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Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe

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Abstract

Natural disturbance regimes are changing substantially in forests around the globe. However, large-scale disturbance change is modulated by a considerable spatiotemporal variation within biomes. This variation remains incompletely understood particularly in the temperate forests of Europe, for which consistent large-scale disturbance information is lacking. Here, our aim was to quantify the spatiotemporal patterns of forest disturbances across temperate forest landscapes in Europe using remote sensing data and determine their underlying drivers. Specifically, we tested two hypotheses: (1) Topography determines the spatial patterns of disturbance, and (2) climatic extremes synchronize natural disturbances across the biome. We used novel Landsat-based maps of forest disturbances 1986–2016 in combination with landscape analysis to compare spatial disturbance patterns across five unmanaged forest landscapes with varying topographic complexity. Furthermore, we analyzed annual estimates of disturbances for synchronies and tested the influence of climatic extremes on temporal disturbance patterns. Spatial variation in disturbance patterns was substantial across temperate forest landscapes. With increasing topographic complexity, natural disturbance patches were smaller, more complex in shape, more dispersed, and affected a smaller portion of the landscape. Temporal disturbance patterns, however, were strongly synchronized across all landscapes, with three distinct waves of high disturbance activity between 1986 and 2016. All three waves followed years of pronounced drought and high peak wind speeds. Natural disturbances in temperate forest landscapes of Europe are thus spatially diverse but temporally synchronized. We conclude that the ecological effect of natural disturbances (i.e., whether they are homogenizing a landscape or increasing its heterogeneity) is strongly determined by the topographic template. Furthermore, as the strong biome-wide synchronization of disturbances was closely linked to climatic extremes, large-scale disturbance episodes are likely in Europe's temperate forests under climate changes.

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1 Introduction

Natural disturbances strongly affect carbon sequestration (Seidl, Schelhaas, Rammer, & Verkerk, 2014), ecosystem services (Thom & Seidl, 2016), and economic value of forests (Dale et al., 2001). They further support resilience through fostering biodiversity and increasing the heterogeneity of ecosystems (Turner, 2010). Natural disturbances are thus of central importance for major challenges of forest ecosystem management, from the mitigation of climate change to the sustainable provisioning of ecosystem services and the conservation of global biodiversity.

Forest disturbances have increased across the temperate forest biome in recent decades (Cohen et al., 2016; Schelhaas, Nabuurs, & Schuck, 2003), and there is evidence that both climate change and forest management have contributed to the observed increase in forest disturbances (Raffa et al., 2008; Seidl, Schelhaas, & Lexer, 2011). As climate change is expected to further facilitate disturbance activity, there is growing concern that future disturbance dynamics will exceed tipping points and cause critical transitions of ecosystems, such as a shift from forests to nonforest areas, or a significant change in the tree species characterizing a system (Millar & Stephenson, 2015; Seidl et al., 2017). Wind and bark beetles are the primary agents of natural disturbance in the temperate forest biome of Europe (Kulakowski et al., 2017; Seidl et al., 2014). Wind disturbances include the uprooting of trees, as well as stem breakage as a result of strong winds during local downbursts, intense low-pressure systems, or topographically induced *foehn* winds (Gardiner et al., 2008). Bark beetle disturbances result from insect-induced tree mortality by beetles of the subfamily *Scolytidae*, of which the European spruce bark beetle (*Ips typographus* L.) is the ecologically and economically most important species in Europe (Kautz, Meddens, Hall, & Arneth, 2017; Müller, Bußler, Goßner, Rettelbach, & Duelli, 2008). Together, wind and bark beetles damaged, on average, 30.2 Mill. m³ of timber per year in the temperate forests of Europe between 1971 and 2010 (Seidl et al., 2014).

Wind and bark beetle disturbances are sensitive to climate variability. The occurrence of wind disturbances is largely driven by intense storm events, with storm duration, maximum gust speed, and preceding precipitation being the major factors determining disturbance severity (Mitchell, 2013). Climate variability also influences the multivoltine life cycle of bark beetles (Baier, Pennerstorfer, & Schopf, 2007) and affects host colonization and defense (Netherer et al., 2015). Hence, climate is a driving force behind bark beetle population dynamics (Marini et al., 2017). Climate-mediated amplifying feedbacks in the insect-host system are particularly important due to an increasing risk of “hotter droughts” in the future (Allen, Breshears, & McDowell, 2015; Millar & Stephenson, 2015). Furthermore, wind and bark beetles strongly interact with each other through increased reproduction success of bark beetles in wind-felled trees (Stadelmann, Bugmann, Wermelinger, & Bigler,

2014). Such interactions can further amplify disturbance dynamics under changing climate conditions (Seidl & Rammer, 2017).

Despite their social and ecological importance and their high climate sensitivity, our knowledge on the spatiotemporal patterns of natural disturbances in the temperate forests of Europe is still limited, compared to, for instance, the forests of North America (Hicke et al., 2012; Meddens, Hicke, & Ferguson, 2012). Centuries of intensive human use mask natural processes in the temperate forests of Europe, and management responses to disturbances often alter their spatiotemporal patterns (Senf, Pflugmacher, Hostert, & Seidl, 2017). Furthermore, the long tradition of European disturbance research has largely focused on detailed studies at the local scale (Kautz, Dworschak, Gruppe, & Schopf, 2011; Mezei et al., 2017; Overbeck & Schmidt, 2012). Yet, recent analyses from other continents suggest that natural disturbance regimes in forests can be synchronized over large geographic extents (Aukema et al., 2006; Jarvis & Kulakowski, 2015). It remains unclear whether synchronization is the case also across temperate forests of Europe, and if so, which factors are able to trigger synchronization at large spatial scales.

In addition to the temporal patterns of disturbance, also their large-scale spatial patterns remain incompletely understood, as the few existing comparative studies in Europe (Marini et al., 2017) use widely differing data sources that do not allow a stringent analysis and attribution of differences in spatial patterns. More generally, a significant gap in data that is systematic and comprehensive in both space and time has hitherto limited our understanding of the biomescale dynamics of forest disturbance (Kautz et al., 2017). However, recent advances in disturbance detection from remote sensing now allow new insights into forest disturbances at the scale of biomes and continents (Banskota et al., 2014).

We here systematically investigate spatiotemporal patterns of natural disturbances and their underlying drivers in the temperate forests of Europe. To consistently address the patterns and processes related to natural disturbances, and exclude the influence of human activity, we focused our analysis on strictly protected landscapes spanning a wide range of ecological conditions in the temperate zone of Europe. Specifically, we used novel Landsat-based maps of forest disturbance (1986–2016) to test the following two hypotheses: (1) Topography is a major driver of biome-wide variability in spatial disturbance patterns, and (2) Climatic extremes synchronize disturbance activity across the temperate forests of Europe.

2 Materials and Methods

2.1 Study sites and disturbance data

In order to exclude confounding effects of forest management, our study focusses on five protected forest landscapes in Austria, the Czech Republic, Germany, and Slovakia (Figure 1a). All landscapes consist of the strictly protected core zones of National Parks (Figure 1b and Table 1), and span a wide gradient of elevations and ecological conditions. The landscapes thus represent a variety of common forest types of the temperate forest biome of Europe (EEA, 2006). Lower elevation areas are characterized by Central European and Carpathian submountainous beech forest types, dominated by European beech (*Fagus sylvatica* L.). Low elevation beech forests transition into Central European and Carpathian

mountainous beech forests at elevations higher than approximately 800 m a.s.l (dominated by *F. sylvatica*, Norway spruce [*Picea abies* (L.) Karst.], and silver fir [*Abies alba* Mill.]). Regions above roughly 1,200 m a.s.l. are characterized by subalpine and mountainous coniferous forests, which are dominated by Norway spruce and silver fir; and European larch (*Larix decidua* Mill.) forests. The tree line (approximately at 1,800 m a.s.l., but varying throughout the region) is characterized by a *krummholz* belt of mountain pine (*Pinus mugo* Turra).

