Both Cyclone-induced and Convective Storms Drive Disturbance Patterns in European Primary Beech Forests

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Abstract Wind is the leading disturbance agent in European forests, and the magnitude of wind impacts on forest mortality has increased over recent decades. However, the atmospheric triggers behind severe winds in Western Europe (large-scale cyclones) differ from those in Southeastern Europe (small-scale convective instability). This geographic difference in wind drivers alters the spatial scale of resulting disturbances and potentially the sensitivity to climate change. Over the 20th century, the severity and prevalence of cyclone-induced windstorms have increased while the prevalence of atmospheric instability has decreased and thus, the trajectory of Europe-wide windthrow remains uncertain. To better predict forest sensitivity and trends of windthrow disturbance we used dendrochronological methods to reconstruct 140 years of disturbance history in beech-dominated primary forests of Central and Eastern Europe. We compared generalized linear mixed models of these disturbance time series to determine whether large-scale cyclones or small-scale convective storms were more responsible for disturbance severity while also accounting for topography and stand character variables likely to influence windthrow susceptibility. More exposed forests, forests with a longer absence of disturbance, and forests lacking recent high severity disturbance showed increased sensitivity to both wind drivers. Large-scale cyclone-induced windstorms were the main driver of disturbance severity at both the plot and stand scale (0.1–100 ha) whereas convective instability effects were more localized (0.1 ha). Though the prevalence and severity of cyclone-induced windstorms have increased over the 20th century, primary beech forests did not display an increase in the severity of windthrow observed over the same period.

Plain Language Summary Two main atmospheric patterns are driving European windthrow with large-scale winter storms being more prevalent in Western Europe and summer thunderstorm-generated winds being more prevalent in Eastern Europe. In central Europe, most forests display a mixed-severity disturbance regime indicating that both large- and small-scale disturbances are occurring. However, few studies have been conducted looking at the prevalence of large-scale winter windstorms and small-scale summer thunderstorms. Here we found evidence for both, but recently large-scale winter windstorms have had a greater impact.

1. Introduction

A total of 40% of Europe is covered with forest (182 million ha; Cook, 2019), and windthrow is directly responsible for more than 50% of damage reported in those forested areas each year (18.6 million m³ on average; Gardiner et al., 2010; Schelhaas, 2008). Furthermore, total wind-induced forest damage has increased since the early 20th century (Schelhaas et al., 2003; Seidl et al., 2017; Usbeck et al., 2010). Shifting disturbance dynamics and managerial responses to disturbance can alter habitat provisioning (Bengtsson et al., 2000; Kozák et al., 2018), regulate carbon storage (Burrascano et al., 2013; Carey et al., 2001; Harmon et al., 1990; Luyssaert et al., 2008; Seedre et al., 2020), and impact the role of forestry in the European economy (Leverkus et al., 2012; Müller et al., 2019). Thus, understanding the drivers of shifting wind disturbance patterns is needed to facilitate informed decision-making for forest and conservation management, and additionally quantify the future role of Europe's forests in global biogeochemical cycles.
Extratropical cyclones are one of two meteorological drivers of intense wind in Europe, and these cyclones can influence forest areas in excess of hundreds of km² (Brázdil et al., 2004). The temperature, pressure, and humidity gradients produced by cyclones, and their associated fronts, can induce winds in excess of 20 m/s across large affected areas (Brázdil et al., 2004). As temperature and related atmospheric humidity values have risen in Europe (Hartmann et al., 2013), fronts associated with cyclones have increased in strength (Schemm et al., 2017). These fronts have caused windstorms in Western Europe, including several recent events (e.g., storms Vivian, Lothar, and Martin) each of which disturbed more than 100 million m³ of debris (Gardiner et al., 2010). The recent increase in strength of cyclones, usually in winter, has led some researchers to suggest that cyclone-induced windstorms are increasing the frequency and severity of windthrow disturbance events (Schelhaas et al., 2003; Usbeck et al., 2010). However, although intense wind prevalence has increased (Figure 1), an increasing disturbance trend is not apparent in disturbance reconstructions from primary and old-growth forests of Central or Eastern Europe (Čada et al., 2020; Firm et al., 2009; Schurman et al., 2018; Zielonka et al., 2010).

Certain disturbance reconstructions from these forests show decreasing trends in disturbance severity over the 20th century. This could be due in part to reductions of other disturbance and mortality agents (Seidl et al., 2017). However, with the majority of European disturbance agents increasing in intensity (Seidl et al., 2017) and the fact that mountain regions of Central and Eastern Europe are subject to significant increases in the prevalence of intense wind speeds (see Figure 3 in Donat et al., 2011 and Figure 1 in this study), we would expect to see increases in disturbance severity if winds produced by cyclonic storms are drastically increasing. Thus, large-scale cyclones may not be the sole windthrow driver in Central and

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**Figure 1.** Average annual (a) wind speed and (b) convective available potential energy (CAPE) based on 20th century reanalysis data. Locations of Carpathian Mountain beech plots (the focal forests of this study) are shown as filled dots. Trends in the prevalence of extreme days per year in Carpathian beech forests plots (open dots) show (c) intense wind speed has increased and (d) severe CAPE has decreased over the 20th century. Local polynomial regression trend lines are shown in red.
Eastern Europe, or some moderator of wind (e.g. stand character and canopy roughness) may be reducing the influence of these storms.

The second major meteorological driver of intense wind in Europe is atmospheric instability, which generates strong winds through microbursts and occasionally, tornados. Despite the fact that severe convective storms are common across Europe (Taszarek et al., 2019), studies of convective storms on European forest disturbance are limited (Brázdil et al., 2018; Furtuna et al., 2018; Nagel et al., 2006, 2017). These convective storm elements can create higher speed winds than extratropical cyclones but at smaller scales and for shorter periods. For example, over the course of a few days, cyclones can elevate winds across hundreds of km²; whereas most convective storms usually only have strong winds that affect less than 1 km² over the course of ca. 1 h (Brázdil et al., 2004). Thus, to help differentiate these drivers, we refer to these phenomena in this text as “large-scale cyclones” and “small-scale convective instability”.

