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Long-term tropical cyclones activity shapes forest structure and reduces tree species diversity of U.S. temperate forests

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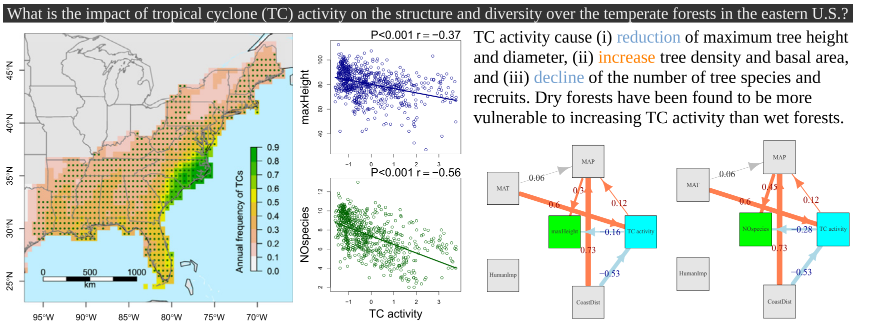
HIGHLIGHTS

- Tropical cyclone (TC) activity is a strong driver of forest structure and diversity.
- TC activity reduced maximum tree size, increased tree density and wood volume.
- TC activity reduced species diversity, with dry forests being more sensitive.
- U.S. temperate forest dynamics is expected to change due changing TC activity.

GRAPHICAL ABSTRACT



What is the impact of tropical cyclone (TC) activity on the structure and diversity over the temperate forests in the eastern U.S.?

TC activity cause (i) reduction of maximum tree height and diameter, (ii) increase tree density and basal area, and (iii) decline of the number of tree species and recruits. Dry forests have been found to be more vulnerable to increasing TC activity than wet forests.

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ABSTRACT

Increasing tropical cyclone (TC) pressure on temperate forests is inevitable under the recent global increase of the intensity and poleward migration of TCs. However, the long-term effects of TCs on large-scale structure and diversity of temperate forests remain unclear. Here, we aim to ascertain the legacy of TCs on forest structure and tree species richness by using structural equation models that consider several environmental gradients and use an extensive dataset containing >140,000 plots with >3 million trees from natural temperate forests across eastern United States impacted by TCs. We found that high TC activity (a combination of TC frequency and intensity) leads to a decrease in maximum tree sizes (height and diameter), an increase in tree density and basal area, and a decline in the number of tree species and recruits. We identified TC activity as the strongest predictor of forest structure and species richness in xeric (dry) forests, while it had a weaker impact on hydric (wet) forests. We highlight the sensitivity of forest structure and tree species richness to impacts of likely further increase of TC activity in interaction with climate extremes, especially drought. Our results show that increased TC activity leads to the homogenization of forest structure and reduced tree species richness in U.S. temperate forests. These findings suggest that further declines in tree species richness may be expected because of the projected increase of future levels of TC activity.

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1. Introduction

Tropical cyclones (TCs) represent one of the most forceful natural hazards with severe environmental and socioeconomic impacts. High wind speed and torrential rain triggering floods or landslides are often associated with TCs and are responsible for the large-scale disturbances of forests and other natural ecosystems (Hall et al., 2020). The most obvious impacts of TC disturbances on forest communities are changes in forest structure, not only through the opening of forest canopies (e.g. due to defoliation, broken or uprooted trees), but also through the adaptation of structural characteristics to specific disturbance regimes, e.g. smooth or lower canopies as responses to winds (Lugo, 2008). TC activities (intensity and frequency) affect tropical and subtropical forests more strongly than temperate forests at higher latitudes (Lugo, 2008). Globally, TC intensity has increased (Elsner et al., 2008; Kossin et al., 2020) and TC landfalls (land crossing) have migrated poleward (Garner et al., 2021; Studholme et al., 2022). Thus, the likelihood of TC disturbance in temperate forests is increasing (Altman et al., 2018; Korznikov et al., 2022; Zampieri et al., 2020). However, the impacts of changing TC activity on forest communities are poorly explored at large spatial scales, especially in temperate forests.

The impacts of high wind speeds and large amounts of rainfall from TCs are widespread, extending hundreds of kilometers outward from the TC center along its entire track. Moreover, they are often followed by other disturbances like storm surges, floods, landslides, or later even fires (e.g. due to accumulated debris; (Lin et al., 2020)). The environmental footprints of TCs are largely heterogeneous and their impacts depend on intensity, frequency, translation speed (moving speed), and complex interactions with ecosystems (Kossin, 2018; Lugo, 2008). On the other hand, the ecosystems have little influence on TCs, which are mainly controlled by temperature, atmospheric pressure and wind conditions (Lugo, 2008; Day and Hodges, 2018). High-resolution TC track data are now available in global databases, e.g. in the International Best Track Archive for Climate Stewardship (IBTrACs, (Knapp et al., 2010)), and therefore provide source for examining footprints of impacts of TCs on forest communities and for projections of TCs activity in a given area into the future. Still, a better understanding of the factors affecting TCs impacts is necessary for forest conservation and management, especially for the implementation of strategies to mitigate ongoing climate change.

