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RESEARCH ARTICLE

Post-disturbance recovery of forest cover and tree height differ with management in Central Europe

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Abstract
Context Recovery from disturbances is a prominent measure of forest ecosystem resilience, with swift recovery indicating resilient systems. The forest ecosystems of Central Europe have recently been affected by unprecedented levels of natural disturbance, yet our understanding of their ability to recover from disturbances is still limited.
Objectives We here integrated satellite and airborne Lidar data to (i) quantify multi-decadal post-disturbance recovery of two indicators of forest structure, and (ii) compare the recovery trajectories of forest structure among managed and un-managed forests.
Methods We developed satellite-based models predicting Lidar-derived estimates of tree cover and stand height at 30 m grain across a 3100 km^2 landscape in the Bohemian Forest Ecosystem (Central Europe). We summarized the percentage of disturbed area that recovered to > 40% tree cover and > 5 m stand height and quantified the variability in both indicators over a 30-year period. The analyses were stratified by three management regimes (managed, protected, strictly protected) and two forest types (beech-dominated, spruce-dominated).
Results We found that on average 84% of the disturbed area met our recovery threshold 30 years post-disturbance. The rate of recovery was slower in un-managed compared to managed forests. Variability in tree cover was more persistent over time in un-managed forests, while managed forests strongly converged after a few decades post-disturbance.
Conclusion We conclude that current management facilitates the recovery of forest structure in Central European forest ecosystems. However, our results underline that forests recovered well from disturbances also in the absence of human intervention. Our analysis highlights the high resilience of Central European forest ecosystems to recent disturbances.

Keywords Recovery · Disturbance · Windthrow · Bark beetles · Forest management · Lidar · Landsat · Temperate forest · Bohemian forest ecosystem

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Introduction

Natural disturbances are important drivers of forest ecosystem dynamics. They shape forest ecosystem structure and functioning by creating biological legacies such as logs and snags (Lindenmayer et al. 2004), and by increasing the heterogeneity of forests from stand to landscape scales (Turner 2010). Yet, there is growing evidence of changing disturbance regimes under climate change (Seidl et al. 2017), requiring forest managers to increasingly focus on the resilience of ecosystems to disturbance (Seidl et al. 2016c). A prerequisite for developing management actions that foster resilience is the ability to measure and quantify indicators of resilience (Scheffer et al. 2015).

Post-disturbance recovery is an important indicator of ecosystem resilience, with fast recovery generally suggesting a high level of resilience (Scheffer et al. 2015; Seidl et al. 2016c). Forest recovery can be measured using different indicators (Frolking et al. 2009; Trumbore et al. 2015), including recovery in forest structural elements (Bolton et al. 2015; Bartels et al. 2016), floristic indicators (McLachlan and Bazely 2001; Nagel et al. 2006), and biomass (Williams et al. 2012; Dobor et al. 2018). As disturbances affect ecosystem service supply predominately negatively (Thom and Seidl 2016), the time it takes to recover important forest properties also is a key determinant of the societal impact of disturbances. However, recovery is a retrospective indicator of resilience that can only be assessed after a perturbation has taken place. A prospective view of resilience can be gleaned, for instance, from spatial heterogeneity. Heterogeneity can dampen the cross-scale interactions and amplifying feedbacks that are necessary for catastrophic events and regime shifts (Peters et al. 2004). Specifically, variability in recovery can have long-lasting effects on the development of forest ecosystems (Meigs et al. 2017), and can decrease the vulnerability of forests to future disturbances by preventing synchronous exceedance of susceptibility thresholds for, e.g., bark beetle outbreaks (Seidl et al. 2016a). Hence, not only the temporal signal of recovery (i.e., recovery rate) but also its spatial pattern (i.e., variability in recovery) needs to be considered for a comprehensive quantification of forest ecosystem resilience to disturbance (Scheffer et al. 2015; Braziunas et al. 2018).

The forests of Central Europe have been strongly affected by natural disturbances from wind and bark beetles recently (Seidl et al. 2014b; Senf et al. 2018), with unprecedented disturbance levels in at least the last century (Schurman et al. 2018). Consequently, the ability of these forests to recover has come into focus. Recent research has addressed the initial establishment of tree-seedlings in the first years after a disturbance, demonstrating that forests affected by bark beetles and wind regenerate well through self-replacement (Svoboda et al. 2010; Zeppenfeld et al. 2015; Macek et al. 2017). These local studies delivered important insights into the potential of Central European forests to recovery from a disturbance. Yet, a landscape-scale perspective on long-term post-disturbance recovery trajectories is still missing to date. We lack, for instance, important information on the overall proportion of forests that have recovered from a disturbance in a given landscape, as well as on the spatial variability of disturbance recovery. Addressing such questions requires a complementary broad-scale approach to estimating recovery, such as the analysis of remote sensing data.

