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RESEARCH ARTICLE

Short-term effects of moderate severity disturbances on forest canopy structure

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Abstract

1. Moderate severity disturbances, those that do not result in stand replacement, play an essential role in ecosystem dynamics. Despite the prevalence of moderate severity disturbances and the significant impacts they impose on forest functioning, little is known about their effects on forest canopy structure and how these effects differ over time across a range of disturbance severities and disturbance types.
2. Using longitudinal data from the National Ecological Observatory Network project, we assessed the effects of three moderate severity press disturbances (beech bark disease, hemlock woolly adelgid and emerald ash borer, which are characterized by continuous disturbance and sustained mortality) and three moderate severity pulse disturbances (spring cankerworm moth, spongy moth and ground fire, which are associated with discrete and relatively short mortalities) on temperate forest canopy structure in eastern US. We studied (1) how light detection and ranging (LiDAR)-derived metrics of canopy structure change in response to disturbance and (2) whether initial canopy complexity offsets impact of disturbances on canopy structure over time. We used a mixed-effects modelling framework which included a non-linear term for time to represent changes in canopy structure caused by disturbance, and interactions between time and both disturbance intensity and initial canopy complexity.
3. We discovered that high intensity of both press and pulse disturbances inhibited canopy height growth while low intensity pulse disturbances facilitated it. In addition, high intensity pulse disturbances facilitated increases in the complexity of the canopy over time. Concerning the impact of initial canopy complexity, we

found that the initial canopy complexity of disturbed plots altered the effects of moderate disturbances, indicating potential resilience effects.

4. *Synthesis*. This study used repeated measurements of LiDAR data to examine the effects of moderate disturbances on various dimensions of forest canopy structure, including height, openness, density and complexity. Our study indicates that both press and pulse disturbances can inhibit canopy height growth over time. However, while the impact of press disturbances on other dimensions of canopy structure could not be clearly detected, likely because of compensatory growth, the impact of pulse disturbances over time was more readily apparent using multi-temporal LiDAR data. Furthermore, our findings suggest that canopy complexity might help to mitigate the impact of moderate disturbances on canopy structures over time. Overall, our research highlights the usefulness of multi-temporal LiDAR data for assessing the structural changes in forest canopies caused by moderate severity disturbances.

KEYWORDS

canopy complexity, canopy structural metrics, forest structure, moderate disturbance, multi-temporal LiDAR, NEON, press and pulse disturbance

1 | INTRODUCTION

Moderate severity forest disturbances (i.e. non-stand replacing) play an essential role in ecosystem dynamics (Gough et al., 2016). These moderate severity events (e.g. groundfire, insects, pathogens, ice, wind) can have variable effects on ecosystem processes such as carbon cycling, structural development and succession by leaving substantial portions of the ecosystem alive (Fahey et al., 2020; Fei et al., 2019; Gough et al., 2013; Nave et al., 2011). Moderate severity disturbances can remove specific forest components (e.g. a single species or size class), which can change canopy structure, resource availability (e.g. light and precipitation transmission/absorption) and microclimate, and subsequently, the competition among individual trees and demographic cohorts (Fahey et al., 2016; Stuart-Haëntjens et al., 2015). In many forested regions, the impacts of frequent but less severe moderate severity disturbances on ecosystem structure and function can outweigh the impacts of less frequent but more severe stand-replacing disturbances, as well as the more common but low-impact single/multiple tree gap formation (Sommerfeld et al., 2018). For instance, a bark beetle outbreak can spread throughout a forest and cause significant damage, including a reduction in biomass and productivity for relatively long periods and may even lead to stand-replacing events (Lovett et al., 2016).

Unlike stand-replacing disturbances (e.g. clear-cut, landslides, strong windstorms and severe wildfire), the effects of moderate severity disturbance on canopy structure or architecture can be highly variable depending on disturbance intensity, disturbance type, initial canopy structure and duration of disturbances. The intensity of moderate disturbances, for example, can affect the extent to which the disturbance alters structure and the duration of its legacy effects (Fahey et al., 2015; Gough et al., 2007; Scheuermann et al., 2018; Stuart-Haëntjens et al., 2015). Different disturbance types (i.e. different causal agents) can have distinctively different impacts on canopy structural attributes such as height, canopy density, openness, interior and exterior complexity (Atkins et al., 2020). Moreover, different canopy structure (i.e. three-dimensional canopy architecture) can influence ecosystem resistance to moderate severity disturbances (Hardiman et al., 2013). Together, these factors can impact the changes in canopy structures (Gough et al., 2022; Millar & Stephenson, 2015) and determine the response pathways of post-disturbance reorganization such as reassembly, restructuring and replacement (Seidl & Turner, 2022).

Moderate severity disturbances can vary widely in their causal agent (and thus the mode of mortality), timing, duration and spatial extent. For instance, insects and pathogens such as beech bark disease (*Cryptococcus fagisuga*, BBD), hemlock woolly adelgid *Adelges tsugae* (HWA) and emerald ash borer *Agrilus planipennis* Fairmaire (EAB) have negative impacts on their hosts that take relatively long periods of time to kill their host trees (deleterious for 1–10 years). In this study, we classified these three disturbances as *press disturbance* since their disturbances were continuous (Jentsch & White, 2019), but non-host species are not directly affected. These prolonged outbreaks disrupt water and nutrient transportation of their hosts (Cale et al., 2017; Herms & McCullough, 2014; Orwig & Foster, 1998). Disturbance magnitude caused by these insects and pathogens can be inferred by detecting changes in the growth rates, canopy density and complexity (Atkins et al., 2020; Edgar & Westfall, 2022). In contrast, *pulse disturbances* (Jentsch & White, 2019) such as insect defoliation (e.g. spongy moth *Lymantria dispar* [SPM] and spring cankerworm moth *Paleacrita vernata* [CAK]), wildfire, windstorm and salvage logging directly cause physical damage to canopy structures indiscriminate of tree species identity within a short period. The consequences of these temporally pulse disturbances often generate canopy openings or physical injuries to the trees (Bae et al., 2022).

Despite the prevalence of moderate severity disturbances and the significant impacts they impose on forest functioning, little is known about their effects on forest canopy structure or how these effects differ over time across a range of disturbance severities and disturbance types. This is primarily due to three reasons. First, moderate disturbances often have a small spatial extent, short duration and leave many live trees standing, creating challenges in detecting mortality and damage, unlike severe disturbance events. Second, there is a lack of adequate tools and datasets, such as repeated measurements of light detection and ranging (LiDAR) and ground observation data necessary to understand the development of ecosystem structure and function as forests respond to these events. Third, different mechanisms of mortality and wide-ranging ecological consequences make it difficult to identify consistent response patterns.

Here, we used data from the National Science Foundation's National Ecological Observatory Network (NEON) to understand the impacts of moderate disturbance on five terrestrial sites across the Eastern United States. More specifically, we aimed to characterize the effects of moderate disturbances (such as diseases insects, and wildfire) on the changes in LiDAR-derived canopy structure and subsequent canopy dynamics over time (Figure 1). We examined whether (1) different types of moderate disturbances inhibit or promote changes in canopy structures (ΔCS) and (2) initial canopy complexity has a significant effect on ΔCS. Combining repeated LiDAR remote sensing measures and ground observations (i.e. tree species, [DBH, cm], health status, disturbance agents) from NEON sites across multiple ecosystems in the United States, we identified patterns in the canopy structural outcomes of press and pulse moderate disturbance types.

2 | MATERIALS AND METHODS

2.1 | NEON study dataset and site

The National Science Foundation's NEON project provides temporal observations in the form of both ground and aerial datasets that can advance understanding of the ecological change and future ecological conditions across the continental United States. NEON monitors 47 terrestrial sites throughout the United States, each site contains a maximum of 50 base plots (including distributed and tower plots) (Thorpe et al., 2016). Each base plot (40×40 m), hereafter plot, is further divided into sub-plots to collect vegetation structure and composition data (see details in NEON (2022) and Thorpe et al. (2016)). Within each subplot, information such as tree species, DBH (cm), health status, disturbance types (i.e. insect, pest, fire, harvest), disturbance agents are recorded. These ground observation data are available from 2014. In addition, NEON provides repeated LiDAR measures for a subset of these sites (NEON, 2021a) since 2013.