In addition to covering all major temperate forest types of Europe (with the exception of oak [*Quercus* spp.] dominated forests, for which no large unmanaged landscapes exist) the five landscapes span a gradient in topographic complexity (Figure 1c). The Bohemian Forest and Harz sites present low mountain ranges and highland landscapes, which are typically found throughout Central Europe (*Mittelgebirge*). They are characterized by gentle topography, with the highest peaks not extending above 1,500 m, and often small-scale gradients in elevation, resulting in a generally low complexity of the terrain (Table 1). On the other end of the spectrum are the Kalkalpen and Berchtesgaden landscapes, both characterized by high peaks extending into the alpine zone (>2,000 m). Both landscapes exhibit large gradients in elevation, and have high terrain complexity (Table 1). The Tatra landscape is inbetween the low mountain and alpine landscapes, as it is located at a relatively high elevation, but is characterized by gentler topography, resulting in overall intermediate terrain complexity (Table 1).

We used novel maps of annual stand-replacing forest disturbances generated from Landsat data (Senf, Pflugmacher et al. 2017) (Figure 1d). The maps are based on the analysis of all available Landsat images and indicate stand-replacing forest disturbances, which were defined as a residual tree cover of less than 50%. Hence, the maps only depict events that substantially impacted forest structure, with non-stand-replacing disturbances such as defoliation or the breakage of individual stems not considered in this study. The disturbance maps were generated at 30 m spatial grain and had overall accuracies (compared to photo-interpreted reference plots) of more than 85%. Disturbance patches smaller than five pixels were omitted to reduce false positives in disturbance detection. The minimum mapping unit is thus 0.5 ha. The disturbance year was also estimated from the Landsat time series, with 80% of the disturbances being estimated within ± 1 year of a reference year obtained from visual image interpretation. No attribution of disturbances to specific agents was conducted, but contextual knowledge of the sites from local field studies suggests that the vast majority of disturbances resulted from either wind or *Ips typographus* infestation. As these two disturbance agents are often difficult to separate at the pixel level using Landsat data (Oeser, Pflugmacher, Senf, Heurich, & Hostert, 2017), we decided to conduct our analyses of spatiotemporal patterns at the level of the disturbance regime, that is jointly addressing wind and bark beetle disturbance. For details on detecting disturbances in European temperate forests from Landsat see Senf, Pflugmacher, et al. (2017).

2.2 Spatial pattern analysis

In order to test our first hypothesis, we utilized landscape pattern analysis. We quantified spatial patch characteristics using two patch-scale and two landscape-scale metrics (Table 2):

(1) area-weighted mean patch size (in the following abbreviated to patch size), (2) area-weighted mean perimeter-area-ratio (in the following abbreviated to patch complexity), (3) probability of adjacent patches (in the following abbreviated to patch aggregation), and (4) the percent of the landscape disturbed (O'Neill et al., 1988). To better characterize differences in spatial disturbance pattern between years of low vs. high disturbance activity, we classified the years into low/high disturbance activity years using the time series median of each landscape as threshold (see Fig. S2). Landscape metrics were subsequently calculated for each subset over the complete study period (1986–2016). For the landscape-scale metrics, we used within site resampling to quantify uncertainties (Coops et al., 2010). To that end, we randomly sampled 100 sub-landscapes representing approximately the dispersal range of *Ips typographus* (500 m radius; Kautz et al. (2011)), and repeatedly calculated landscape metrics within each sub-landscape. For comparison of the patch- and landscape-scale metrics among sites and disturbance activity classes, we used linear models (LM), except for patch area and percent of landscape disturbed, where generalized linear models (GLM) with Gamma distribution and log-link function were used.

2.3 Temporal pattern analysis

In order to test our second hypothesis, we first investigated the synchrony of temporal disturbance dynamics across sites. For doing so, we created time series of annual disturbance area for each landscape, and standardized the time series via dividing it by its standard deviation. Subsequently, we combined all five time series by calculating their mean. If the time series exhibit no synchrony, we would expect to find no distinct temporal pattern in this standardized mean across landscapes (i.e., the temporal dynamics of the individual time series would be expected to cancel each other out). If the time series exhibit synchrony, we would expect a temporal pattern emerging from the combination of the individual standardized time series. Finally, to account for potential errors in the disturbance year estimate and in order to increase signal-to-noise ratio, we applied a 3-year moving average filter.

We tested data on drought and storm variability as potential climate drivers of disturbance synchrony. For quantifying drought variability, we used time series of monthly Standardized Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano, Begueria, and Lopez-Moreno (2010)). The SPEI takes into account both precipitation and evapotranspiration, with the latter being estimated from monthly mean temperature time series following Thornthwaite (1948). Hence, the SPEI index includes variability in precipitation and temperature, which both were found important for bark beetle dynamics in previous research (Marini et al., 2017). For calculating monthly SPEI time series for each landscape, we used precipitation and temperature data from the E-OBS European high-resolution gridded data set (Hofstra, Haylock, New, & Jones, 2009). For one landscape (Tatra), we observed that no precipitation data was available after 2005. We gap-filled the missing data points using information from 84 climate stations located in a buffer of 250 km around the center location of the landscape. One advantage of the SPEI index is that it incorporates past observations in order to reflect the memory of ecosystems to past drought conditions (Vicente-Serrano et al., 2010). We here used a time scale of 36 months to identify multiyear, regional- to continental-scale drought patterns instead of year-to-year variation in precipitation and

temperature (see Figs S3 and S4). Subsequently, we averaged the individual SPEI time series to obtain an indicator of synchrony in drought across landscapes, and aggregated the monthly values to annual values using the arithmetic mean. Finally, as the time series were trend-stationary (Kwiatkowski-Phillips-Schmidt-Shin (KPSS) test; KPSS trend = 0.04, truncation lag parameter = 1, p -value >.1), we removed the trend using linear regression in order to prevent the detection of spurious correlations between time series (see Fig. S5).

For quantifying storm activity, we used time series of daily maximum windspeed acquired from climate stations in a buffer of 250 km around the center location of each landscape. Climate station data were obtained from the Global Surface Summary of the Day (GSOD) database (Smith, Lott, & Vose, 2011). The number of available climate stations varied between 84 (Tatra) and 279 (Kalkalpen). From these daily time series, we calculated yearly maxima, standardized them using z -scores, and averaged the standardized annual time series across landscapes (see Fig. S6). As the resulting time series of the average standardized maximum windspeed was also trend-stationary (KPSS trend = 0.07, truncation lag parameter = 1, p -value >.1), we similarly removed the trend using linear regression (see Fig. S7).