Remote sensing has emerged as an important tool for quantitative assessments in the field of disturbance ecology. While mapping forest disturbances from remote sensing data is now feasible (Banskota et al. 2014), the analysis of post-disturbance recovery has received less attention to date. Recent studies have used data from active sensors such as light detecting and ranging (Lidar) to quantify post-disturbance structural characteristics and recovery trajectories (Bolton et al. 2015; Vogeler et al. 2016; Latifi et al. 2016; Bolton et al. 2017; Hill et al. 2017). However, as those approaches are limited in their spatial and temporal extent, it might be beneficial to also utilize data from passive, satellite-borne sensors—such as Landsat—for mapping post-disturbance recovery across extended spatio-temporal scales (Kennedy et al. 2007; Schroeder et al. 2007). Trends in spectral recovery derived from Landsat time series can give valuable insights into the regrowth of vegetation after large-scale disturbances such as clear-cutting and fire in the boreal forests (Frazier et al. 2015; White et al. 2017; Frazier et al. 2018). It remains unclear, however, whether Landsat is also suited for characterizing post-disturbance recovery in more fine-grained landscapes such as the forests of Central Europe.

Forests in Central Europe are by large parts managed ecosystem, with approximately 70% of the total forest area being under active management and only 4% of Europe's forests being without impact by humans (Forest Europe 2015). Management in Central Europe includes clear-cut harvest, salvage harvesting in response to natural disturbances (Stadelmann et al. 2013), gap and shelter-wood cutting to induce advanced regeneration, and planting after clear-cut or natural disturbance. The latter is intended to foster post-disturbance recovery, with managers often questioning the ability of forests to recover naturally after disturbance. However, as planting is executed largely uniformly in space, it could at the same time decrease the structural diversity in early- to mid-successional stages of forest development relative to natural forest regeneration (Donato et al. 2012). Furthermore, salvage harvesting in response to natural disturbances frequently removes important pre-disturbance legacies, reducing structural diversity (Bace et al. 2015) and habitat quality of the resulting managed early-seral forests (Swanson et al. 2011; Thorn et al. 2017). It therefore remains an open question whether management improves the recovery from natural disturbances, or if forests of Central Europe are resilient to the current disturbance regimes even without human intervention.

Here, our aim was to quantify and compare long-term post-disturbance forest recovery in managed and un-managed forests in Central Europe. We used satellite data to predict Lidar-based estimates of tree cover and stand height across a 3100 km^2 landscape at the border of Austria, Czechia, and Germany (including two major National Parks). We then assessed the performance of varying spectral indices and remote sensing metrics, as well as the effect of training sample size on model performance. Furthermore, we combined the predicted tree cover and stand height maps with satellite-based maps of past forest disturbance (from 1985 onwards), allowing us to summarize and compare recovery and variability in both tree cover and stand height between managed and un-managed forests, as well as between different elevation bands. Elevation hereby served as proxy for different dominant tree species in the region (Röder et al. 2010; Bässler et al. 2016). In sum, our objectives were: (i) quantify multi-decadal post-disturbance recovery focusing on two indicators of stand structure, and (ii) compare recovery trajectories of stand structure between managed and un-managed forests.

Materials and methods

Study landscape

Our study landscape is situated in the Bohemian Forest ecosystem (48° 57′ N 13° 26′ E; Fig. 1), which is a typical *Mittelgebirge* mountain range situated along the border of Austria, Czechia and Germany. Elevation ranges from 300 m a.s.l. in valleys to 1,450 m a.s.l. along the main mountain ridge. The climate is characterized by a moderate to cool montane climate (3 to 4 °C mean annual temperature) with relatively high precipitation levels (annual total of 1300 to 1800 mm) that decreases from west to east. The centre of the area is formed by two conjoined protected areas, the Bavarian Forest National Park in Germany (240 km^2; established 1970) and the Šumava National Park in Czechia (690 km^2; established 1991). The most important tree species are Norway spruce (*Picea abies* (L.) Karst.), European beech (*Fagus sylvatica* L.), and silver fir (*Abies alba* Mill.).

The study landscape can broadly be divided into three management regimes (Fig. 1): (1) *Strictly protected*, (2) *protected*, and (3) *managed* forests. The first regime, *strictly protected*, characterizes areas that were not managed at all during the analysis period 1985–2016 (i.e., core zones of national parks[1]). In those areas, no human intervention is allowed, and disturbance and recovery reflect natural ecosystem dynamics, developing without human interference (Senf and Seidl 2018). The major disturbance agents in the *strictly protected* areas are bark beetles and wind storms. The second management regime, *protected*, contains all areas which are within the boundaries of national parks, but which were subject to some human intervention during the study period. Interventions in the *protected* management regime included salvaging or other treatments of natural disturbances to contain the spread of bark beetles to areas outside the national park. The second management regime thus comprises

[1] Please note that the current core zones of the national parks are larger than shown in Fig. 1, yet we here focus on areas where management was excluded over the entire study period 1985–2016.

