Application of multidimensional structural characterization to detect and describe moderate forest disturbance

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Abstract. The study of vegetation community and structural change has been central to ecology for over a century, yet the ways in which disturbances reshape the physical structure of forest canopies remain relatively unknown. Moderate severity disturbances affect different canopy strata and plant species, resulting in variable structural outcomes and ecological consequences. Terrestrial lidar (light detection and ranging) offers an unprecedented view of the interior arrangement and distribution of canopy elements, permitting the derivation of multidimensional measures of canopy structure that describe several canopy structural traits (CSTs) with known links to ecosystem function. We used lidar-derived CSTs within a machine learning framework to detect and describe the structural changes that result from various disturbance agents, including moderate severity fire, ice storm damage, age-related senescence, hemlock woolly adelgid, beech bark disease, and chronic acidification. We found that fire and ice storms primarily affected the amount and position of vegetation within canopies, while acidification, senescence, pathogen, and insect infestation altered canopy arrangement and complexity. Only two of the six disturbance agents significantly reduced leaf area, counter to common assumptions regarding many moderate severity disturbances. While findings are limited in their generalizability due to lack of replication among disturbances, they do suggest that the current limitations of standard disturbance detection methods—such as optical-based remote sensing platforms, which are often above-canopy perspectives—limit our ability to understand the full ecological and structural impacts of disturbance, and to evaluate the consistency of structural patterns within and among disturbance agents. A more broadly inclusive definition of ecological disturbance that incorporates multiple aspects of canopy structural change may potentially improve the modeling, detection, and prediction of functional implications of moderate severity disturbance as well as broaden our understanding of the ecological impacts of disturbance.

Key words: disturbance; ecosystem ecology; forest structure; lidar; NEON; remote sensing.

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INTRODUCTION

Disturbances generally alter forest structure, but variation in the severity, intensity, and frequency of disturbance leads to variable structural outcomes. Shifting vegetation composition, abundance, and distribution patterns further shape disturbance response (Pickett and White 1985, Frelich and Lorimer 1991, Frelich and Reich 1999, Frolking et al. 2009). While ecologists have long studied how disturbance severity, intensity, and frequency reshape vegetation structure (Connell 1978, Johnstone et al. 2016, Turner et al. 2016, Cale et al. 2017), the structural differentiation as a function of the agent of disturbance has not been systematically characterized across forested ecosystems using standardized methods (Jimenez et al. 1985, Foster et al. 1999, Amiro 2001, Łaska 2001, Hanson and Lorimer 2007, Buma 2015).

Moderate severity disturbances (i.e., non-stand replacing or partial disturbances, also referred to as lower magnitude change) can produce a wide array of structural outcomes, including highly heterogeneous structural conditions across a variety of spatial scales (Woods 2004, Hanson and Lorimer 2007, Fahey et al. 2015). At moderate severities, the importance of disturbance agent in driving variable structural and functional outcomes may be equivalent in magnitude to other well-characterized factors such as severity, intensity, and frequency (Hardiman et al. 2013). Without considering the structural divergence associated with different disturbance agents, our ability to construct generalized frameworks to characterize disturbance effects and make inferences about structure–function relationships following moderate disturbance is limited (Turner et al. 2001, White and Jentsch 2001).

Separate investigations of extreme weather, fire, windthrow, insect invasion, and pathogen outbreak events suggest disturbance agents imprint quantifiably distinct patterns of vegetation redistribution and structural change (Dale 2001, Hanson and Lorimer 2007, Frolking et al. 2009, Plotkin et al. 2013, Oldfield and Peterson 2019, Peterson 2019, Fig. 1). Some disturbance agents affect the vertical distribution of vegetation—ice and windthrow reduce foliage in the upper canopy (Frolking et al. 2009, Weeks et al. 2009, Fig. 1A), while ground fires may disproportionately remove subcanopy vegetation (Turner et al. 2001; Fig. 1B). Host-specific insects and pathogens, including beech bark disease and hemlock woolly adelgid, alter the horizontal distribution of vegetation through the creation of canopy gaps and canopy thinning (Orwig and Foster 1998, Fahey et al. 2015, Arthur et al. 2017, Fig. 1C).

Most evidence that disturbance agents create divergent structural outcomes comes from studies that are either solely qualitative or limited in the structural outcomes they consider (Franklin et al. 2002, Roberts 2007). Disturbance effects on vegetation structure are inherently multidimensional and may not be easily summarized, or detected, using a single structural parameter (Lowman and Rinker 2004, Frolking et al. 2009), yet the effects of disturbance on vegetation structure are typically described using dimensionless structural parameters (Waring and Schlesinger 1985) or as unidimensional shifts in vegetation canopy height or openness (Parker and Brown 2000, Weeks et al. 2009, McMahon et al. 2015). For example, leaf area index (LAI) is an estimate of leaf area often used to characterize structural change resulting from disturbance (Waring and Schlesinger 1985). It may change only minimally following a low-to-moderate severity disturbance event which may limit its utility as a disturbance detection measure (Cohen et al. 2016). Although disturbances frequently alter several canopy structural traits concurrently, the relative performance of LAI versus canopy structural trait metrics in characterizing forest disturbances has not been addressed.

Multidimensional approaches may help detect and differentiate moderate severity disturbance agents. One promising framework describes several aspects of canopy structure to define a suite of canopy structural traits (CSTs; Fahey et al. 2019*b*) including vegetation density, height, arrangement, cover, and structural complexity (Atkins et al. 2018*a*; Table 1; Fig. 2). Canopy
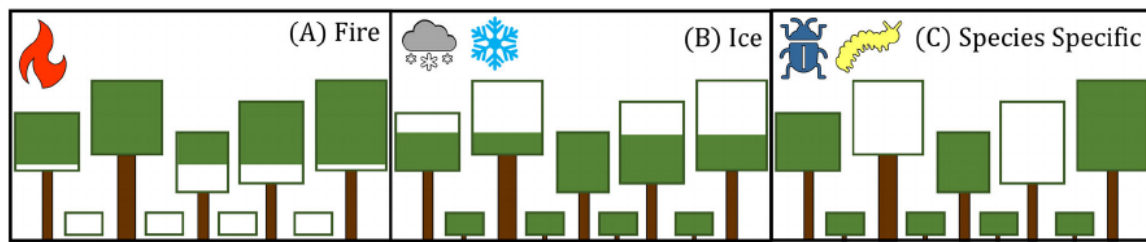
Fig. 1. Hypothesized structural outcomes of disturbance agents informed by previous studies. Moderate severity fire will affect the lower canopy (A), while ice and wind will affect the upper canopy (B). Species-specific disturbances work at the individual level (e.g., targeting individual trees), creating canopy gaps as a result of induced tree mortality (C).

structural trait metrics are derived from terrestrial lidar (Hardiman et al. 2011, McMahon et al. 2015, Ehbrecht et al. 2016, Atkins et al. 2018d, Shiklomanov et al. 2019) and linked with a variety of ecosystem functions, including primary production (Hardiman et al. 2011, Gough et al. 2019, LaRue et al. 2019), light acquisition (Stark 2012, Atkins et al. 2018b), microclimate (Ehbrecht et al. 2017), and resource-use efficiency (Hardiman et al. 2011). The CST framework includes integrative, multidimensional measures of canopy structure (Table 2), including metrics that quantify canopy complexity, such as canopy rugosity. Canopy rugosity is a metric that summarizes vertical and horizontal variance in vegetation density and is a robust indicator of functional change (Gough et al. 2019). CSTs provide a powerful, standardized methodology for characterizing multiple aspects of structural change following disturbance, thus potentially enabling the detection of disturbances not sufficiently characterized by single measures of structural change.