Since there might be varying lag effects between remote sensing based estimates of disturbance activity and drought/storm variability (Seidl, Muller et al., 2016), we used a modeling approach loosely based on distributed lag models (Baltagi, 2008). In principal, our model is based on a linear relationship between the change in standardized disturbance area

($Y'_t = Y_t - Y_{t-1}$; see Fig. S8) and drought/storm activity: $Y'_t = \beta_0 + \beta_1 * x_t$. To account for varying lags between drought/storm activity and disturbance, we added a lag component to

the linear model: $Y'_t = \beta_0 + \beta_1 * x_{t-l}$, with l being the lag distance (i.e., a $l = 1$ means a relationship between drought/storm index values from the previous year are related to current year disturbance estimates). However, disturbance dynamics might not only be influenced by one specific lag, but by several preceding years (e.g., due to cumulative drought effects or several storm events). We hence include a weighted lag that takes into

account also neighboring lags: $Y'_t = \beta_0 + \beta_1 * \left(\sum_{i=-\lfloor s/2 \rfloor}^{\lfloor s/2 \rfloor} w * x_{(t-1)+i} \right)$. Given equal weights ($w = 1/n_s$), this formulation presents a moving average with width s of the lagged drought/storm index values. To identify the best combination of l and s , we applied a heuristic grid-search that compares varying lag distances and window widths using the Akaike Information Criteria corrected for small sample sizes (AICc). The values tested were $l = \{1, 2, 3, 4, 5, 6, 7, 8\}$ and $s = \{1, 3, 5, 7, 9\}$. As we identified temporally auto-correlated residuals during initial model fitting, we used a generalized least squares (GLS) estimator with a first-order autoregressive process (AR(1)) as estimation technique (Korner-Nievergelt et al., 2015).

3 Results

3.1 Spatial patterns of natural disturbances in across temperate forest landscapes in Europe

The landscapes showed substantial differences in their spatial patterns of disturbance (Figure 2). Patch size was significantly different between sites and high/low activity years

(Difference in deviance = -2.93 ; p -value $<.01$; Figure 2a). During high activity years, patch size decreased with increasing terrain complexity of the landscape (Figure 2a). The by far largest patch sizes were found in the Bohemian forest landscape (area-weighted mean of 3,550 ha). The Harz and Tatra landscapes showed intermediate mean patch sizes (area-weighted mean of 58 and 60 ha, respectively), while the area-weighted mean patch size was below 10 ha for both alpine sites (Kalkalpen and Berchtesgaden). During low activity years, patch sizes were generally smaller (area-weighted mean <10 ha).

Patch complexity was significantly different between sites and high/low activity years ($F_{9,5210} = 593.9$; p -value $<.01$; Figure 2b), yet differences were smaller than for patch size. In general, patch complexity increased with increasing terrain complexity. Trends were similar between low/high activity years, yet patches were generally less complex in high activity years.

Patch aggregation showed a similar pattern to patch complexity, with significant differences observed between landscapes and high/low activity years ($F_{9,532} = 77.05$; p -value $<.01$). For high activity years, there was a very high probability that two randomly chosen patches were adjacent in the Bohemian forest landscape (0.79; Figure 2c), with a lower probability for the other landscapes (0.51 [Berchtesgaden] to 0.58 [Tatra]). Hence, disturbance patches were more aggregated in landscapes of low topographic complexity, while landscapes of higher topographic complexity showed more dispersed disturbance pattern. Patch aggregation dropped to <0.41 for all landscapes during low activity years.

With increasing terrain complexity, the percentage of the landscape that was disturbed decreased significantly (Difference in deviance = -762.93 ; p -value $<.01$). While during years of high disturbance activity nearly 50% of the landscape was disturbed in the Bohemian forest, it was only 4% for the Kalkalpen and Berchtesgaden landscapes (Figure 2d).

3.2 Temporal patterns of forest disturbances across temperate forest landscapes in Europe

Disturbances were strongly synchronized across landscapes. Periods of high disturbance activity occurred at approximately decadal intervals, with three distinct waves in the late 1980s, 1990s, and 2000s (Figure 3 and Fig. S10). Furthermore, there was a marked increase in overall disturbance activity from one wave to the next, and each disturbance wave had a longer duration than the previous one.

Comparing the change in standardized disturbance area and the SPEI time series we found congruent temporal patterns between disturbance activity and drought occurrence (Figure 4a). In particular, all three waves of high disturbance activity followed dryer than average periods (i.e., 1983–1985, 1989–1995, and 2001–2004); and peaked during phases of wetter than average conditions (i.e., 1986–1988, 1996–2000, and 2005–2007). Changes in disturbance activity were best predicted by SPEI with a lag distance of 3 years and a smoothing width of 3 years (Fig. S11a). Hence, drier conditions in the 3 preceding years triggered a significant increase in disturbance activity (Figure 4b; Difference in AIC to

intercept-only model = 10.87; Likelihood-ratio = 16.60, p -value <.01; see Table S12 for estimates).

We also found a significant relationship between storm variability and disturbance activity (Figure 4c; Difference in AIC to intercept-only model = 3.79; log-likelihood-ratio = 9.75, p -value <.01; see Table S12 for estimates). The lag distance and smoothing width most supported by the data were also 3 years (Fig. S11b), being congruent with the relationship between SPEI and disturbance activity. Hence, years of high disturbance activity always followed years of above-average wind speed, indicating years of elevated windthrow risk.

4 Discussion

We here used novel Landsat-based maps of natural disturbances in temperate forests of Europe to explore spatiotemporal disturbance patterns at the biome scale. We were particularly interested if and how regional-scale climate drivers synchronize temporal disturbance dynamics, and how disturbances manifest spatially at the landscape scale. Our results show that while drought and storm activity synchronized temporal disturbance dynamics, the spatial patterns of disturbances are diverse and largely follow a gradient in topographic complexity.

We identified topographic complexity as a major factor influencing the within-biome variability in spatial patterns of natural disturbances. A higher topographic complexity can substantially increase the exposure of forest stands to wind (Mitchell, 2013), and modulates forest landscape structure and composition (Zald et al., 2016). Forest landscape structure and composition, in turn, significantly affect the spatial development of bark beetle outbreaks through connectivity (Seidl, Muller et al., 2016), and increase wind exposure through fragmentation and the creation of edges (Harper et al., 2005). Landscapes with a higher topographic complexity often show a higher degree of fragmentation, mainly due to small-scale variation in land cover (e.g., rock-outcrops). Furthermore, topographically complex landscapes often have a higher variability in tree species, resulting from a high local variation in environmental conditions (Kitagawa, Mimura, Mori, & Sakai, 2015). Hence, once a localized eruption of bark beetle is triggered (e.g., due to small-scale wind damage), the spread of those localized populations is inhibited in landscapes of higher topographic complexity, leading to a more dispersed pattern at the landscape scale (e.g., Berchtesgaden). In landscapes with lower topographic complexity—and thus lower degree of fragmentation and more homogenous species composition—localized eruptions can spread unimpeded and merge into larger disturbance patches (e.g., Bohemian forest). In addition, there are many geoclimatic barriers in alpine landscapes, such as mountain tops or (tree-less) ridges, which directly prohibit the dispersal of bark beetles. Those barriers can thus further dampen the coalescence of localized eruptions into larger disturbance patches. Finally, local topographic complexity might also directly affect bark beetle dispersal, for example, via local wind systems or microclimatic gradients (Kautz, Imron, Dworschak, & Schopf, 2016).