Alongside the impacts of TCs on the environmental conditions, mainly driven by increased amount of wind and precipitation, TCs have also direct short- and long-term effects on forest structure, composition, and succession (Lin et al., 2020; Lugo, 2008). In addition, the severity of forest damage during TCs also depends on forest moisture types (Ibanez et al., 2019; Van Bloem et al., 2005; Van Bloem and Martin, 2021) and amount of TC-related rainfall (Hall et al., 2020; Lin et al., 2020; Lugo, 2008). In general, TCs induce tree damage and mortality, causing a direct short-term decrease in stem basal area, leading to improved light conditions under the canopy and a subsequent increase in stem density due to rapid tree regeneration (Uriarte et al., 2004; Van Bloem et al., 2007). TCs also strongly affect tree height and architecture due to the broken tips of large trees exposed to winds. Hence, forests with high TCs activity have been found to have lower canopies in temperate forests (Putz and Sharitz, 1991), subtropical wet and rain forests (Brokaw and Grear, 1991), tropical and subtropical forests (Harley et al., 2015, 2012; Ibanez et al., 2019) and mangrove wetlands (Simard et al., 2019). In the long term (up to several decades after a TC), smooth and uniform canopy structures with cohorts of distinct size classes are observed to be legacies of past TCs (Chi et al., 2015; Van Bloem et al., 2007).

As a consequence of the TC impact on forest structure, there is a tight connection between TC activity and species diversity (Marks et al., 2016), an immediate drop in species diversity due to high tree mortality was observed after TC disturbance, followed by an increase in species richness due to rapid regeneration (Chi et al., 2015; Lugo, 2008; Murphy et al., 2014). Such tree replacement also leads to high temporal species turnover (Tanner et al., 1991), e.g. reduction of disturbance-intolerant species (Xi et al., 2019), while the effects of TC activity on species diversity are highly dependent on forest type, site condition, and time scale of study (Altman, 2020; Van Bloem and Martin, 2021). In particular, most studies come from the tropical forest (e.g. (Ibanez et al., 2019)), focus on the effect of individual TCs (e.g. (Tanner and Bellingham, 2006)), or have a small spatial scale (e.g. (Putz and Sharitz, 1991)). Consequently, existing studies from temperate forests differ in their conclusion about the impact of TC activity on tree species diversity, with some identifying increased diversity after TC disturbance (e.g. (Xi et al., 2019)), while others find a decrease in diversity (e.g. (Putz and Sharitz, 1991)).

Although ongoing shifts in species composition have recently been observed in temperate forests in the United States (U.S.) (Au et al., 2020; Foster, 1988; McEwan et al., 2011; Umaña et al., 2022), studies investigating the large-scale impact of TCs on temperate forest structure and diversity are still rare, and existing studies are limited in their spatiotemporal extent (Lin et al., 2020; Lugo, 2008). Here, we present the results of TC impacts on community structure in the U.S. Eastern Deciduous Forest (EDF) temperature biome. In particular, we tested the impact of environmental conditions, represented by TC activity, temperature, precipitation, human impact and moisture type, on the structure and diversity of the forests characterized by (i) maximum forest height and tree diameter, (ii) tree height and diameter distributions (skewness), (iii) the number of trees, species and recruits, (iv) and stand basal area. We hypothesize that TC activity significantly affects forest structure and diversity, even after accounting for other environmental characteristics, and the impact of TC activity varies by forest moisture type. Our study combines a large-scale inventory of U.S. forests with the impact of TC effects on stand structure and diversity reflecting multiple environmental conditions in the EDF.

2. Materials and methods

2.1. Study sites – forest structure, moisture type and plot selection

We used USDA-Forest Service Forest Inventory and Analysis (FIA) data from the U.S. East Coast TC-prone region, which included 24 states from Texas to Maine (Bechtold and Patterson, 2005) (Fig. 1). This region contained >600,000 plots, each consisting of four subplots with a fixed radius covering 168 m^2 for overstory vegetation and four 13 m^2 subplots for understory vegetation (tree's recruits). Height, diameter at breast height (DBH), and species identity were retained for trees with DBH $\geq$ 1 in. (2.54 cm). The number of individuals was retained for recruits, defined as trees with DBH < 1 in. and either >6 in. tall for conifers or > 12 in. tall for hardwoods. Within each plot, total number of trees (density), total number of recruits, total number of tree species, sum of tree basal area, and maximum and skewness of tree height and DBH were calculated. Skewness values were included to characterize the size distribution in the plots, in which high skewness values (right-tailed distribution) reflect the prevalence of smaller individuals, while low skewness values (left-tailed distribution) reflect the prevalence of larger individuals. The plots in FIA are classified into three forest moisture types based on landform, topographical position, and soil moisture available to trees (Fig. S1; (Bechtold and Patterson, 2005)), in particular, there are: (i) xeric plots where moisture availability is low, e.g. dry ridgetops, steep slopes, or sandy soils, (ii) mesic plots where soil moisture is adequate, and (iii) hydric plots where soil moisture is abundant, e.g. swamps, bogs, small drains, or pocosins.