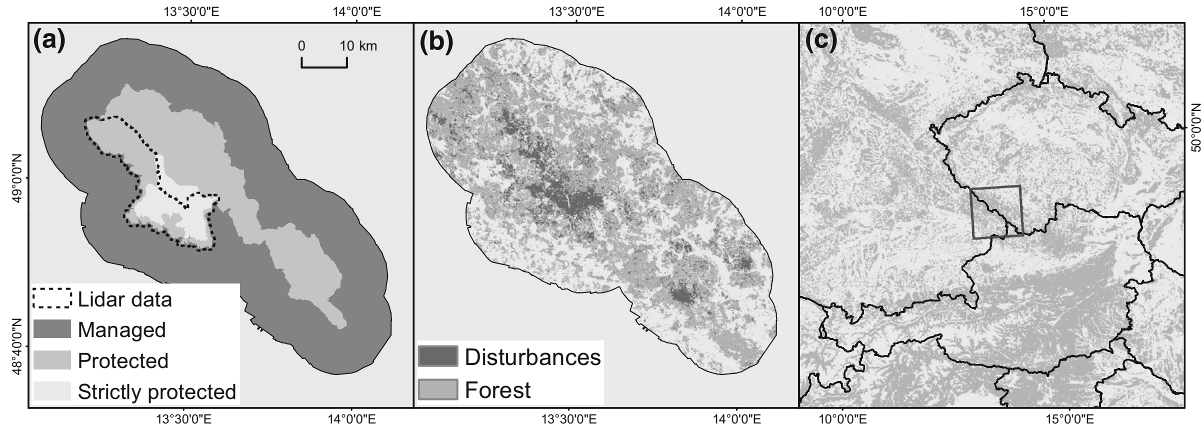

Fig. 1 Study landscape with the three management regimes and availability of Lidar data (**a**), disturbance patches and forest area mapped from Landsat data (**b**), and location of the study landscape in Central Europe (**c**)

only management interventions in response to natural disturbances, but does not include regular, planned harvesting interventions. The third management regime, *managed*, comprises forests of varying ownership (private and public) and management objectives. The disturbance regime in this last area can be characterized as human-dominated, with typical management interventions including clearcut harvesting with and without planting, as well as gap and shelterwood cutting to support natural regeneration. Hence, the *management* areas include mostly human-caused forest disturbances. However, also the area under this third management regime was subject to natural disturbances by wind and bark beetles during the study period. However, usual management responses to natural disturbances include sanitation and salvage logging as well as replanting to facilitate swift recovery.

Mapping post-disturbance forest structure

Landsat-based disturbance and recovery metrics

All Landsat data from the United States Geological Survey (USGS) and European Space Agency (ESA) archives were downloaded and processed to annual best observation composites following the methods described in Senf et al. (2017). In essence, processing involved the calculation of surface reflectance values, the creation of cloud and cloud-shadow masks, and the creation of median spectral reflectance composites including only clear growing-season observations (between June 1st and August 31st) during the study period (1985–2016). Additionally, we acquired maps of stand-replacing forest disturbances and disturbance onset (i.e., the first year of disturbance; Point A in Fig. 2) from Senf et al. (2017). The disturbance maps had an overall accuracy of 87% with error of commission/omission for the disturbances class being 5% and 3%, respectively. The year of disturbance was estimated correctly for 80% of the disturbances given a ± 1-year tolerance.

We transferred the multi-spectral median composites from Landsat into three spectral indices commonly used for disturbance and recovery mapping: the normalized burn ratio (NBR; Key 2006), the Tasseled Cap wetness component (TCW; Crist 1985), and the disturbance index (DI; Healey et al. 2005). The NBR has been employed in a variety of studies mapping disturbances (Meigs et al. 2011; Kennedy et al. 2012; Hermosilla et al. 2015) and recovery (Pickell et al. 2015; White et al. 2017) and is linked to structural changes in disturbed and recovering vegetation. Similarly, the TCW has been employed for assessing disturbance and recovery (Hais et al. 2009; Senf et al. 2015), also being sensitive to structural changes in the tree canopy. The DI integrates all Tasseled Cap components (brightness, greenness and wetness), thus delivering a more holistic view on forest changes (see, for example, Hais et al. 2009). In order to remove residual clouds and outliers from the spectral index time series—which might obscure further analysis—we followed Kennedy et al. (2010) in detecting and

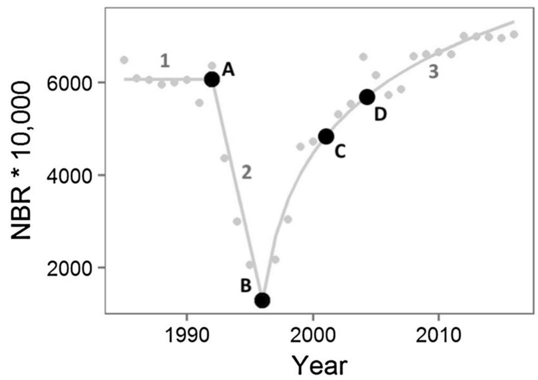

Fig. 2 Example Landsat spectral trajectory. Note that the disturbance and recovery metrics are here exemplified using the NBR trajectory. Each grey dot is an annual Landsat observation of one example pixel. Point A indicates the start of disturbance. Point B indicates the end of disturbances and hence the start of recovery. Point C indicates the spectral recovery after 5 years (short-term spectral recovery), whereas point D indicates the 80% spectral recovery (long-term spectral recovery). Segment 1 indicates the pre-disturbance observations. Segment 2 indicates the disturbance segment, from which the disturbance magnitude and duration are derived. Segment 3 indicates the recovery model

removing spikes based on a normalized difference measure between neighboring observations.