We hypothesized that the multivariate CST-based approach would better describe structural change than a unidimensional, leaf-area-only approach among a series of moderate severity disturbances, including ice storm, low-severity ground fire, age-related senescence, chronic acidification, and pathogens and insect outbreaks within eastern temperate forests (Table 1). Further, we hypothesized that disturbance agents would differ in which CSTs they most strongly alter (i.e., canopy height, area/density, arrangement, openness, and complexity; Fig. 2) due to agent-specific effects on canopy structure (Atkins et al. 2018a, Fahey et al. 2019a). We expected fire

and ice storm damage to preferentially affect total leaf area, as well as area/density and canopy height. Both fire and ice storms are pulse disturbances that occur over acute time intervals often resulting in reductions in canopy leaf area and vegetation height throughout and across the canopy (Plotkin et al. 2013, Cote et al. 2014, Turner et al. 2016, Oldfield and Peterson 2019, Fahey et al. 2019b). We expected species-specific disturbances surveyed would primarily alter canopy traits such as arrangement, height, complexity, and openness (Fig. 3).

Methods

We surveyed six temperate forest sites (Table 1), each of which was moderately disturbed by a different agent, including disturbances from age-related senescence, chronic acidification, insect, and pathogen outbreaks. We estimated how each agent altered canopy structure through surveys of pulse disturbed sites before and after disturbance and, in the case of temporally diffuse press disturbances, by sampling disturbed and nearby control (undisturbed) sites concurrently. The use of different sampling schema is not ideal but allows for comparisons among or between disturbed and undisturbed areas. We adopted a case-study approach whereby analyses were made only within sites—comparing disturbed to undisturbed areas. Given varying site characteristics, sampling times, and data limitations, it is important to note that the potential to confound site with disturbance type. Therefore, we limit or inferences and descriptions to how each disturbance event changes ecological structure at that singular site.

Table 1. Site, data collection, and disturbance information.

Location	Coordinates	Data period	Disturbance type	Details
Great Smoky Mountains National Park (TN)	35.709° N, −83.395° W	2016–2017	Fire	Wildfires burned over 6800 ha in and around Great Smoky Mountains National Park in TN. Many plots associated with the NEON GRSM site were affected, but not severely burned (low to moderate damage). We compared pre-fire data collected in 2016 to post-fire data from 2017.
Fernow Experimental Forest (WV)	39.054° N, −79.670° W	2016	Chronic acidification	Since 1989, ammonium sulfate (35.5 kg $N \cdot ha^{-1} \cdot yr^{-1}$ and 40.5 5 kg $S \cdot ha^{-1} \cdot yr^{-1}$) has been applied yearly to watershed 3 (WS3) a deciduous, hardwood forested watershed. Watershed 7 (WS7), an adjacent watershed, serves as a control. Here, we compare data collected in 2016.
Indian Point (MI)	45.484° N, −84.680° W	2014, 2017	Pathogen	Indian Point is a protected forest in northern Michigan that has been affected by beech bark disease over the past half-decade. We compare data from the same plots collected in 2014 and 2017.
UMBS (MI)	45.555° N, −84.721° W	2012, 2016	Succession or mechanical damage	The Forest Accelerated Succession Experiment (FASET; US-UMd) facilitated the stem girdling of over 6700 trees over 39 ha on the property of the University of Michigan Biological Station (UMBS). We compare data from the treatment (US-UMd) to the control (the adjacent AMERIFLUX site, US-UMB) for both the years 2012 and 2016. Each as a separate analysis to account for change over time.
Hubbard Brook (NH)	3.942° N, −71.745° W	2015–2017	Ice storm	The ISE was established in a 70- to 100-year-old mixed hardwood stand dominated by American beech (*Fagus grandifolia*), sugar maple (Acer saccharum), red maple (Acer rubrum), and yellow birch (*Betula alleghaniensis*). Ten 20 × 30 m plots were established in summer 2015, and pre-treatment measurement collections were initiated. Two plots were randomly assigned to each of five treatments with variable ice intensity targets and frequency: (1) control; no experimental icing applied, that is, 0 mm; (2) low; 6.4 mm of ice in year 1 only; (3) moderate; 12.7 mm of ice in year 1 only; (4) double; 12.7 mm of ice in year 1 and year 2; and, (5) high; 19.0 mm of ice in year 1 only. Ice treatments were implemented during subfreezing conditions in 2016 (year 1; across five different dates) and 2017 (year 2; January 14). Ice addition was targeted toward the inner 10 × 20 m of the plots, with a 10 m wide buffer that was not unaffected by the treatment making up the balance of the plot.
Harvard Forest (HF)	42.531° N, −72.188° W	2017	Hemlock woolly adelgid	HWA first seen in HF in 2008 and was widely distributed by 2012. Significant tree decline and noticeable tree mortality were noted by 2016. We focused on a 60 × 150 m section of the ForestGEO plot located on Prospect Hill where there were concurrent tree mortality and lidar data. Low severity plots were chosen as those with less than 10% basal area mortality threshold (Appendix S1).

This approach offers a novel and informative way to characterize and differentiate moderate severity disturbances, but requires further validation, replication, and examination to reach its full potential.