Throughout Europe, the temporal and regional patterns of small-scale convective instability differ from cyclones (Figure 1). Atmospheric conditions associated with strong cyclones (elevated atmospheric humidity and subsequent front strength, Schemm et al., 2017) are on the rise, whereas conditions associated with strong convective storms (high relative humidity which influences air parcel buoyancy; Del Genio et al., 2007) are decreasing in prevalence as Northern Hemisphere temperatures rise (Hartmann et al., 2013). In Southeastern Europe convective instability is more common (Furtuna et al., 2018; Nagel et al., 2017; Taszarek et al., 2019), whereas cyclones dominate in Western Europe. Despite the lower prevalence of cyclone-induced winds in Central, Southern, and Eastern Europe, windthrow is still a major disturbance agent driving forest dynamics there (Nagel et al., 2017; Sommerfeld et al., 2018; Synek et al., 2020). Disturbance reconstructions in old-growth European beech (Fagus sylvatica L.) dominated forests from Slovenia to Montenegro show that windthrow is the most prevalent disturbance agent but large-scale stand-leveling windstorms are not the norm (Furtuna et al., 2018; Nagel et al., 2017). Instead, smaller-scale windthrow events (<10 ha) are more common, and most occur during the summer suggesting that small-scale convective instability is the main driver and not large-scale cyclonic storms.

These two drivers of wind form a cline of disturbance size across Europe with large-scale disturbance being common in Western Europe (e.g., France and Germany) and smaller-scale disturbance more common in Southeastern Europe (e.g., Slovenia to Montenegro) coincident with the prevalence of intense windstorms in the west (Bett et al., 2017) and intense convective instability in the southeast (Brooks et al., 2003; Taszarek et al., 2019). Based on disturbance reconstructions from the Carpathian Mountains at the border of Central and Eastern Europe, most disturbances are smaller scale (<10 ha; Čada et al., 2020) and thus, if large-scale cyclones are driving windthrow dynamics in these forests, some moderator of wind is increasing forest resistance to large-scale disturbance. Otherwise, it may be that small-scale convective instability is at least partially responsible for the smaller disturbance patch size there, just as it is in Southeastern Europe. It should be noted, however, that most studies describing the large-scale wind disturbance in Western European forests come from commercially managed forests where forest structure and composition have been altered from a natural state, which has the potential to temporarily increase forest vulnerability to windthrow, possibly biasing disturbance events toward the severe end of the spectrum (Everham & Brokaw, 1996; Gardiner et al., 2005, 2010; Quine & Gardiner, 2007; Schelhaas et al., 2003). Thus, studies attempting to discern the relative influence of large-scale cyclones and small-scale convective instability should analyze forests that lack or control for evidence of management practices including stand thinning and lengthening of rotation periods to reduce this possible disturbance severity and scale bias.

Regardless of the relative presence of large-scale cyclones or small-scale convective instability, forest exposure and disturbance history can mediate windthrow severity. Variables influencing forest vulnerability to windthrow that can be estimated or reconstructed across the 20th century include topographic exposure (Quine & White, 1998; Senf & Seidl, 2018), and time series of forest disturbance severity and time since the last disturbance (Janda et al., 2017). Topographic exposure is a measure of shielding based on a virtual horizon angle at a fixed distance from a point on the map. Points at valley bottoms are more shielded from wind than points at the peak of a mountain. Thus, forests on ridges and mountain peaks are more vulnerable than those in valleys (Ruel et al., 2002). When measuring the windthrow risk of a particular stand, forest dynamics can also influence susceptibility to windthrow. For example, a recently disturbed forest with few living stems remaining will need adequate time for trees to regenerate before becoming susceptible to disturbance.
again. Thus, variables like time since the last disturbance and the severity of the last disturbance are likely to mediate future susceptibility to wind disturbance (Schurman et al., 2018). Also, as we discuss above, longitude and its association with temperature and humidity patterns can influence windthrow risk through the relative presence of large-scale cyclone-induced windstorms (more common in Western Europe) versus small-scale convective instability (more common in Southeastern Europe (Brázdil et al., 2004). Finally, the presence of a temporal trend in disturbance severity datasets and the differing trends for the two main drivers of European wind (Figures 1c and 1d) imply that storm severity or forest vulnerability are changing through time (Schelhaas et al., 2003; Usbeck et al., 2010). Quantifying the effects of these wind moderating variables will inform forest susceptibility models of windthrow disturbance and elucidate atmospheric drivers of wind.

Our objective in this study was to use a large network of primary forest plots, where the main disturbance agent is wind, to determine the relative influence of wind drivers at two spatial scales and examine trends in wind-induced forest disturbance over the 20th century. We checked for evidence of large-scale cyclone-induced windstorms and small-scale convective instability in European beech forests at the plot (ca. 0.1 ha) and forest stand scales (ca. 100 ha) while also controlling for windthrow susceptibility variables acting at local and continental scales. By addressing these objectives, we can inform hypotheses presented in the literature on the reason for recent increases in European windthrow disturbance which include an increase in intense wind frequency (which we account for) and increases in forest management and cover (which our methods exclude).