We here provide the first evidence that natural disturbance dynamics are synchronized at subcontinental spatial scale in the temperate forest of Europe, and show that synchronization correlated with drought and storm activity. This finding is in agreement with studies on other

bark beetle-dominated systems (Jarvis & Kulakowski, 2015). Our data suggests that regional-scale climate variability is a key factor synchronizing natural disturbance dynamics, in particular through drought and storm activity (see also Pederson et al. (2014)). Drought—here defined as the combined effect of low water availability and high temperature—directly influences the temporal dynamics of natural disturbance in Europe through controlling bark beetle population dynamics (Marini et al., 2017). In particular, hot years improve bark beetle development and survival and lead to a higher probability of the completion of a second or third generational cycle per year. Water stress additionally weakens tree defenses and increases the colonization success of bark beetles. Thus, regional-scale drought patterns can facilitate bark beetle population development across landscapes, which in turn results in a synchronized eruption of outbreaks across large areas. Furthermore, variability in storm activity directly drives disturbance dynamics by increasing the risk of wind disturbances. Increased wind disturbances trigger localized eruptions of bark beetles (Stadelmann et al., 2014), which in turn amplify climate-driven fluctuations in bark beetle populations (Seidl & Rammer, 2017). Hence, it is the combined effect of dry and hot periods with above-average storm activity that likely synchronized natural disturbance dynamics across the temperate forests of Europe.

Besides the synchronizing effect from regional-scale climate variability, there are also other factors that likely contribute to a synchronized development of natural disturbances. In Europe, forest structure could be an important factor synchronizing forest disturbances across large scales. Past forest land use has shaped current forest structure across large parts of Europe (Bebi et al., 2017; Munteanu et al., 2015), and high natural disturbance activity in the second half of the nineteenth century resulted in an aging and increasingly disturbance-prone cohort in the remaining unmanaged forests (Janda et al., 2017). However, the synchronizing effect of past disturbances and management (i.e., creating homogeneous stands of susceptible species and age cohorts) likely has a considerably longer periodicity (in the order of multiple decades to centuries) than the one identified here. Hence, past management and disturbances are unlikely to be the driver of the short-term synchronies identified here (approximate periodicity of 8 years).

Our study has important implications in the context of forest management. Based on our findings, the effect disturbances have on ecosystems—that is whether disturbances are homogenizing the landscape via large high severity disturbance patches, or rather create a mosaic of small patches and heterogeneous structures—is strongly modulated by the topographic template of a landscape. Hence, in more heterogeneous landscapes (as in the alpine landscapes in our study) disturbances further increase heterogeneity in structures. In less topographically complex landscapes (as in the lower elevation landscapes in our study), however, disturbances could homogenize forest structures at the landscape scale. A recent study on the biodiversity effects of disturbance change found generally positive effects of disturbances on biodiversity, but highlighted that exceedingly large disturbance patches could result in negative impacts on biological diversity (Thom et al., 2017). Consequently, increasing structural variability in management is particularly important in topographically less complex landscapes, and could be achieved by retaining disturbance legacies on the landscape, as well as by allowing variable recovery trajectories to form heterogeneous postdisturbance stands (Bace et al., 2015; Seidl, Donato, Raffa, & Turner, 2016).

Climate change is expected to affect forest disturbances in forest around the globe (Seidl et al., 2017). We here present evidence that changes in climatic extremes could be particularly relevant in this regard. Extreme events such as drought and storm events have long been recognized as triggers of forest disturbances (Dale et al., 2001). We here show that their influence goes significantly beyond initiating disturbances, as they have the ability to synchronize disturbance activity across subcontinental scales. Such large-scale synchronies are not only ecologically relevant but are also noteworthy in the context of forest economics, as large fluctuations in timber supply—resulting from pulses of salvaged wood after disturbance—can cause significant drops in timber prices and contribute to the substantial economic losses from forest disturbances (Gardiner et al., 2008). Future increases in extreme droughts and wind events, as expected as the consequence of climate change (Field, 2012), could thus further impact disturbance regimes and subsequently forest structure by an increased synchronization across large scales. In this regard, the congruence of high drought and storm activity identified here for the last 30 years is particularly noteworthy. Both large-scale drought and storm activity are driven by atmospheric and oceanic circulation patterns, in particular, the North Atlantic Oscillation (NAO) in the case of Europe (Donat, Leckebusch, Pinto, & Ulbrich, 2010; López-Moreno & Vicente-Serrano, 2008). Consequently, processes such as NAO (which shifted from mostly negative to mostly positive during our observation period (Visbeck, Hurrell, Polvani, & Cullen, 2001)) should receive increased attention in the context of temporal patterns of forest disturbance. More broadly, our results highlight that spatiotemporal dynamics of natural disturbances in the temperate forests of Europe are significantly affected by processes operating at large spatial scales, such as inter-biome topographic gradients and regional- to continental-scale climate variability. Our analysis thus supports the recently emerging insight (Raffa et al., 2008; Seidl, Muller et al., 2016; Senf, Campbell, Pflugmacher, Wulder, & Hostert, 2017) that understanding the spatiotemporal dynamics of natural disturbances (and their response to a changing climate) does not only require a solid understanding of processes at the tree- to stand-scale, but also necessitates the consideration of landscape- to biome-scale processes.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

- Allen CD, Breshears DD, McDowell NG. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*. 2015; 6(8) art129. doi: 10.1890/Es15-00203.1
- Aukema BH, Carroll AL, Zhu J, Raffa KF, Sickley TA, Taylor SW. Landscape level analysis of mountain pine beetle in British Columbia, Canada: Spatiotemporal development and spatial synchrony within the present outbreak. *Ecography*. 2006; 29(3):427–441. DOI: 10.1111/j.2006.0906-7590.04445.x
- Bace R, Svoboda M, Janda P, Morrissey RC, Wild J, Clear JL, et al. Donato DC. Legacy of pre-disturbance spatial pattern determines early structural diversity following severe disturbance in Montane spruce forests. *PLoS ONE*. 2015; 10(9):e0139214. doi: 10.1371/journal.pone.0139214 [PubMed: 26421726]
- Baier P, Pennerstorfer J, Schopf A. PHENIPS – A comprehensive phenology model of *Ips typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. *Forest Ecology and Management*. 2007; 249(3):171–186. DOI: 10.1016/j.foreco.2007.05.020
- Baltagi, BH. Distributed lags and dynamic models. *Econometrics*. Baltagi, BH., editor. Berlin, Heidelberg: Springer; 2008. p. 129-145.
- Banskota A, Kayastha N, Falkowski MJ, Wulder MA, Froese RE, White JC. Forest monitoring using Landsat time series data: A review. *Canadian Journal of Remote Sensing*. 2014; 40(5):362–384. DOI: 10.1080/07038992.2014.987376
- Bebi P, Seidl R, Motta R, Fuhr M, Firm D, Krumm F, et al. Kulakowski D. Changes of forest cover and disturbance regimes in the mountain forests of the Alps. *Forest Ecology and Management*. 2017; 388:43–56. DOI: 10.1016/j.foreco.2016.10.028 [PubMed: 28860675]
- Cohen WB, Yang ZQ, Stehman SV, Schroeder TA, Bell DM, Masek JG, et al. Meigs GW. Forest disturbance across the conterminous United States from 1985-2012: The emerging dominance of forest decline. *Forest Ecology and Management*. 2016; 360:242–252. DOI: 10.1016/j.foreco.2015.10.042
- Coops NC, Gillanders SN, Wulder MA, Gergel SE, Nelson T, Goodwin NR. Assessing changes in forest fragmentation following infestation using time series Landsat imagery. *Forest Ecology and Management*. 2010; 259(12):2355–2365. DOI: 10.1016/j.foreco.2010.03.008
- Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, et al. Wotton BM. Climate change and forest disturbances. *BioScience*. 2001; 51(9):723–734. DOI: 10.1641/0006-3568(2001)051[0723:ccafd]2.0.co;2
- Donat MG, Leckebusch GC, Pinto JG, Ulbrich U. Examination of wind storms over Central Europe with respect to circulation weather types and NAO phases. *International Journal of Climatology*. 2010; 30(9):1289–1300. DOI: 10.1002/joc.1982
- European Environmental Agency (EEA). European forest types – Categories and types for sustainable forest management reporting and policy. Copenhagen: European Environmental Agency; 2006.
- Field, CB. Managing the risks of extreme events and disasters to advance climate change adaptation: Special report of the intergovernmental panel on climate change. Cambridge: Cambridge University Press; 2012.
- Gardiner B, Byrne K, Hale S, Kamimura K, Mitchell SJ, Peltola H, Ruel JC. A review of mechanistic modelling of wind damage risk to forests. *Forestry*. 2008; 81(3):447–463. DOI: 10.1093/forestry/cpn022
- Harper KA, Macdonald SE, Burton PJ, Chen J, Broszofski KD, Saunders SC, et al. Esseen P. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*. 2005; 19(3):768–782. DOI: 10.1111/j.1523-1739.2005.00045.x
- Hicke JA, Allen CD, Desai AR, Dietze MC, Hall RJ, Hogg EH, et al. Vogelmann J. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology*. 2012; 18(1):7–34. DOI: 10.1111/j.1365-2486.2011.02543.x
- Hofstra N, Haylock M, New M, Jones PD. Testing E-OBS European high-resolution gridded data set of daily precipitation and surface temperature. *Journal of Geophysical Research: Atmospheres*. 2009; 114(D21):1–16. DOI: 10.1029/2009JD011799