Site and disturbance descriptions

Fire, Great Smoky Mountains National Park, Tennessee.—In November–December of 2016, a series of arson fires swept through the Great Smoky Mountains National Park, burning over 6800 ha. Portions of the affected range fell within the study area of the National Ecological Observatory Network (NEON) Twin Creeks relocatable terrestrial site (GRSM). We compared pre- (2016) and post-fire (2017) lidar data collected from six NEON forest inventory plots (Atkins et al. 2018*d*). Forests in GRSM are dominated by overstory tulip poplar (*Liriodendron tulipifera*), oak (*Quercus spp.*), and red maple (*Acer rubrum*), with rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) prominent in the understory.
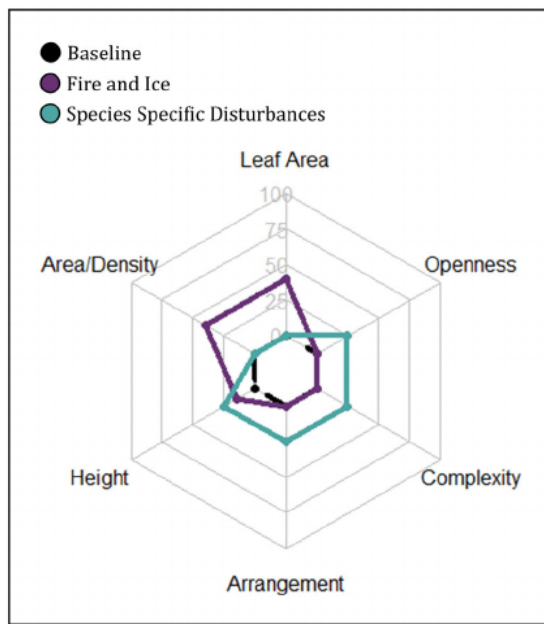
Fig. 2. Hypothesized relative change from baseline conditions (in units of absolute value of percentage change) for leaf area as well as canopy structural traits defined in Table 2 (Atkins et al. 2018a). Hypothesized change is based on empirical data for moderate severity fire (Kinnaird and O'Brien 1998, Alencar et al. 2006, Boer et al. 2008), ice storm damage (Rhoads et al. 2002, Weeks et al., 2009), while species-specific hypotheses are informed from conservative extrapolations based on qualitative descriptions of related disturbances (Orwig and Foster 1998, Gough et al. 2013). Disturbances such as fire and ice are expected to alter leaf area, density, and canopy height, while acidification, senescence, insect, and pathogen outbreaks are expected to alter canopy height, openness, complexity, and arrangement.

Ice storm damage, Hubbard Brook Experimental Forest, New Hampshire.—Ice storms are ecologically influential disturbance agents in many areas of the eastern USA, including the forests of New England where return intervals can be fewer than 5 yr (Irland 2000, Changnon 2003). The Ice Storm Experiment (ISE) at Hubbard Brook Experimental Forest (HBEF) was initiated in 2015 to mimic the mechanical damage resulting from severe ice storms (Rustad and Campbell 2012). Water was applied to vegetation during sub-zero conditions in 2015 to achieve varying levels of ice thickness—light (6 mm), moderate (12 mm), and heavy (19 mm). Lidar data were compared to assess the effects of ice on canopy structure by comparing pre- and post-treatment data across severity levels (e.g., light, moderate, heavy) in 2015, 2016, and 2017 (Fahey et al. 2019b). Forests in HBEF are dominated by American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*).

Pathogen, beech bark disease at Indian Point, Michigan.—American beech bark disease (BBD) occurs following the invasion of a beech scale insect, *Cryptococcus fagisuga* (Ehrlich 1934), and is widespread in North America (Cale et al. 2017). Feeding by this insect causes two opportunistic fungi (*Neonectria faginata* and *Neonectria ditissima*) to produce cankers on the bark, the continuous formation of which results in stem girdling and subsequent tree death (Ehrlich 1934, Arthur et al. 2017). To examine the canopy structural change resulting from BBD, we compared CSTs from 2014 to 2017 for Indian Point (IP) in northern, lower Michigan. IP is a relict forest dominated by large eastern hemlock (*Tsuga canadensis*), American beech (*Fagus grandifolia*), and white pine (*Pinus strobus*). IP is also known as Colonial Point Memorial Forest and is land held in trust by the Burt Lake Band of Chippewa and Ottawa Indians as well as the University of Michigan Biological Station. We have opted to use the former name of the area, Indian Point, after consultation with the Burt Lake Band.

Insect infestation, Hemlock woolly Adelgid at Harvard Forest, Massachusetts.—Hemlock woolly adelgid (HWA) is an invasive, aphid-like insect first reported in the USA in Virginia in 1951 (Havill et al. 2006). Since its introduction, HWA has spread to 19 states from Georgia to southern Maine, affecting millions of trees and threatening the range of eastern hemlock. The insect can feed on all sizes and age classes of hemlock trees, often killing trees within 10 yr (Orwig and Foster 1998). At Harvard Forest, HWA was first seen on Prospect Hill in 2008 and was widespread by 2012. By 2016, significant hemlock decline and noticeable mortality began to occur (Orwig and Foster 1998). We compared CSTs in 2017 from areas of low and moderate infection—with low infection classified as less than 10% basal area mortality (Appendix S1: Fig. S1) at Prospect Hill. While this represents a deviation from the strictly disturbed to undisturbed method used at other sites, it was a necessity given the lack of completely undisturbed areas at Harvard Forest.

Table 2. Detailed description of canopy structural parameters derived from terrestrial lidar using the forestr package in R.

Parameters	Symbol	Units	Description
Area and density			
Vegetation area index (VAI)	VAI		Ratio of vegetation area of the canopy per ground area
Maximum VAI	VAI_{max}		The VAI of the densest 1 m^2 of the canopy (x, z) in units of VAI
Mean peak VAI	VAI_{peak}		Mean of VAI_{max} for a plot, measured at 1-m intervals
SD of height of max VAI	σZ_{VAI}		Standard deviation of the height of VAI_{max} for each column
Height			
Mean leaf height	H	m	Mean of column measured density-adjusted vegetation height (i.e., lidar return densities adjusted for occlusion using the Beer-Lambert Law (Beer 1852; Lambert 1760)
Height^2	σH	m	Standard deviation of column mean leaf height
Mean outer canopy height	MOCH	m	Mean of the column maximum canopy height
Maximum canopy height	H_{max}	m	Maximum canopy height as on one measure for the entire plot (i.e., the greatest measured lidar height)
Arrangement			
Canopy porosity	P_C	ratio	Ratio of bins with no lidar returns to the total number of bins
Cover and openness			
Gap fraction	Θ	ratio	Transect mean of column ratio of sky hits relative to total leaf returns
Complexity/ heterogeneity			
Canopy rugosity	R_C	m	Transect variance of column leaf density variance
Top rugosity	R_T	m	Standard deviation of column maximum canopy height
Effective no. layers	ENL		Description of vertical canopy structure based on the occupation of 1 m wide vertical layers by canopy elements relative to the total space occupation of a stand

Note: Table adapted from Atkins et al. (2018).

Successional change/senescence, University of Michigan Biological Station, Michigan.—The Forest Accelerated Succession Experiment (FASET; for continuity, we will use the AmerifFlux ID for this site, US-UMd), located in northern lower Michigan, is a large-scale manipulative experiment, in which 6700 mature aspen (*Populus* spp.) and birch (*Betula* spp.) trees were stem-girdled within a 39-ha area during 2008 to accelerate successional processes leading to the decline of these early successional species (Nave et al. 2011, Gough et al. 2013). The treatment forest is paired with a nearby undisturbed control site of similar forest composition (University of Michigan Biological Station AmeriFlux Core Site, US-UMB). We compared CSTs for control and treatment to each other for both 2012 and 2016, respectively, with the supposition that 2016 represents further successional progress compared to the control.

