We note that some ambiguity exists with regard to the silvicultural terminology used in the literature. What we here describe as uneven-aged forests has also been referred to as continuous cover forests (Pommerening, 2023), irregularly structured forests (Schütz 2002b), and full-storied forests (Ekholm et al. 2023) in other contexts. We use the term uneven-aged (see e.g., Schall et al. 2018), as it best discriminates our four study sites from the surrounding control group. Surrounding forests are, for instance, often managed in small strip- or shelterwood cuts aimed to establish advanced regeneration before clearing, and thus often also feature two canopy layers and a continuous forest cover. Yet, these forests are managed in a rotation system and have a homogeneous age structure within stands, which clearly distinguishes them from the uneven-aged stands of our study sites (cf. Fig. 1 B, C).

## 2.2. Data

### 2.2.1. Disturbance

We extracted disturbance information from the European forest disturbance map (Senf and Seidl 2021a). The map is based on Landsat satellite data and manual satellite image interpretation for more than 19,000 locations throughout Europe. It provides information on canopy openings across Europe for the period 1986–2020 at 30 m spatial grain. While Senf and Seidl (2021a) mapped all canopy openings in Europe regardless of their cause, subsequent work has attributed canopy openings to specific disturbance agents. We here focused our analysis exclusively on natural disturbances, using the agent attribution of Seibald et al. (2021). This study trained a random forest model to attribute disturbance agents based on the spectral signal, patch form and landscape context of each patch, using an empirical disturbance database from Austria. Specifically, we focused on wind and bark beetle disturbances, the two most important disturbance agents in Austria (Thom et al. 2013). The mean share of wind disturbance was 87% of all natural disturbances in uneven-aged forests and 86% in even-aged forests (Figure S3).

We studied the effect of uneven-aged forest management on four indicators of the forest disturbance regime: disturbance rate, disturbance frequency, maximum patch size, and the proportion of area disturbed with high severity. Having  $n$  years of observations (1986 – 2020) and  $m$  30 m cells in a sublandscape, we calculated disturbance rate as (Eq. 1)

$$\frac{1}{n} * \sum_{i=1}^n \frac{disturbed_i}{m} \quad (1)$$

with  $disturbed_i$  being the number of disturbed cells in year  $i$ . Disturbance frequency was derived as (Eq. 2)

$$\frac{1}{n} * \sum_{i=1}^n event_i \quad (2)$$

with  $event_i$  being the binary value indicating if a disturbance event occurred in year  $i$ . Disturbance patch size was calculated as the number of connected cells (queens' contiguity) affected by disturbances in the same year or the following year (to account for errors in the predicted disturbance year, see Senf and Seidl, 2021a) multiplied by cell size (0.09 ha). Only patches that had their centroid within the sublandscape were considered in the analysis. Maximum disturbance patch size was calculated as (Eq. 3):

$$\max_{i \in \{1, \dots, n\}} (size_i) \quad (3)$$

with  $size_i$  being the maximum disturbance patch size in year  $i$ . Finally, we calculated the proportion of high severity disturbances on the total area disturbed. For this we used the severity indicator provided by the European forest disturbance map, ranging from zero to one and indicating the probability of complete canopy loss (Senf and Seidl 2021a). Here, we classified disturbances as highly severe if the severity indicator exceeded 0.8. The proportion of high severity disturbances was calculated as (Eq. 4)

$$\frac{\sum_{i=1}^n severe_i}{\sum_{i=1}^n disturbed_i} \quad (4)$$

with  $severe_i$  being the number of cells severely disturbed in the year  $i$ .

We note that the disturbance rate is by definition correlated with disturbance frequency and patch size (Pearson's correlation coefficients in our dataset: 0.57 and 0.77, respectively). Nonetheless, the frequency and size metrics provide complementary information about different processes within the disturbance regime, since the same disturbance rate

may result from a single large or several small events. We hence retained all four metrics in our analysis.

### 2.2.2. Auxiliary information

We used a digital elevation model provided by the Austrian government on a spatial grain of 10 m (Geoland, 2015) to characterize topography. We aggregated this data to 30 m spatial resolution to match the disturbance map and subsequently computed slope and aspect for each cell. We further calculated topographic exposure (topex) following the method proposed by Mikita and Klimánek (2010) as the stack-sum of low-angled (5°) hillshades from eight different directions. A north-westerness index (representing the dominant wind direction in the area) was calculated by taking the cosine of aspect rotated by 45 degrees counterclockwise. All raster calculations were done using the *terra* package (Hijmans, 2023) within the R programming environment (R Core Team, 2022). Information on species composition was obtained from the Copernicus dominant leaf type map (Copernicus, 2020). This map contains information on whether the dominant leaf type of a 10 m cell is coniferous or deciduous. The information was aggregated to match the resolution of our disturbance information by calculating the proportion of dominant coniferous species for each 30 m cell.

## 2.3. Study design

We conducted a pairwise comparison of sublandscapes sampled from our study sites representing uneven-aged forests (i.e., treatment group) to similar (in terms of environmental conditions and species composition) forests in their proximity, representing even-aged forests (i.e., control group). Specifically, we randomly sampled (without replacement but possibly overlapping) 2500 sublandscapes with 36 ha in size (20 by 20 pixels of 30 × 30 m in size) from each uneven-aged study site. Sublandscape size was chosen to be more than 50 times the mean disturbance size (i.e., 0.69 ha in Austria according to Seibald et al. 2021), following recommendations for equilibrium landscape sizes by Urban et al. (1987). Analyses focused only on forested pixels within sublandscapes, and sublandscapes with a forest cover of less than 30 ha (83.3%) were excluded. To each uneven-aged sublandscape we matched an even-aged counterpart from a moving window of 20 × 20 km outside our uneven-aged study sites. We chose this relatively short distance between paired landscapes to ensure similar geological and climate conditions, and to safeguard that the same climatic extremes (e.g., storms) affected both landscapes. We conducted a sensitivity analysis to assess the effect of the matching window size on our results and found only minor differences (Figure S4).

We used elevation (because both climatic conditions and disturbance regimes change with elevation), slope (representing accessibility and soil conditions), topographic exposure (as an indicator of exposure to strong winds) and north-westerness (representing wind exposure in the main wind direction as well climatic differences due to solar radiation) as site conditions in the matching process (see Table 1 and the section on auxiliary information above). Conifer share was included as an important stand-level variable because conifers are considerably more susceptible to disturbances in our study area than broadleaved species (Thom et al. 2013; Pasztor et al. 2014; Jactel et al. 2017).

We calculated the similarity between sublandscapes using the Mahalanobis distance across the five indicators of site and stand conditions. For every uneven-aged sublandscape, the even-aged sublandscape with the lowest Mahalanobis distance was selected as the matching sublandscape. Next, potentially poor matches were filtered out by considering only sublandscape pairs with a Mahalanobis distance of one or lower, retaining the 80% best matches. In a sensitivity analysis, we found only small differences in our results when applying other distance thresholds (Figure S5). From the remaining set of matching sublandscapes we randomly sampled 1250 pairs per study area. This approach gives equal weight to the four study sites despite their differences in size (Table 1).