For characterizing disturbances and recovery—and subsequently predicting forest structure after disturbance—we developed a set of metrics describing the spectral and temporal characteristics of disturbance and recovery. We first determined the end of disturbance for each disturbed pixel by identifying the minimum spectral value after the onset of a disturbance (Point B in Fig. 2). This step was necessary as particular disturbances by biotic agents often extend over several years, and the start of recovery is thus not accurately characterized by the disturbance onset (see, for example, Fig. 2). Once the end of a disturbance was identified, we calculated the spectral magnitude of disturbance (*absolute disturbance magnitude*), defined as the spectral difference between the mean of all observations before the disturbance onset (*pre-disturbance spectral value*; segment 1 in Fig. 2) and the spectral value at the end of a disturbance segment (segment 2 in Fig. 2). We also calculated the *relative disturbance magnitude* by dividing the absolute disturbance magnitude by the pre-disturbance spectral value. We assessed the *length of disturbance* as the difference in years between disturbance onset and end (point A and B in Fig. 2, respectively). For further characterizing the pre-disturbance spectral characteristics, we also calculated the slope of all observations before disturbance (*pre-disturbance slope*; Hais et al. 2016).

For characterising recovery, we fit a linear-log model to the spectral recovery trajectory (segment 3 in Fig. 2), providing a good approximation of short-term spectral recovery (i.e., initial rapid changes in spectral signal) and longer-term spectral trends (saturation of the spectral signal after approx. 10–15 years; see Fig. 2). We also tested linear, exponential, power and logit models, but found that the linear-log model provided the best balance between model fit and stable model performance. No model was fit if less than five observations were available. From the linear-log model we derived two metrics summarizing the spectral recovery trend: The absolute and relative short-term spectral recovery and the time until spectral recovery (Kennedy et al. 2010; White et al. 2017). The first metric is derived by the absolute spectral change 5 years after the end of disturbance (*absolute short-term recovery*; point C in Fig. 2), which is divided by the disturbance magnitude for deriving the *relative short-term recovery*. The second metric (*long-term spectral recovery*) is derived by counting the number of years until the model reaches 80% of the pre-disturbance spectral value (point D in Fig. 2). We also tested a variety of other thresholds for the short- and long-term recovery metrics (i.e., recovery after 3, 10 or 15 years; pre-spectral threshold of 60%, 90% or 100%), but found generally high correlation between metrics (Pearson $r > 0.90$) and thus decided to follow the metrics recommended in White et al. (2017). Finally, we estimated the *time since disturbance* as the length of the recovery trajectory in years.

Lidar-based estimates of tree cover and stand height

We used a Lidar-based 1 m spatial resolution canopy height model (CHM) from 2012 to derive post-disturbance structural variables at Landsat spatial resolution (i.e., 30 m pixels). The CHM data was generated by the national park authorities from full-waveform Lidar data (Riegl 680i laser scanner, 350 kHz, nominal point density of 30–40 points per m^2) acquired from an average altitude of 650 m above ground (ca. 300–400 m swath width) over 3 days in June under leaf-on conditions. We followed Bolton et al. (2015) and Bolton et al. (2017) in deriving metrics of post-disturbance tree cover and stand height, respectively. Tree cover was calculated as the share of 1 m CHM pixels that had a height greater 2 m, including both regenerating (2 to 5 m) and mature (> 5 m) trees, but excluding taller shrub and herbs (Latifi et al. 2016). Stand height was calculated as the 75% quantile of all 1 m CHM pixels. The 75% quantile, in contrast to upper quantiles (i.e., 99%), is more closely linked to the height structure of recovering trees, and likely less influenced by residual trees (Bolton et al. 2017). Yet, correlation analysis between the 75% quantile and other quantiles commonly used (i.e., 50%, 95% and 99%) indicated high similarity among stand height metrics (Pearson $r > 0.8$).

Predictive models of post-disturbance tree cover and stand height

Using the two Lidar-based forest structural metrics as response variables and the disturbance and recovery metrics described in the previous section as predictors (Table 1), we built predictive models using random forest regression (Breiman 2001; Ahmed et al. 2015). We build three models for each of the three spectral indices compared in this study (NBR, TCW, and DI). Further, we trained models with an increasing proportion of pixels used for training (0.25, 0.5, 1, 2.5, 5, 10, 20%), thus testing the effect of training sample size on model performance. To ensure that the full data space is utilized for training, we applied a stratified sampling design that first cuts all data points into quintiles and following selects n/5 samples at random from each quintile. Finally, to prevent including disturbances that occurred after Lidar data acquisition, we restricted the analysis to disturbances before 2009 (Lidar acquisition minus 3 years, which is the median disturbance duration). For assessing model performance, we randomly sampled an independent (i.e., not used for training) sample of n = 5000 pixels. From this validation sample, we calculated the root mean squared error (RMSE), the relative RMSE (divided by the mean), and the squared Pearson correlation coefficient (r^2). Finally, we used the best performing model with minimum amount of training data (i.e., the most parsimonious and computationally least intensive model) to predict post-disturbance tree canopy cover and stand height for each disturbed pixel. By doing so we yielded continuous maps of post-disturbance tree cover and stand height for the year 2016, and thus with variable time since disturbance (5–30 years).