Chronic acidification, Fernow Experimental Forest.—Chronic atmospheric acid deposition is a persistent stress on many forests across the USA but is of acute concern in the Allegheny and Appalachian Mountains of West Virginia, Ohio, Pennsylvania, and New York. Even though reductions in acid deposition spurred by the 1990 Clean Air act amendments have helped mitigate this environmental stressor (Mathias and Thomas 2018), its legacy persists in altered soil chemistry, forest composition, and forest structure (Warby et al. 2008, Horn 2018). Manipulative experiments that include experimental additions of acid-precursor compounds have been deployed across the country to address ecosystem-related questions surrounding acid deposition. Among these is a long-term experiment at the Fernow Experimental Forest in West Virginia. Continuous, annual additions of ammonium sulfate (35.5 kg N·ha^{-1}·yr^{-1} and 40.5 kg S·ha^{-1}·yr^{-1}) began in watershed 3 of the Fernow Experimental Forest in 1989 (Adams et al. 2007). This treatment watershed was paired with control watershed 7 as part of the long-term Fernow Watershed Acidification Study. The treatment watershed exhibited depletion of both calcium (Ca$^+$) and magnesium (Mg$^+$; Adams et al. 2007)
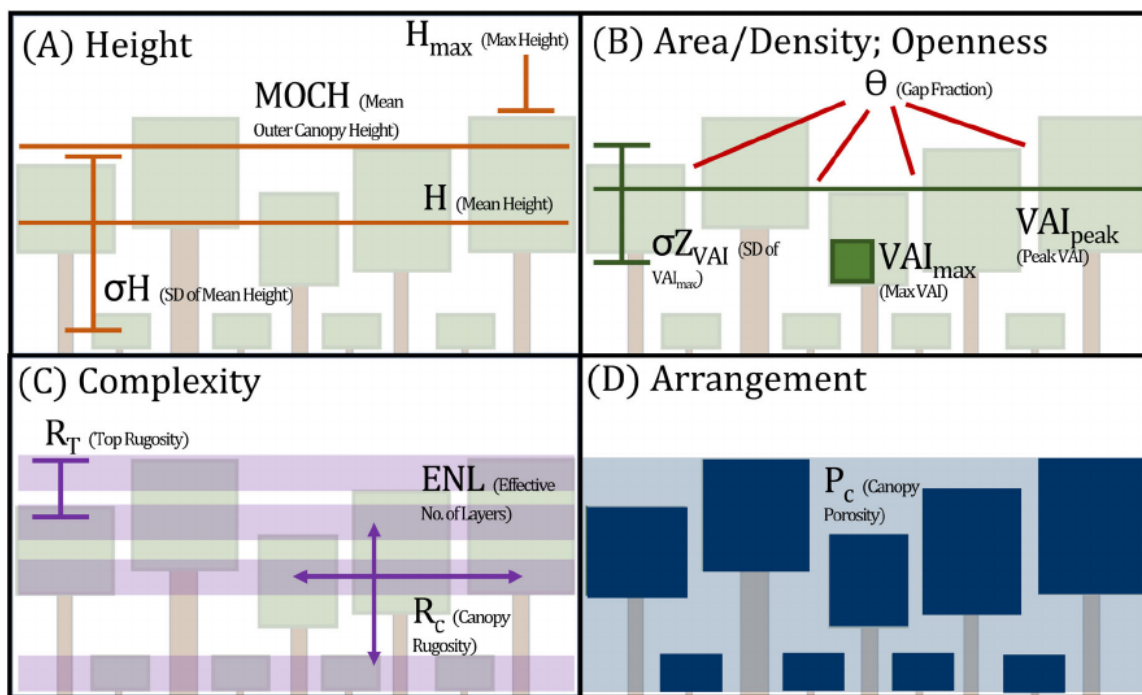
Fig. 3. Graphical representations of canopy structural measures for all five CSTs describe in Table 2: height (A) area and density, (B) openness, (C) complexity, and (D) arrangement categories described in full in Table 1 and defined mathematically in Atkins et al. 2018*b*.

with cascading effects on vegetation. The control watershed is now a mixed-hardwood forest comprised primarily of maple (*Acer* spp.), red oak (*Quercus rubra*), and tulip poplar (*Liriodendron tulipifera*), while the treatment watershed is a mixed-hardwood forest dominated by black cherry (*Prunus serotina*) and red maple (*Acer rubrum*). We compared CSTs from treatment (watershed 3) and control watersheds (watershed 7) —each with similar climate and topography and are located adjacent to each other within the Fernow Experimental Forest.

Data collection and analyses

Canopy structural complexity.—We collected canopy structural data with a user-mounted, portable canopy lidar system equipped with an upward facing, Riegl LD90 3100VHS near-infrared pulsed-laser operating at 2000 Hz (Riegl USA, Orlando, Florida, USA). This system generates continuous LiDAR returns from a slice of the canopy as it is walked along a measured transect. Plot dimensions and sampling areas varied

by site, but data collected at each site included 60–120 m total scan lengths per plot, comprised 2–3 linear transects per each plot, beyond the range required to achieve stable landscape-level measures of canopy structure (Hardiman et al. 2018). A more detailed description of the development and operation of this terrestrial laser scanning system is available in Parker et al. (2004) and Hardiman et al. (2011). We derived CST metrics at the plot level using the forestr package (Atkins et al. 2018*a*, *d*) in R 3.5 (R Core Team 2018). forestr produces a suite of CST metrics that describe canopy area/density, openness, height, complexity, and arrangement (Table 2)— greater detail is available in Atkins et al. (2018*a*).

Random forest classification.—We identified structural models for each disturbance agent using a random forest machine learning classification approach with the randomForest package (Liaw and Wiener 2002) in R 3.5. This algorithm produces a series of iterative decision trees using binary, recursive partitioning that is based on predictor values and known classes (Breiman

Table 3. Signature structural model output and error.