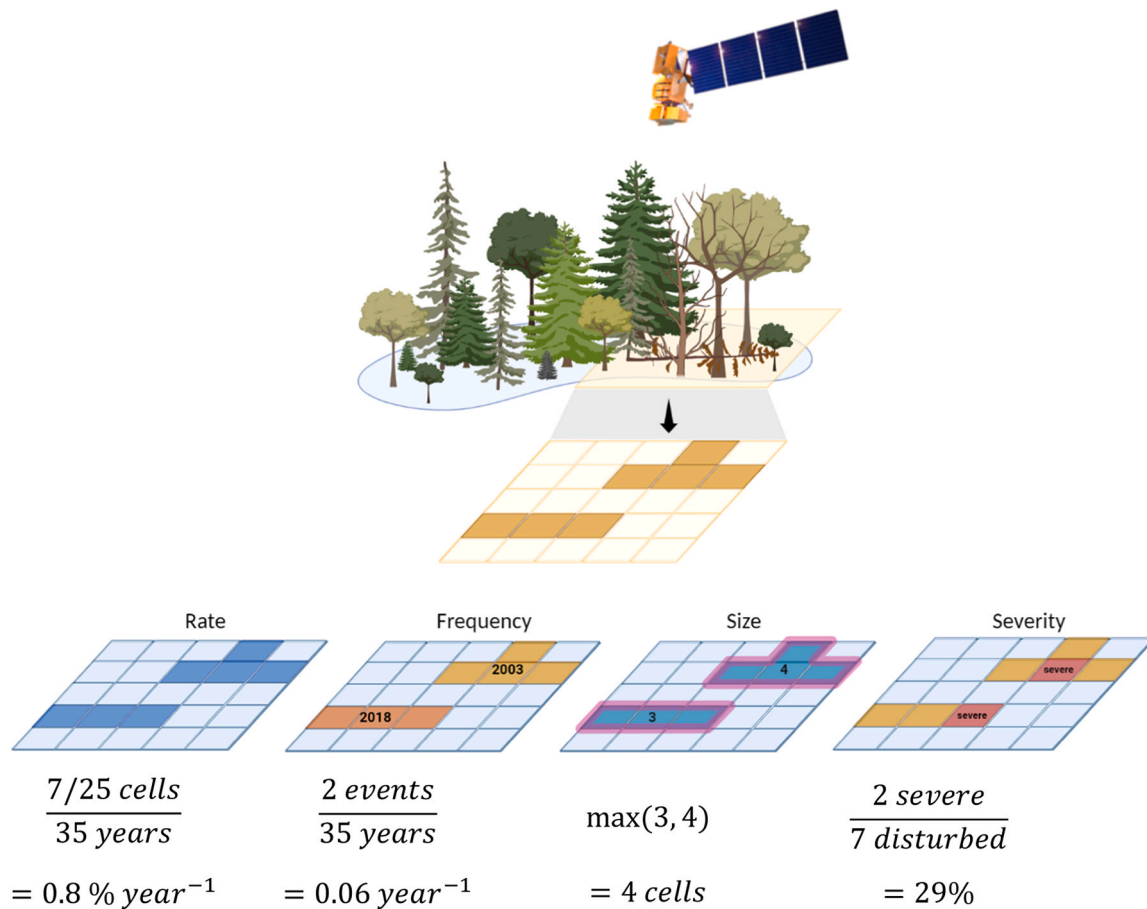


Fig. 2. : Visual explanation of the four metrics used to characterize disturbance regimes in this study. Note that the illustration does not represent the true size of the analysis units in terms of number of cells analyzed but was simplified here for illustration purposes (created with BioRender.com).

Overall, the sublandscape pairs had similar site conditions and species compositions (Table 2, Figure S1). The careful matching of sublandscapes thus controls for differences in site conditions and species composition, ensuring that differences in disturbance metrics obtained from this comparison can be attributed to the differences in uneven-aged and even-aged forest management. For each of the 5000 sublandscape pairs, we computed disturbance metrics (see above), and compared them between uneven-aged and even-aged systems. We note that uncertainty exists with regard to the attribution of canopy disturbances detected by remote sensing to different disturbance agents. To account for this uncertainty (overall attribution accuracy was 63%, Sebald et al. 2021) we performed a Monte Carlo Simulation in which we assigned the disturbance agent of each disturbed cell in our study area with a probability determined by the user’s accuracy in the original attribution study (Sebald et al. 2021). We then calculated the resulting mean values of annual disturbance rates for uneven-aged and even-aged forests in

each Monte Carlo run and analyzed the variation in disturbance rates and the effect of attribution uncertainty on our findings.

#### 2.4. Analyses

We analyzed differences in the disturbance regime between pairs of uneven-aged and even-aged sublandscapes. First, we compared uneven-aged and even-aged forests for each of the four disturbance metrics: (i) disturbance rate, (ii) frequency, (iii) maximum patch size and (iv) proportion of high severity (question 1). To test for statistical significance, we calculated the differences of each disturbance metric within each sublandscape pair. After a visual inspection for normality (Figure S6), we employed two-sided t-tests to identify statistically significant differences, with the null hypothesis that uneven-aged and even-aged forests have the same disturbance regime (cf. our question 1). We, however, focus our interpretation on ecological rather than statistical significance, as even small differences can be statistically significant when using remote sensing data due to the high sample size. Subsequently, we visually assessed variation in disturbance rates over time. To investigate whether and how topography modifies management effects on disturbance regimes (question 2), we fitted separate generalized additive models (GAMs) for even-aged and uneven-aged forests, with disturbance metrics as response variables and site variables as predictors. In addition, we controlled for conifer share as a confounding factor to improve the interpretation of the effects of topography on management effects. We fitted GAMs with three knots for each predictor to avoid overfitting, using *quasibinomial* as distribution family and *logit* as link function. We assessed model fits using residual plots, which yielded distributions close to normality (Figure S7). The predictors were

Table 2

Summary statistics of the sublandscapes analyzed for the two different management systems (see also Figure S1 for a graphical representation). Presented are median values and the 5th and 95th percentiles (in parentheses). n= number of sublandscapes analyzed.

Variable	Uneven-aged (n= 5000)	Even-aged (n= 5000)
Elevation	1191 m (700 m, 1 549 m)	1213 m (707 m, 1537 m)
Slope	16.1° (3.8°, 25.3°)	16.7° (4.2°, 25.0°)
Topex	5.0 (4.5, 7.6)	4.9 (4.5, 7.6)
North-westerness	0.1 (-1.0, 1.0)	0.2 (-1.0, 1.0)
Share of conifers	99.0% (76.7%, 100.0%)	98.1% (75.0%, 100.0%)

tested for multi-collinearity by calculating concurrency values. After excluding topex as a predictor variable, all concurrency values were  $<0.7$ , indicating no issues with multi-collinearity (Dormann et al. 2013). The four models explained between 13.1% and 24.9% of the deviance of the data.

We used the software R (R Core Team, 2022) for all analyses, specifically employing the packages *dplyr* (Wickham et al. 2022) and *tidyr* (Wickham and Girlich M. 2022) for data preparation, *terra* (Hijmans, 2023) for spatial analyses, *MatchIt* (Ho et al. 2011) for the matching of sublandscapes with different management and *mgcv* (Wood, 2011) for fitting GAMs. For visualization we used the packages *ggplot2* (Wickham, 2016) and *ggpubr* (Kassambara, 2022) as well as *rnaturalearth* (Massicotte and South, 2023).