Analyzing structural recovery rates

We assumed a pixel to be structurally recovered if a minimum tree cover of 40% and a minimum stand height of 5 m were reached, closely following common forest definitions (Chazdon et al. 2016). We thus only assess whether a pixel can be considered reforested, but do not address recovery in floristic composition or biomass. To assess rates of structural recovery, we calculated the percentage of pixels meeting our recovery threshold for each year after disturbance (5–30 years). The calculation was stratified by the management regimes described in Sect. 2.1 (Fig. 1), as well as by elevation bands. Elevation was split into < 1150 m and ≥ 1150 m, with the former representing beech-dominated and the latter representing spruce-dominated forests (Röder et al. 2010; Bässler et al. 2016). To test for differences in recovery trajectories, we fit logistic functions to the recovery trajectories using non-linear regression. We weighted the parameter estimation by the number of observations, avoiding years with only few pixels to distort the

Table 1 Average percentage of disturbed areas that structurally recovered at 30 years post-disturbance

Stratum	Percent of disturbed area structurally recovered	
	Beech-zone	Spruce-zone
Strictly protected	86 (83–90)	92 (89–94)
Protected	84 (80–88)	79 (75–84)
Managed	55 (47–63)	60 (52–68)

Estimates are derived from logistic functions shown in Fig. 5. Values in brackets indicate the 95% prediction interval derived from parametric bootstrap model fit. From the logistic model, we derived the percentage of pixels recovered after 30 years as comparable measure across management regimes and elevation bands. Uncertainties in the logistic model were quantified using parametric bootstrap with 10,000 replications (Bates and Watts 2007).

Analyzing variability in tree cover and stand height

To assess the variability in tree cover and stand height after disturbance, we calculated the coefficient of variation for both indicators. To calculate the coefficient of variation—which needs a vector of data points and thus can't be calculated at the pixel level—we aggregated the tree cover and stand height maps to a grid of five times five Landsat pixels (equalling 2.25 ha). The coefficient of variation thus serves as a proxy for the variability of tree cover and stand height among neighboring pixels, with a higher value indicating a higher local variability. We also calculated the median time since disturbance and the mean elevation for each grid cell, thus allowing us to stratify the analysis by time since disturbance and elevation, as described above.

Result

Mapping post-disturbance tree cover and stand height

The best predictive performance with minimum training data was achieved by the random forest models using the NBR-based disturbance and recovery metrics and 10% (n = 9424) of the total data for training (see Fig. 7 in the "Appendix"). In the following we thus report results for these models only. The final tree-cover model had an r^2 of 0.71, a RMSE of 0.15 and a relative RMSE of 57% (Fig. 3). The final stand height model had an r^2 of 0.58, a RMSE of 3.33 and a relative RMSE of 102% (Fig. 3).

Maps of post-disturbance tree cover and stand height provide a detailed picture of the spatial variability in both structural variables across the landscape (Fig. 4). Well visible is the large area disturbed by bark beetles in the strictly protected part of the study area, with highly variable tree cover and stand height (Fig. 4a). In contrast, areas

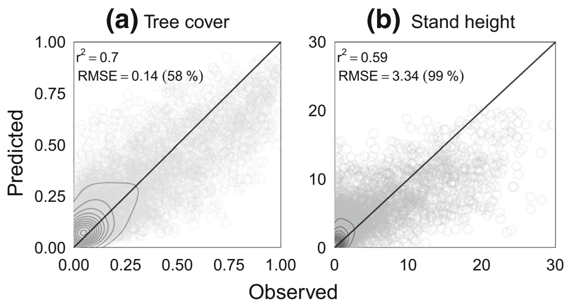

Fig. 3 Scatterplots between predicted and observed post-disturbance canopy cover and stand height. Grey isolines indicate data density. The black horizontal line indicates the 1:1 line. Reported are the squared correlation coefficient (r^2), the root mean squared error (RMSE), and the relative RMSE (relative to the mean; in brackets)

predominantly characterized by small-scale disturbance patches and forest management showed a more homogeneous tree cover and stand height (Fig. 4b).

Rates of structural recovery

The rate of structural recovery after disturbance was high, with on average 84 (79–88[2]) % of the disturbed areas reaching our recovery thresholds (i.e., a minimum tree cover of 40% and minimum stand height of 5 m) after 30 years. Recovery rates varied, however, significantly between management regimes (i.e., no overlap of the 95% confidence intervals in Fig. 5 and Table 1). Fastest recovery was always found in *managed forests*, with on average 86 (83–90) % of the disturbed area in the beech-zone and 92 (89–94) % in the spruce-zone being recovered after 30 years. In *strictly protected* forests, only 55 (47–63) % of the disturbed area in the beech-zone and 60 (52–68) % in the spruce-zone reached the recovery threshold after 30 years. Recovery rates in *protected* forests—that is where natural disturbances are salvage harvested but not planted—were similar to *managed* forests in the beech-zone (84 [80–88]% of the disturbed area reaching the recovery threshold after 30 years), whereas recovery in *protected* forests of the spruce-zone was slower than in *managed* forests, but faster than in *strictly protected* forests (79 [75–84] % of the disturbances reaching the recovery threshold after 30 years).

[2] We here always report the 95% prediction interval derived from parametric bootstrap with 10,000 replications.