2. Materials and Methods

2.1. Study Plots

We assessed the historical disturbance of 20 beech-dominated primary mixed forests stands within the Carpathian Mountains of Slovakia and Romania. The presence of primary forests was determined through forest inventories in Slovakia (Kozák et al., 2018; Mikoláš et al., 2019; Sabatini et al., 2018; also see http://remoteforests.org) and Romania (Kozák et al., 2018; Sabatini et al., 2018) and detailed descriptions of these primary forest inventories can be found in the study by Mikoláš et al., (2019). Primary forest stands occurred in four geographic clusters which we refer to as landscapes (West Slovakia, East Slovakia, North Romania, and South Romania) covering 42°–50° latitude and 14°–25° longitude, with plots ranging in elevation from 615 to 1,324 m a.s.l (Figure 2a). To obtain historical disturbance data from stands, we collected tree cores from 280 circular plots randomly positioned within primary forests. We used ArcGIS 10.7 to randomly place the 280 plots in non-overlapping pairs oriented along topography contours with plot pair centers positioned 80 m apart (Figure 2b). Only beech-dominated mixed forest plots were included in this study to ensure that windthrow was the predominant disturbance agent (Nagel et al., 2006) and because beech-dominated mixed forest is the most abundant forest type across temperate Europe, increasing comparability of these results to other windthrow studies in Europe. The most common tree species within stands in order of abundance were Fagus sylvatica (71%), Abies alba (15%), Picea abies (6%), and Acer pseudoplatanus (4%).

2.2. Historical Disturbance Chronology Calculation

Annual records of percent canopy area removed were created based on tree-ring data for each plot and stand. At each plot, trees were selected for coring based on a hierarchy of size classes in a nested circle design. All trees ≥6 cm diameter at breast height (DBH) were cored up to 8 m from the plot center. Also, a quarter of canopy and subcanopy trees 10–20 cm DBH, and all trees ≥20 cm DBH were cored up to 17.84 m from the plot center. These cores were dried prior to mounting and sanding using consecutively finer grit sandpaper (up to 1000 ANSI grit). Cores were visually crossdated and ring widths were measured using a Lintab measuring machine and TSAP-Win software. Crossdating was verified with Cofecha and CDendro software (Holmes, 1983; Larsson, 2003).

Within crossdated tree-ring series, we used two types of disturbance-indicating growth patterns to reconstruct disturbance events: (1) Rapid early growth of trees established under an open canopy and (2) abrupt increases in growth, called releases (Altman et al., 2018). Open canopy established trees were identified as individuals that exceeded a threshold value of mean growth from 5 to 15 years of growth.
These threshold values were calculated based on logistic regressions comparing empirical data from collected plot seedlings growing in the open canopy or closed canopy conditions (Janda et al., 2017). Separate regressions were performed for common tree species present (Fagus sylvatica, Abies alba, Picea abies, Acer pseudoplatanus, and a group of all other species present pooled in an additional group) in each landscape (i.e., five species groups × 4 landscapes = 20 species: landscape critical values). Releases, our second disturbance indicating growth pattern, were identified using the absolute increase method (Fraver & White, 2005b; Trotsiuk et al., 2014). This method compares the mean growth in the 10 years before a focal year and the 10 subsequent years including the focal year at all possible positions along an individual tree growth series. If the absolute increase in growth is greater than a threshold value, then a release event is recorded at the focal year. We limit recorded releases to one every 20 years and no tree may record a release above a DBH where they are considered to have attained canopy status. Because the average growth of the species within beech-dominated mixed forests was different, we calculated absolute increase threshold values for each species group in each landscape separately and the canopy position DBH cutoff for each species individually. Thus, release events were defined as years when the growth comparisons indicate a growth increase exceeding 1.25 the standard deviation of increases in the landscape-species combination (Fraver & White, 2005b; Trotsiuk et al., 2014).

Both of these disturbance-indicating growth patterns were then transformed to a measure of canopy area removed using methods of Lorimer and Frelich (1989) and Schurman et al., (2018). We used power function models that estimated canopy area from a disturbance indicating the tree's current DBH (Lorimer & Frelich, 1989). Power functions were specific to each tree species group in each landscape.
To better characterize the plot and stand level timing and severity of all tree level disturbance events of both disturbance types, we created a raw chronology of pooled canopy area removed before fitting a kernel density estimation (KDE) function to temporally smooth the disturbance chronology. Yearly values of tree level canopy area removed were pooled at the plot (Figure 2c) and subsequently stand level (Figure 2d) to create raw disturbance chronologies. Then, a kernel density function with a 30-year window was fit to plot and stand chronologies of raw canopy area removed to create two spatial hierarchies of disturbance chronologies (Trotsiuk et al., 2014).

Peaks in the plot and stand kernel density disturbance chronologies were used for identifying the timing and severity of disturbance events and for calculating time series describing the time since the last disturbance and last disturbance severity for each plot and stand (Schurman et al., 2018). We used three criteria for determining a plot peak: (1) The kernel density disturbance chronology had to be increasing for at least the 5 previous years, (2) it had to exceed 10% canopy area removed, and (3) subsequent peaks had to be separated by at least 10 years. Because disturbance chronologies include data from the young growth of trees and because trees that could record recent disturbance may not have reached our criteria diameter classes at the time of sampling (median age of all trees in plots at 6 cm DBH, the minimum sampling size, was 31 years), we truncated the historical disturbance chronologies so that 1989 represented the most recent year.

2.3. Windthrow Susceptibility Variables

Because past disturbance influences the susceptibility of a stand to future disturbance (Schurman et al., 2018), we calculated the time series of time since the last disturbance and the severity of that last disturbance for plots and stands based on kernel density function peaks (Figure S1). Beginning in the year 1600, values of time since the last disturbance and severity of the last disturbance were set to zero, and time since the last disturbance increased by one every year without disturbance. After detecting the first disturbance peak greater than 10% canopy area removed in a kernel density disturbance chronology, the “severity of last disturbance” variable was set to the peak severity of the disturbance and the “time since last disturbance” was reset to zero. After the first disturbance peak, the last disturbance severity and time since the last disturbance values only changed if a disturbance peak with a magnitude greater than 10% of the canopy area of the plot or stand occurred more than 10 years after the last disturbance peak. We shifted values of time since last disturbance and severity of last disturbance to 15 years after the peak disturbance year (half the length of the KDE function window; Figure S1), because kernel density peaks occur at the temporal center of raw disturbance events. Thus, a 15-years shift is necessary to ensure that evidence of previous disturbance, not disturbance during the focal period, was used to predict disturbance severity of the focal year.