To focus on longer-term forest responses, we restricted our analysis to natural forests that have not been recently disturbed to not get our analysis bias by the short-term effect of disturbances. Therefore we excluded plots that have undergone recent disturbances (recorded in FIA) as well as any special purpose forests including silviculture treatments, plantations, or agricultural forests (detailed list of excluded plots is in Text S1). For plots with multiple measurements, we chose the most recent inventory for analysis. This period includes the years 1967–2020. To download the data, we used the R package rFIA (version 0.2.4 downloaded in 5.2.2021; (Stanke et al., 2020)).

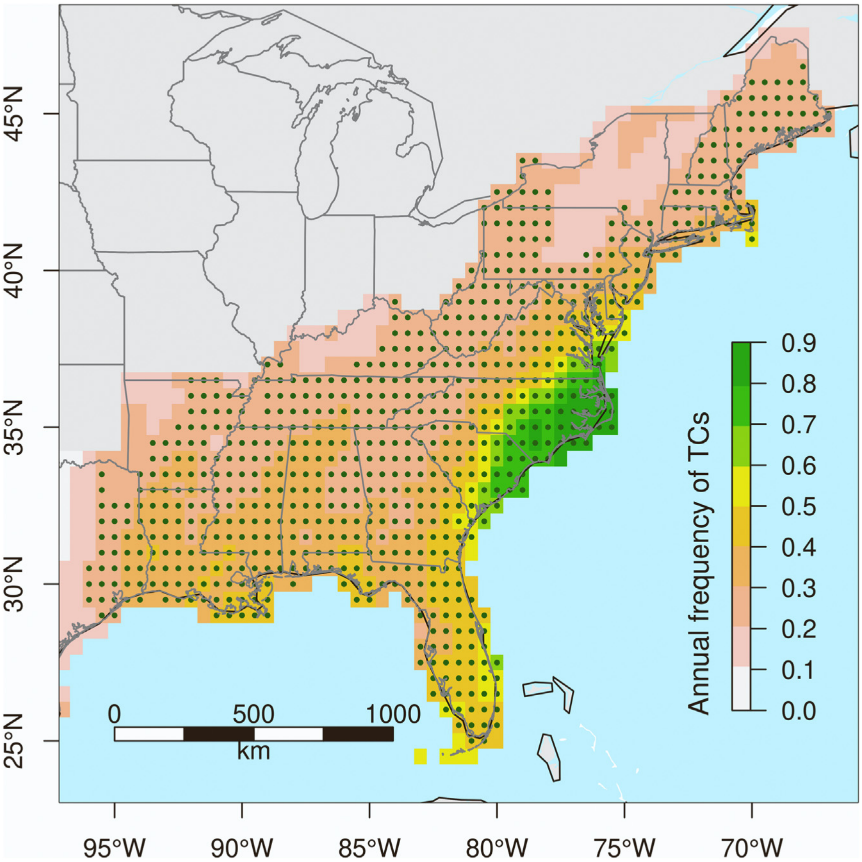

Fig. 1. Mean annual frequency of cyclones from Knapp et al. (2010) averaged in 0.5° × 0.5° for all forest plots up to 200 km from their tracks on the east shore of the U.S. over 40 years (1980–2019). Focal grids affected by at least 10 TCs over 40 years are drawn with green dots.

2.2. TC activity and other environmental characteristics

Data on TC activity were collected from the global IBTrACs database for the 40-year period from 1980 to 2019 (Knapp et al., 2010). For each plot, we used annual intensity, represented by the sum of wind speed, and TC frequency including tracks within 200 km of individual plots, given that TCs can affect forest communities at such distances (Miller et al., 2006; Trouet et al., 2016). We only considered category 1 to 5 TCs on the Saffir-Simpson Hurricane Wind Scale. From these values a principal component analysis (based on scaled and centred values) was conducted, then we extracted the first axis (providing 80 % of the variability, loadings of both variables with the axis were 0.71) to obtain one composite characteristic of tropical cyclone frequency and intensity (hereafter referred to as TC activity; Fig. S2).

Several environmental characteristics were extracted from the databases for individual plot coordinates. As temperature and water availability are strongly associated with species composition (Chase, 2010; Grosso et al., 2008), mean annual temperature (MAT) and mean annual precipitation (MAP) were extracted from the WorldClim 2.0 database at 10-min resolution (http://www.worldclim.org/version2, (Fick and Hijmans, 2017)) to characterize large-scale long term environmental conditions. The human footprint index at 1 km^2 resolution (hereafter referred to as human impact, Human Footprint 2009, available from http://wcshumanfootprint.org/) was used as a proxy for potential human disturbance of forests (Venter et al., 2016). Moreover, the distance to the coast was calculated using the R package rnaturalearth (in 1:110 m scale) as an indicator of continentality, which is linked to MAT, MAP and TC activity. During the analyses we fitted multiple models, but some combinations of explanatory variables were excluded. In particular, 1) latitudinal gradient was not considered to avoid collinearity with MAT (Pearson $r = -0.92$; Fig. S2), 2) altitude was not analysed because of the high intercorrelation with MAT and MAP (Pearson $r > 0.5$), 3) and distance to the shoreline was not considered in one model with TC activity to avoid collinearity (Pearson $r = -0.76$; Fig. S2). If highly correlated explanatory variables are in one model, small changes in the model or data may lead to erratic changes in the coefficient estimates (Graham, 2003).