Site	n	Signature model constituents	CE (OOB)	VAI model CE (OOB)	Description of change
GRSM, ground fire	37	VAI, MOCH, VAI_{peak}	18.52	25.93	Decrease in overall VAI, primarily from the densest areas.
HBEF					
Light, ice storm	20	VAI_{peak}, VAI_{max},	15.00	50	The average maximum heights, height of peak leaf area
Moderate, ice storm	20	VAI_{peak}, σZ_{VAI}	2.5	37.5	Height and leaf area decrease, while complexity of the forest increases
Heavy, ice storm	10	VAI_{peak}, σZ_{VAI}	0	25	Height and leaf area decrease, while complexity of the forest increases
IP, beech bark disease	61	P_G VAI_{max}	6.56	42.62	A more open canopy, but dense areas become denser
HARV, hemlock woolly adelgid	38	R_T, ENL	21.3	35.7	Forest complexity increases with progressing infestation and increasing mortality
UMBS					
2012, senescence	175	P_G H, R_G σZ_{VAI}	13.14	48	Height and leaf area variance decrease, while the forest becomes more porous and less complex
2016, senescence	62	R_G R_T, P_C	20.97	53.23	Complexity and height variance decrease
FERN, chronic acidification	30	MOCH, P_G σZ_{VAI}, σH	20	50	Increases canopy height and makes the canopy less open

Note: n represents number of plots for analysis. CE, classification error; OOB, out of bag.

2001, Cutler et al. 2007). Random forest uses a series of uncorrelated models (decisions trees) to build a composite classification with a statistical breakdown that shows which variables are the most significant in contrasting known classes by describing how influential they are to model accuracy. Variables that lead to a larger mean decrease in accuracy when removed from the model are more influential in the classification process. This technique has been useful in other related, data-rich ecological applications (Juel et al. 2015, Belgiu and Draguţ 2016, Atkins et al. 2018*e*) including forest cover and disturbance detection using remote sensing (Healey et al. 2018).

We used a two-step procedure to produce parsimonious random forest structural models separately for each disturbance agent—comparing disturbed and non-disturbed areas at each site. We first built kitchen sink models using the full suite of canopy structural metrics as predictors (Table 2) and then built more parsimonious models through an iterative process of parameter selection retaining only the most influential parameters, minimizing out-of-bag error while constraining the number of input parameters. We compared the resulting multivariate models

to single-variable models that use vegetation area index (VAI)—a proxy for leaf area that is derived from terrestrial lidar—as the only predictor. This was done for each disturbance, at each site, independently. VAI-only models were evaluated using the same random forest classification procedure in order to evaluate whether additional information is supplied by multidimensional structural models over leaf-area-only models via classification accuracy. We also included a parametric statistical approach using Student's *t*-test (Appendix S1: Table S1) with effect size calculations (Cohen's *d*) to examine significant changes between disturbance and undisturbed areas.

RESULTS

Fire, Great Smoky Mountains National Park, Tennessee

Ground fire at GRSM reduced VAI primarily in the understory. The structural model included reductions to vegetation area (VAI), the peak canopy VAI, or the average height of maximum VAI (VAI_{peak}) and increases in mean outer canopy height (MOCH). VAI decreased from 7.3 ± 0.4 in 2016 (pre-fire) to 6.4 ± 0.8 in 2017 (post-fire; values following $\pm$ are standard

deviations here and following through the manuscript). VAI_{peak} decreased from 3.2 ± 0.6 to 2.5 ± 0.4, while MOCH increased from 20.0 ± 3.5 m to 24.2 ± 4.8 m as the allocation of vegetation in the upper canopy increased relative to the fire-impacted subcanopy. Of the 13 post-fire scans, 11 were correctly classified, as were 11 of the 14 pre-fire scans, for a 15.4–21.4% classification error rate, respectively, with a total out-of-bag (OOB) error of 18.5% compared to the VAI-only model which had a classification error of 25.9% (Table 3). t-Test results indicate that fire significantly reduced overall VAI ($P = 0.002$) with a very large effect observed between pre- and post-disturbance plots ($d = 1.33$; Appendix S1: Table S1).

Ice storm, Hubbard Brook Experimental Forest

Across all severity levels (light, moderate, and heavy), ice primarily affected VAI in the upper canopy. The structural model included decreases in the height of peak vegetation area (VAI_{peak}), while the heavy and moderate severity levels showed increased variability in canopy height. In the heavy ice treatment, VAI_{peak} shifted downward from 3.4 ± 0.2 to 2.2 ± 0.6, in the moderate treatment from 3.4 ± 0.4 to 2.6 ± 0.5, and in the light treatment from 3.6 ± 0.7 to 2.9 ± 0.3. Structural variability, expressed in the model as σZ_{VAI}—the standard deviation of the height of peak VAI—increased in the heavy treatment from 3.8 ± 0.7 to 6.6 ± 0.7 m, and in the moderate treatment from 3.9 ± 0.7 to 5.4 ± 0.9 m. The structural model of the light ice treatment retained overall maximum leaf area (VAI_{max}), which decreased from 6.7 ± 1.1 to 5.4 ± 0.6. Classification accuracy increased with disturbance severity, indicating severe ice disturbance modified the canopy in a more consistent way. All 20 of the scans for the heavy treatment were classified correctly for an OOB error rate of 0%. 39 of the 40 moderate severity scans were classified correctly for an OOB error rate of 2.5%. 17 of 20 light severity scans were classified correctly for an OOB rate of 15%. Classification errors for VAI-only models were higher for all treatments (Table 3). Significant differences with large effects in VAI using the parametric, t-test approach were only observed for moderate ($P = 0.002$; $d = 1.06$) and heavy ($P = <0.001$; $d = 1.96$) treatments.

Pathogen, beech bark disease at Indian Point, Michigan

Beech bark disease made canopies more porous and open over time as diffuse mortality of canopy trees advanced. However, the overall density of vegetation area in the densest areas of the forest increased, likely a function of increased forest floor light availability resulting in the growth release of lower canopy seedlings and saplings. Canopy porosity (P_C) increased as the infestation progressed from 0.6 ± 0.4 in 2014 to 0.7 ± 0.03 in 2017, while VAI_{max} increased from 5.1 ± 0.8 to 6.7 ± 0.7. 17 of 19 scans for 2014 and 40 of 43 scans for 2017 classified correctly, 10.5% and 4.7% success rate, respectively, for a total OOB error rate of 6.6%. Classification errors for the VAI-only model were higher (42.6%), and no significant differences or effects were observed in VAI from the parametric approach.

Insect defoliation, Hemlock woolly adelgid at Harvard Forest, Massachusetts

Areas more severely affected by hemlock woolly adelgid were more structurally complex, with increased canopy layering and more variable heights resulting from disturbance. A change in canopy layering is likely caused by a progression of foliar loss from the lower to upper crown as infection expands. The CST model included top rugosity (R_T) and the effective number of layers (ENL). High mortality areas of the forest were more complex ($R_T = 3.5 \pm 0.6$ m; ENL $= 17.3 \pm 1.5$) than low mortality areas ($R_T = 2.9 \pm 0.5$ m; ENL $= 15.3 \pm 1.4$). Four of the 6 high mortality scans were classified correctly by the model, as were 7 of the 8 low mortality scans for an overall OOB error rate of 21.4%. Classification error for the VAI-only model was higher (35.7%), and no significant differences or effects were observed in VAI from the parametric approach.