### 3. Results

#### 3.1. Management effects on the forest disturbance regime

Uneven-aged forests were overall less affected by natural disturbances than even-aged forests. The average disturbance rate in uneven-aged forests was 31.3% lower compared to even-aged forests across all four study sites (uneven-aged:  $0.10\% \text{ yr}^{-1}$ ; even-aged:  $0.14\% \text{ yr}^{-1}$ ) (Fig. 3). Uneven-aged forests experienced disturbances 36.3% less frequently on average (uneven-aged:  $0.033 \text{ events yr}^{-1}$ ; even-aged:  $0.051 \text{ events yr}^{-1}$ ) and had on average 15.7% smaller maximum disturbance patch sizes (uneven-aged: 0.80 ha; even-aged: 0.95 ha). The average proportion of high severity disturbance events was only marginally lower (3.8%) in uneven-aged forests compared to even-aged forests (uneven-aged: 30.3%; even-aged: 31.5%). All differences were highly statistically significant ( $p < 0.001$ ) (Table 3). Uncertainties due to potential misclassification of disturbance agents did not substantially alter our findings (Figure S8)

Disturbance rates in the four study sites showed high temporal variability, mainly as a result of major storm events in the years 2007, 2008 and 2014. In background years (i.e., years without a major storm event), uneven-aged forests mostly had lower disturbance rates than even-aged forests (Fig. 4). In some storm years, uneven-aged forests exhibited higher disturbance rates in study sites characterized by rugged terrain (sites A and B), while uneven-aged forests in comparatively simple terrain (sites C and D) were always less affected by disturbance.

#### 3.2. Factors modulating management effects

Differences in disturbance regimes between management strategies

were substantially modulated by topography. While the disturbance rate was generally lower in uneven-aged forests, it exceeded the rate of even-aged forests in areas with slopes  $>20^\circ$  and elevations  $>1\,500 \text{ m asl}$  (Fig. 5). This effect was mainly driven by an increase in disturbance frequency on steeper slopes and larger disturbance patch sizes in higher elevations. However, the proportion of high severity disturbances decreased on steep slopes, indicating more but less severe disturbances in uneven-aged mountain forests.

Uneven-aged forests also had a higher disturbance rate than even-aged forests in sublandscapes below 700 m in elevation. This was mainly the effect of an elevated disturbance frequency, yet maximum disturbance patch sizes were very small in both uneven-aged and even-aged low-elevation forests. For all other site conditions uneven-aged forests had lower disturbance rates than even-aged forests. Lower disturbance rates in uneven-aged forests were particularly pronounced in mid-elevation forests and on gentle slopes. Apart from a small increase in high severity disturbances in northwest-exposed forests, north-westerness had no notable modulating effect on the disturbance regime.

### 4. Discussion

Changing disturbance regimes pose a major challenge for the sustainable management of forest ecosystems (Kulakowski et al. 2017; Turner and Seidl, 2023). We here show that uneven-aged management can substantially mitigate the impact of natural disturbances on forests in Central Europe. Our findings are in line with previous studies (Mohr and Schori, 1999; Dvořák et al., 2001; Hanewinkel et al., 2014; Pukkala et al., 2016; Diaci et al., 2017; Díaz-Yáñez et al., 2017) and support our hypothesis of a positive effect of uneven-aged management on resistance to disturbance. Managing for structural complexity (Pommerening and Murphy, 2004; Keeton, 2006; Ehbrecht et al. 2017) can thus be an efficient means for coping with increasing disturbances in the conifer-dominated forests of Central Europe. Depending on disturbance metric, we found that disturbance activity was reduced by between 3.8% and 36.3%, with the strongest dampening effect of uneven-aged management on disturbance frequency. However, disturbance rates have also increased by between 55% and 78% in Central and Eastern Europe since 1986 (Senf et al. 2021); the reduction of disturbance rates by 29% in uneven-aged forests found here is thus unlikely to completely cancel future changes in forest disturbance regimes. This is underscored by the finding that severe storms do affect forests regardless of their management (Fig. 4), with sometimes even higher disturbance impacts in uneven-aged compared to even-aged forests. Increasing structural complexity through uneven-aged forest management can thus make an

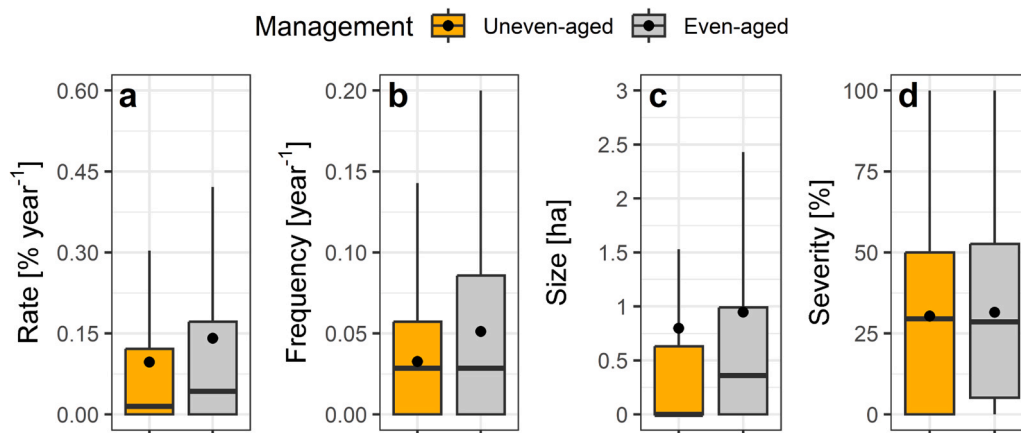
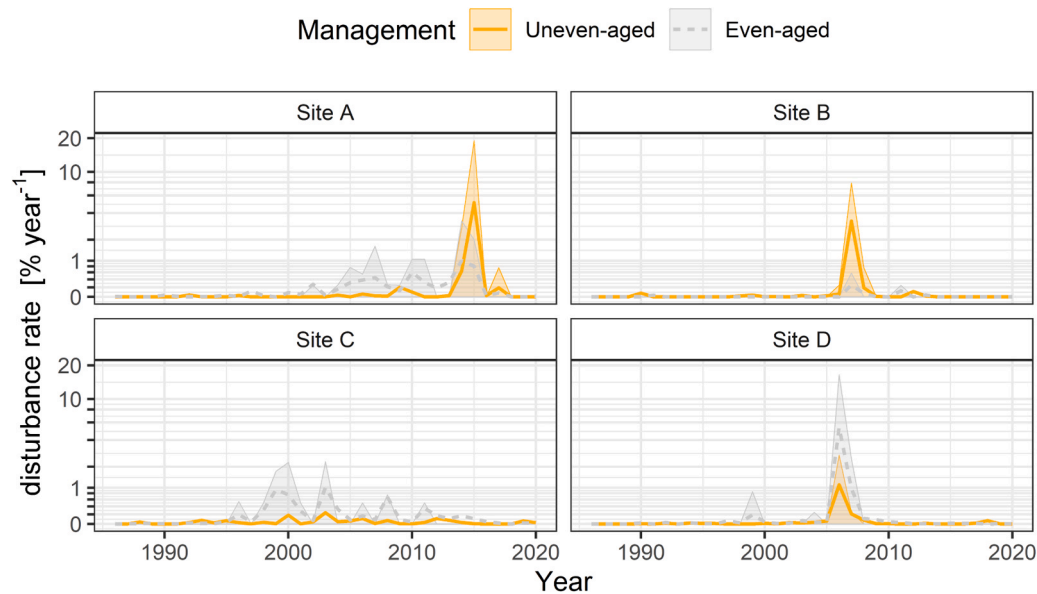


Fig. 3. Uneven-aged forests are less affected by natural disturbances than even-aged forests. Differences in the disturbance regimes of uneven-aged and even-aged forests: a) disturbance rate, b) disturbance frequency, c) maximum patch size, and d) the proportion of high severity disturbances. Mean values are depicted as points, medians as horizontal lines, and interquartile ranges (IQR) as boxes, while whiskers illustrate data points within the range of  $Q1 - 1.5IQR$  to  $Q3 + 1.5IQR$ , with  $Q1$  and  $Q3$  representing the first and third quartiles, respectively.

**Table 3**

Results of two-sided t-tests to test for differences in the disturbance regime of uneven-aged and even-aged forests. Please note that we computed severity only when disturbances actually occurred, resulting in a lower degree of freedom (df) for the proportion of high severity disturbances.