2.3. Analyses

Only forests affected by TC activity and defined as areas with at least 10 TCs over a 40-year period were selected for analysis ($n = 149{,}822$ plots with > 3 million trees). Sites with lower TC occurrence were mostly not affected by TCs at all, especially as these sites are located far from the coast, thus the intensity is also very low and we do not expect impact of TC activity at these sites. Hence, the forest structure and diversity is driven there by different factors than TC activity and disentangling these factors is out of the focus of our study intended to examine the patterns driven by TC activity. We aggregated (compute mean) the data in 0.5° × 0.5° grid cells (~ 55 km × 55 km): 1) regardless of moisture type (all forests, altogether 718 grid cells, Fig. 1), 2) and then separately for each forest moisture type (xeric 316, mesic 706, and hydric 443 grid cells), to aggregate nearby plots with similar environmental conditions and thereby reduce the pseudo-replication problem.

The relative importance of TC activity and other environmental conditions on forests was tested by fitting piecewise structural equation models (SEM; (Lefcheck, 2016)). Because our data were spatially structured, we implemented SEMs using simultaneous autoregressive error models (SAR) that account for spatial autocorrelation by including near-neighbor weights (Kissling and Carl, 2008). The distance between neighboring grids up to 100, 250, 500, 750 and 1000 km was used in the SAR models separately. The distance with the lowest Akaike information criterion (AIC) was selected for each response variable. We formulated a hypothetical causal model based on a priori knowledge of TC activity and other environmental effects on forest communities (Fig. S3) and used it to test the fit of the models to the data using SEM. Fitting a causal model to the data allows us to test for both direct and indirect effects (e.g. TC activity on the number of species via MAP). In particular, we assumed the direct effects of environmental variables (TC activity, MAT, MAP, and human impact) on indicators of forest structure and species richness (it allows us to compare the net effects of environmental variables, Fig. S3). TC activity was expected to be affected by distance from the coast (TC activity is decreasing along land distance from the coast and is affected by land masses, Fig. 1, Lugo, 2008) and MAT (temperature regulates TCs; Day and Hodges, 2018). Finally MAP was fitted based on TC activity (TCs come with high precipitation; Hall et al., 2020, Maxwell et al., 2021), distance from shoreline (precipitation tends to decrease with the distance from the coast; Ogino et al., 2016) and MAT (temperature and precipitation are closely related; Grosso et al., 2008). The final model for each indicator of forest structure and species richness was obtained iteratively by including and removing combinations of predictors to obtain the best-fitting model that minimizes Fisher's C statistics and maximizes the *P* value of the full SEM. It was computed within and across all forest moisture types separately. The goodness-of-fit was evaluated by Fisher's C for the whole model and Nagelkerke pseudo-R^2 values were reported to show the explained variation (Lefcheck, 2016). Because many of the variables included in our SEM were correlated (see Fig. S2), we estimated a variance inflation factor (VIF) to assess whether multi-collinearity affected parameter estimates; the VIF threshold for linearized SEMs was set to 3, as in (Craven et al., 2018).

Correlations between forest structural and environmental characteristics are presented by scatter plots with Pearson correlation coefficients. Environmental variables were scaled and log-transformed and forest structural characteristics were also log-transformed to residuals meet model assumptions of normality. SEMs were fitted by 'piecewiseSEM' package version 2.1.2 (Lefcheck, 2016), SAR models by 'spdep' package version 1.2-1, VIF was computed by 'car' package version 3.0-12, all in R version 4.1.1.

3. Results

We found strong direct correlations between forest structure and species richness and individual TC activity and other environmental characteristics (Figs. 2, S4). TC activity had a negative impact on all structural forest characteristics, except for the density (positive impact) and stand basal area (non-significant impact). MAT had a negative effect on the tree height and DBH skewness and the number of species and recruits. MAP had a positive effect on all structural and species richness characteristics, except for no effect on tree height skewness. Human impact had a negative effect on the density, species and recruits, and a positive effect on maximum tree DBH.

The direct relationships were explored using a structural equation model (SEM, Fig. S3), which provides additional information of the simultaneous effects of environmental characteristics on forest structural characteristics and species richness. TC activity directly negatively affects the maximum tree height and DBH (std. estimate -0.16, $P \leq 0.001$), the number of species (std. estimate -0.28, $P \leq 0.001$), the number of recruits (std. estimate -0.32, $P \leq 0.001$), height skewness (std. estimate -0.08, $P \leq 0.01$) and DBH skewness (std. estimate -0.19, $P \leq 0.001$) for all forests (Figs. 3, S5, Tables 1, S1). The negative effects of TC activity on tree height and DBH distribution skewness caused an increasing number of large trees compared to the number of small trees. On the other hand, higher TC activity induced higher tree density (std. estimate 0.24, $P \leq 0.001$) and stand basal area (std. estimate 0.11, $P \leq 0.001$) in all forests (Fig. 3). With a few exceptions, TC activity had mostly similar effects for all forest types grouped together and individual moisture-type forests (Tables 1, S1). TC activity was mostly the strongest predictor for all structural characteristics in xeric forests and mostly the weakest predictor in hydric forests. Contrasting results were observed for tree density and stand basal area, which were negatively affected by TC activity in xeric forests and positively in hydric forests.