Successional change/senescence, University of Michigan Biological Station, Michigan

Senescence of early successional trees reduced canopy complexity, lowering the height of the densest concentration of leaves. This resulted in a more open canopy, pointing to a homogenization of canopy structure as a function of the mortality of the tallest trees. The structural model included R_C, σZ_{VAI}, P_C, and H. Four years

following the commencement of tree decline, treatment and control, R_C was 10.5 ± 3.2 m and 13.1 ± 5.3 m, H was 8.1 ± 1.3 m and 9.2 ± 1.7 m, P_C was 0.67 ± 0.04 and 0.70 ± 0.04, and σZ_{VAI} was 4.6 ± 0.9 m and 5.4 ± 1.0, respectively. Eight years after treatment, disturbed and control forest canopy complexity, maximum canopy height, and the variability of canopy height diverged even more. The 8-yr structural model included R_C, P_C, and R_T, which were 8.0 ± 3.4 m to 14.3 ± 6.8 m, 0.70 ± 0.06 to 0.70 ± 0.04, and 4.6 ± 1.0 m to 5.9 ± 1.7 m in treatment and control forests, respectively. For 2012 scans, 90 of the 99 control scans (US-UMB) were classified correctly, while 62 of 76 treatment scans (US-UMd) were classified correctly for a total OOB error rate of 13.1%. For 2016 scans, 40 of the 44 control scans (US-UMB) were classified correctly, while 9 of 18 treatment scans (US-UMd) were classified correctly for a total OOB error rate of 20.9%. No significant differences or effects were observed in VAI. Classification errors for VAI-only models were higher for both years (2012, 48.0%; 2016, 53.2%), and no significant differences or effects were observed in VAI from the parametric approach.

Chronic acidification, Fernow Experimental Forest

Chronic acid deposition resulted in a taller canopy that was more porous, open, and variable than the control. Vegetation in the treatment forest was concentrated at higher canopy positions and coincided with a more open subcanopy. The control canopy was shorter and vegetation more dispersed. The nitrogen and sulfur amended forest was associated with a higher canopy, suggesting growth stimulation of the upper canopy, and a loss of subcanopy vegetation. The structural model included maximum canopy height (H_{max}), canopy porosity (P_C), the standard deviation of the height of maximum VAI density (σZ_{VAI}), and the standard deviation of mean leaf height (σH), respectively, acid deposition increased canopy porosity from 0.6 ± 0.03 to 0.7 ± 0.04, elevated H_{max} from 24.6 ± 1.5 m to 27 ± 2.4 m, enhanced variance in the height of VAI_{max} from 6.2 ± 1.2 to 7.8 ± 1.8, and raised the variance in mean leaf height from 4.5 ± 0.8 m to 5.5 ± 1.2 m. 14 of 17 scans from the treatment watershed and 10 of 13 scans from the control

watershed were classified correctly, 17.6% and 23.0% success rates, respectively, with a total OOB error rate of 20%. Classification error for the VAI-only model was higher (50%), and no significant differences or effects were observed in VAI from the parametric approach.

Synthesis: patterns of change among disturbance agents

Though our ability to make broad generalizations about disturbance patterns from this study is limited by lack of replication, similarities among disturbance agents (Fig. 4) were suggestive and interesting. Ice and fire, both pulse disturbances, primarily reduced vegetation area/density and height; in contrast, age-related senescence, pathogens, and acidification-affected vegetation arrangement and complexity (Fig. 4A, B; Table 3). Structural differentiation from beech bark disease, which is both a pathogen and an insect syndrome disturbance, was characterized by changes in area/density and arrangement (Table 2). Not only was there direct, physical loss of vegetation through defoliation, but also whole tree mortality created gaps in the canopy that change measures such as canopy porosity. This is in stark contrast to disturbance agents such as fire, ice, or acidification that at low to moderate levels rarely result in whole tree senescence. These emergent similarities inform areas of future inquiry of structural differentiation we observe among disturbance agents.

DISCUSSION

Our findings support our hypothesis that canopy structural differentiation may be viewed as a function of the individual agent of a given disturbance, as each disturbance agent altered a unique combination of canopy structural traits (Table 3). As hypothesized, fire and ice modified the amount and distribution of leaf area within the canopy, while pathogens, insect, age-related senescence, and acidification changed canopy arrangement, height, and/or complexity. Among the six disturbance agents examined, only two statistically, significantly reduced leaf area (Appendix S1: Table S1) and only fire retained VAI as an influential model parameter, demonstrating that moderate severity disturbances can be more effectively and consistently
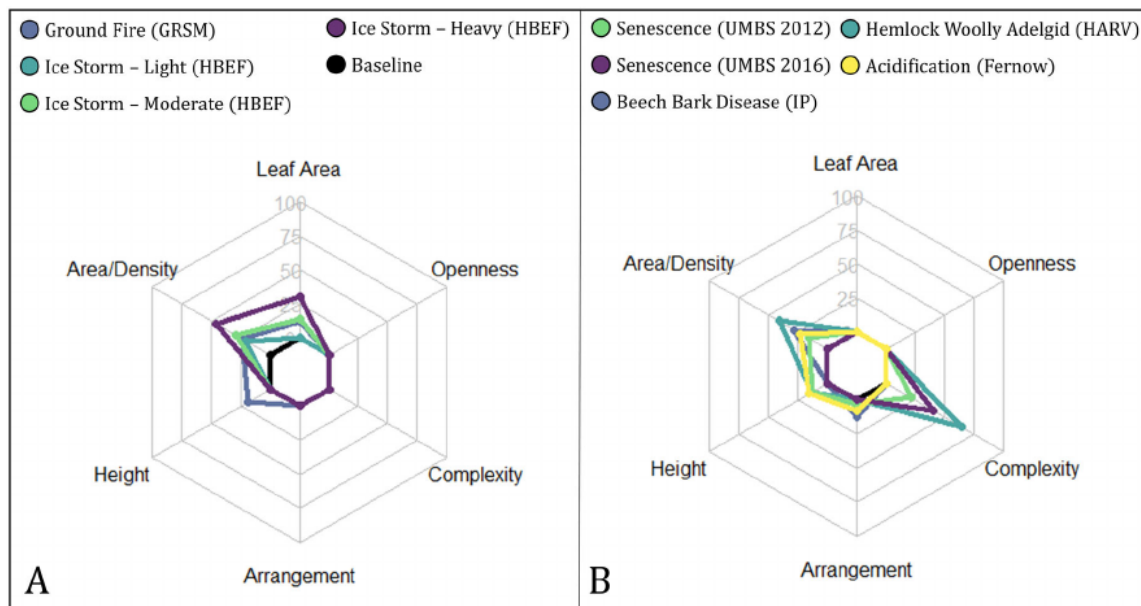
Fig. 4. Relative change (%) for ground fire and ice (A) and senescence, hemlock woolly adelgid, beech bark disease, and chronic acidification (B) based on the absolute value of percentage change for leaf area, and for canopy structural traits defined in Table 2 and illustrated in Fig. 3.

distinguished from undisturbed areas using CSTs (Fig 5, Table 3; Appendix S1: Table S1). There was no uniform modification of a single structural trait such as leaf area. Rather, disturbance agents typically altered multiple, different CST metrics. Patterns, however, were evident among disturbance agents. Fire and ice were best described by how they affect the amount and variability of leaf area, while other disturbances were best described by how they alter canopy complexity (Fig. 4).