Disturbance metric	t-value	df	p-value	Mean difference	95% confidence interval	
					lower	upper
Rate	-10.692	4999	< 0.001	-0.044% year <sup>-1</sup>	-0.052% year <sup>-1</sup>	-0.036% year <sup>-1</sup>
Max. patch size	-3.343	4999	< 0.001	-0.149 ha	-0.237 ha	-0.062 ha
Frequency	-18.047	4999	< 0.001	-0.019 year <sup>-1</sup>	-0.021 year <sup>-1</sup>	-0.017 year <sup>-1</sup>
Proportion of high severity	-3.788	1699	< 0.001	-3.194%	-4.849%	-1.540%



**Fig. 4.** : Temporal trajectories of disturbance rate in the four study sites. Lines indicate the average disturbance rate across all sublandscapes of a study site while ribbons show the interdecile range (range between the 10th and 90th percentile of the data). Sites A and B are characterized by rugged terrain, whereas the terrain of Sites C and D is comparatively simple.

important contribution to address increasing disturbances, but it needs to be applied in concert with other silvicultural measures (e.g., converting species compositions to more climate-adapted tree species, Kuuluvainen et al. 2012; Jactel et al. 2017; Messier et al. 2019; Aszalós et al. 2022).

**4.1. Study design and limitations**

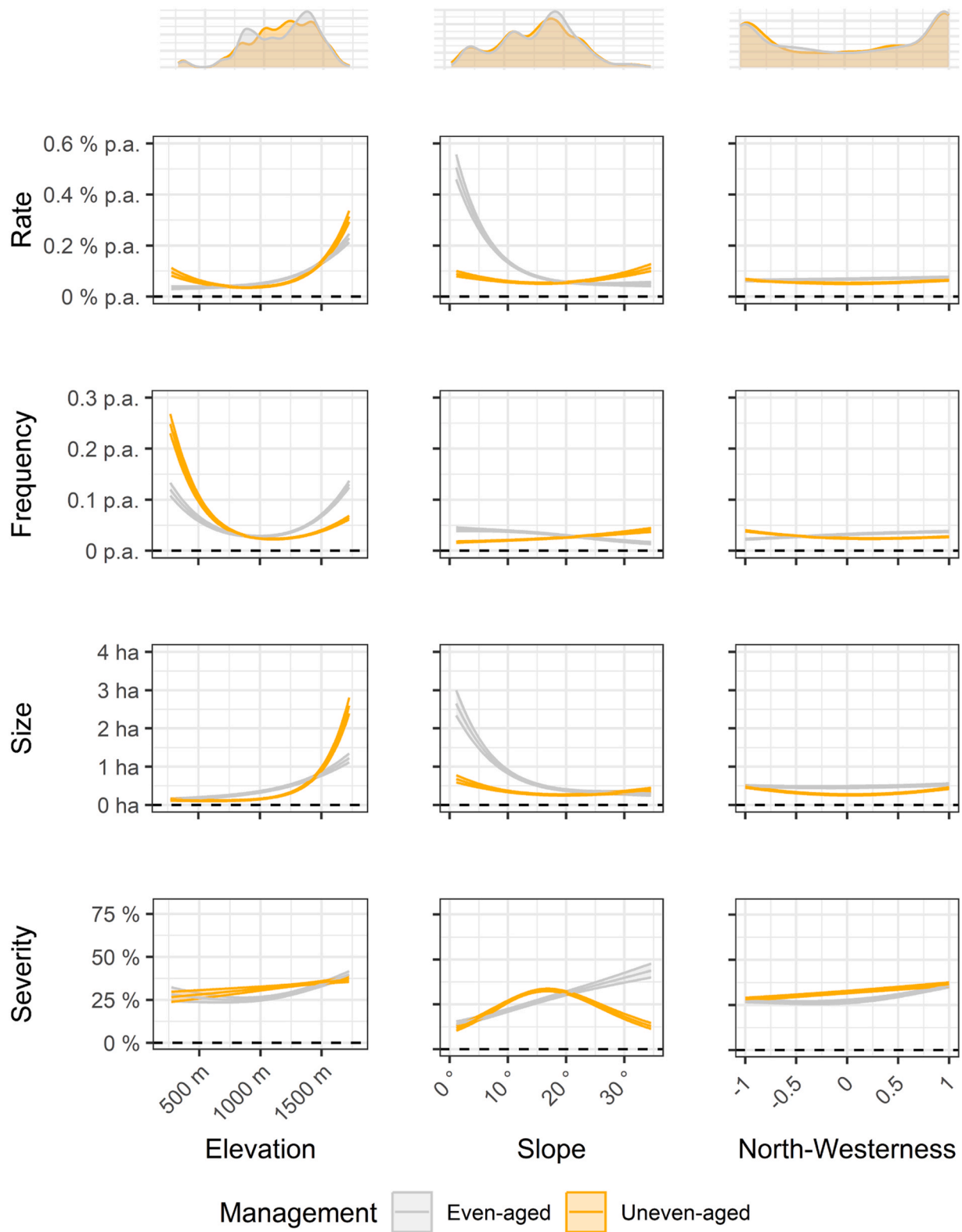
A key strength of this study design is the paired-landscape approach, which identifies comparable sublandscapes with similar attributes except for the treatment effect under study. Similar approaches of comparing a special management case to a surrounding counterfactual of business as usual management has been successfully applied previously to assess the effect of uneven-aged management on biodiversity (Schall et al. 2018), and the effect of the cessation of management on disturbance regimes (Sommerfeld et al., 2018). Here, we go beyond these previous analyses by explicitly controlling for differences in site and stand conditions between the two strata via a pairwise comparison of carefully matched sublandscapes (Ho et al. 2007). We note that our pairwise comparison deliberately controlled for differences in the share of conifers, i.e., we here only analyzed the effect of structural differences between uneven-aged and even-aged forests, while controlling for potential differences in species composition.

Nonetheless, important limitations should be considered when interpreting our findings. First, we identified uneven-aged forests via the general management system applied at the company level and did not analyze forest structure of each sampled sublandscape explicitly (Ehbrecht et al. 2017). Specifically, we implicitly assumed that forests

surrounding our uneven-aged study sites represented a meaningful counterfactual for our analysis. Given that the share of uneven-aged forests in general and of Plenter forests in particular is very low in Austria (cf. Schütz, 2001, 2002a, 2002b; BFW 2023), we conclude that it is highly likely that areas randomly selected from the surrounding of our study sites are even-aged forests. A further limitation is that we do not have information on disturbance history prior to 1986 for our study sites and hence could not control for potential differences in disturbance legacy on current disturbance dynamics (Sommerfeld et al., 2021).

Uncertainty in our results also stems from the use of remote sensing data. Specifically, uncertainties include the risk of misclassification of disturbed areas (e.g., the omission of small disturbed patches in the satellite analysis) and incorrect disturbance agent attribution (e.g., attributing regular management interventions to natural disturbances). Previous work found that especially the differentiation between disturbances caused by bark beetles and those caused by wind is challenging (Sebold et al. 2021). As a consequence, we here analyzed both agents jointly. Furthermore, we performed a Monte Carlo analysis to quantify the effect of attribution uncertainty on our analysis, finding that our results were robust to potential errors in the agent attribution of the underlying disturbance data. We also note that we here solely focused on management-related differences in the natural disturbance regime. Future studies could use similar approaches as the one presented here to also study the imprint of management interventions on forest canopies in more detail, e.g. studying differences between managed and unmanaged ecosystems.