Two strong indirect effects on forest structure and species richness were observed (Table S1, Fig. S6). MAT had mostly negative indirect effects on forest structure (except positive effect on basal area and number of trees) and species richness via a positive effect on TC activity. For example, considering DBH, MAT had a positive effect on TC activity (std. estimate 0.67), which has a negative effect on DBH (std. estimate -0.26), and this together gives a negative indirect effect of MAT on DBH (std. estimate $-0.18 \sim -0.26 * 0.68$). Opposite, positive, indirect effects on the forest structure and species richness were observed for coastal distance via TC activity. Overall, the fit of the hypothetical model depends on the structural variable ranging from low R^2 for skewness characteristics (less than $R^2 = 0.1$) to $R^2 = 0.59$ for species richness, but in all models Fisher's C was $P > 0.05$ (Table S1). The concordance of TC activity by coastal distance and MAT was high in all forests ($R^2 > 0.61$), similarly to the fit of MAP by TC activity, coastal distance, and MAT ($R^2 > 0.5$). The human impact did not have significant effects on the forest structure of any of the SEMs.

4. Discussion

Our findings suggest that TC activity may have significant long-term effects on the structure and species richness of temperate forests in the east part of the U.S. even with consideration of other large-scale environmental variables in our models. Moreover, the strength of these effects varies considerably according to the forest moisture types.

4.1. TC effects on the forest structure

We observed the negative impact of TC activity on maximum tree heights in eastern U.S. temperate forests. Tall trees are more exposed to TC winds and therefore more likely to be disturbed than trees with crowns below or in canopy layer (Brokaw and Grear, 1991), and thus wind appears to be one of universal factors controlling a maximum tree height (e.g. with site productivity). Lower tree height relative to radial growth has been observed in several tropical regions (Blanchard et al., 2016; Thomas et al., 2015) along with increased resprouting or formation of multiple stems, which may lead to lower investment in vertical growth (Van Bloem et al., 2007; Zimmerman et al., 1994). Moreover, we observed negative correlations of TCs with maximum tree DBH and positive correlations with basal area, suggesting a response by increased stem density under high TC activity. TC disturbance generally resulted in increased stem density due to short-term increased light availability through defoliation and opening of the forest canopy accelerating establishment (Lin et al., 2020). Although our analyses focus on the long-term perspective (recently disturbed sites where not included), we also observed positive effects of TC activity on the density of trees with DBH ≥ 1 in., but negative on the number of recruits (DBH < 1 in.). A similar pattern was observed in temperate longleaf pine forests in Florida, where the recovery was attributed to several potential negative effects of pests, invasive species, effort to remove fallen trees or other following disturbances like fire (Zampieri et al., 2020). Moreover, high TC activity was reflected in shifts of tree size distribution toward large tree sizes. TC activity thus mainly increases tree mortality of small trees (including recruits) more strongly than for large trees (Lugo, 2008). The reduced number of recruits and small size trees under high TC activity may be also a long-term result of low light availability bellow the canopy due to increased stem and multi stems density.

When considering forest moisture types, TC activity was observed to be the strongest predictor for forest structure and tree species richness in xeric forests, but the weakest predictor in hydric forests. In general, hydric stands in temperate forests have lower TC mortality than xeric areas, partly due to different species composition and topographic location (Putz and Sharitz, 1991). On the other hand, in tropical and subtropical regions, xeric forests with lower tree size (DBH and height) were less affected by TCs than humid and hydric forests with larger trees (Ibanez et al., 2019; Van Bloem et al., 2005). Moisture type is also closely related to topographical position and soil properties, which affect forest resistance to TCs (Clinton and Baker, 2000; Everham and Brokaw, 1996; Martin and Ogden, 2006). In particular,