In this study, we chose five NEON sites based on the presence of specific disturbance types in vegetation structure data (NEON, 2022) or the presence of their occurrences in site event reports (NEON, 2022): Bartlett Experimental Forest (BART), Harvard Forest (HARV), Smithsonian Conservation Biology Institute (SCBI), Mountain Lake Biological Station (MLBS), Great Smoky Mountains National Park (GRSM) (Figure 2). Within each site, we selected plots based on the availability of co-occurring ground observations and the NEON Airborne Observation Platform (AOP) LiDAR data that met two conditions: (1) contained at least 15 plots and (2) the mean of annual canopy height changes in each plot did not exceed and aberration threshold (<2.5 standard deviations from the mean of maximum height at each site). We excluded aberrations that exceeded this threshold as they were likely due to either stand-replacing disturbances (thus, severe rather than moderate) or unknown events. This resulted in 35, 31, 21, 23 and 21 plots for each year in BART, HARV, SCBI, MLBS and GRSM

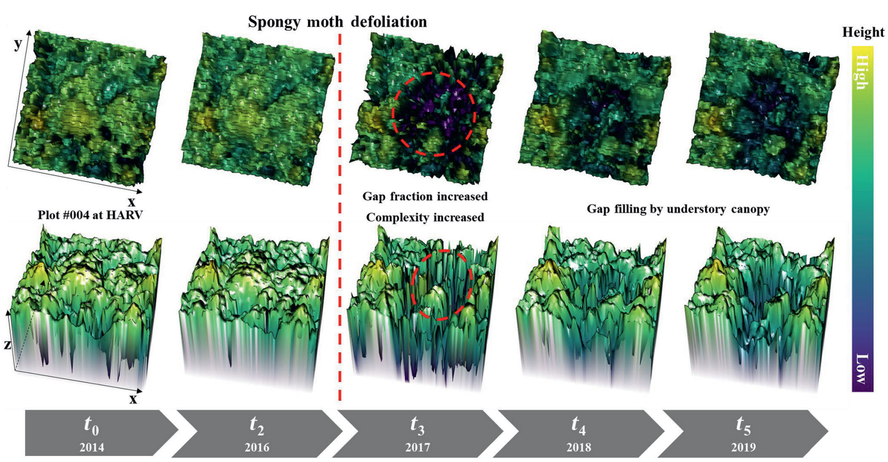

FIGURE 1 Example of moderate disturbance impact on canopy structure over time. Illustration of $0.5\times0.5\,m^2$ canopy height models of the National Ecological Observatory Network (NEON)'s no. 4 plot at Harvard Forest (HARV) site from t_0 (2014) to t_5 (2019) using NEON Airborne Observation Platform light detection and ranging data. Here, pre- and post-defoliation impacts of spongy moth *Lymantria dispar* (SPM) on canopy heights (blue to yellow gradient colours: low to high canopy height; red dashed line: SPM defoliation occurred time; red dashed circle: physical canopy reduction by SPM defoliation).

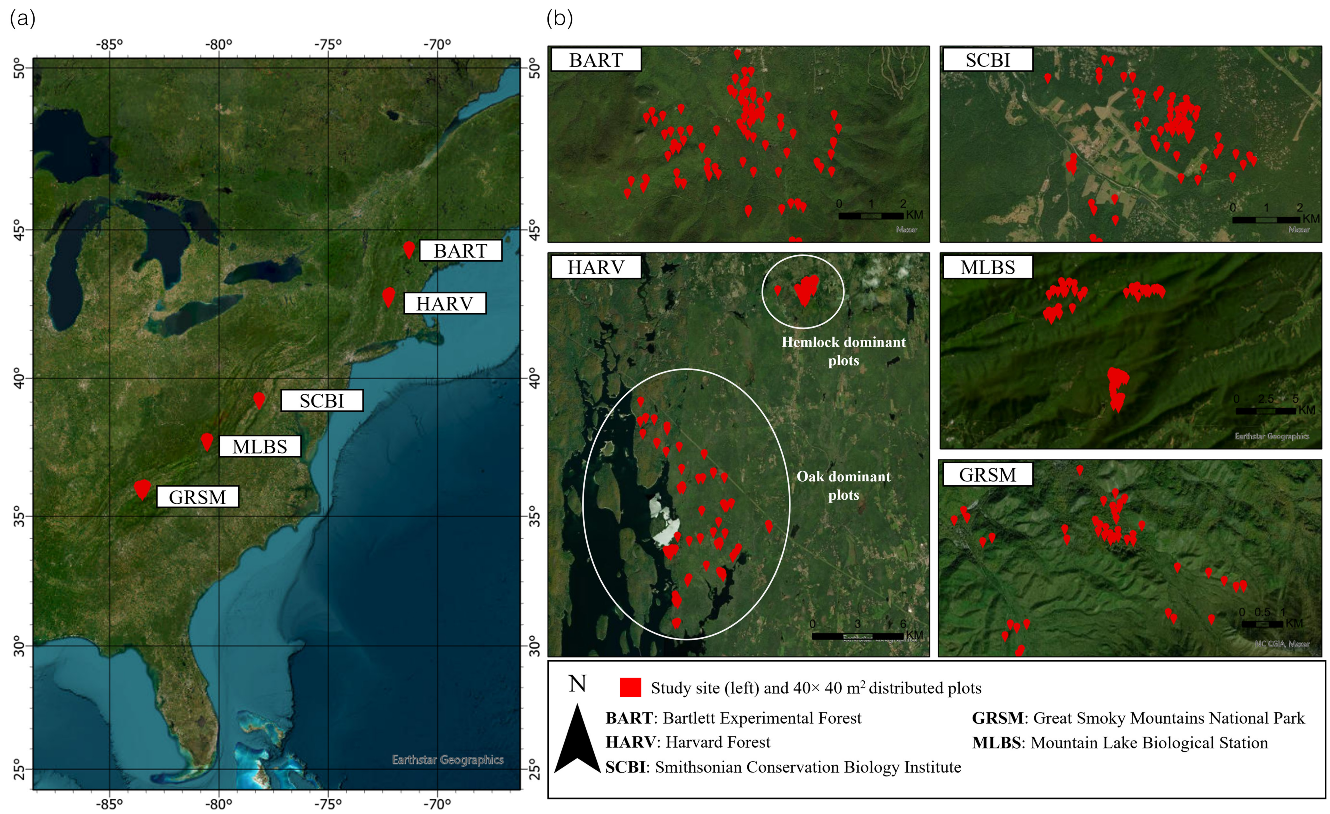

FIGURE 2 National Ecological Observatory Network study sites located across the eastern United States (a) and spatial locations of plots (b).

sites, respectively (Figure 2; Table S1). Each site had a distinct single moderate disturbance, except for HARV which experienced both SPM defoliation and (HWA; Table 1). In all, we included one pathogen, four insect diseases and one fire event in this study.

2.2 | Press and pulse moderate severity disturbances

We categorized disturbances into two types—press and pulse—based on their mortality mechanisms (Table 1) (Jentsch & White, 2019; White & Jentsch, 2001); press disturbances are characterized by continuous disturbance and sustained mortality. In contrast, pulse disturbances are associated with discrete and relatively short mortalities. Here, we included three press disturbances: BBD, HWA and EAB, which showed high host specificity and prolonged effects over multiple years; and three pulse disturbances: SPM and spring CAK, which caused repeated annual defoliations, and ground fire, which affected the tree canopies once or twice over a 10-year period (2013–2021).

2.2.1 | Press disturbances

Beech bark disease at Bartlett Experimental Forest

BBD (*Neonectria faginata* and *Neonectria ditissima*) is an insect–pathogen complex that can kill up to 20% of mature American beech trees (*Fagus grandifolia*) within 2 years and 50% within 10 years, with larger trees dying more quickly than smaller trees (McCullough et al., 2001). BBD has adverse effects on radial growth and the health of the host canopy, as evidenced by chlorosis and dieback of the leaves. BBD infection girdles the trunk and kills upper portions of the trees; the likelihood of this happening increases with tree size because small trees have fewer cankers on average (Cale et al., 2017; McCullough et al., 2001).