The reason for incorporating time since the last disturbance and severity of the last disturbance is twofold. First, those variables have been shown to influence the susceptibility of forests to future disturbance. Second, because disturbance changes the structure of the forest, these variables can be interpreted as a rough proxy for forest structural complexity. Forests with lower severity disturbance and disturbance that happened further in the past are more likely to display higher structural complexity (Janda et al., 2017; Meigs et al., 2017). Thus, we are examining the direct effect of past disturbance on future disturbance as well as approximating an indirect effect of structure on disturbance susceptibility.

Beyond time since the last disturbance and severity of the last disturbance, wind-induced disturbance in forests is also likely moderated by factors including topographic exposure, longitude, and time period. Landscapes that are more exposed are more likely to experience higher severity disturbance with elevated wind levels, thus, to account for topographic exposure, we calculated a distance-limited “topex” value for every plot. Distance limited topex is $-1 \times \text{average of the virtual horizon angles up to a distance of 1 km from each plot center at the eight cardinal and intercardinal directions} \ (Quine & White, 1998; Ruel et al., 2002; Schmidt et al., 2010). We calculated topographic exposure values in ArcMap 10.7 based on digital elevation model layers retrieved from the USGS Earth Explorer (https://earthexplorer.usgs.gov/). Using this method, more positive values occur on mountain tops where trees are more exposed to wind whereas lower values occur in valleys where trees are more shielded from the wind. Longitude moderates the wind-induced disturbance because of the strength of various drivers of wind change as the climate becomes more continental. Areas closer to the west coast experience higher average wind speeds and more intense cyclones and more continental areas experience more convective instability (Siedlecki, 2009). Finally, there is some
evidence that the effect of wind speed and convection on forest disturbance may vary across the 20th century (Gardiner et al., 2010; Schelhaas et al., 2003; Usbeck et al., 2010) possibly due to global change. Thus, we also account for the influence of “time period” (i.e., year) as an explanatory variable in order to examine temporal changes in susceptibility to wind.

2.4. Historical Meteorology Data

We use the 20th Century Reanalysis version 3 data set as a source of estimated atmospheric and wind conditions from 1850 to 1989 (Compo et al., 2006, 2011). At the time of writing, this reanalysis product represents the most temporally extensive data set with the highest resolution which models wind speed and convective instability. This reanalysis has been tested for accuracy (Slivinski et al., 2019) and has been compared to other reanalysis datasets (Bett et al., 2017). Values for surface u-wind (zonal or east-west), surface v-wind (meridional or north-south), and convective available potential energy (CAPE), a measure of small-scale convective instability, were extracted at each plot and stand centroid for all 3-h time steps from January 1, 1850 to December 31, 1989. Measures of vector wind were calculated from u-wind and v-wind values at every time step as these are estimated from the temperature and pressure gradients produced by large-scale patterns including extratropical cyclone windstorms (Leckebusch & Ulbrich, 2004). Because CAPE and wind speed values within the 20th century reanalysis data set are estimates from an ensemble of models (Compo et al., 2006) and because trees in each area are likely adapted to the prevailing average wind and storminess (Quine & Gardiner, 2007), we create an annual time series of the number of time steps where wind speed or CAPE were greater than two standard deviations above the mean for that area. This method is analogous to using the 98th percentile as a threshold as Leckebusch et al. (2008) and Donat et al. (2011) did when examining the influence of extreme storms on regions of Europe. Also, the number of extreme wind speed and CAPE periods have previously been shown to correspond to storminess (Anyomi et al., 2016; Leckebusch et al., 2008; Usbeck et al., 2010).

2.5. Models

Some uncertainty in the timing of disturbance events exists in the reconstructed disturbance dataset because there are lags in tree growth and recruitment after disturbance. We chose to address this uncertainty by analyzing the historic dataset in 5-year periods. Our dependent variable, proportion canopy area removed, and independent variables, time since last disturbance (≥10% canopy area removed), the severity of last disturbance (≥10% canopy area removed), number of high windspeed 3-h intervals, and number of high CAPE 3-h intervals were averaged into a time series of 5-year periods. Values for distance-limited topographic exposure and longitude (additional explanatory variables) were static through time.

To address our primary goal of describing the influence of wind speed and storminess on primary mixed forest disturbance, we fit seven univariate and four multivariate Bayesian regression models (Table 1) to the historical disturbance data set and compared models using leave-one-out cross validation which ranks models based on predictive ability using an information theory approach. Because many plots had 5-year periods without observed disturbance and because certain susceptibility criteria must be met for a plot to be vulnerable to wind disturbance (e.g., just after a large disturbance there may not be live trees in the plot and thus the plot will not be able to record disturbance regardless of wind speeds) we chose to use a two-part zero-inflated beta model structure. This structure allows us to model and account for variables that increase the probability of observing disturbance as well as modeling variables influencing disturbance severity. In the disturbance presence portion of the model, we use a beta distribution model because we are modeling disturbance severity as the proportion of plot or stand canopy area disturbed, which is bound between zero and one. The model formula for all models tested can be summarized with the following equations:

\[
Y_i \sim ZIBeta(p_i; \phi_i) \tag{1}
\]

\[
\text{logit}(p_i) = \alpha_p + \beta_p x_i \tag{2}
\]