- Janda P, Trotsiuk V, Mikolas M, Bace R, Nagel TA, Seidl R, et al. Syoboda M. The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. *Forest Ecology and Management*. 2017; 388:67–78. DOI: 10.1016/j.foreco.2016.08.014 [PubMed: 28860676]
- Jarvis DS, Kulakowski D. Long-term history and synchrony of mountain pine beetle outbreaks in lodgepole pine forests. *Journal of Biogeography*. 2015; 42(6):1029–1039. DOI: 10.1111/jbi.12489
- Kautz M, Dworschak K, Gruppe A, Schopf R. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. *Forest Ecology and Management*. 2011; 262(4):598–608. DOI: 10.1016/j.foreco.2011.04.023
- Kautz M, Imron MA, Dworschak K, Schopf R. Dispersal variability and associated population-level consequences in tree-killing bark beetles. *Movement Ecology*. 2016; 4:9.doi: 10.1186/s40462-016-0074-9 [PubMed: 27087978]
- Kautz M, Meddens AJH, Hall RJ, Arneith A. Biotic disturbances in Northern Hemisphere forests – A synthesis of recent data, uncertainties and implications for forest monitoring and modelling. *Global Ecology and Biogeography*. 2017; 26(5):533–552. DOI: 10.1111/geb.12558
- Kitagawa R, Mimura M, Mori AS, Sakai A. Topographic patterns in the phylogenetic structure of temperate forests on steep mountainous terrain. *AoB Plants*. 2015; 7:1–12. DOI: 10.1093/aobpla/plv134
- Korner-Nievergelt, F. Chapter 6 – Assessing model assumptions: Residual analysis. Bayesian data analysis in ecology using linear models with R, BUGS, and STAN. Korner-Nievergelt, F.Roth, T.von Felten, S.Guélat, J.Almasi, B., Korner-Nievergelt, P., editors. Boston, MA: Academic Press; 2015. p. 75-94.
- Kulakowski D, Seidl R, Holeksa J, Kuuluvainen T, Nagel TA, Panayotov M, et al. Bebi P. A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. *Forest Ecology and Management*. 2017; 388:120–131. DOI: 10.1016/j.foreco.2016.07.037 [PubMed: 28860677]
- López-Moreno JI, Vicente-Serrano SM. Positive and negative phases of the wintertime North Atlantic oscillation and drought occurrence over Europe: A multitemporal-scale approach. *Journal of Climate*. 2008; 21(6):1220–1243. DOI: 10.1175/2007jcli1739.1
- Marini L, Økland B, Jönsson AM, Bentz B, Carroll A, Forster B, et al. Schroeder M. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography*. 2017; doi: 10.1111/ecog.02769
- Meddens AJ, Hicke JA, Ferguson CA. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications*. 2012; 22(7):1876–1891. DOI: 10.1890/11-1785.1 [PubMed: 23210306]
- Mezei P, Jakus R, Pennerstorfer J, Havasova M, Skvarenina J, Ferencik J, et al. Netherer S. Storms, temperature maxima and the Eurasian spruce bark beetle *Ips typographus*-An infernal trio in Norway spruce forests of the Central European High Tatra Mountains. *Agricultural and Forest Meteorology*. 2017; 242:85–95. DOI: 10.1016/j.agrformet.2017.04.004
- Millar CI, Stephenson NL. Temperate forest health in an era of emerging megadisturbances. *Science*. 2015; 349(6250):823–826. [PubMed: 26293954]
- Mitchell SJ. Wind as a natural disturbance agent in forests: A synthesis. *Forestry*. 2013; 86(2):147–157. DOI: 10.1093/forestry/cps058
- Müller J, Bußler H, Goßner M, Rettelbach T, Duelli P. The European spruce bark beetle *Ips typographus* in a national park: From pest to keystone species. *Biodiversity and Conservation*. 2008; 17(12):2979–3001. DOI: 10.1007/s10531-008-9409-1
- Munteanu C, Kuemmerle T, Keuler NS, Muller D, Balazs P, Dobosz M, et al. Radeloff VC. Legacies of 19th century land use shape contemporary forest cover. *Global Environmental Change-Human and Policy Dimensions*. 2015; 34:83–94. DOI: 10.1016/j.gloenvcha.2015.06.015
- Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, et al. Schopf A. Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist*. 2015; 205(3):1128–1141. DOI: 10.1111/nph.13166 [PubMed: 25417785]