BBD was first reported at BART in the 1940s (Leak, 2006; NEON, 2021b) and a majority of the American beech trees in BART plots were infested with BBD at the time of the initial survey (NEON, 2022). As a result, we were unable to pinpoint the year of BBD's introduction to specific plots at the site and considered that BBD had affected the BART plots for at least a decade. To assess the canopy structural change caused by BBD, we compared the canopy structures of BART site in 2014 (t_0) to those of 2016 (t_2), 2017 (t_3), 2018 (t_4) and 2019 (t_5) (Table 1) to quantify progressive changes in canopy structure.

Hemlock woolly adelgid at Harvard Forest NEON

HWA; *Adelges tsugae* is a phloem-feeding insect that afflicts hemlock trees (*Tsuga canadensis*), causing distinct and lasting impacts to forest structure throughout the Eastern United States (Havill et al., 2014). HWA depletes the stored starches of a tree and impedes the flow of nutrients to the twigs and needles of the host tree (HWA kills the host from the inside out, resulting in intra-crown defoliation first

TABLE 1 Disturbance types at study sites.

Disturbance type		Host	Estimated effects on canopy structure based on the reference listed in this table	Detected site and year	Mean disturbance intensity (proportion of affected basal area) ± standard deviation	No. plots	No. of classified plots by the disturbance intensity		Reference
Press disturbance	Beech bark disease (BBD)	*Fagus grandifolia*	Canopy height growth reduction, gap fraction increase, canopy density reduction	BART, 1940s	20.98 ± 17.49 (%)	35	High Moderate Low	5 25 5	NEON (2022) Atkins et al. (2018) Cale et al. (2017)
	Emerald ash borer (EAB)	*Fraxinus* spp.	Canopy height growth reduction, gap fraction increase, canopy density reduction	SCBI, 2015	10.39 ± 8.86 (%)	21	High Moderate Low	4 13 4	Anderson-Teixeira et al. (2021) Gonzalez-Akre et al. (2016) Knight et al. (2010)
	Hemlock woolly adelgid (HWA)	*Tsuga canadensis*	Canopy height growth reduction, gap fraction increase canopy density reduction	HARV, 2008	30.34 ± 24.11 (%)	17	High Moderate Low	3 11 3	Havill et al. (2014) Atkins et al. (2018)
Pulse disturbance	Spongy moth (SPM)	Generalist	Gap fraction increase, canopy density reduction, rapid recovery rate	HARV, 2016, 2017	22.17 ± 18.91 (%)	20	High Moderate Low	3 13 4	NEON (2021b) NEON (2022) Conrad-Rooney et al. (2020)
	Cankerworm moth (CAK)	Generalist (deciduous tree)	Gap fraction increase canopy density reduction rapid recovery rate	MLBS, 2018	63.22 ± 18.46 (%) (*Quercus* spp. ratio)	23	High Moderate Low	4 15 4	NEON (2021b) NEON (2022) Darr and Coyle (2021)
	Ground fire (wildfire)	–	Gap fraction increase, canopy density reduction, rapid recovery rate	GRSM, 2016	34.49 ± 30.52	21	High Moderate Low	3 13 5	NEON (2022) Atkins et al. (2018)

then progressing outwards). Canopy gaps created by HWA-induced mortality significantly increases the amount of light reaching the forest floor and results in rapid understorey vegetation responses (Orwig & Foster, 1998). Hemlock trees can survive for many years after HWA infestation, with some surviving more than 15 years in northeastern US (Havill et al., 2014).

To study the canopy structural changes caused by HWA, we compared the CSs of 2014 (t_0) to those of 2016 (t_2), 2017 (t_3), 2018 (t_4) and 2019 (t_5) at HARV (Table S1). In 2008, HWA was observed for the first time in HARV, and by 2012, its dispersion was extensive. In 2016, significant tree mortality was recorded (Atkins et al., 2020).

Emerald ash borer at Smithsonian Conservation Biology Institute NEON

EAB; *Agrilus planipennis* is an invasive insect whose larvae damage the xylem tissue beneath the bark of trees, impeding water transfer and ultimately killing ash trees by stem girdling (complete mortality of ash stands), usually within 5 years of initial infestation (Knight et al., 2010, 2012). Canopy thinning and branch diebacks can be used to detect their damage (Herms & McCullough, 2014).

This invasive insect was first reported at SCBI in 2015. In 2016, EAB's distribution was widespread and considerable tree mortality was observed (NEON, 2022). To capture canopy structural dynamics in SCBI, we compared the CSs of 2016 (t_0) to those of 2017 (t_1), 2018 (t_2), 2019 (t_3) and 2021 (t_5) (Table 1).

2.2.2 | Pulse disturbances

Spongy moth at Harvard Forest NEON

SPM; *Lymantria dispar* is one of the most significant insect defoliators in the northeastern United States. Larva of the SPM feed on the leaves of their several host species, causing rapid and often complete defoliation. Insect defoliation is normally sub-lethal but can reduce host growth and repeated defoliation occurrences can potentially kill trees, especially when defoliation co-occurs with other disturbances such as drought that impair the carbon balance of the host trees (Conrad-Rooney et al., 2020; Dietze & Matthes, 2014).

In 2016 and 2017, entire oak-dominated stands were completely defoliated by SPM at HARV plots (NEON, 2021b). HARV experienced a severe drought during the 2016 growing season, amplifying the lethality of the impacts by SPM (NEON, 2021b) (drought stress can reduce trees' resistance to disturbances and make it more difficult to regenerate leaves after defoliation caused by SPM). To study the canopy structural change caused by SPM, we compared the CSs for HARV of 2014 (t_0) to those of 2016 (t_2), 2017 (t_3), 2018 (t_4) and 2019 (t_5) (Table 1).

Spring cankerworm moth disturbance at Mountain Lake Biological Station NEON

Spring CAK; *Paleacrita vernata* is a defoliator and outbreaks can cause serious damage to trees (Darr & Coyle, 2021). In May 2018, all oak trees in the identified plots at MLBS suffered from a severe defoliation and moderate recovery in the spring from CAK. This resulted in increased light penetration to the forest floor (NEON, 2021b). Therefore, we considered all oak trees in the plots were defoliated by CAK to calculate disturbance severity described in Section 2.3. To investigate the impact of defoliation by CAK, we compared the CSs for MLBS of 2017 (t_0) to those of 2018 (t_1) and 2021 (t_4) (Table 1).

Wildfire at Great Smoky Mountains National Park NEON

In November 2016, there was a wildfire in GRSM. The wildfire burned only a few GRSM plots severely, and it burned the ground vegetation of the majority of plots (groundfire) (Atkins et al., 2020). Low severity fires modify mainly the understorey vegetation and have modest effects on the overstorey (Atkins et al., 2020; Minor et al., 2017). To investigate the impact of wildfire at GRSM site, we compared the CSs of 2015 (t_0) to those of 2016 (t_1), 2017 (t_2), 2018 (t_3) and 2021 (t_4) (Table 1).

2.3 | Calculating disturbance intensity

The vegetation structure data (NEON, 2022) have records at individual tree level, including species, DBH, height and specific disturbance agent. For BBD, HWA, EAB, CAK and SPM, the intensity of disturbance was determined by the mean proportion of disturbed basal area to total basal area. We first calculated the basal area of each tree (DBH > 5 cm) and summed over all individuals (disturbed and undisturbed) to estimate total basal area of each plot. Then, we calculated the proportion of disturbed basal area to total basal area for each plot for each year (if ground surveys were conducted multiple times in a single year, we used the mean DHB values for calculating the basal area for that year). We then calculated the intensity of disturbance by taking the average of the proportion of disturbed basal area to total basal area of each plot across the years for all plots within five sites (equation 1).

$$\text{Disturbance intensity}\,(\%) = \text{Average of}\left(\frac{\sum \text{Basal area of disturbed(trees/plot)}}{\sum \text{Basal area of total(trees/plot)}} \times 100\right) \text{by year.} \tag{1}$$

Lastly, we classified high, moderate and low intensity levels by standard deviation of the affected basal areas across each disturbance agent (high intensity: more than 1 standard deviation greater than the mean; moderate intensity: between −1 and 1 standard deviations from the mean; low intensity: <−1 standard deviation below the mean). To prevent misunderstanding when discussing the relative impact of different moderate severity disturbances, we adopted the word disturbance intensity to indicate the magnitude or degree of impact observed among the moderate severity disturbances included in this study.