\[
\log(\phi_i) = \alpha_\phi + \beta_\phi x_i + \{1|\text{stand}\} \tag{3}
\]
Equation 1 represents the full two-part mixture model where $Y_i$ is the modeled disturbance severity of period $i$, $p_i$ is the probability that a period will exhibit zero disturbance, and $\phi_i$ is the mean of the beta distribution model which estimates disturbance severity given certain forest and atmospheric conditions. Equation 2 and 3 represent the respective forms of the zero-inflated and beta portions of the model where the terms $\alpha_p$ and $\alpha_\phi$ are the zero-inflated and beta intercepts, the $\beta_p x_i$ and $\beta_\phi x_i$ terms represent a general-form parameter estimate for the independent variables in the models, and (1|stand) represents the random factor of stand used to account for our nested design. Equation 4, 5, and 6 are prior distributions used for the intercept ($\alpha$) and parameter estimates ($\beta$) for the zero-inflated and beta portions of the model (Equation 2 and 3). All variable 5-year period averages were scaled to z-scores to increase computational efficiency and so that a flat prior with a half Student’s t distribution with 3 degrees of freedom and a scale parameter of 10 could be used in Bayesian regression models. Our four multivariate models (table 1) can be described as (1) the susceptibility variables model, where we account only for factors influencing forest susceptibility to the wind (see windthrow susceptibility variables section above) but no wind or convective-instability term is present. This model can be interpreted as a test of the influence of wind on forest disturbance. If this is the best model, neither CAPE nor wind speed significantly influences forest disturbance. Multivariate model 2 is the wind speed + susceptibility model, where the wind speed and all two-way interactions with wind speed are added to the zero-inflation and beta portion of the model. This model tests for the influence of extratropical cyclones. Multivariate model 3 is the convective instability + susceptibility model which matches the form of the wind speed + susceptibility model with CAPE substituted for wind speed and it tests for the influence of convective instability on forest disturbance. Multivariate model 4 is the global model which includes all terms from the wind speed model and convective instability model but also includes

$$
\alpha_p \sim \text{logit}(0,1)
$$

$$
\alpha_\phi \sim \text{student t}(3,0,10)
$$

$$
\beta x_i \sim \text{student t}(3,0,10)
$$

**Table 1**

| Model                      | Form                                                                 |
|----------------------------|----------------------------------------------------------------------|
| Time since last dist. only | $\alpha + \beta$ time since dist.                                    |
| Severity of last dist. only| $\alpha + \beta$ dist. severity                                      |
| Topographic exposure only  | $\alpha + \beta$ topographic exposure                                |
| Time period only           | $\alpha + \beta$ time period                                         |
| Lng. only                  | $\alpha + \beta$ Lng.                                               |
| Cyclone wind only          | $\alpha + \beta$ WSPD                                               |
| Convective inst. only      | $\alpha + \beta$ CAPE                                               |
| Susceptibility vars.       | $\alpha + \beta$ time since dist. + $\beta$ dist. severity + $\beta$ topographic exposure + $\beta$ Lng. + $\beta$ time period |
| Cyclone wind + susceptibility| $\alpha + (\beta$ time since dist. + $\beta$ dist. severity + $\beta$ topographic exposure + $\beta$ Lng. + $\beta$ time period) * $\beta$ WSPD |
| Convective inst. + sus.    | $\alpha + (\beta$ time since dist. + $\beta$ dist. severity + $\beta$ topographic exposure + $\beta$ Lng. + $\beta$ time period) * $\beta$ CAPE |

Note. WSPD represents the number 3-h periods with intense cyclone-induced wind speeds and CAPE represents the number of 3-h periods with intense convective instability.
the two-way interaction between wind speed and CAPE. These same model forms were fit to both the plot level and stand level datasets.

3. Results

3.1. Disturbance Reconstruction

All plots within mixed primary forests showed evidence of disturbance based on our reconstruction methods. When tree level disturbance events were aggregated to the stand level, reconstructions showed evidence of disturbances covering larger areas but the maximum severity observed, measured as canopy area removed, was 60% lower at the coarser stand level than at the plot level (see variability in Figure 3 and Figure S2). The 5-year interval with the most severe disturbance event on the plot level was one in which 99% of the canopy area was removed. This occurred in a plot within the Vihorlat stand in Slovakia during the 1885–1890 period. At the stand level, the largest reconstructed disturbance only removed 39% of the canopy area and occurred in the Belia stand of Romania from 1895 to 1900 (Figure S2).

Figure 3. Raw disturbance data observed in beech dominated mixed primary forest plots (blue dots) and stands (red dots) in comparison to hypothesized wind disturbance moderating forest and location traits. Beta regression and logit $\beta$ values are given for zero-inflated beta mixture models. The model predicted values are displayed as a line with a 95% credible interval.
Even though the range of maximum disturbance severity differed between plots and stands, many other aspects of the plot and stand disturbance regimes were very similar. Plots had an average of 2.03 ± 0.91 (1 SD) disturbance peaks from 1850 to 1989 where stands averaged 2.21 ± 1.03. This implies a disturbance return interval of 68 years on the plot level and 62 years on the stand level. Plot level disturbance averaged over all plots from 1850 to 1989 was 7.5% ± 12.4% canopy area removed, and plot disturbance was below 10% canopy area removed for 75.7% ± 0.1% of the analyzed period. Stand level disturbance severity averaged over all stands from 1850 to 1989 was 7.5% ± 6.2% canopy area removed and stand disturbance was below 10% canopy area removed for 75.0% ± 0.1 of the analyzed period.