Our results were derived from four forest enterprises situated spanning a range of elevations and geological conditions in the forests of



**Fig. 5. : Topography modulates disturbance regimes in forests under even-aged and uneven-aged management.** Rate: disturbance rate in % area disturbed per year, Frequency: disturbance frequency per year, Size: maximum patch size per year, and Severity: proportion of high severity disturbances. Ribbons indicate average responses and standard errors derived by GAMs. Each panel shows the variation of disturbance metrics over one site variable, while the other two site variables were set to the median values of their distribution (see Table 2).



Central Europe. Whether our findings on the effect of uneven-aged management can be generalized to e.g., low-elevation forests, remains unclear and should be the focus of future investigations. For instance, most forests investigated here were dominated by coniferous species, which are particularly prone to disturbances by wind and bark beetles (Jactel et al., 2017; Scherrer et al., 2022; Patacca et al., 2023). How uneven-aged management would affect broadleaved-dominated forest types in Central Europe remains largely unknown. More broadly, we here quantified disturbance differences between two management systems, while elucidating the underlying mechanisms leading to these differences was beyond the scope of our analysis. Previous work indicated that structural complexity and high single tree vitality increase the resistance against wind and snow of uneven-aged conifer forests (Díaz-Yáñez et al. 2017). Further research is required to assess whether these or other factors are driving the lower disturbance rates of uneven-aged forests observed in this study. We also note that focusing on the past provides limited insights into how uneven-aged forests will be affected by novel disturbance regimes emerging under climate change (Turner and Seidl, 2023). Therefore, further work is needed to better understand the underlying mechanisms and conclusively answer whether uneven-aged forests will also be less impacted by natural disturbances under future climate.

#### 4.2. Implications for forest management

We found that uneven-aged management had a distinct effect on forest disturbance regimes (Fig. 3), leading to a substantial reduction in disturbance rate. Therefore, uneven-aged management could be an important tool in the arsenal of forest managers for addressing ongoing changes in disturbance regimes (Pommerening and Murphy, 2004; Turner and Seidl, 2023; Thom and Spathelf, 2023). Forest disturbances are expected to increase further in the coming decades, with projections for our study area suggesting a two- to six-fold increase in disturbances by the end of the 21st century (Seidl et al. 2009; Thom et al. 2022). Considering these drastic changes expected for the future, it is unlikely that the adoption of uneven-aged management alone will be sufficient to mitigate the effects of increasing forest disturbances. Reducing the share of coniferous tree species may, for instance, additionally dampen disturbance activity (Jactel et al. 2017; Aszalós et al. 2022). The fact that uneven-aged management cannot substitute such a species change to broadleaved forests particularly in low elevation areas is underscored by our finding of high disturbance activity in uneven-aged, low-elevation conifer forests. We thus see uneven-aged management as but one element of a broader strategy to address the emerging novel disturbance regimes in forest management (Leverkus et al. 2021; Thom and Spathelf, 2023; Turner and Seidl, 2023).

Our results emphasize that management decisions to mitigate increasing disturbances need to be tailored to local context. We here found that terrain strongly modulated the effect of management on disturbances. Specifically, on steep slopes and in high elevations, uneven-aged forests were more prone to disturbance than even-aged forests. This could result from increased canopy roughness in uneven-aged forests on steep slopes, e.g. increasing the exposure to wind (Bodin and Wiman, 2007). Partly, this could also be an artifact of the remotely sensed disturbance data, as irregular management in an already highly patchy system (i.e. subalpine forests in our study area) could lead to analysis thresholds (e.g., the 1 800 m<sup>2</sup> minimum mapping unit of the disturbance map used) being crossed more frequently, resulting in larger apparent patch sizes with lower shares of severe disturbances (cf. Fig. 5). Furthermore, there are differences in how uneven-aged forests are achieved by management in different terrain: High elevation forests are often managed in a group selection approach using cable yarding systems (Schönenberger, 2001; Spinelli et al. 2015), which increase stand edges that potentially lead to higher disturbance impacts compared to single tree selection systems (Matlack and Litvaitis, 2001; Kautz et al., 2013).

The reduction of disturbance impacts in uneven-aged forests was very effective in simpler terrain (<20° slopes) and in mid-elevation areas, where single-tree selection is feasible. However, managing for uneven-aged stand characteristics in group selection systems has many other benefits in steep, high elevation mountain forests (e.g., in the context of protection against gravitational natural hazards, Moos et al. 2016). It might thus still be the desirable management approach also in rugged terrain, as e.g., the ability of forests to recover ecosystem functioning after disturbance (i.e., disturbance resilience, not assessed here) is considerably elevated in uneven-aged stands (Diaci et al. 2017).

The advantages and disadvantages of uneven-aged management have been intensively discussed among forest scientists and management decision makers (Kuuluvainen et al. 2012; Redon et al. 2014; Nolte et al. 2018; Schall et al. 2018; Ekholm et al. 2023). Our results show, that uneven-aged management is no silver bullet solution for managing forest change (Kuuluvainen et al. 2012; Messier et al. 2019), and highlight that the benefits and drawbacks of each management system need to be assessed against and adapted to local needs and conditions. However, we found evidence that in Central Europe, forests under uneven-aged management are less affected by natural disturbances than even-aged forests. Managing for uneven-aged conditions and associated structural complexity can therefore be an important element in a broader management strategy of addressing increasing disturbances in the future.

#### CRediT authorship contribution statement

**Johannes Mohr:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Dominik Thom:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Rupert Seidl:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Hubert Hase-nauer:** Writing – review & editing, Resources.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Code Availability

The code for processing the data and reproducing all analyses is available at <https://github.com/MohrJohannes/UEAForestResistance.git>.

#### Acknowledgements

We thank the four forest enterprises investigated here for their data and their interest in this study, in particular Johannes Wohlmacher, Clemens Spörk, Alberich Lodron, and Thomas Zanker. Thanks to Dr. Kristin Braziunas for proofreading the manuscript. J.M. and R.S. acknowledge support from European Research Council under the European Union's Horizon 2020 research and innovation program (Grant Agreement 101001905, FORWARD). The analyses presented here were initiated as part of a visit by J.M. at the Institute of Silviculture at the University of Natural Resources and Life Sciences (BOKU), Vienna. Moreover, we thank two anonymous reviewers for their helpful comments on an earlier version of this manuscript.

#### Conflict of interest statement

The authors declare no conflict of interest.

## Author contributions

D.T. and R.S. conceived the ideas for the study; J.M., D.T. and R.S. designed the methodology for the study; J.M. developed the algorithms for matching the sublandscapes and calculating disturbance metrics; J. M., D.T. and R.S. analyzed the data; J.M. wrote the first draft of the manuscript; J.M., D.T., H.H. and R.S. contributed to further versions of the manuscript. All authors have read and agreed to the published version of the manuscript.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121816](https://doi.org/10.1016/j.foreco.2024.121816).