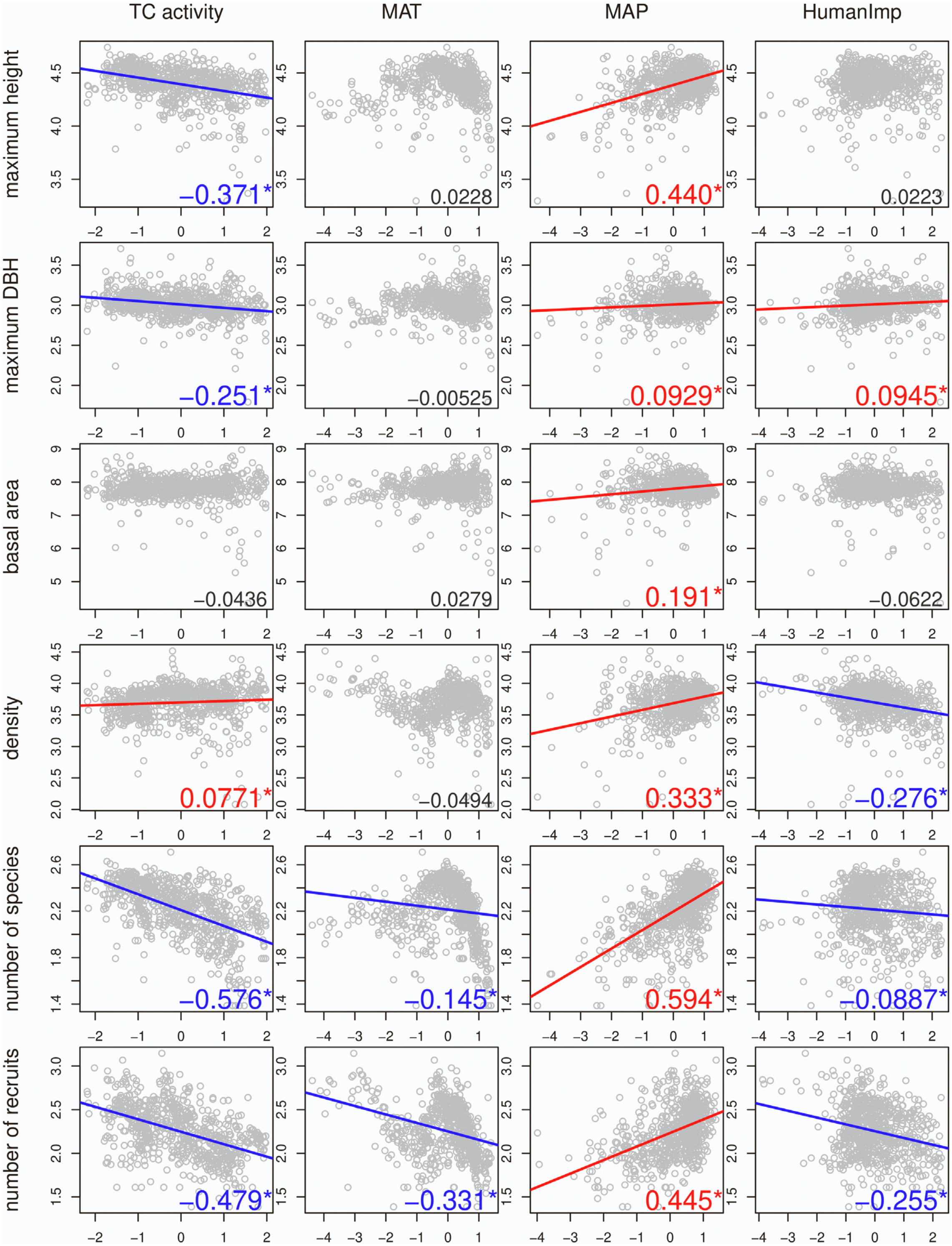

Fig. 2. Correlations between structural characteristics (log-transformed) and environmental characteristics (scaled and log-transformed) for all gridded forests ($n = 718$). Correlation coefficients are shown along with lines visualizing a significant ($*P \leq 0.05$) trend of linear relationships (red for positive, blue for negative, while black correlation coefficient and no trend line indicate a non-significant relationship; $P > 0.05$).

the lowest mortality due to winds was observed in plateaus that are common for hydric forests with deep soils, while the highest mortality is on slopes and ridges that often host xeric forests with shallow soils (Korznikov et al., 2022). Xeric forests have also low productivity (Hoover and Smith, 2012) and TC effects may be more negative than in productive sites, e.g. by slow growth and regeneration, or sparse distribution of trees more susceptible to wind damage than in closed-canopy forests in productive sites.

From the long-term perspective and repeating occurrence of TCs, forest resistance to TC activity may appear, e.g. by production of flexure wood and altered forest structure (Lugo, 2008). For example, lower disturbance effects were recorded after the second TC in hydric forests in Puerto Rico and were attributed to altered forest structure (i.e. shorter stature, smaller stem diameter, and high sprouting response) and post-disturbance water availability (Van Bloem et al., 2005). Such observations are consistent with our results showing strong effects of TC activity on temperate forest