### 3.2. Wind Disturbance Models

In our model comparison of wind drivers (e.g., large-scale extratropical cyclones and small-scale convective instability) and susceptibility variables, multivariate models that included both wind drivers and their interactions with susceptibility variables outperformed models without wind as well as single predictor models (Table 2). Single predictor models (e.g., wind speed only, time since disturbance only, etc.) were outperformed in every instance by multivariate models when predicting patterns of disturbance in forests of Central and Eastern Europe. At the plot level, the best model overall was the global model which included both cyclonic and convective wind drivers, the interactions between them, and the interactions between drivers and susceptibility variables. A measure of model quality, the expected log predictive density (ELPD) of the best model, estimated using leave-one-out cross-validation was >2.9 times better than the next best model which only contained susceptibility variables and wind speed. However, when aggregating evidence of disturbance to the stand level, two models show almost equal evidence toward best-describing patterns in disturbance. These models are the global model and the wind speed and susceptibility model. Both models include wind speed driven by large-scale cyclone-induced windstorms and two-way interactions between wind speed and susceptibility variables, but the global model also contained convective instability and interactions. Because the global model explains more variance, has a lower leave-one-out information criterion score, shows a slightly better ELPD, and can be used to interpret all interactions, we focus discussion on this model.

Examining the influence of susceptibility variables on historical disturbance severity, independent of changes in wind driver variables, we saw that topographic exposure, the severity of the last disturbance, time since last disturbance, and time interval were strong predictors of the presence and severity of plot level disturbance (Figure 3). Longitude, independent of wind variables, was not a good predictor of disturbance...
severity in plots as both zero-inflated and beta parameter estimate credible intervals overlapped zero. High values of topographic exposure increased the probability of disturbance. High values of time since the last disturbance increased disturbance probability and severity. High values of the severity of the last disturbance and time period decreased the probability and severity of disturbance. At the stand level, only severity of the last disturbance, time since last disturbance, and time period increased disturbance severity. The directions of these relationships were the same as when analyzing at the plot level: high values of previous disturbance severity, recent time periods, and longer times since last disturbance increased disturbance severity observed.

3.3. Wind Moderators

When interactions between susceptibility variables and wind drivers were considered, we saw some generalizable patterns. Regardless of the wind driver or the scale, intense wind conditions lost their impact over time. This trend was much more pronounced for the “CAPE:time period” interaction than for the “wind speed:time period” interaction. When the intense cyclone-induced wind was observed in plots or stands lacking previous high severity disturbance, predicted disturbance severity was higher. Strong interactions of wind drivers with time since the last disturbance was apparent at the plot level only. When increased time since the last disturbance was paired with intense wind or CAPE conditions, disturbance severity increased. When greater topographic exposure was paired with intense wind or CAPE conditions, the result was greater severity or probability of disturbance at the plot level, but when plot level estimates of exposure were averaged to the stand level, parameter estimate credible intervals began to overlap zero (Figure S3 and S4). Interestingly, the influence of high wind speeds produced from extratropical cyclones did not taper with longitude as expected, but the influence of convective instability did increase with longitude as expected.

When we plotted conditional effects of wind interactions with multiple forest susceptibility traits (e.g., time since last disturbance, severity of last disturbance, and topographic exposure), it was apparent that winds from large-scale cyclone-induced windstorms were more influential to disturbance severity in mixed beech primary forests of Central and Eastern Europe than winds from small-scale convective instability, especially in susceptible plots and stands. Susceptible plots were defined as those with susceptibility variables one standard deviation higher than the mean (e.g., plots with >77 years since the last disturbance [66 for stands], the severity of last disturbance removed >50% of the canopy area [26% for stands], and had an exposure value of >1.6° [−4.17° for stands]). At the plot and stand levels, the slope of the “wind speed-susceptible” predicted line was greater than that of the “convective instability-susceptible” line and higher values of disturbance severity were reached (ca. 5% more severe at 20 severe days per year; see Figure 4). Wind from cyclone-induced windstorms was interacting with forest susceptibility at the plot level, and this interaction was maintained even when aggregating to the stand level so that regardless of scale, higher cyclone-induced wind speeds caused higher severity disturbance in susceptible forests. However, when examining how convective instability interacts with forest susceptibility, more susceptible plots exhibited higher severity disturbance when instability was high (Figure 4a), but at the stand level, the impact of convective storms were reduced (Figure 4c).

4. Discussion

In this study, we showed that intense wind speed prevalence, driven by large-scale extratropical cyclones, was the main driver of windthrow disturbance especially in susceptible plots and stands of primary mixed forest in Central and Eastern Europe. The influence of smaller-scale convective instability on disturbance was also supported by models. Based on these data, increases in intense wind speed prevalence observed over the 20th century have not resulted in an increase in the scale of disturbance events observed. Additionally, coincident reductions in the prevalence of intense convective storms, have resulted in a net decline of disturbance severity. Because this study was conducted in fixed area plots located only in primary forests, changes in forest area and management do not influence these results.
4.1. Intense Convective Instability