- Oeser J, Pflugmacher D, Senf C, Heurich M, Hostert P. Using intra-annual Landsat time series for attributing forest disturbance agents in Central Europe. *Forests*. 2017; 8(7):251. doi: 10.3390/f8070251
- O'Neill RV, Krummel JR, Gardner RH, Sugihara G, Jackson B, DeAngelis DL, et al. Graham RL. Indices of landscape pattern. *Landscape Ecology*. 1988; 1(3):153–162. DOI: 10.1007/Bf00162741
- Overbeck M, Schmidt M. Modelling infestation risk of Norway spruce by *Ips typographus* (L.) in the Lower Saxon Harz Mountains (Germany). *Forest Ecology and Management*. 2012; 266:115–125. DOI: 10.1016/j.foreco.2011.11.011
- Pederson N, Dyer JM, McEwan RW, Hessel AE, Mock CJ, Orwig DA, et al. Cook BI. The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs*. 2014; 84(4):599–620. DOI: 10.1890/13-1025.1
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience*. 2008; 58(6):501–517. DOI: 10.1641/B580607
- Riley SJ. Index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*. 1999; 5(1–4):23–27.
- Schelhaas MJ, Nabuurs GJ, Schuck A. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*. 2003; 9(11):1620–1633. DOI: 10.1046/j.1529-8817.2003.00684.x
- Seidl R, Donato DC, Raffa KF, Turner MG. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. *Proceedings of the National Academy of Sciences of the United States of America*. 2016; 113(46):13075–13080. DOI: 10.1073/pnas.1615263113 [PubMed: 27821739]
- Seidl R, Muller J, Hothorn T, Bassler C, Heurich M, Kautz M. Small beetle, large-scale drivers: How regional and landscape factors affect outbreaks of the European spruce bark beetle. *Journal of Applied Ecology*. 2016; 53(2):530–540. DOI: 10.1111/1365-2664.12540
- Seidl R, Rammer W. Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. *Landscape Ecology*. 2017; 32:1385–1498. DOI: 10.1007/s10980-016-0396-4
- Seidl R, Schelhaas MJ, Lexer MJ. Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Global Change Biology*. 2011; 17(9):2842–2852. DOI: 10.1111/j.1365-2486.2011.02452.x
- Seidl R, Schelhaas MJ, Rammer W, Verkerk PJ. Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*. 2014; 4(9):806–810. DOI: 10.1038/nclimate2318
- Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, et al. Reyer CPO. Forest disturbances under climate change. *Nature Climate Change*. 2017; 7(6):395–402. DOI: 10.1038/nclimate3303
- Senf C, Campbell EM, Pflugmacher D, Wulder MA, Hostert P. A multi-scale analysis of western spruce budworm outbreak dynamics. *Landscape Ecology*. 2017; 32(3):501–514. DOI: 10.1007/s10980-016-0460-0
- Senf C, Pflugmacher D, Hostert P, Seidl R. Using Landsat time series for characterizing forest disturbance dynamics in the coupled human and natural systems of Central Europe. *ISPRS Journal of Photogrammetry and Remote Sensing*. 2017; 130:453–463. DOI: 10.1016/j.isprsjprs.2017.07.004 [PubMed: 28860678]
- Smith A, Lott N, Vose R. The integrated surface database recent developments and partnerships. *Bulletin of the American Meteorological Society*. 2011; 92(6):704–708. DOI: 10.1175/2011bams3015.1
- Stadelmann G, Bugmann H, Wermelinger B, Bigler C. Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. *Forest Ecology and Management*. 2014; 318:167–174. DOI: 10.1016/j.foreco.2014.01.022
- Thom D, Rammer W, Dirnbock T, Muller J, Kobler J, Katzensteiner K, et al. Seidl R. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest

- landscape. *Journal of Applied Ecology*. 2017; 54(1):28–38. DOI: 10.1111/1365-2664.12644 [PubMed: 28111479]
- Thom D, Seidl R. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Review*. 2016; 91(3):760–781. DOI: 10.1111/brv.12193
- Thornthwaite CW. An approach toward a rational classification of climate. *Geographical Review*. 1948; 38(1):55–94.
- Turner MG. Disturbance and landscape dynamics in a changing world. *Ecology*. 2010; 91(10):2833–2849. DOI: 10.1890/10-0097.1 [PubMed: 21058545]
- Vicente-Serrano SM, Begueria S, Lopez-Moreno JI. A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate*. 2010; 23(7):1696–1718. DOI: 10.1175/2009jcli2909.1
- Visbeck MH, Hurrell JW, Polvani L, Cullen HM. The North Atlantic Oscillation: Past, present, and future. *Proceedings of the National Academy of Sciences of the United States of America*. 2001; 98(23):12876–12877. DOI: 10.1073/pnas.231391598 [PubMed: 11687629]
- Zald HS, Spies TA, Seidl R, Pabst RJ, Olsen KA, Steel EA. Complex mountain terrain and disturbance history drive variation in forest aboveground live carbon density in the western Oregon Cascades, USA. *Forest Ecology and Management*. 2016; 366:193–207. DOI: 10.1016/j.foreco.2016.01.036 [PubMed: 27041818]

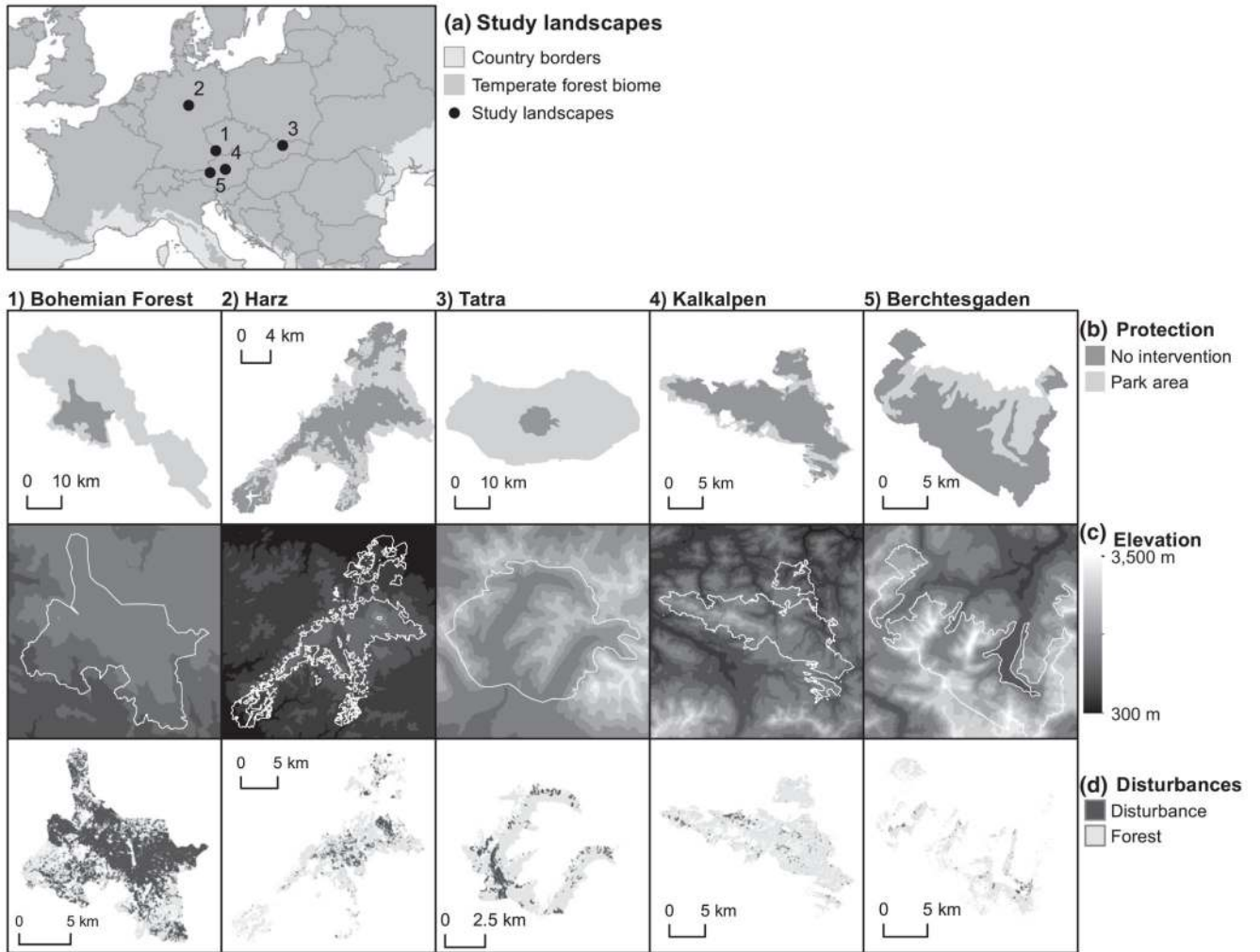


Figure 1. Study landscape location (a), protection status (b), topography (based on SRTM data) (c), and natural stand-replacing disturbances between 1986 and 2016 mapped from Landsat (d)