2.4 | Deriving canopy structural metrics from NEON AOP LiDAR data

2.4.1 | Calculating canopy structures and their changes(ΔCS), and initial canopy complexity

We quantified forest structure over time using NEON's annual AOP airborne LiDAR (Table S2). We calculated mean of maximum canopy height (MOMCH), leaf area index (LAI), subcanopy leaf area index (LAIsub), deep gap fraction (DGF), top rugosity (TR) and Gini index (Gini) which are robust for low to medium point density of discrete return LiDAR (LaRue et al., 2019, 2022) (Table S2). Since the LiDAR densities are different among years, we standardized the density to 4 points/m^2 by randomly selecting points from raw LiDAR point clouds in all plots and sites (Figure S1). Then, we calculated the point-based canopy metrics, such as LAI and Gini. Lastly, we generated a 1-m resolution canopy height model (CHM) using the pit free function, assuring that there were not any unintended canopy gaps on CHM due to artefacts of data processing and calculated CHM-based metrics, such as MOMCH, DGF and TR. All LiDAR data processing and analysis was done using the LIDR package (Roussel et al., 2020). The distributions of these metrics are found in Figures S1 and S2.

The changes in LiDAR-derived canopy structures (ΔCSs) were calculated by subtracting structural metrics of each year following the initial disturbance (t_n) from the first year (t_0) (i.e. ΔCS = canopy structures of T_n − canopy structures of T_0). The initial time (t_0 in Figure 1) was determined as the first year available in NEON's AOP data at each site. Therefore, it does not represent the pre-disturbance status of the plots at some sites (e.g. BBD at BART, CAK at MLBS, EAB at SCBI, and HWA at HARV sites) but rather the degree of change from the initial round of measurements.

We considered TR, a height variation of CHM (Table S2), to describe initial canopy complexity using the first available LiDAR acquisition year (t_0) at each NEON site, hypothesizing that initial canopy complexity would influence subsequent canopy dynamics and potentially resist against the disturbances (Hardiman et al., 2013). We classified high, medium and low complexity levels by standard deviation of rugosity (high complexity: more than 1 standard deviation; medium complexity: between −1 and 1 standard deviations; low complexity: <−1 standard deviation).

2.5 | Statistical analysis

To evaluate the impacts of moderate disturbance magnitude and direction (e.g. inhibition or facilitation) on canopy dynamics at the study sites, we applied a mixed-effects modelling framework (six disturbances and five ΔCSs: overall 30 models) (Figure 3). We embedded longitudinal observations (level 1) within NEON plot ID (level 2). In addition, because the trend and intercepts of ΔCSs are variable over time, the time term was allocated as random slope and intercept. The corAR1 function, a first-order autoregressive error structure for time measured at fixed intervals, was added to the models to address autocorrelation resulting from repeated measurements. Statistical analyses were conducted using the NLME package (Pinheiro, 2021) in R 4.1.2 software (R Core Team, 2021).

To test our hypotheses, we included (1) non-linear terms for time in the models (Billings et al., 2015; Stuart-Haëntjens et al., 2015) to describe the dynamics of canopy structures over time (Ryo et al., 2019), (2) two interactions terms of linear time term with disturbance severity and with initial canopy complexity to determine their moderator effects (i.e. to determine whether legacies of initial conditions and disturbance severity are related in impeding or facilitating ΔCS) (Figure 3). We normalized plot-level intensity and initial canopy complexity variables with each site (depending on the severity distribution of the data, we used log transformation or square root transformation). Here we used marginal R^2 and conditional R^2 to measure model performance. Marginal R^2 describes the variance explained by fixed effects, while conditional R^2 describes the variance explained by

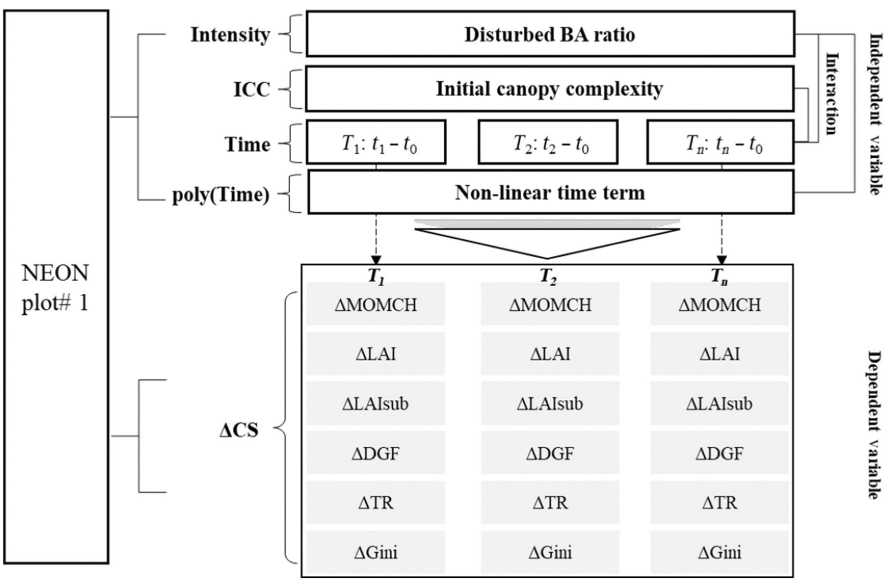

FIGURE 3 Illustration of the structures of repeated measured data and mixed models in this study.

both fixed and random effects (Nakagawa & Schielzeth, 2013). Therefore, marginal R^2 close to 1 indicate that the fixed effects adequately explain variance, and conditional R^2 close to 1 indicate that the majority of unexplained variation is across groups (in this case, years) rather than between measures within years. Lastly, we generated predictor effect plots using the EFFECT package in R (Fox & Weisberg, 2018) to understand the interaction effects between disturbance intensity and time and initial canopy complexity and times.

We also conducted a non-parametric Friedman test for comparing yearly repeated measurements (i.e. multi comparisons) with Bonferroni test for correcting the significance level, $\alpha=0.05$ to $\alpha=0.05/c$, where c is the number of comparisons. By conducting this test, we derived the significant differences of the LiDAR-derived canopy structural metrics among the measured years at each site.

3 | RESULTS

In this study, we tested statistical interaction effects between disturbance intensity and time and between initial canopy complexity and time for changes in canopy structures. Briefly, the findings indicated that press disturbances inhibited canopy height changes over time, while no significant interaction effects were observed between the intensity of press disturbances and time for other canopy structure changes. Conversely, pulse disturbances displayed significant interaction effects with time for alterations in canopy structures. Furthermore, we found that the interaction effects between initial canopy complexity and time for changes in canopy structures exhibited opposite trends in comparison to the interactions between disturbance intensity and time.

3.1 | Changes in canopy structures over time by disturbance type and severity

3.1.1 | Press disturbances: BBD, HWA and EAB

Changes in height

Changes in canopy height showed non-linear trends over time ($p<0.1$) (height row on Figure 4). BBD- and HWA-disturbed plots showed similar trends showing accretionary changes in their canopy heights, while EAB-disturbed plots did not. For example, during the study periods (i.e. between first and last years) canopy height (i.e. MOMCH) significantly increased in BBD- (median increased by nearly 6%, $p<0.01$) and HWA- (median increased by nearly 8%, $p<0.01$) disturbed plots (Figure 4a-1,b-1). In contrary, canopy height in EAB-disturbed plots was not significantly changed up to 3 years (t_0–t_3) but then its median value declined by about 2% between t_3 and t_5 ($p<0.01$, Figure S3).