The highest-ranked models for plots and stands both included evidence of convective storms which indicates that, in mixed forests of Central and Eastern Europe, thunderstorms with microbursts and tornadoes are significantly impacting forest dynamics, a fact that has largely been ignored in the European windthrow literature (Antonescu et al., 2017; Gardiner et al., 2010; Schelhaas et al., 2003; Usbeck et al., 2010). The influence of small-scale convective storms on forest disturbance has only been recorded in mixed forests of the Dinaric Mountains of Southeastern Europe (Nagel et al., 2017), mixed forests of the Romanian Carpathian Mountains (Furtuna et al., 2018), and in the deciduous forests of North America (Canham et al., 2001; Peterson & Pickett, 1991). Interestingly, these studies as well as the current study all focus on mixed forests dominated by a deciduous species which likely reduces the susceptibility of forests to windthrow in winter when trees lack leaves. Thus, we would not expect to see the same relative influence of convective storms in coniferous forests lacking deciduous trees. Additionally, the lack of convective forest disturbance studies is probably due to the smaller and more heterogeneous average footprint of convective-induced windthrow events, usually much less than 1 km² (Canham et al., 2001; Nagel et al., 2017). Thus, because the average area covered by stands analyzed here was 1 km², the influence of convective winds was not as influential at the stand scale. Disturbance from small-scale convective storms may have only affected one plot or a few trees and could be averaged out when calculating the disturbance severity at the stand scale. However, small-scale disturbance dynamics such as those created by small-scale convective storms cannot be ignored as they create forests of high structural complexity by opening up gaps in which recruitment can diversify the age and size profile of the forest (Franklin et al., 2002; Lorimer & Halpin, 2014; Meigs et al., 2017; Tepley et al., 2013). These localized events increase forest horizontal and vertical heterogeneity by creating gaps for seedling/sapling recruitment.
In addition to the smaller size of the intense wind footprint of convective storms, dynamics specific to convective instability also played a part in reducing the predicted impact of convective instability in forests. The CAPE values from 20th century reanalysis data used as our measure of convective instability are modeled on a 1° × 1° grid and represent conditions favorable for producing uplift in the atmosphere but should not be interpreted as implying that a disturbance-inducing storm will form or that a storm will cover the entire grid cell. Thus, high values of CAPE are not always associated with forest disturbance and only increase the probability of exposure to high winds. We accounted for this in two ways: (1) We used zero-inflated models in order to account for the probability of observing no disturbance despite having elevated CAPE and (2) we used the number of extreme events per year as an independent variable which has been shown to influence windthrow (Leckebusch et al., 2008; Usbeck et al., 2010).

Convective storms had a greater influence with increasing longitude, potentially indicating the influence of a more continental climate. Also, there was a strong and consistent interaction between longitude and intense CAPE observed in the plot level global model (Figure S4). Thus, the forests of Romania are more vulnerable to convective storms, probably because convective instability is more likely to be intense in many areas of Romania compared to Slovakia (Taszarek et al., 2019). This pattern of more intense conditions with continentality has been noted in previous research on storm prevalence across Europe (Antonescu et al., 2017; Brooks et al., 2003) and is probably playing a role in driving this pattern. However, this is one of the first studies to show this pattern with empirical forest disturbance data.

### 4.2. Intense Wind Speed

Intense wind speeds were a primary driver of disturbance severity regardless of the scale measured. This pattern was true across the longitudinal cline of this study making this one of a limited number of studies attributing large-scale cyclone-induced windstorms to forest disturbance in Romania (Gardiner et al., 2010). The interactions between the prevalence of intense cyclone-induced wind speeds and susceptibility variables were also stronger and more consistent than those of the smaller scale intense winds created by small-scale convective instability, likely reflecting the larger footprint of cyclones (Brázdil et al., 2018; Gardiner et al., 2010; Leckebusch et al., 2008; Leckebusch & Ulbrich, 2004; Usbeck et al., 2010). It is even likely that this pattern would have been observed at the landscape scale based on the average size of large-scale cyclone-induced windstorms (Brázdil et al., 2004) and the strength of these patterns in these data.

The fact that cyclone-induced windstorms are driving disturbance dynamics at stand scales has implications for stand structure. Large severe disturbances can reduce local structural complexity (Janda et al., 2017; Meigs et al., 2017), however, even the most severe stand level disturbance observed here would only be classified as low or possibly moderate severity in the global/European context (see predicted disturbance severities around 0.15 proportion canopy area removed in Figure 4). So, even the stand scale disturbances observed here are still increasing structural complexity of stands through gap creation and patch dynamics, only the gap sizes are likely a bit larger than those produced through convective instability.

### 4.3. Trends Over Time

The link between both convective storms and cyclone-induced windstorms and forest disturbance severity has weakened over the 20th century. This trend is more understandable for intense CAPE, which has decreased in prevalence over the 20th century and will likely continue to do so (Figure 1). Reductions in CAPE values are caused by reductions in relative humidity with warming and the subsequent changes in air parcel buoyancy based on adiabatic lapse rates (Riemann-Campe et al., 2009). As temperatures continue to increase, atmospheric humidity values will increase but relative humidity values will continue to decline (Hartmann et al., 2013). Rising atmospheric humidity will cause intense wind speed prevalence to rise, though some uncertainty in the extent of this pattern exists due to changes in cyclone storm path changes (Sepp et al., 2005). Despite the observed increases in intense wind speed prevalence over the 20th century, we observed a reduction in the influence of wind on disturbance severity (i.e. the same prevalence of intense wind causes lower severity disturbance today than in the past). This result is in direct contrast to hypotheses made in previous studies of windthrow disturbance in European forests that, based on data from salvage logging and reported damage, surmise increasing prevalence of intense winds may be responsible for
disproportionate increases in catastrophic windthrow damage (Gardiner et al., 2010; Schelhaas et al., 2003; Usbeck et al., 2010). However, these studies rightly list the caveat that windthrow and salvage logging reports are spatially and temporally inconsistent and reports may be disproportionately more common from intensively managed stands and in recent periods, reducing the applicability of their results for unmanaged primary forest ecosystems (Everham & Brokaw, 1996). These studies, however, are able to incorporate data from recent periods which our study was not able to do, due to the ca. 30 years time delay required when using dendrochronological methods to reconstruct disturbance history. Thus, we could not incorporate data from recent severe windstorms like Lothar, Martin, and Kyrill, which would have almost certainly inflated the impact of recent wind speed increases on forest disturbance. All time periods analyzed here maintain a sufficient presence of trees with the potential to record disturbance (Figure S5). Based on the number of trees with the ability to record disturbance, we see that the recent portion of the 20th century that we analyzed was well represented and if the disturbance was present, it could have been recorded by trees.