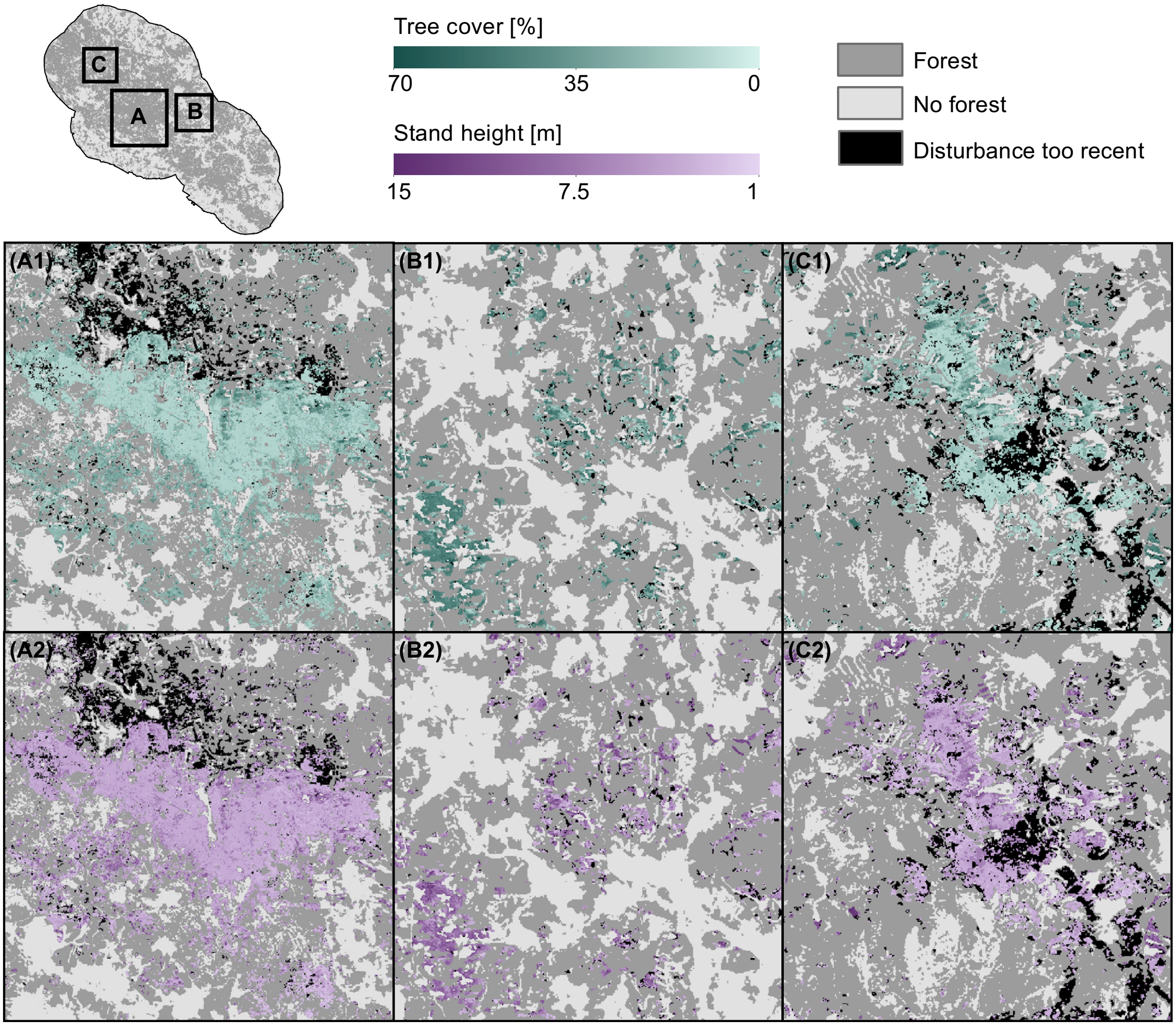

Fig. 4 Maps of post-disturbance tree cover and stand height for the study landscape in the year 2016. Close-up A shows an unmanaged bark beetle outbreak (ca. 1995) with high variability in tree cover and stand height. Close-up B shows a managed forest with small-scale harvests, and homogeneous tree cover and stand height after disturbance. Close-up C shows a managed wind-throw (i.e. a combination of natural and human disturbance) with variable post-disturbance tree cover and stand height. Disturbances after 2011 were not included in the analysis and are here labeled as *disturbance too recent*

Variability in post-disturbance tree cover and stand height

Differences in the variability of both tree cover and stand height between management regimes were generally low (Fig. 6). However, two important insights emerged. First, variability in stand height was significantly higher in *strictly protected* forests compared to *managed* forests in the beech-zone. Second, while variability in tree cover among all three management regimes was more similar in the initial years post-disturbance, variability in tree cover in *managed* and *protected* forests sharply declined after 25 years post-disturbance. *Strictly protected* forests, in turn, didn't show this decline, and had a significantly higher variability in tree cover than managed forests 25 to 30 years post-disturbance, especially in the beech zone.

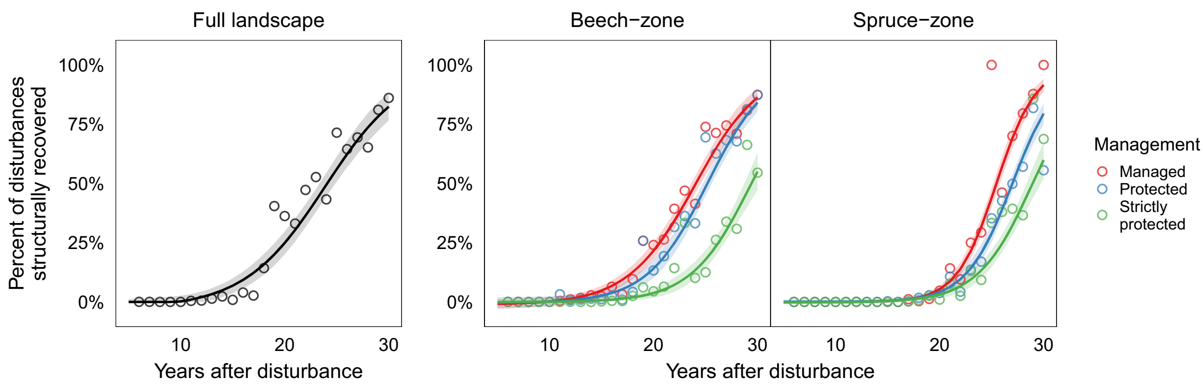

Fig. 5 Structural recovery trajectories after disturbance for the full landscape (left) as well as stratified by elevation bands and management regimes (right). Recovery is here defined as reaching a minimum tree cover of 40% and a minimum stand height of 5 m. The ribbons indicate the 95% prediction interval