We discovered a significant interaction between time since disturbance and disturbance intensity, with canopy growth being slower after disturbances of greater intensity ($p<0.01$ and $p<0.1$, respectively) (Figure 5a-1,c-1, respectively). On the contrary, the canopy height growth was not inhibited by the HWA disturbance (the interaction between HWA intensity and time did not show significances for the changes in canopy height over time, $p>0.1$) (Figure 5; Table S3).

Changes in openness and density

Changes in canopy density (i.e. LAI) affected by press disturbances describe non-linear trends over time, while canopy openness does not (openness row on Figure 4). Unlike accretionary changes in their canopy heights, changes in LAI fluctuated in BBD- and HWA-affected plots over time resulting in non-significant differences between first and last years of observations (Figure 4a-3,b-3; Figure S3). Moreover, changes in subcanopy density (i.e. LAIsub) of BBD-affected plots declined by 26% between t_3 and t_5 ($p<0.05$, Figure 4a-4; Figure S3) and that of HWA-affected plots did not change significantly over time (Figure 4b-4). EAB-affected LAI also declined by about 1% between t_0 and t_3 and increased by about 33% between t_3 and t_5 (Figure S3).

Although canopy densities affected by press disturbances changed significantly over time, we could not find significant interaction effects between intensities of press disturbances and time for changes in ΔDGF, ΔLAI and ΔLAIsub (Figure 5). These non-significant interactions may indicate the intensity of press disturbances did not suppress the canopy densities or expand canopy openings during the study periods contrary to what we expected (shown in Table 1).

Changes in canopy complexity

Canopy complexity (both TR and Gini) changed non-linearly over time (Figure 4a-5,a-6, b-5,b-6, c-5,c-6). For example, ΔTR of canopies affected by BBD and HWA exhibited repeated increase and decrease, but overall (comparison between initial year and last year) medians of ΔTRs declined by about 7% and 10%, respectively (Figure S3). ΔGini of canopies affected by BBD and HWA also responded non-linearly (Figure 4a-6,b-6), but overall changes were not significant (Figure S3). On the other hand, TR and Gini of EAB-affected plots did not show fluctuations (Figure 4c-5,c-6), but they significantly increased by 23% and 14%, respectively, over time (Figure S3).

Only BBD intensity had a negative impact (impeding) on their changes in canopy complexity TR over time ($p<0.1$) (Figure 5a-6; Table S3), indicating that BBD intensity made canopy complexity stable or less complex than in previous times.

3.1.2 | Pulse disturbances: SPM, CAK and fire

Pulse disturbance intensities showed more substantial interaction effects with time than the impact of press disturbances on canopy structures (Figure 5).

Changes in height

Changes in canopy height (i.e. MOMCH) of SPM- and wildfire-disturbed plots exhibited reductions and following increments after

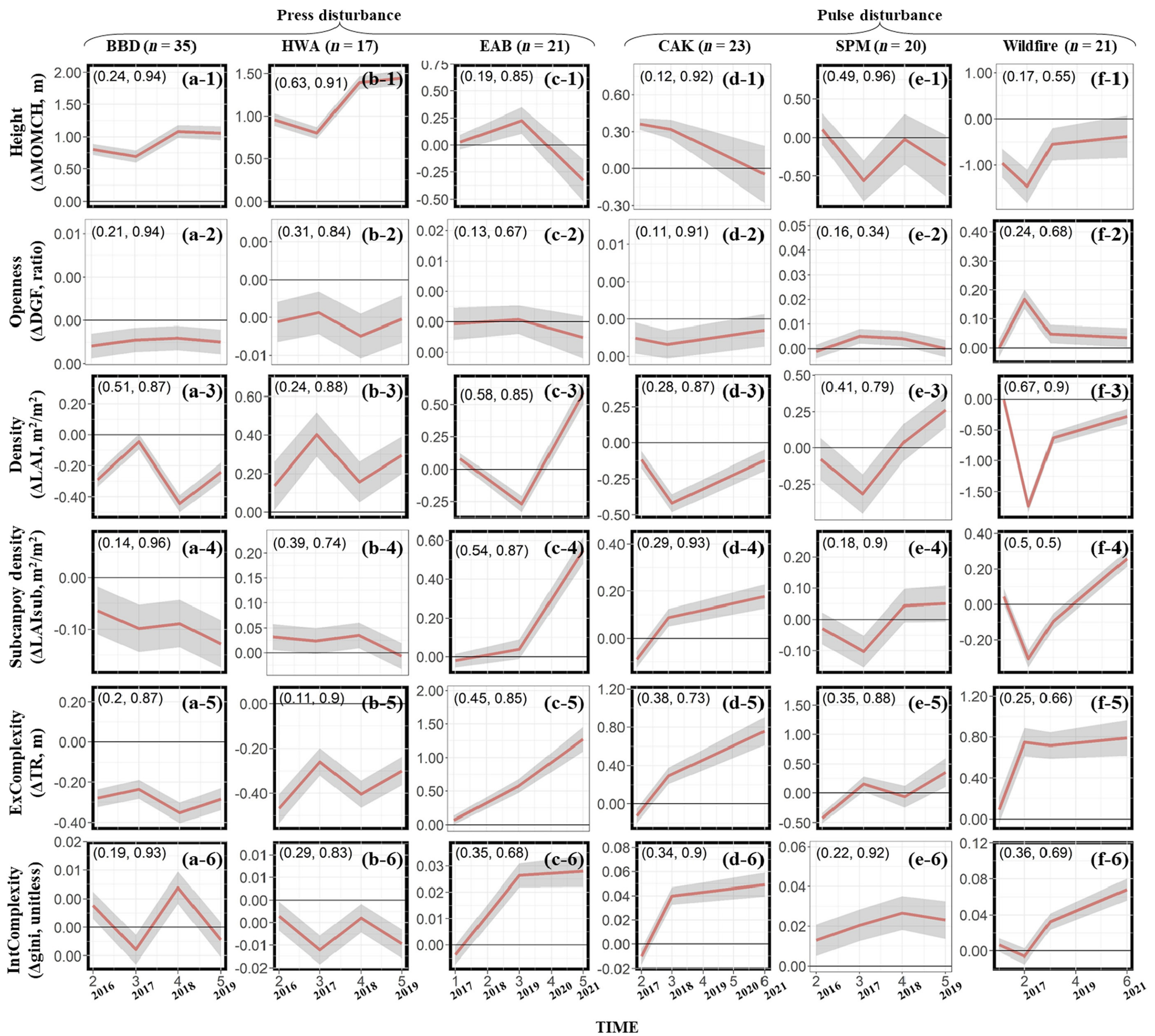

FIGURE 4 Temporal changes in canopy structures. The figure shows the predictor effects plots displaying changes in height, deep gap fraction, LAI, top rugosity and Gini index over time (marginal and conditional R^2 values are at the top of each panel [i.e. (marginal R^2, conditional R^2)] and thick black box denotes the significant model [$p<0.05$] for time term; shaded areas indicate 95% confidence interval; vertical dashed line indicates pulse disturbances occurred times). LAI: leaf area index.

the disturbances ($p<0.1$) (Figure 4; Table S3), while that of CAK-disturbed plots did not ($p>0.1$).

We found significant interaction effects between disturbance intensity and time of two pulse disturbances (SPM and wildfire) (Figure 5e-1,f-1). High intensity of SPM- and wildfire-inhibited canopy height growth (i.e. negative interaction effect, $p<0.05$, Figure 5e-1,f-1; Table S3), while their low intensity facilitated canopy height growth over time.

Changes in openness and density

We found that ground wildfire increased canopy opening immediately after the disturbances (i.e. ΔDGF showed non-linear relationship with time in wildfire-disturbed plots) (Figure 4; Figure S3). After the groundfire, the opening areas increased by 150% between t_1 and t_2 (Figure S3), and then they decreased by 114% between t_2 and t_3. In case of the impacts of the interaction between disturbance intensity and time, only CAK intensity showed significant interaction with time for ΔDGF (i.e. high CAK intensity facilitated opening canopies) ($p<0.05$, Figure 5).