## References

- Aszalós, Réka, Thom, Dominik, Aakala, Tuomas, Angelstam, Per, Brümelis, Guntis, Gálhidy, L.ászló, et al., 2022. Natural disturbance regimes as a guide for sustainable forest management in Europe. *Ecol. Appl.*: a Publ. Ecol. Soc. Am. 32 (5), e2596 <https://doi.org/10.1002/eap.2596>.
- Bastit, Félix, Brunette, Marielle, Montagné-Huck, Claire, 2023. Pests, wind and fire: a multi-hazard risk review for natural disturbances in forests. *Ecol. Econ.* 205, 107702 <https://doi.org/10.1016/j.ecolecon.2022.107702>.
- Bauhus, Juergen, Puettmann, Klaus, Kühne, Christian, 2013. Close-to-nature forest management in Europe. Does it support complexity and adaptability of forest ecosystems? In: *Managing forests as complex adaptive systems. Building resilience to the challenge of global change*. With assistance of K. Dave Coates, Christian C. Messier, Klaus J. Puettmann. London, New York: Earthscan from Routledge (Earthscan forest library).
- 2023 BFW (Ed.), 2023. ÖWI 2023. Österreichische Waldinventur 2023. Bundesforschungs- und Ausbildungszentrum für Wald. Available online at <https://waldinventur.at/>, checked on 11/17/2023.
- Bodin, Per, Wiman, Bo L.B., 2007. The usefulness of stability concepts in forest management when coping with increasing climate uncertainties. *For. Ecol. Manag.* 242 (2–3), 541–552. <https://doi.org/10.1016/j.foreco.2007.01.066>.
- Bohn, Friedrich J., Huth, Andreas, 2017. The importance of forest structure to biodiversity-productivity relationships. *R. Soc. Open Sci.* 4 (1), 160521 <https://doi.org/10.1098/rsos.160521>.
- Copernicus, 2020. High Resolution Layer: Dominant Leaf Type (DLT) 2018. Edited by European Environment Agency. Available online at <https://land.copernicus.eu/pan-european/high-resolution-layers/forests/dominant-leaf-type/status-maps/dominant-leaf-type-2018>, checked on 9/22/2023.
- Diaci, Jurij, Rozenberger, Dusan, Fidej, Gal, Nagel, Thomas A., 2017. Challenges for uneven-aged silviculture in restoration of post-disturbance forests in Central Europe: a synthesis. *Forests* 8 (10), 378. <https://doi.org/10.3390/f8100378>.
- Díaz-Yáñez, Olalla, Mola-Yudego, Blas, González-Olabarria, José Ramón, Pukkala, Timo, 2017. How does forest composition and structure affect the stability against wind and snow? *For. Ecol. Manag.* 401, 215–222. <https://doi.org/10.1016/j.foreco.2017.06.054>.
- Dormann, Carsten F., Elith, Jane, Bacher, Sven, Buchmann, Carsten, Carl, Gudrun, Carré, Gabriel, et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36 (1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Dvořák, Lubor, Bachmann, Peter, Mandallaz, Daniel, 2001. Sturmschäden in ungleichförmigen Beständen | Storm damage in irregular stands. *Schweiz. Z. für Forstwes.* 152 (11), 445–452. <https://doi.org/10.3188/szf.2001.0445>.
- Ehbrecht, Martin, Schall, Peter, Ammer, Christian, Seidel, Dominik, 2017. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. *Agric. For. Meteorol.* 242, 1–9. <https://doi.org/10.1016/j.agrformet.2017.04.012>.
- Ekhholm, Adam, Lundqvist, Lars, Petter Axelsson, E., Egnell, Gustaf, Hjältén, Joakim, Lundmark, Tomas, Sjögren, Jörgen, 2023. Long-term yield and biodiversity in stands managed with the selection system and the rotation forestry system: a qualitative review. *For. Ecol. Manag.* 537, 120920 <https://doi.org/10.1016/j.foreco.2023.120920>.
- Forest Europe, 2020. State of Europe's Forests 2020. Available online at [https://foresteu.ropa.org/wp-content/uploads/2016/08/SoEF\\_2020.pdf](https://foresteu.ropa.org/wp-content/uploads/2016/08/SoEF_2020.pdf), checked on 9/1/2023.
- Geoland, 2015. Digitales Geländemodell (DGM) Österreich. Edited by Österreich Bundesministerium für Finanzen. Available online at <https://www.data.gov.at/katalog/dataset/dgm#resources>, updated on 3/17/2015, checked on 9/22/2023.
- Gough, Christopher M., Atkins, Jeff W., Fahey, Robert T., Hardiman, Brady S., 2019. High rates of primary production in structurally complex forests. *Ecology* 100 (10), e02864. <https://doi.org/10.1002/ecy.2864>.
- Hanewinkel, M., Kuhn, T., Bugmann, H., Lanz, A., Brang, P., 2014. Vulnerability of uneven-aged forests to storm damage. *Forestry* 87 (4), 525–534. <https://doi.org/10.1093/forestry/cpu008>.
- Hijmans, Robert J., 2023. terra: Spatial Data Analysis. Available online at (<https://CRAN.R-project.org/package=terra>).
- Ho, Daniel E., Imai, Kosuke, King, Gary, Stuart, Elizabeth A., 2007. Matching as nonparametric preprocessing for reducing model dependence in parametric causal inference. *Polit. Anal.* 15 (3), 199–236. <https://doi.org/10.1093/pan/mp1013>.
- Ho, Daniel E., Imai, Kosuke, King, Gary, Stuart, Elizabeth A., 2011. MatchIt: nonparametric preprocessing for parametric causal inference. *J. Stat. Soft.* 42 (8), 1–28. <https://doi.org/10.18637/jss.v042.i08>.
- J.-P., Schütz, 2002a. Die Plenterung und ihre unterschiedlichen Formen. Skript zu Vorlesung Waldbau II und Waldbau IV. ETH Zurich, Zurich. Available online at: <https://ethz.ch/content/dam/ethz/special-interest/usys/ites/waldmgmt-waldbau-dam/documents/Lehrmaterialien/Skripte/Waldbau/plenterskript-02-03>.