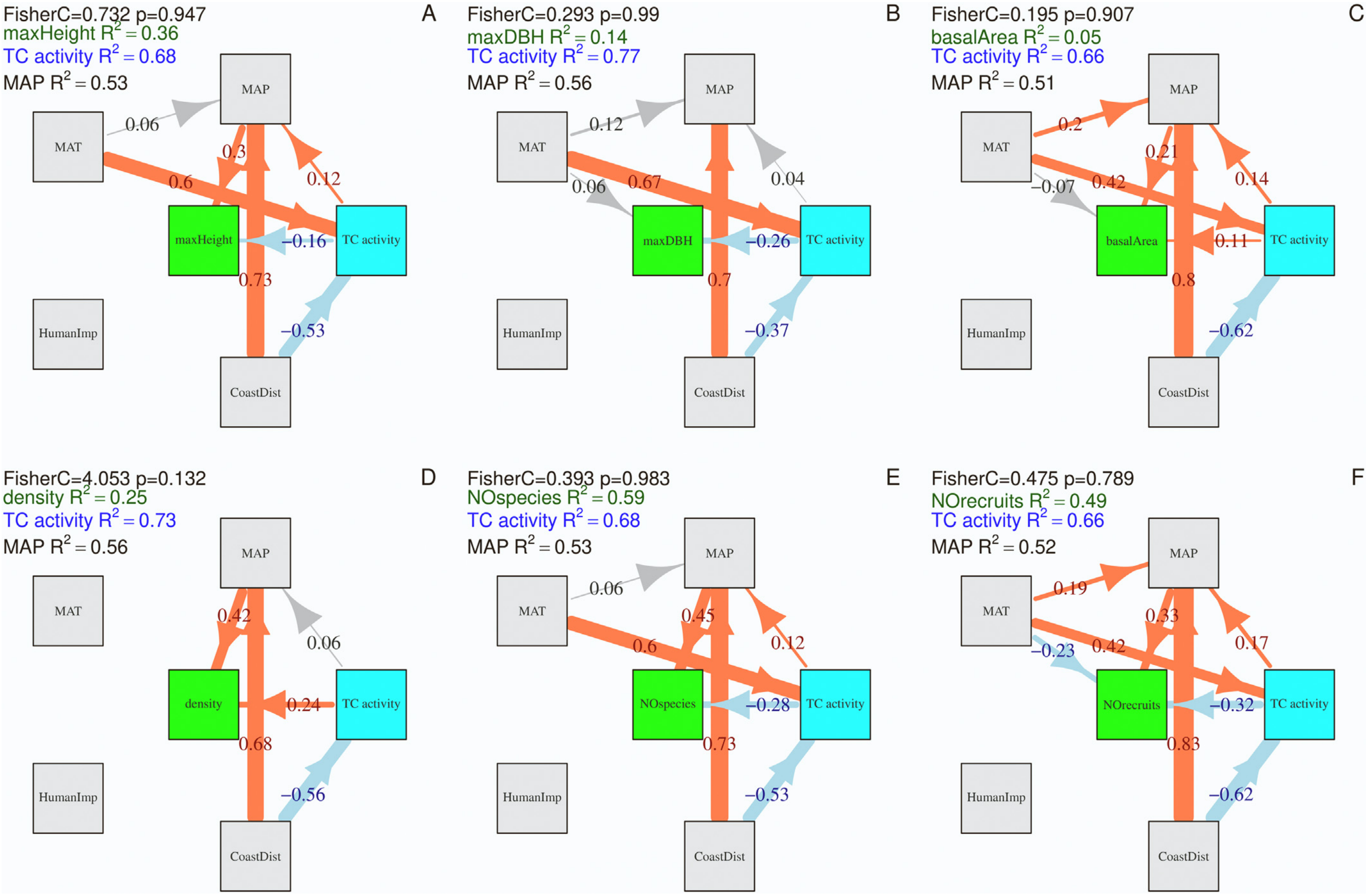

Fig. 3. Standardized SEM coefficients for environmental characteristics explaining structural and species richness forest characteristics for all forests. Diagrams show significant positive effects (orange colour), significant negative effects (in blue) and non-significant effects (in gray) in SEMs and their statistics (Fisher's C, P and Nagelkerke pseudo-R^2). Detailed model information is available in Table S1 and further variables in Figs. S5–6.

structure, e.g. reduced maximum tree height and DBH, and increased tree density in response to high TC activity. However, shifts in forest structure may also be the result of altered species composition in TC- affected forests, i.e. shade-tolerant species survive and sprout more vigorously after TC than pioneer species (Everham and Brokaw, 1996; Xi et al., 2019). There were also strong intercorrelations among TC activity, altitude and coastal distance, that all may act simultaneously in forming forest communities.

4.2. TC effects on tree species richness

In addition to altered forest structure, we observed negative correlations of TC activity with species richness of temperate trees. It was previously reported in tropical forests (Lin et al., 2020), but such studies have limited spatial extent or inconsistent trends observed in temperate forests (Xi et al., 2019). In general, species richness is expected to stabilize biomass productivity via enhanced asynchrony in the performance of co-occurring species (Craven et al., 2018; Dolezal et al., 2020) and increase community resistance to disturbances and climatic events (Jactel et al., 2017). Here, it is possible that 1) a strong synchronous community-wide disturbance of TCs disrupts and reduces stabilizing effect of species asynchrony (individuals of all species are damaged concurrently), and 2) the limited size of the species pool in temperate forests leads to a less rapid and successful regeneration in response to specific forest conditions after disturbances (e.g. by having low number of pioneer species) as is the case in tropical forests with a significantly larger species pool (Lugo, 2008). In tropical forests, TCs mostly have short-term positive effects on tree species richness (Lin et al., 2020; Lugo, 2008; Uriarte et al., 2004), but may lead to species richness declines on the long term (Lugo, 2008). On the other hand, short-term negative effects have also been observed in temperate hydric forests (Putz and Sharitz, 1991). In parallel, hydric forests have been observed to be more resistant to hurricanes (Tanner and Bellingham, 2006), which is consistent with our observation of the weakest effect of TC activity on species number (as well as other forest characteristics) in hydric forests. TC activity may have little effect on hydric forests due to their species composition that is adapted to tolerate high levels of water that is coming with TCs (Maxwell et al., 2021) and is one of the main drivers of increasing overall mortality because of TC disturbance (Hall et al., 2020).