Changes in canopy densities (both LAI and LAIsub) showed non-linear trends in plots affected by pulse disturbances throughout time (Figure 4). LAI of canopies impacted by pulse disturbances (CAK, SPM and wildfire) declined by 18% (t_3), 12% (t_3) and 65% (t_2) and afterwards increased by 17% (t_6), 16% (t_4) and 255% (t_3), respectively (Figure 4; Figure S3). LAIsub of SPM- and wildfire-disturbed plots also declined by 25% and 97%, respectively, and afterwards increased over 100% (Figure 4; Figure S3).

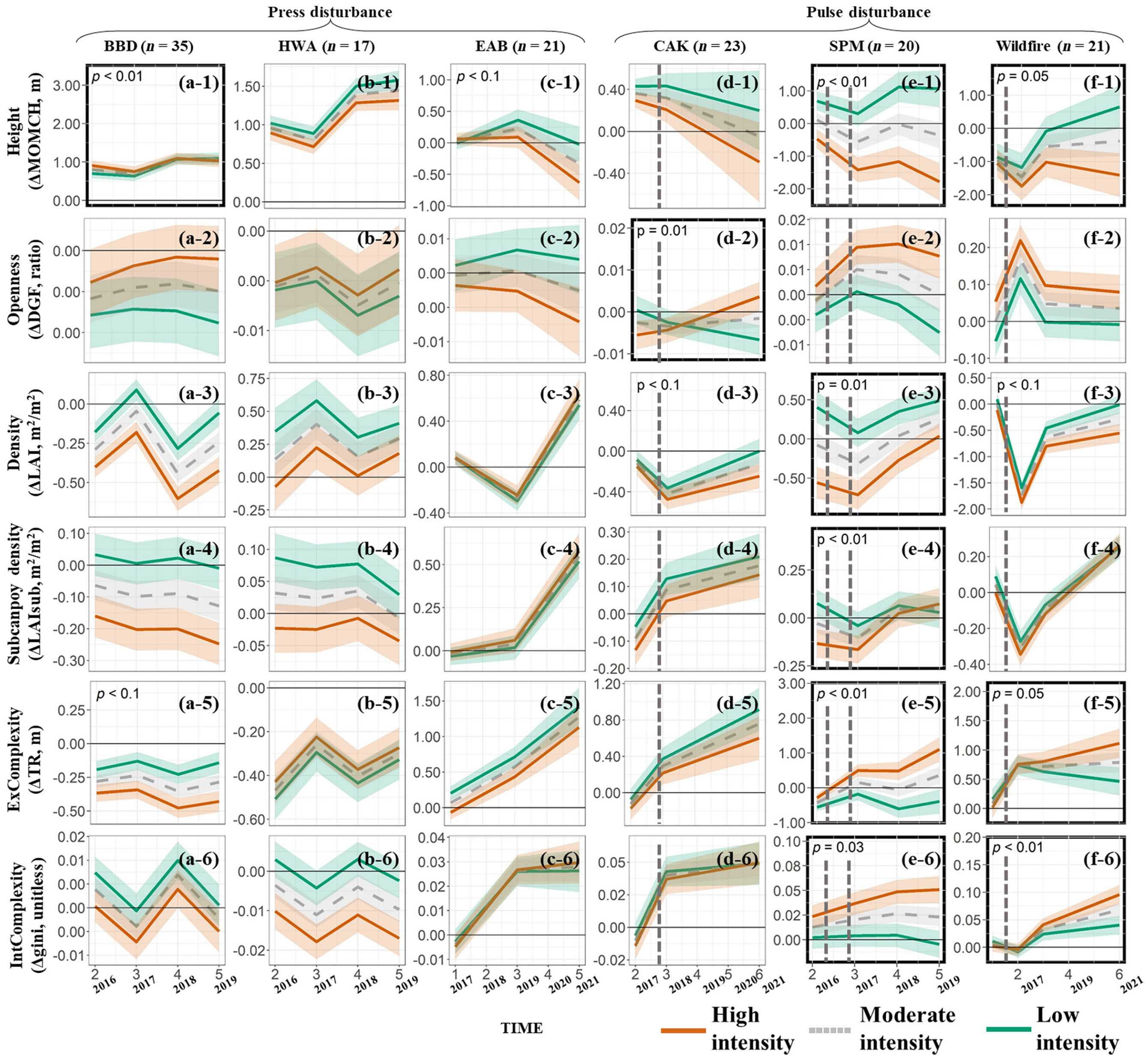

FIGURE 5 The effects of disturbance intensity on changes in canopy structures over time. The figure shows the interaction effects between disturbance intensity and time for changes in height, deep gap fraction, leaf area index, top rugosity and Gini index. Each plot shows predictor effects displaying how high, moderate and low disturbance intensity levels impact on canopy structures over time (high intensity: more than 1 standard deviation; medium intensity: between −1 and 1 standard deviations; low intensity: <−1 standard deviation) (black boundary denotes $p < 0.05$ for interaction term between time and disturbance severity; shaded areas indicate 95% confidence interval; vertical dashed line indicates pulse disturbances occurred times).

We found that high intensities of CAK and wildfire inhibited increase in canopy density (i.e. negative interaction effects for ΔLAI, $p < 0.1$). Moreover, we found high SPM intensity facilitated increase in both canopy density and subcanopy density (i.e. positive interaction effect for ΔLAI and ΔLAIsub, $p < 0.01$) unlike other those of CAK and wildfire.

Changes in canopy complexity

Exterior and interior canopy complexities (i.e. TR and Gini, respectively) in general increased after pulse disturbances (Figure 4). For example, median values of TR significantly increased by more than 20% after the pulse disturbances occurred ($p < 0.05$, Figure S3). In addition, median values of Gini significantly increased by more than 40% after the CAK defoliation, but not significant after SPM and wildfire disturbances occurred (Figure S3).

Changes in exterior and interior complexities were significantly facilitated by high intensities of SPM and wildfire over time ($p < 0.05$, Figure 5e-5,e-6, f-5,f-6). This finding describes how canopy surface became more complex and vertical canopy distribution became more heterogeneous in SPM- and wildfire-disturbed plots than before the disturbances occurred.

3.2 | Interaction effects between initial canopy complexity and time for changes in canopy structures

3.2.1 | Press disturbances

Changes in height

Initial canopy complexity positively correlated with changes in canopy height, while it exhibited negative interactions with time on changes in canopy height (i.e. MOMCH) in BBD- and HWA-disturbed plots (Figure 6; Table S2). This finding may suggest that the initial canopy complexity of the canopy has a positive influence on canopy height growth following disturbances; however, this effect was not sustained over time and resulted in a reduction in canopy surface complexity over time (negative interaction with time) (Figure 6a-1,b-1; Table S2).

Changes in density and openness

High initial canopy complexity promoted increase in canopy density in HWA-affected plots (Figure 6b-3) (positive interaction between initial canopy complexity and ΔLAI; $p<0.05$, Table S2). Moreover,