- Jactel, Hervé, Bauhus, Jürgen, Boberg, Johanna, Bonal, Damien, Castagnérol, Bastien, Gardiner, Barry, et al., 2017. Tree diversity drives forest stand resistance to natural disturbances. *Curr. For. Rep.* 3 (3), 223–243. <https://doi.org/10.1007/s40725-017-0064-1>.
- Jin, Suming, Sader, Steven A., 2005. MODIS time-series imagery for forest disturbance detection and quantification of patch size effects. *Remote Sens. Environ.* 99 (4), 462–470. <https://doi.org/10.1016/j.rse.2005.09.017>.
- Kassambara, A., 2022. ggpubr: 'ggplot2' Based Publication Ready Plots. Available online at <https://CRAN.R-project.org/package=ggpubr>.
- Kautz, Markus, Schopf, Reinhard, Ohsner, Joachim, 2013. The "sun-effect": microclimatic alterations predispose forest edges to bark beetle infestations. *Eur. J. For. Res* 132 (3), 453–465. <https://doi.org/10.1007/s10342-013-0685-2>.
- Keeton, William S., 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *For. Ecol. Manag.* 235 (1–3), 129–142. <https://doi.org/10.1016/j.foreco.2006.08.005>.
- Knoke, Thomas, 1997. Ökonomische Aspekte der Holzproduktion in ungleichaltrigen Wäldern: einführende Untersuchungen zur Forstbetriebsplanung im Kreuzberger Gemeinwald. Economic aspects on timber production in uneven-aged forests: preliminary studies on forest management planning in the Kreuzberg Municipal Forest. In *Forstw 116* (1–6), 178–196. <https://doi.org/10.1007/BF02766893>. Cbl.
- Knoke, Thomas, 2012. The Economics of Continuous Cover Forestry. In: Pukkala, Timo, von Gadow, Klaus (Eds.), *Continuous Cover Forestry*, 23. Springer Netherlands (Managing Forest Ecosystems, Dordrecht, pp. 167–193).
- Knoke, Thomas, Paul, Carola, Gosling, Elizabeth, Jarisch, Isabelle, Mohr, Johannes, Seidl, Rupert, 2023. Assessing the economic resilience of different management systems to severe forest disturbance. *Environ. Resour. Econ.* 84 (2), 343–381. <https://doi.org/10.1007/s10640-022-00719-5>.
- Kulakowski, Dominik, Seidl, Rupert, Holeksa, Jan, Kuuluvainen, Timo, Nagel, Thomas A., Panayotov, Momchil, et al., 2017. A walk on the wild side: disturbance dynamics and the conservation and management of European mountain forest ecosystems. *For. Ecol. Manag.* 388, 120–131. <https://doi.org/10.1016/j.foreco.2016.07.037>.
- Kuuluvainen, Timo, Tahvonen, Olli, Aakala, Tuomas, 2012. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. *Ambio* 41 (7), 720–737. <https://doi.org/10.1007/s13280-012-0289-y>.
- Leverkus, Alexander B., Thorn, Simon, Gustafsson, Lena, Noss, Reed, Müller, Jörg, Pausas, Juli G., Lindenmayer, David B., 2021. Environmental policies to cope with novel disturbance regimes—steps to address a world scientists' warning to humanity. *Environ. Res. Lett.* 16 (2), 21003. <https://doi.org/10.1088/1748-9326/abc5a>.
- Lindner, Marcus, Maroschek, Michael, Netherer, Sigrid, Kremer, Antoine, Barbati, Anna, Garcia-Gonzalo, Jordi, et al., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manag.* 259 (4), 698–709. <https://doi.org/10.1016/j.foreco.2009.09.023>.
- Ma, Qin, Su, Yanjun, Niu, Chunyue, Hu, Tianyu, Luo, Xiangzhong, Tai, Xiaonan, et al., 2023. Tree mortality during long-term droughts is lower in structurally complex forest stands. *Nat. Commun.* 14 (1), 7467. <https://doi.org/10.1038/s41467-023-43083-8>.
- Mason, W.L., 2002. Are irregular stands more windfirm? *Forestry* 75 (4), 347–355. <https://doi.org/10.1093/forestry/75.4.347>.
- Massicotte, P., South, A. (2023). *naturalearth: World Map Data from Natural Earth*. Available online at (<https://CRAN.R-project.org/package=naturalearth>).
- Matlack, Glenn R., Litvaitis, John A., 2001. Forest edges. In: *Malcolm, L.Hunter (Ed.), Maintaining biodiversity in forest ecosystems*. Repr. Cambridge Univ. Press, Cambridge.
- McElhinny, Chris, Gibbons, Phillip, Brack, Cris, Bauhus, Jürgen, 2005. Forest and woodland stand structural complexity: its definition and measurement. *For. Ecol. Manag.* 218 (1–3), 1–24. <https://doi.org/10.1016/j.foreco.2005.08.034>.
- Messier, Christian, Bauhus, Jürgen, Doyon, Frederik, Maure, Fanny, Sousa-Silva, Rita, Nolet, Philippe, et al., 2019. The functional complex network approach to foster forest resilience to global changes. *Ecosyst.* 6 (1) <https://doi.org/10.1186/s40663-019-0166-2>.
- Mikita, Tomáš, Klimánek, Martin, 2010. Topographic exposure and its practical applications. *J. Landsc. Ecol.* 3 (1), 42–51. <https://doi.org/10.2478/s10285-012-0022-3>.
- Mohr, Conradin, Schori, Christian (1999): Femelschlag oder Plenterung – Ein Vergleich aus betriebswirtschaftlicher Sicht | Irregular Shelterwood System or Selection ("Plenter") System – a Comparison from an Economic Point of View. In *Schweizerische Zeitschrift für Forstwesen* 150 (2), pp. 49–55. doi: 10.3188/szf.1999.0049.
- Moos, Christine, Bebi, Peter, Graf, Frank, Mattli, Josias, Rickli, Christian, Schwarz, Massimiliano, 2016. How does forest structure affect root reinforcement and susceptibility to shallow landslides? *Earth Surf. Process. Land.* 41 (7), 951–960. <https://doi.org/10.1002/esp.3887>.
- Müller, Mortimer M., Vacik, Harald, Diendorfer, Gerhard, Arpaci, Alexander, Formayer, Herbert, Gossow, Hartmut, 2013. Analysis of lightning-induced forest fires in Austria. *Theor. Appl. Clim.* 111 (1–2), 183–193. <https://doi.org/10.1007/s00704-012-0653-7>.