Beyond singular measures of structural change

We found moderate severity disturbance agents can, but often do not, reduce total leaf area. This finding suggests that the characterization of disturbance-related structural changes based on leaf area alone fails to describe structural outcomes observed in disturbed sites relative to undisturbed areas. This is likely due to how slower acting disturbances (e.g., certain pathogens and insects, as well as age-related senescence) allow sufficient time for compensatory foliar replacement to occur as mortality progresses (Raffa et al. 2008, Gherlenda et al. 2016)—either through regrowth or subcanopy

response. In contrast, disturbances such as fire and extreme weather events occur abruptly and may temporarily reduce leaf area (Bond-Lamberty et al. 2002, Beringer et al. 2003). Additionally, insect or pathogen outbreaks, such as bark beetle infestations, are pulse disturbances and occur over much shorter time frames than similar disturbances we surveyed. This would not necessarily allow time for compensatory regrowth, making the likely structural outcomes more similar to those of fire or ice surveyed here.

Four of the disturbance agents surveyed were best characterized by metrics that describe changes in leaf area location, density, or variance rather than total leaf area. In our study, only two of the disturbance agents we examined significantly reduced leaf area based on traditional parametric statistical tests—fire (GRSM) with a 10.2% reduction and ice with 13.9% and 26.2% reductions at moderate and heavy ice loads, respectively (Appendix S1: Table S1)—but again, only fire included leaf area as parameter in the multivariate structural model (Table 2). These observed reductions in leaf area are within the range of other similar disturbances including a 2–25% reduction in leaf area following an ice
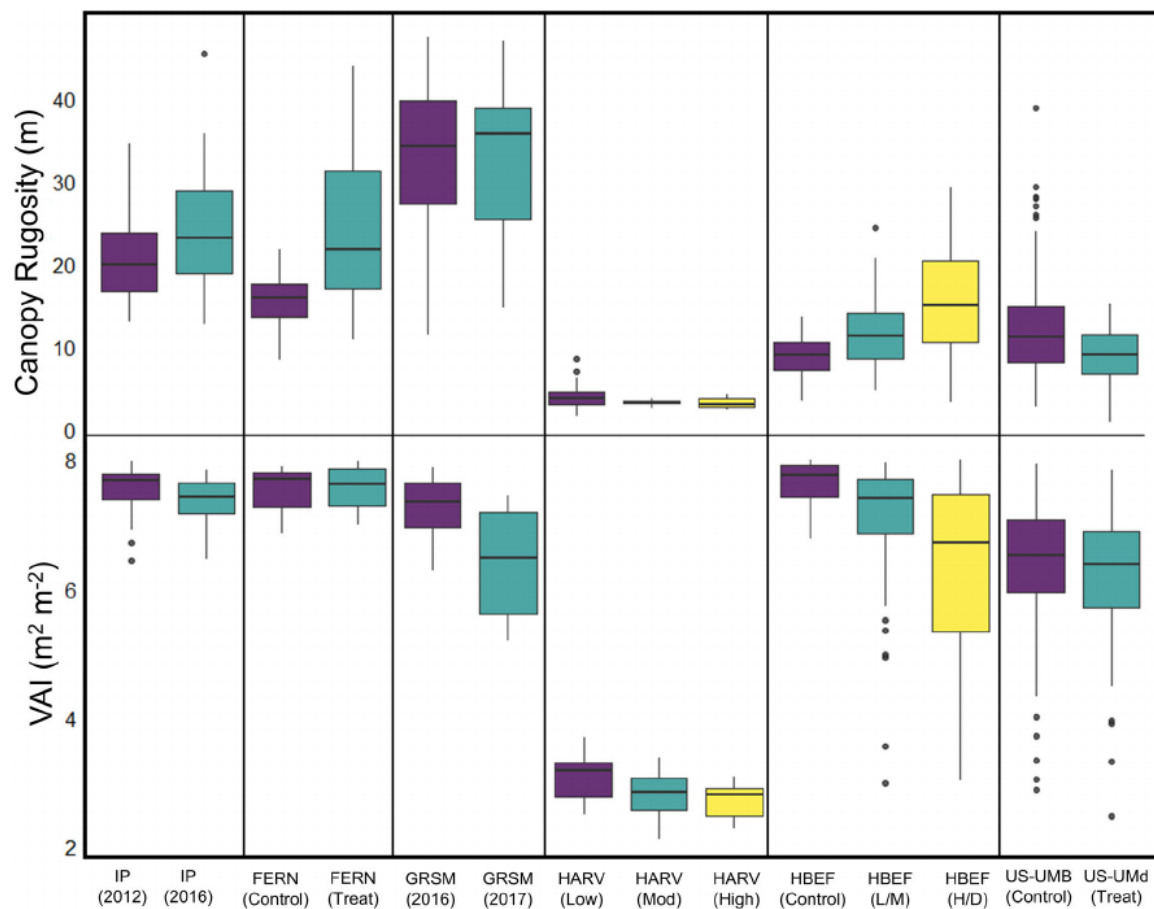
Fig. 5. At top, canopy rugosity by site and disturbance (e.g., control vs treatment, low to high, pre and post). At bottom, vegetation area index as same. For HBEF, L/M is the combination of the low and moderate treatments, and H/D is the average of the heavy and double treatments.

storm in Quebec (Colpron-Tremblay and Lavoie 2010); a 10–30% reduction in canopy cover following hurricane-force winds in North Carolina (Busing et al. 2009); 33% reduction in leaf area following ice storms in the northeastern USA (Rhoads et al. 2002); and a 30% reduction in leaf area following drought in northern Arizona (Classen et al. 2006). Despite similarities in the magnitude of change relative to those studies, reductions in leaf area from fire and ice were concentrated in different canopy strata (Appendix S2 and S3), a dimensional structural change not captured by dimensionless measures of total leaf area. Using only statistical parametric approaches focused on leaf area, the ice and fire would be the only detectable disturbances.

Beyond leaf area, our analysis shows that changes in individual measures of canopy traits, even integrative measures, are insufficient to characterize structural differentiation among disturbance agents. For example, canopy rugosity, an integrative complexity measure strongly tied to ecosystem functioning (Atkins et al. 2018c, Gough et al. 2019), changed in response to disturbance in only half of the disturbance agents surveyed (Fig. 5). Moreover, the directionality of change in canopy complexity, when it occurred, was mixed. Ice storms (HBEF) and insect invasion (HARV) increased canopy complexity, while age-related senescence (US-UMd) decreased canopy complexity (Fig. 5).