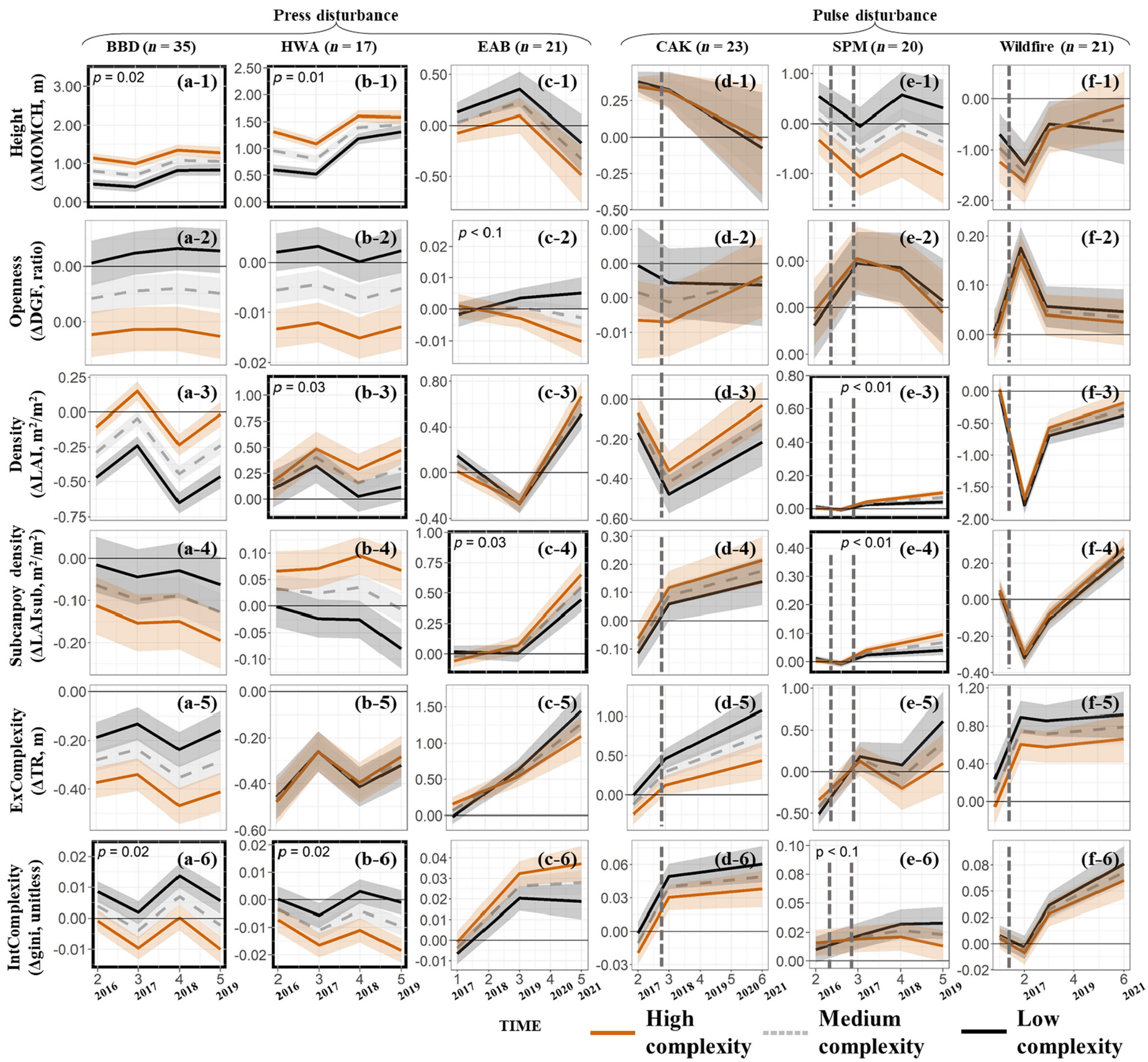

FIGURE 6 The effects of initial canopy complexity on changes in canopy structures over time. The figure shows the interaction effects between initial canopy complexity and time for changes in height, deep gap fraction, leaf area index, top rugosity and Gini index. Plots show predictor effects displaying how levels of initial canopy complexity impact on canopy structures over time (high complexity: more than 1 standard deviation; medium complexity: between −1 and 1 standard deviations; low complexity: <−1 standard deviation) (black boundary denotes $p<0.05$ for interaction term between time and disturbance severity; shaded areas indicate 95% confidence interval; vertical dashed line indicates pulse disturbances occurred times).

in EAB-disturbed plots, high initial canopy complexity facilitated subcanopy increase (increase in LAIsub in Figure 6c-4) and canopy closure (negative interaction with time on ΔDGF).

Changes in canopy complexity

Initial canopy complexity had negative interaction effects with time only for changes in interior canopy complexity (i.e. Gini) at BBD- and HWA-affected plots. Complexity of the canopy in both affected plots declined continuously over time (Figure 6a-6,b-6).

3.2.2 | Pulse disturbances

We only observed significant interaction effects between initial canopy complexity and time in plots impacted by SPM among the pulse disturbances. Initial canopy complexity had positive interaction effects with time for changes in canopy density (i.e. LAI and LAIsub). These findings show high initial canopy complexity help increasing the quantity of leaves in canopy in SPM-disturbed plots than before the disturbances occurred.

4 | DISCUSSION

We investigated whether moderate severity disturbances increased or decreased changes in an array of canopy structure metrics over time. We discovered that the intensity of moderate severity disturbances inhibited canopy height growth (in both press and pulse disturbance-affected plots) and decreased canopy density (in pulse disturbance-affected plots), while facilitating short-term increases in canopy openness and complexity.

We found BBD and EAB disturbances among press disturbances can suppress canopy height growth over time ($p<0.1$) (Figure 5a-1,c-1). While we observed that general changes in canopy structures responding to the intensity of press disturbances were not significant (Figure 5). These findings could be attributable to the following reasons. First, press disturbances do not physically alter the canopies directly, and their impacts on canopies do not manifest for one to several years after infection, or do not manifest at all (Cale et al., 2017; Hoven et al., 2020; Knight et al., 2012; Orwig & Foster, 1998; Stadler et al., 2005). Second, while suppressions of canopies by press disturbances proceed slowly, non-host tree species can grow rapidly when released from competition for resources (McDowell et al., 2020). These replacements of host tree species by non-host or subcanopy tree species after the infections (Cale et al., 2017; Fahey et al., 2016; Hoven et al., 2020; Knight et al., 2012; Stuart-Haëntjens et al., 2015) will obscure the impacts of press disturbances, eventually making them difficult to detect in yearly collected LiDAR data (Gao et al., 2020).

Our results showed similarities and dissimilarities with results from previous studies. Atkins et al. (2020) discovered BBD-affected plots formed more open volume inside (empty or unoccupied space) canopies. However, they discovered that the total density of vegetation in the forest's densest places increased, most likely as a result of enhanced forest floor light availability leading in the release of seedlings and saplings from the lower canopy (Atkins et al., 2020). Our results also revealed that canopy density had decreased between initial and final years of observation (median values of LAI decreased from 3.94 to 3.69 m^2/m^2), but there were fluctuations (repetitive increase and decrease) in between the study periods (Figure 4), likely due to canopy replacements and infilling from the sides of gaps. In addition, Atkins et al. (2020) examined the CS from low to moderate HWA infections at HARV (ForestGeo plots). They observed that high HWA intensity caused forest complexity to rise as infestation and mortality progressed. Furthermore, Boucher et al. (2020) discovered a substantial drop in canopy density in HARV ForestGeo plots caused by HWA between 2012 and 2016. We could not find significant main and interaction impacts of the HWA intensity on canopy structures ($p > 0.05$); however, we observed that the HWA-disturbed plots became less complex than before over time (median values of TR were 2.83 at t_0 and 2.54 at t_5, Figure S3) and very weak negative effects of the intensity on canopy density ($p=0.11$). These differences in results may be caused by the differences in proportion of hemlock tree distribution; our NEON plots consisted of more subcanopy species compared to the ForestGeo plot studied by Atkins et al. (2020). Furthermore, we suspected that accelerated growth of subcanopy species responding to increased light availability caused by increased canopy openings might fill the gaps, obscuring changes in canopy density (positive correlation between DGF and LAIsub [0.411, $p<0.001$]) (Figure S2). Lastly, we found that canopy height declined in EAB-plots 3 years after the infection. Based on the findings from Knight et al. (2012) and Hoven et al. (2020), we speculated this EAB impact might drive the canopy replacement by understorey species, such as *Asimina triloba* (shrub species, height <2 m).

In contrast to press disturbances, canopy structures responded immediately to pulse disturbances, such as CAK, SPM and wildfire (Figure 5). These responses are characterized by substantial abruptness, with large magnitudes and quick recoveries over time (Figure 5; Figure S3). In general, the intensity and time interactions of the pulse disturbances evaluated in this study exhibited similar temporal patterns, inhibiting canopy height growth and density increase and facilitating canopy opening and structural heterogeneities (Figure 4).