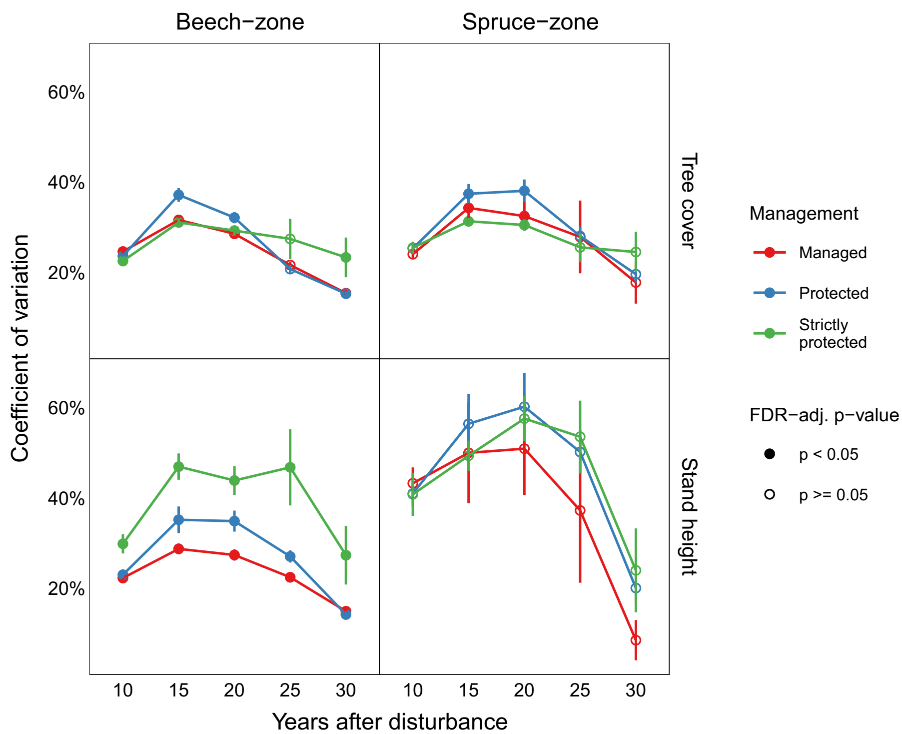

Fig. 6 Variability in tree cover and stand height in five-year time-steps after disturbance. Variability is expressed as the coefficient of variation in a 2.25 ha forest patch (i.e., five times five Landsat pixels). Error bars indicate the 95% confidence interval. Shape of the dots indicate whether there were significant ($p < 0.05$) differences after FDR-correction

Discussion

Differences in structural recovery rates

Our results underline the high potential of Central European forests to recover from recent disturbance events, with 84 (79–88) % of the disturbed area exceeding 40% tree cover and 5 m stand height after 30 years. These rates are in the same order of magnitude as those found for other temperate forest ecosystems recovering from large, severe natural disturbance events (e.g., recovery after the Yellowstone fire, see Turner et al. (2016)). The speed of recovery differed substantially between managed and un-managed forests, meeting our expectations of faster recovery in managed forests. The faster recovery in managed forests can most likely be attributed to planned canopy openings via silvicultural interventions (resulting in advanced regeneration) and planting on disturbed sites, both facilitating a rapid and successful recovery. Yet, while slower in their recovery, forests also recovered from disturbance in the absence of any human intervention. Our results at the landscape scale are thus in line with local field-based evidence of high regeneration success following natural disturbances (Svoboda et al. 2010; Nováková and Edwards-Jonášová 2015; Zeppenfeld et al. 2015). Central European forests ecosystems are thus highly resilient to recent disturbance events. The future resilience of forests, however, remains an open question to be addressed in future work. Climate change has the potential to reduce resilience, causing larger disturbed areas and thus longer distances to seed source, while regenerating trees could increasingly suffer from extreme climatic events (Hansen et al. 2018; Johnstone et al. 2016).

It is important to note that we here only addressed one component of forest recovery, namely recovery in stand structure. While tree cover and stand height are important indicators of forest recovery that can be readily assessed over large areas (Bolton et al. 2013, 2015, 2017), other important indicators of recovery exist (Trumbore et al. 2015; Seidl et al. 2016c). For example, we did not assess floristic indicators here, yet tree species composition has been generally found to recover more slowly from disturbances than forest structure (Seidl et al. 2014a). However, for our study system there is strong evidence that recent disturbances have not changed species composition (Svoboda et al. 2010; Nováková and Edwards-Jonášová 2015; Zeppenfeld et al. 2015; Macek et al. 2017). Also, non-native tree species are of limited concern in our study system, as managers typically plant fast-growing and economically valuable native tree species such as Norway spruce.