Other hypotheses given for the elevated levels of recently reported damage in Western Europe windthrow studies are an increase in forest cover across Europe (Gardiner et al., 2010) and increases in the age of the average European forest (Schelhaas et al., 2003). Increases in forest area likely led to increases in forest disturbance, however by using data from a plot census in this study, the area represented by disturbance recording trees has not drastically changed. Thus, our data do not directly test this hypothesis but do exclude forest cover increases as a potential bias. As for the increasing age of European forests due to the lengthening of rotation periods, this may make even-aged managed forests more vulnerable to wind disturbance. However, primary forest plots are usually older on average and their lack of stand-leveling disturbance events implies that older trees remain present within forests. Despite this presence of old trees, which suggests primary forests should be more vulnerable, we observed a decrease in disturbance severity. Thus, based on these data, it may be more likely that disproportionate increases in wind disturbance observed in Western Europe may be due both to forest area increases and the prevalence of maturing, even-aged monocultures in commercial forests there.

4.4. Structural Complexity

Previous studies have hypothesized the potential for stands high in structural complexity to have increased resistance to windthrow (Everham & Brokaw, 1996; Gardiner et al., 2010; Mitchell, 2013). Stands in this study show increasing resistance to windthrow and likely have high structural complexity induced by changes in the mixed-severity disturbance regime (Figures 3 b and 3c). Across the time period analyzed, disturbance severity decreased and the time since disturbance increased on average. Both of these variable trajectories can be interpreted as increases in forest structural complexity based on previous research in spruce forests (Janda et al., 2017; Meigs et al., 2017). Also, as the forests in this study are aging and increasingly exhibit old-growth structure traits (e.g. increased canopy height roughness), their resistance to wind disturbance may be increasing as well (Mitchell, 1995). However, the link between structure and disturbance was not directly measured here and should be interpreted with caution. Previous studies that have attempted to account for stand structure as a susceptibility variable have not shown a clear and obvious influence of structure on windthrow susceptibility (Barry Gardiner et al., 2005; Mitchell, 2013). Regardless, the fact that disturbance probability is lower recently even when the intense wind is controlled for (Figure 3e), is evidence that something about these forests has changed and increased resistance. Thus, future research on the influence of structural complexity on windthrow vulnerability is warranted.

4.5. Susceptibility to Windthrow

Here we controlled for five variables that we hypothesized moderated wind-induced disturbance in beech dominated mixed forests of Central and Eastern Europe, all influenced disturbance in the hypothesized manner, but patterns were scale specific or only interacted with one of the two wind drivers. Longitude only interacted with small-scale convective instability at smaller, plot scales. The fact that longitude did not show strong interactions with the larger-scale cyclone-induced windstorms indicates that intense winds were ubiquitous across the Carpathian Mountains and the influence of intense wind speeds was consistent across the longitudinal gradient. Despite evidence that extratropical cyclones are not likely to reach deep into continental Europe due to the East-Central European High (Di Rita et al., 2018) and the
poleward movement trend of extratropical cyclones making landfall in Europe (Leckebusch et al., 2008; Sepp et al., 2005), the absolute area of elevated wind speeds that cyclones produce covers the full gradient of longitudes studied here (14°–25°). Topographic exposure was consistent as a moderator of wind disturbance regardless of the wind driver but only at the plot scale. This result has been observed before and, thus, many windthrow susceptibility models include distance-limited topographic exposure as a predictor (Quine & White, 1998; Ruel et al., 2002; Schmidt et al., 2010). The reduced interaction between winds and topographic exposure at the stand scale was expected because stand measures of topographic exposure represented an average of plot level exposure, which reduced differences between stand measurements. Beyond topographic exposure, topographic roughness has been shown to moderate the scale of disturbances, which may be an additional reason that we did not observe severe disturbances at the larger stand scale as our stands are mostly in or near mountainous areas (Senf & Seidl, 2018). Previous disturbance also influenced future disturbance severity as expected, with shorter time interval since the last disturbance and higher severity of the last disturbance associated with higher severity forest leveling, i.e., when more trees are present, more forest can be disturbed (Janda et al., 2017; Meigs et al., 2017).

There are variables that we do not include in this analysis that are known moderators of windthrow disturbance. These include soil depth, soil moisture, tree height, and stand density (Canham et al., 2001; Gardiner et al., 2008; Nicoll et al., 2008; Usbeck et al., 2010), yet reliably reconstructing these variables over the analysis period is a large feat outside of the scope of this analysis. Because our main goals were to determine if large-scale cyclone-induced storms were the only source of wind disturbance in Central and Eastern European forests and to describe changes in the influence of wind drivers over the 20th century, maximizing model fit was not essential to achieve these goals. Inclusion of other drivers and moderators of forest dynamics would almost certainly increase the fit of models, and the low estimated R² values observed for plot scale models are evidence of this, but finding strong and significant trends of cyclones, convection, and wind moderators across the 20th century had never been accomplished prior to this study. Thus, this study provides essential information based on readily available forest positions and past disturbance data that can be used to predict the risk of future windthrow disturbance.

Though large-scale cyclone-induced windstorms are driving small- and large-scale disturbances in primary forests, the influence of convective storms cannot be ignored. The fact that both intense windstorms and intense convective instability are less influential in recent years may be evidence that primary forests are less susceptible to windthrow due to changes in the disturbance regime. Forest susceptibility variables used here can be extrapolated to many forests. Forest exposure, time since the last disturbance, and severity of the last disturbance can be incorporated into censuses to map and monitor forest vulnerability in response to predicted increases in intense cyclone activity.

Data Availability Statement

Datasets for this research are available in these in-text data citation references (Pettit, 2020), with CC 4.0 license https://doi.org/10.6084/m9.figshare.12983003.v1.

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