- Nolet, Philippe, Kneeshaw, Daniel, Messier, Christian, Bédard, Martin, 2018. Comparing the effects of even- and uneven-aged silviculture on ecological diversity and processes: a review. *Ecol. Evol.* 8 (2), 1217–1226. <https://doi.org/10.1002/ece3.3737>.
- O'Hara, K.L., Ramage, B.S., 2013. Silviculture in an uncertain world: utilizing multi-aged management systems to integrate disturbance. *Forestry* 86 (4), 401–410. <https://doi.org/10.1093/forestry/cpt012>.
- Passtor, Ferenc, Matulla, Christoph, Rammer, Werner, Lexer, Manfred J., 2014. Drivers of the bark beetle disturbance regime in Alpine forests in Austria. *For. Ecol. Manag.* 318, 349–358. <https://doi.org/10.1016/j.foreco.2014.01.044>.
- Patacca, Marco, Lindner, Marcus, Lucas-Borja, Manuel Esteban, Cordonnier, Thomas, Fidej, Gal, Gardiner, Barry, et al., 2023. Significant increase in natural disturbance impacts on European forests since 1950. *Global Change Biology* 29 (5), pp. 1359–1376. doi: 10.1111/gcb.16531.
- Peck, JeriLynn E., Zenner, Eric K., Brang, Peter, Zingg, Andreas, 2014. Tree size distribution and abundance explain structural complexity differentially within stands of even-aged and uneven-aged structure types. *Eur. J. For. Res* 133 (2), 335–346. <https://doi.org/10.1007/s10342-013-0765-3>.
- Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77 (1), 27–44. <https://doi.org/10.1093/forestry/77.1.27>.
- Pommerening, Arne, 2023. *Continuous Cover Forestry: Theories, Concepts, and Implementation*. John Wiley & Sons.
- Pukkala, Timo, Gadow, Klaus von, 2012. *Managing Forest Ecosystems*. In: *Continuous Cover Forestry*. Springer Netherlands, Dordrecht.
- Pukkala, Timo, Laiho, Olavi, Lähde, Erkki, 2016. Continuous cover management reduces wind damage. *For. Ecol. Manag.* 372, 120–127. <https://doi.org/10.1016/j.foreco.2016.04.014>.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. Available online at <https://www.R-project.org/>.
- Rämö, Janne, Tahvonen, Olli, 2014. Economics of harvesting uneven-aged forest stands in Fennoscandia. *Scand. J. For. Res.* 29 (8), 777–792. <https://doi.org/10.1080/02827581.2014.982166>.
- Redon, Mathilde, Luque, Sandra, Gosselin, Frédéric, Cordonnier, Thomas, 2014. Is generalisation of uneven-aged management in mountain forests the key to improve biodiversity conservation within forest landscape mosaics? *Ann. For. Sci.* 71 (7), 751–760. <https://doi.org/10.1007/s13595-014-0371-7>.
- Röhrig, Ernst, Bartsch, Norbert, Lüpke, Burghard von, 2006. *Waldbau auf ökologischer Grundlage*. 91 Table 7., vollst. aktualisierte Aufl. Stuttgart (Hohenheim). Ulmer (UTB Forst- und Agrarwissenschaften, Ökologie, Biologie).
- Schall, Gossner, Peter, Heinrichs, Martin M., Fischer, Steffi, Boch, Markus, Prati, Steffen, Daniel, et al., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* 55 (1), 267–278. <https://doi.org/10.1111/1365-2664.12950>.
- Scherrer, Daniel, Ascoli, Davide, Conedera, Marco, Fischer, Christoph, Maringer, Janet, Moser, Barbara, et al., 2022. Canopy disturbances catalyse tree species shifts in Swiss Forests. *Ecosystems* 25 (1), 199–214. <https://doi.org/10.1007/s10021-021-00649-1>.
- Schmidt, Matthias, Hanewinkel, Marc, Kändler, Gerald, Kublin, Edgar, Kohnle, Ulrich, 2010. An inventory-based approach for modeling single-tree storm damage — experiences with the winter storm of 1999 in southwestern Germany. *Can. J. Res.* 40 (8), 1636–1652. <https://doi.org/10.1139/X10-099>.
- Schönenberger, Walter, 2001. Trends in mountain forest management in Switzerland. *Schweiz. Z. für Forstwes.* 152 (4), 152–156. <https://doi.org/10.3188/szf.2001.0152>.
- Schütz, J.-P., 2001. *Der Plenterwald und weitere Formen strukturierter und gemischter Wälder*. Parey Buchverlag, Berlin.
- Schütz, J.-P., 2002b. Silvicultural tools to develop irregular and diverse forest structures. *Forestry* 75 (4), 329–337. <https://doi.org/10.1093/forestry/75.4.329>.
- Sebold, Julius, Senf, Cornelius, Seidl, Rupert, 2021. Human or natural? Landscape context improves the attribution of forest disturbances mapped from Landsat in Central Europe. *Remote Sens. Environ.* 262, 112502 <https://doi.org/10.1016/j.rse.2021.112502>.
- Seidl, Rupert, Rammer, Werner, Jäger, Dietmar, Lexer, Manfred J., 2008. Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. *For. Ecol. Manag.* 256 (3), 209–220. <https://doi.org/10.1016/j.foreco.2008.04.002>.
- Seidl, Rupert, Schelhaas, Mart-Jan, Lindner, Marcus, Lexer, Manfred J., 2009. Modelling bark beetle disturbances in a large scale forest scenario model to assess climate change impacts and evaluate adaptive management strategies. *Reg. Environ. Change* 9 (2), 101–119. <https://doi.org/10.1007/s10113-008-0068-2>.
- Seidl, Rupert, Thom, Dominik, Kautz, Markus, Martin-Benito, Dario, Peltoniemi, Mikko, Vacciano, Giorgio, et al., 2017. Forest disturbances under climate change. *Nat. Clim. Change* 7, 395–402. <https://doi.org/10.1038/nclimate3303>.
- Senf, Cornelius, Seidl, Rupert, 2021a. Mapping the forest disturbance regimes of Europe. *Nat. Sustain* 4 (1), 63–70. <https://doi.org/10.1038/s41893-020-00609-y>.
- Senf, Cornelius, Seidl, Rupert, 2021b. Storm and fire disturbances in Europe: Distribution and trends. *Glob. Change Biol.* 27 (15), 3605–3619. <https://doi.org/10.1111/gcb.15679>.
- Senf, Cornelius, Sebold, Julius, Seidl, Rupert, 2021. Increasing canopy mortality affects the future demographic structure of Europe's forests. *One Earth* 4 (5), 749–755. <https://doi.org/10.1016/j.oneear.2021.04.008>.
- Senf, Cornelius, Buras, Allan, Zang, Christian S., Rammig, Anja, Seidl, Rupert, 2020. Excess forest mortality is consistently linked to drought across Europe. *Nat. Commun.* 11 (1), 6200. <https://doi.org/10.1038/s41467-020-19924-1>.
- Sharma, Ajay, Bohn, Kimberly, Jose, Shibu, Dwivedi, Puneet, 2016. Even-Aged vs. Uneven-Aged Silviculture: implications for multifunctional management of Southern Pine Ecosystems. *Forests* 7 (12), 86. <https://doi.org/10.3390/f7040086>.
- Sommerfeld, Andreas, Rammer, Werner, Heurich, Marco, Hilmers, Torben, Müller, Jörg, Seidl, Rupert, 2021. Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe? *J Ecol* 109, 737–749. <https://doi.org/10.1111/1365-2745.13502>.
- Sommerfeld, Andreas, Senf, Cornelius, Buma, Brian, D'Amato, Anthony W., Després, Tiphaine, Diaz-Hormazabal, Ignacio, et al., 2018. Patterns and drivers of recent disturbances across the temperate forest biome. In *Nature Communications* 9 (1), p. 4355. doi:10.1038/s41467-018-06788-9.
- Spinelli, R., Maganotti, N., Visser, R., 2015. Productivity Models for Cable Yarding in Alpine Forests. In *European Journal of Forest Engineering* 1 (1), pp. 9–14. Available online at <https://dergipark.org.tr/en/pub/ejfe/issue/5186/70454>, checked on 11/9/2023.
- Streit, Kathrin, Wunder, Jan, Brang, Peter, 2009. Slit-shaped gaps are a successful silvicultural technique to promote *Picea abies* regeneration in mountain forests of the Swiss Alps. *For. Ecol. Manag.* 257 (9), 1902–1909. <https://doi.org/10.1016/j.foreco.2008.12.018>.
- Strith, Ana, Bebi, Peter, Rossi, Christian, Grêt-Regamey, Adrienne, 2021. Addressing disturbance risk to mountain forest ecosystem services. *J. Environ. Manag.* 296, 113188 <https://doi.org/10.1016/j.jenvman.2021.113188>.
- Thom, Dominik, Seidl, Rupert, 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biol. Rev. Camb. Philos. Soc.* 91 (3), 760–781. <https://doi.org/10.1111/brv.12193>.
- Thom, Dominik, Spatelf, Peter, 2023. Adaptive Waldbewirtschaftung zur Minderung von Störungen. *Schweiz. Z. für Forstwes.* 174 (2), 70–75. <https://doi.org/10.3188/szf.2023.0070>.
- Thom, Dominik, Seidl, Rupert, Steyrer, Gottfried, Krehan, Hannes, Formayer, Herbert, 2013. Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. *For. Ecol. Manag.* 307, 293–302. <https://doi.org/10.1016/j.foreco.2013.07.017>.
- Thom, Dominik, Rammer, Werner, Laux, Patrick, Smiatek, Gerhard, Kunstmann, Harald, Seibold, Sebastian, Seidl, Rupert, 2022. Will forest dynamics continue to accelerate throughout the 21st century in the Northern Alps? *Glob. Change Biol.* 28 (10), 3260–3274. <https://doi.org/10.1111/gcb.16133>.
- Turner, Monica G., Seidl, Rupert, 2023. Novel disturbance regimes and ecological responses. *Annu. Rev. Ecol. Syst.* 54 (1), 63–83. <https://doi.org/10.1146/annurev-ecolsys-110421-101120>.
- Urban, Dean, L., O'Neill, Robert, V., Shugart, Herman, H., 1987. *Landscape Ecology*. In: *BioScience* 37 (2), 119–127. doi:10.2307/1310366.
- Weinfurter, Peter, 2013. *Waldbau in Österreich auf ökologischer Grundlage. Eine Orientierungshilfe für die Praxis*. 1st ed. Edited by Landwirtschaftskammer Österreich. Available online at <https://waldbauberater.at/downloads/waldbau.pdf>.
- Wickham, Hadley, 2016. *ggplot2. Elegant graphics for data analysis*. With assistance of Carson Sievert, Second ed. Springer, Switzerland.
- Wickham, H., François, R., Henry, L., Müller, K., 2022. *dplyr: A Grammar of Data Manipulation*. Available online at <https://CRAN.R-project.org/package=dplyr>.
- Wickham, H., Girlich, M., 2022. *tidyr: Tidy Messy Data*. Available online at (<https://CRAN.R-project.org/package=tidyr>).
- Wood, Simon N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B: Stat. Methodol.* 73 (1), 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>.