4.3. Expected shift in forest structure and diversity

Although we did not directly analysed changes in TC activity over time, we take advantage of the large spatial scale of eastern U.S. temperate forests that allowed us to study a wide range of TC activity. In the long term, high TC activity should lead to an increase in the proportion of species tolerant to wind disturbances- (e.g. slow-growing and drought-tolerant species with high wood density and deep root systems; (Chi et al., 2015)) and provide more opportunities for light-demanding pioneer species (Curran et al., 2008). In parallel, high TC activity is thought to reduce the number of disturbance-intolerant species that are not adapted to sustain frequent TC impact (e.g. fast-growing resource-acquisitive species with low wood density; (Chi et al., 2015)). In addition, U.S. temperate forests undergo long-term succession where pioneer tree species with low wood density are replaced by old-growth forest species (Foster, 1988). These dynamics have been observed to be driven by life history and plant traits that drive forest stability and rapid taxonomic turnover, particularly small-seeded and low wood density (pioneer) species favoring faster turnover than species with the opposite traits contributing to forest stability (Umaña et al., 2022). New trees emerge shortly after a TC disturbance

Table 1
Summary of forest structural and species richness response variables explained by environmental characteristics based on forest moisture type. Standardized coefficients of environmental characteristics are shown for the PiecewiseSEMs. In particular, direct effects of TC activity, MAT and MAP on forest structure and species richness characteristics (response). Asterisks and ‘ denote significance level: ‘ for $P \leq 0.1$, * for $P \leq 0.05$, ** for $P \leq 0.01$ and *** for $P \leq 0.001$. Model details include Fisher's C statistics, corresponding *P* value, and Akaike information criterion (AIC). Detailed model information is available in Table S1.

Response	Forest	TC activity	MAT	MAP	Fisher' C	P
Maximum height	all	−0.1626***		0.3015***	0.732	0.947
	xeric	−0.5144***		0.0938*	1.962	0.743
	mesic	−0.1937***		0.2365***	1.413	0.842
	hydric	0.0438		0.3059***	0.919	0.632
Maximum DBH	all	−0.2553***	0.0569		0.293	0.99
	xeric	−0.5820***		−0.1605**	0.786	0.675
	mesic	−0.2770***		−0.1247**	5.793	0.215
	hydric	−0.1358*	0.2767*		11.81	0.066
Basal area	all	0.1073*	−0.0679	0.2117***	0.195	0.907
	xeric	−0.5185***		−0.0313	3.2	0.202
	mesic	0.0691	−0.6252***	0.0966‘	1.876	0.759
	hydric	0.1533*	0.1086	0.1895***	1.21	0.976
Density	all	0.2446***		0.4182***	4.053	0.132
	xeric	−0.1511*		0.2421***	5.025	0.081
	mesic	0.2688***		0.4055***	0.282	0.868
	hydric	0.2751***		0.2014***	6.308	0.613
Number of species	all	−0.2799***		0.4470***	0.393	0.983
	xeric	−0.3747***		0.1899***	0.149	0.928
	mesic	−0.2743***		0.4416***	1.346	0.853
	hydric	−0.0565		0.3739***	3.481	0.746
Number of recruits	all	−0.3167***	−0.2288***	0.3320***	0.475	0.789
	xeric	−0.2935***		0.1016	3.965	0.138
	mesic	−0.2345**		0.3399***	2.344	0.31
	hydric	−0.1733*		0.2251***	0.04	0.98

and regenerating young stands, especially when dominated by pioneer species, suffer from a high overall vulnerability to disturbances (e.g. interaction between TCs and fires; (Ibanez et al., 2022)) and drought (Curran et al., 2008; Smith-Martin et al., 2022). This may prevent the establishment of diverse and structurally complex forests. The outcomes of the vulnerabilities are concordant with our observations of the shifts in the distribution of tree sizes toward larger trees and lower tree species richness under high TC activity.

Our results along the TC activity gradient provide a framework for predicting future TC impacts and changes on U.S. temperate forests as part of the ongoing poleward migration of TCs (Garner et al., 2021; Studholme et al., 2022), leading to increased TC activity in the temperate zone (Altman et al., 2018) and even boreal forests (Korznikov et al., 2022). The most surprising observations from our work are: 1) the negative effects of TCs on tree species richness suggest that forests previously not or rarely disturbed by TCs are likely to experience declines in tree species richness due to changes in disturbance dynamics, and 2) the structure and species richness of xeric forests will be most threatened by the increasing pressure of TC induced disturbances for the following reasons: a) xeric forest are strongly affected by other disturbances that occur concurrently with TCs (e.g. fire; (Ibanez et al., 2022)), b) low productivity and often wind-exposed sites of xeric forests results in TC-vulnerable forest structure (e.g. open canopies on high slopes in dry forests are highly vulnerable to wind damage; (Van Bloem et al., 2005)), and c) low adaptation of xeric forest species to tolerate high water levels (Jones et al., 2006) that come with high precipitation during TCs (Maxwell et al., 2021) significantly increase tree mortality (Hall et al., 2020). With recent climate change, drought frequency will increase (Herrera and Ault, 2017), so shifts in forest moisture types are expected in the future, especially along the moisture gradient from hydric to xeric forests. Hence, we expect that a combination of future shifts in TC activity and increasing frequency of climate extremes could affect vast forest areas and may reduce tree species richness of U.S. temperate forests.

CRediT authorship contribution statement

PF and JA designed the study. PF aggregated data and did analyses. PF wrote the first draft of the manuscript with the contribution of JA, and all authors review & edit the manuscript.

Code for analyses

Available in https://github.com/pavel-fibich/fia-pub.

Data availability

R package rFIA (version 0.2.4) was applied to download the data in 5.2.2021.

Declaration of competing interest

Authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.163852.

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