Differences in variability in tree cover and stand height

We found slightly higher structural variability in un-managed forests, especially > 25 years post-disturbance. This finding is well in line with theoretical considerations suggesting that initial variability in recovery and pre-disturbance structural legacies lead to high structural diversity already in early stages of forest development (Donato et al. 2012; Bace et al. 2015), which can persist throughout stand development (Braziunas et al. 2018; Meigs et al. 2017). Especially the higher variability in stand heights for beech-dominated forests suggests the development of a more diverse canopy structure in unmanaged forests compared to managed forests. The slightly higher variability in tree cover found here further suggests that un-managed forests have a more irregular spacing and a higher fraction of gaps. However, differences in structural diversity were less obvious in forests characterized by only a single species that is in the spruce-zone. Our results thus highlight the concurrent importance of species diversity, in addition to structural diversity.

While a higher structural variability in un-managed forests likely means a reduced primary productivity (Bohn and Huth 2017; Zeller et al. 2018), it favors habitat diversity and thus is beneficial for biodiversity (Hilmers et al. 2018; Donato et al. 2012). Specifically, the diverse structures emerging after natural disturbances in unmanaged forests have recently been shown to harbor equal levels of plant and animal diversity as old-growth forest systems (Hilmers et al. 2018). Furthermore, a more diverse and patchy recovery—as shown for beech-dominated forests here—will benefit light-demanding early-seral species (Swanson et al. 2011; Lehnert et al. 2013) and could prevent the formation of homogeneous and species-poor pole-stage stands. In addition to benefiting biodiversity, variable recovery trajectories can also increase the future resilience of the system (Seidl et al. 2016a). As the primary species regenerating in our system is spruce (Svoboda et al. 2010; Zeppenfeld et al. 2015; Macek et al. 2017), the future risk for large-scale outbreaks of the European spruce bark beetle (*Ips typographus* L.) is high. Variability in recovery could prevent the synchronous exceedance of tree-size related susceptibility thresholds (Raffa et al. 2008; Seidl et al. 2016b), thus increasing the future stability of the system. However, as we found differences in structural diversity to be less distinct in areas dominated by spruce, further research is needed to test this hypothesis.

Methodological considerations

We here showed that Landsat time series—in conjunction with airborne Lidar data—can be successfully utilized for mapping post-disturbance tree cover and stand height in Central European forests. Yet, prediction accuracies were lower than those reported for landscapes in North America (Pflugmacher et al. 2012; Ahmed et al. 2015; Vogeler et al. 2018), especially for tree height. Differences might be explained by the higher spatial complexity of disturbances in our landscape (i.e., many mixed pixels containing disturbed and undisturbed areas due to the fine grain of the prevailing disturbance regime; Senf et al. 2017). We also note that most of the disturbances happened relatively recently (median time since disturbance: 11 years), leading to an overall low central tendency and variance in both tree cover and stand height, and thus a relatively high relative predictive error (Fig. 3). A further limitation lies in the fact that the Lidar data available for the current analysis was not evenly distributed across the three management regimes. While the uncertainties in our models might thus be higher than those obtained from terrestrial inventories, our approach—for the first time—allowed for a landscape-scale mapping of forest recovery for the Bohemian Forest. As such, Landsat—in combination with auxiliary Lidar data—is a promising tool for complementing existing data from field studies and modelling.

Conclusions and management implications

Our results have important implications for foresters and conservation managers. We here provide quantitative evidence that forest management did indeed facilitate the structural recovery of forests over unmanaged conditions. This indicates that targeted management activities such as planting and fostering advanced regeneration might increase forest resilience to disturbances. At the same time, however, active management also tended to decrease the structural heterogeneity in the recovering forest, which has the potential to erode the future resilience of the system. This underlines that new management responses to disturbance are needed that maintain resilience, both in the short- and long-term. In the context of protected area management, we here show that natural disturbances—while killing trees—do not kill the forest, and that forests of Central Europe are well able to recover naturally from such large and severe disturbance events. Salvage harvesting and sanitation cutting in the buffer zones of protected areas did not significantly impede structural recovery, but showed a tendency to reduce structural variability in at least one of the two studied forest types. The increased diversity in naturally recovering forests is likely benefiting biodiversity, and thus contributing to the specific management objectives in protected areas. In conclusion, our analysis provides quantitative evidence for a high resilience of the forests of Central Europe to recent natural disturbance events.

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Appendix

See Fig. 7.

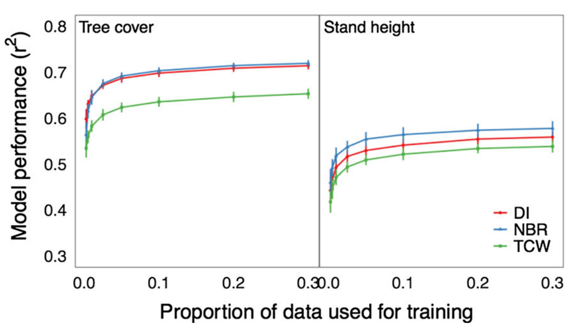

Fig. 7 Comparison of several sample sizes and the three spectral indices for predicting post-disturbance tree cover and stand height derived from Lidar data. Error bars indicate the 95% confidence interval derived from repeating the model calibration/validation 30 times

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