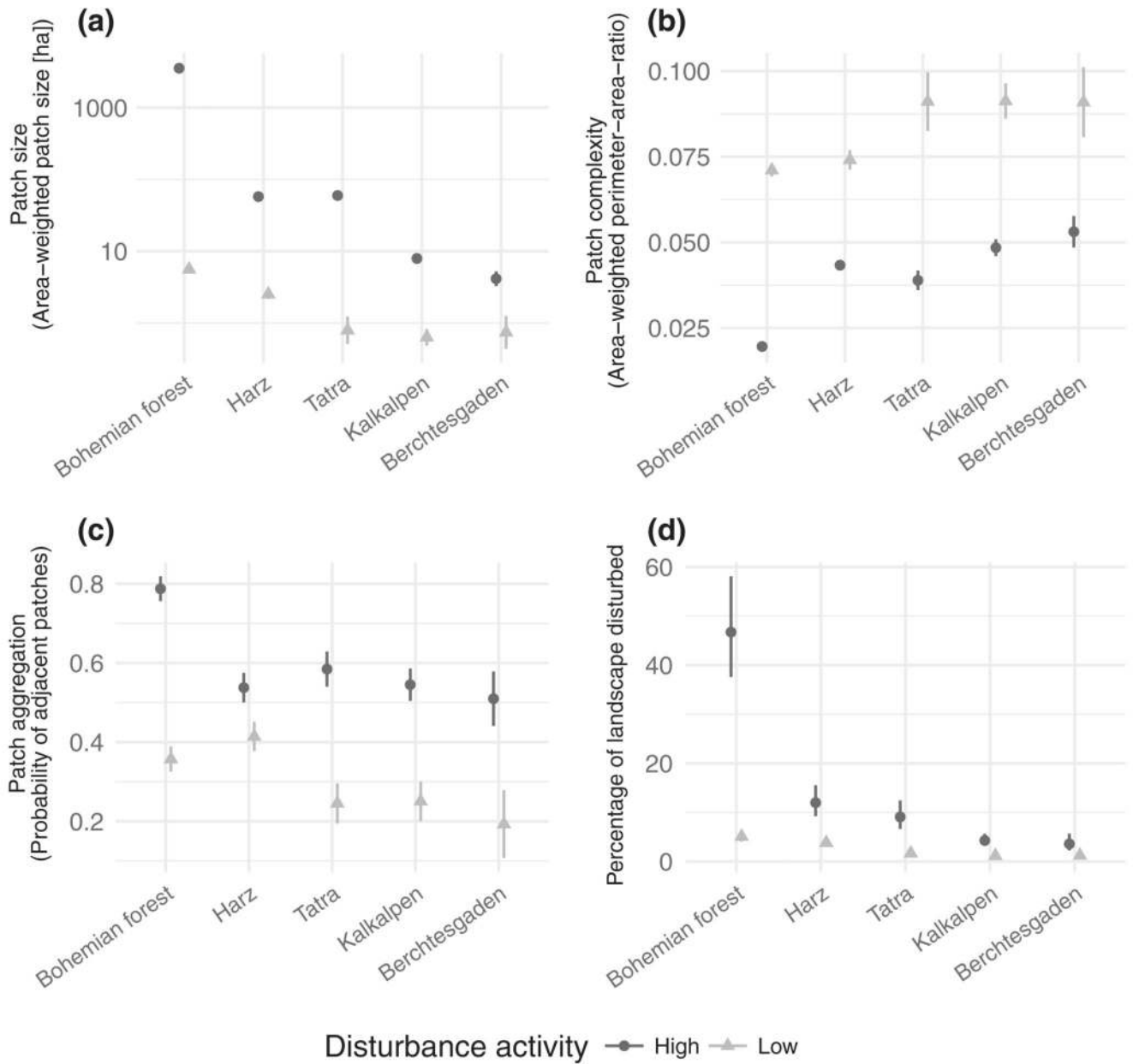


Figure 2.

Differences in landscape patterns between sites and high/low disturbance activity years. The metrics used to describe landscape pattern are (a) patch size, (b) patch complexity, (c) patch aggregation, and (d) percentage of landscape disturbed. Estimates show the mean and standard error obtained from the LM/GLM model and—for the landscape metrics (Probability of adjacent patches and Percentage of landscape disturbed)—are based on 1,000 sublandscapes randomly resampled within each landscape. Landscapes are in order of increasing terrain complexity from left to right (see Section 2.1 and Fig. S1). A statistical summary of the patch/landscape metrics is given in Table S9. For details on the patch/landscape metrics, we refer the reader to Table 2. Note that for (a) the y -axis is \log_{10} -scaled