CAK and SPM are representatives of defoliation-type disturbances. Frequent defoliations can weaken the health of trees and ultimately increase tree mortality (McDowell et al., 2020; Townsend et al., 2012). CAK and SPM exhibited different short-term impacts. We found CAK intensity facilitated opening canopies as we expected (Table 1), whereas SPM intensity inhibited canopy height growth and facilitated canopy density increase after disturbances occurred (Figure 5d,e; Figure S3). Inhibition of canopy height growth by SPM intensity could be due to oak tree mortality by successive years of defoliation in 2016 and 2017 at HARV (Conrad-Rooney et al., 2020; Morin & Liebhold, 2015; NEON, 2021b). Furthermore, we postulated that the observed increase in canopy density resulting from SPM intensity could be attributed to the defoliation caused by SPM, which leads to the creation of gaps within the upper canopies and subsequently increases light availability (Rozendaal & Kobe, 2014) for the understory canopy. This process of gap creation may, in turn, facilitate the establishment and growth of subcanopy species in SPM-affected areas.

In case of wildfire, we found canopy density (i.e. LAI) immediately decreased by about 65% (Figure 4f-3; Figure S2) similar to Atkins et al. (2020)'s study. In addition, we observed that in intensely burnt plots, canopy height and density did not recover, while low intensity fire seems to facilitate the canopy growth and canopy density increase between 2016 to 2021, which were shown in significant negative interaction effects between disturbance intensity and time (Figure 5f-1,f-3). These findings imply that low intense ground fire facilitates canopy dynamics and boosts forest growth and productivity.

Finally, we investigated whether the initial canopy complexity mitigated the effects of disturbance intensity on canopy structural changes. We found initial canopy complexity supported both resistance and resilience of canopy structure (Fahey et al., 2016; Gough et al., 2013; Hardiman et al., 2013) to the press disturbances in terms of maintaining their canopy structures. For instance, the plots affected by BBD and HWA showed that their initial canopy complexity had a positive relationship (i.e. main effect) with canopy height growth while disturbance intensity inhibited canopy height growth over time (Figure 6a-1,b-1; Table S3). As the interaction effects between initial canopy complexity and time exhibited negative relationships with changes in canopy height, we could speculate that this resistance would not persist for longer periods as canopy complexity decreased with time (Figure 6a-1,b-1; Figure S3). Furthermore, for HWA- and EAB-disturbed plots, high initial canopy complexity seemed to increase the quantity of leaves in the canopy (LAI and LAIsub of HWA and EAB, respectively) by increasing fraction of available light (Figure 6b-3,c-4; Figure S2) (Hardiman et al., 2011).

Similar to BBD- and HWA-infested plots, the initial canopy complexity of SPM-defoliated plots may result in stable vegetation structure (negative interaction effect between initial canopy complexity and time for ΔGini, $p<0.1$) (Figure 6). Defoliation of upper canopies will likely increase understorey light availability on the forest floor, and subsequently promote the rapid growth of subcanopy species (positive interaction effects between initial canopy complexity and time for ΔLAI and ΔLAIsub, $p<0.01$). As seen in Figure 6 by the suppression of Gini in SPM-disturbed plots, rapid growth of subcanopies caused by an increase in understorey light availability after SPM may have caused a more uniform vertical distribution than before SPM (positive correlations between Gini and LAIsub [correlation coefficient = 0.670, $p<0.001$]) (Figure S2).

The impacts of press disturbances could be influenced by multiple factors that are related to LiDAR sensing configurations and the relationships between LiDAR-derived metrics. First, while annual remeasurement LiDAR data is rarely available, annual data may not have sufficient temporal resolution (Table 1) to capture the cascade of canopy structure which hinders our ability to detect the effects of press disturbances. Since press disturbances deleterious affect trees for relatively long periods (1–10 years), frequent and long-term data may be required to differentiate between the effects of growth and those of disturbances on changes in canopy structures. Second, the cascading effects could influence the impacts of the disturbances. As shown in Figure S2, there were high correlations among the LiDAR metrics. In this study, we did not analyse the cascading effects of changes in canopy structures (i.e. the cascade of canopy structure changes) as a result of the disturbances. For instance, disturbances can accelerate subcanopy growth by creating the canopy openings; the resulting expansion of subcanopy in these forests could be then associated with a rise in canopy complexity. Therefore, future studies are required to figure out how various types of structural responses to disturbance are linked. Lastly, different LiDAR densities across years may also influence the values of the structural metrics that were derived (Figure S2). Despite our attempts to homogenize the point density in this study, vertical point distribution may be influenced by the beam strength of LiDAR sensors, resulting in variations in point density and canopy structural metrics. Using the same configurations and settings of LiDAR sensors could improve the ability to detect the effects of moderate severity disturbances on canopy structure over time.

5 | CONCLUSIONS

Our study examined the short-term impacts of moderate severity disturbances on changes in canopy structures over time, as well as the mitigating effects of initial canopy complexity over time. We found that moderate severity disturbances in general inhibit canopy height growth. Pulse disturbances quickly produced marked changes in canopy structure and appeared to drive development of subcanopies by expanding canopy openings in the upper canopy. Moreover, initial canopy complexity mitigated with the impacts of moderate disturbances on changes in canopy structures, suggesting a potential ecological mechanism supporting resistance.

Our findings also provided insights into how forest structures stabilize during or following moderate severity disturbances, which may be interpreted as structural resilience. As responses to press disturbances indicate, structural resilience might obscure the influence of interaction effects between disturbance intensity and time since disturbance on canopy structures except for the canopy height growth. Therefore, future work will characterize feedback loops between the impacts of disturbances and the mitigation effects of initial canopy complexity in terms of canopy structural resilience. In addition, this study may hold promise for ecological research, including the effects of moderate severity disturbances on forest productivity and the effects on biodiversity (e.g. changes in niche spaces) (LaRue, Fahey, et al., 2023; LaRue, Knott, et al., 2023).

AUTHOR CONTRIBUTIONS

All authors contributed to the intellectual development and conception of this manuscript; Dennis Heejoon Choi, Songlin Fei, and Brady S. Hardiman conceived and designed the study; Dennis Heejoon Choi analysed the data with support from Songlin Fei, Brady S. Hardiman, Jeff W. Atkins, Elizabeth A. LaRue, Jane R. Foster, Jaclyn Hatala Matthes, Robert T. Fahey and Bina Thapa; Dennis Heejoon Choi wrote the first draft of the manuscript; all authors contributed equally to revising subsequent drafts of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14145.

DATA AVAILABILITY STATEMENT

NEON's Discrete return LiDAR point cloud data (DP1.30003.001) are available at: https://doi.org/10.48443/6E8K-3343 (NEON, 2021a). NEON's Vegetation structure data (DP1.10098.001) are available at: https://doi.org/10.48443/RE8N-TN87 (NEON, 2022). R scripts for calculating canopy metrics are available at the Environmental Data Initiative (EDI): https://doi.org/10.6073/pasta/97f8092c10aecbc62aec12557ecb52bd (Hardiman et al., 2021). Derived data are available at Zenodo: https://doi.org/10.5281/zenodo.7966264 (Choi et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. National Ecological Observatory Network (NEON) site description.

Table S2. Canopy structural metrics and their description (LaRue et al., 2019).

Table S3. Modelling results showing estimates and significances (*$p<0.1$, **$p<0.05$, ***$p<0.01$) (from top to bottom: beech bark disease, hemlock woolly adelgid, and emerald ash borer, canker worm moth, spongy moth, and ground fire).

Figure S1. Violin plots of light detection and ranging (LiDAR)-derived metrics by the different years (A–G: years of LiDAR data acquisition; colours: National Ecological Observatory Network sites).

Figure S2. Correlograms showing correlations among the light detection and ranging metric. Colours indicate different five National Ecological Observatory Network sites selected in this study.

Figure S3. Repeated measures Friedman test by the disturbance types (row) and canopy structural metrics (column) (horizontal black lines and red coloured numbers inside bar graph indicate median values; horizontal bar lines on the plots indicate significant differences between comparing 2 years.)

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