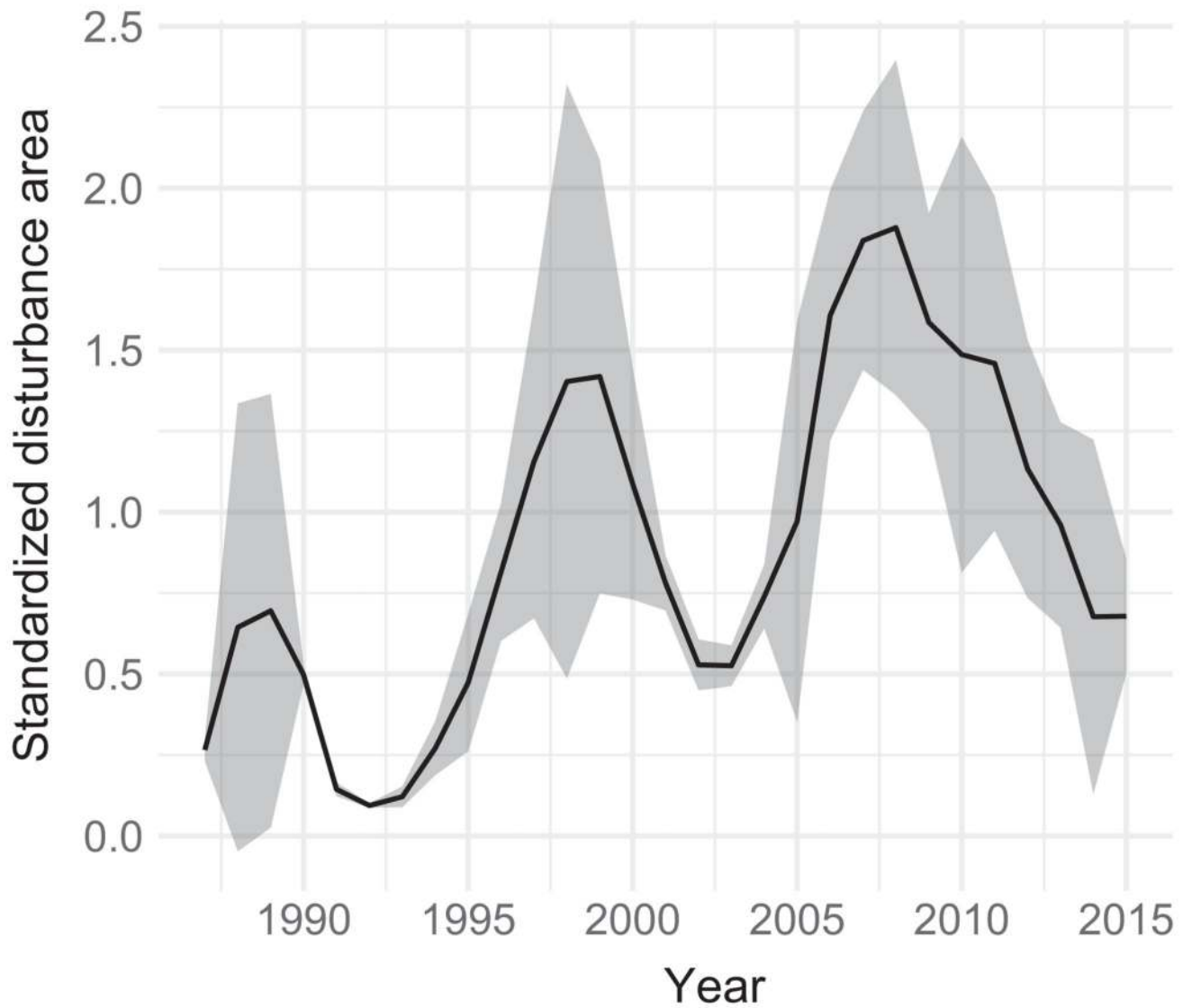


Figure 3. Synchrony in temporal disturbance dynamics across the temperate forest biome of Europe. The values shown are the mean and standard error over the standardized disturbance time series of the five different landscapes. The y -axis is given in units of standard deviation. If there would be no temporal synchrony between landscapes, the time series would be a flat line close to one. (see also Fig. S10)

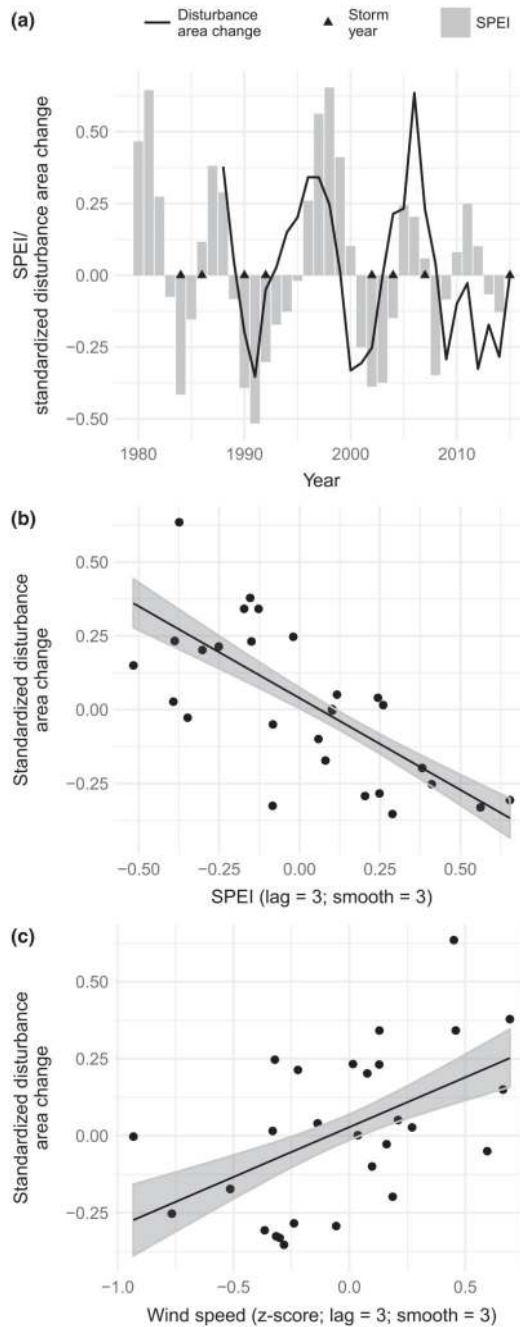


Figure 4.

(a) Temporal variability in drought and storm activity in relation to forest disturbance activity across temperate forests of Europe. Storm years are years with mean daily maximum wind speed >0.5 standard deviations above the long-term average. Low SPEI values indicate drought periods. (b) Relationship between annual drought (lag of 3 years and smoothing of 3 years) and changes in forest disturbance area as estimated from the GLS model. (c)

Relationship between annual peak wind speeds (lag of 3 years and smoothing of 3 years) and changes in forest disturbance area as estimated from the GLS model

Table 1

Summary of the study landscapes. Study sites are sorted along their mean terrain ruggedness index, that is from low to high topographic complexity

Landscape	National park	Year of establishment	Size of study landscape (no intervention area, cf. Figure 1b; km²)	Elevation range (m)	Mean (maximum) of terrain ruggedness index^a (m)	Major forest types^b
Bohemian forest	Bavarian Forest National Park (GER)/Šumava National Park (CZ)	1970 (Bavarian Forest)/1991 (Šumava)	140	737–1,439	11 (55)	Central European submountainous beech forest; Central European mountainous beech forests; Subalpine and mountainous spruce and mountainous mixed spruce-silver fir forests
Harz	Harz National Park (GER)	1990 (East-Germany)/1994 (West-Germany)	129	249–1,143	13 (61)	Central European submountainous beech forest; Central European mountainous beech forests; Subalpine and mountainous spruce and mountainous mixed spruce-silver fir forests
Tatra	High Tatra National Park (SK)	1949	65	1,001–2,044	37 (205)	Carpathian submountainous beech forest, Carpathian mountainous beech forests; Subalpine and mountainous spruce and mountainous mixed spruce-silver fir forests; Subalpine larch-arolla pine and dwarf pine forests
Kalkalpen	Kalkalpen National Park (AUT)	1997	156	394–1,933	40 (191)	Central European mountainous beech forests; Subalpine and mountainous spruce and mountainous mixed spruce-silver fir forests; Subalpine larch-arolla pine and dwarf pine forests
Berchtesgaden	Berchtesgaden National Park (GER)	1978	139	648–2,646	51 (288)	Central European mountainous beech forests; Subalpine and mountainous spruce and mountainous mixed spruce-silver fir forests; Subalpine larch-arolla pine and dwarf pine forests

^aAfter Riley (1999) using a moving window of 3×3 30 m cells obtained from the Shuttle Radar Topographic Mission (SRTM) dataset. The terrain ruggedness index expresses the mean sum changes in elevation between a focal cell and its eight neighboring cells. See also Fig. S1.

^bAfter the European Environmental Agency European forest types classification (EEA 2006).

Table 2

Landscape metrics utilized in this study

Name	Metric	Description	Unit
Patch size	Area-weighted mean patch size	The average patch size weighted by patch size	Hectare
Patch complexity	Area-weighted mean perimeter-area-ratio	The average perimeter-area-ratio weighted by patch size	Dimensionless
Patch aggregation	Probability of adjacent patches	The probability of randomly choosing two disturbance patches that are adjacent to each other	Probability
Percent of landscape disturbed	Percent of landscape disturbed	The total number of pixels disturbed between 1986 and 2016, divided by the total number of forested pixels within the landscape	Percent