Consistency of agent-specific structural differentiation

We found that model classification error differed among disturbance agents, indicating variability in the consistency of structural differentiation among disturbance agents. Low model classification error for ice storms, pathogens, and beech bark disease suggests these disturbances imposed similar, more uniform structural changes within sampled landscapes—that any affected section of the canopy looked like other affected areas within the same ecosystem. In contrast, models of age-related senescence, acidification, hemlock woolly adelgid, and fire had higher classification errors, which suggests structural differentiation from these disturbances was more spatially variable, and less well constrained.

The degree of consistency in structural change among sites may be related to the distribution and timing of tree mortality as a function of a given disturbance agent. For example, both the rate and spatial pattern of pest and pathogen tree mortality are linked to invader-specific feeding (Orwig and Foster 1998), mating, and dispersal patterns (Walter et al. 2016). Our models for pathogen and insect infestation may be more well constrained, compared to other disturbance agents, because the tree species these disturbance agents target are distributed evenly on the landscape. For example, hemlocks, including those at Harvard Forest surveyed here, often grow in dense monospecific stands on uniform soils. At the individual tree scale, the advance of wooly adelgid within an infected crown proceeds uniformly from the lower to upper crown (Orwig and Foster 1998). In contrast, the distribution of tree mortality following ground fires in compositionally diverse forests, such as GRSM, may be much more variable because large spatial differences in burn severity are associated with small-scale changes in microclimate, topography, fuel load, and the abundance of fire-susceptible species and individuals (Hengst and Dawson 1994, Morton et al. 2011, Turner et al. 2016).

Despite apparent differences in structural outcomes among disturbance agents, we cannot discard the possibility that our observations were dependent upon site conditions, such as spatial variation in vegetation composition, stand age, and existing structure, which could affect the uniformity of structural change within each disturbed landscape. While this analysis provides novel insight into how disturbance agents alter canopy and forest structure, we are limited in our ability to generate any generalized model of CSTs and disturbance due to a lack of replication. In our analysis, site and disturbance agent are confounding variables. Alternatively, it could be argued disturbance agents with lower model classification errors simply create greater structural differentiation between disturbed and undisturbed areas than those with higher classification errors, or that sites differed in some substantial, yet unaccounted for manner. Without further replication, there are limitations and caveats that must be made, even if this approach provides novel insight.

Application: the detection of moderate severity disturbance through remote sensing

Our findings suggest that the detection of moderate severity disturbance requires an approach that relies less heavily on vegetation area or quantity but rather considers multiple dimensions of structural change. Disturbance detection via conventional passive optical remote sensing (e.g., Landsat, MODIS) relies heavily on observable changes in leaf area (Foster et al. 1999, Cohen and Goward 2004, Classen et al. 2006, Frolking et al. 2009, Cohen et al. 2016), vegetation cover (Cohen and Goward 2004, Stojanova et al. 2010), or greenness (Atkins et al. 2018c). As a result, optical remote sensing methods may fail to detect low-to-moderate severity disturbances that rearrange, rather than reduce total leaf area. Optical remote sensing from air- and spaceborne platforms has been repeatedly shown to successfully detect rapidly occurring, coarse-scale disturbances that severely reduce leaf area or canopy cover (Frolking et al. 2009, Healy et al. 2018). However, these methods are ill-suited for small-scale, diffuse, and/or low-to-moderate severity disturbances (McDowell 2015, Cohen et al. 2016) which are increasing globally (Hicke et al. 2012, Simler-Williamson et al. 2019). This may be due to the relatively coarse spatial resolution of many optical methods, resolutions often higher than that necessary to detect disturbance; for example, the spatial resolution of Landsat is 30 m, while MODIS is 250 m across, both notably larger than single tree crowns; or it

may be a function of viewpoint, as optical methods only see the forest from the top-of-the-canopy, thus lacking any multidimensionality that can be gained through under-canopy or through-canopy measures of structure.

A reliance on changes in leaf area or cover also limits the ability of optical remote sensing to detect disturbance agent or source. Newer spaceborne, active sensors (e.g., Global Ecosystem Dynamics Investigation [GEDI] and IceSAT2) that explicitly map multidimensional ecosystem structure offer a means to surmount these detection gaps and offer many potential scaling advantages (Stavros et al. 2017, Hancock 2019, Patterson et al. 2019, Dubayah 2020). In the future, the integration of long-term data records from optical remote sensing platforms (e.g., Landsat, MODIS) with the structural detection abilities of active sensors (e.g., GEDI, IceSAT2) will expand our ability to detect, identify, and estimate disturbance (McDowell 2015) as well as describe structural change post-disturbance.

While our study lays the foundation for future work by demonstrating the utility of CSTs to characterize and detect moderate disturbance, we acknowledge the caveats and limitations. Our case-study, observational approach shows the potential for this work, but does not control for site effects or site interactions with disturbance, which could alter how ecosystems respond to a given disturbance (Johnstone et al. 2016, Hillebrand et al. 2018). Additional investigation is necessary to evaluate the consistency of structural patterns within and among disturbance agents. Additionally, we did not consider the effect of co-occurring or compounding disturbances, nor did we investigate important disturbances such as drought, which will increasingly affect larger areas at greater severities over this century (Adams et al. 2012, Gutierrez-Velez et al. 2014, McDowell and Allen 2015, Clark 2016, Atkins and Agee 2019, Stovall et al. 2019, Stovall et al. 2019). Finally, our approach did not standardize for time since disturbance, a difficulty given large agent-specific variation in the timing and duration of defoliation and/or tree mortality. Despite these limitations, our work lays a foundation for how to characterize the structural differentiation of disturbance agents and shows the degree, breadth, variation, and functional implications of structural change among disturbance agents.

Conclusions

Disturbance agents differ in how they reshape forest structure. We have shown that the structural changes that result from disturbance are multidimensional, and the direction and magnitude of structural change cannot be adequately summarized using individual parameters. Instead, multiple measures of CSTs, in addition to leaf area, better characterize disturbance. We conclude that a multidimensional-based approached that considers several elements of structural differentiation may be useful to improve disturbance diagnostics, ecological forecasting, forest management, and earth system modeling (Dietze and Matthes 2014, Fisher 2018, Fahey 2018); however, we must build off of this work before broad generalizations can be made. Future inquiry via manipulative experiments and replicated empirical surveys is needed to understand functional significance of canopy structural change (Matheny et al. 2014, Stuart-Haentjens et al. 2015, Aron et al. 2019, Smith et al. 2019). Linking terrestrial lidar-derived measures of canopy complexity to emergent air- and spaceborne platforms will further scale our ability to detect disturbance-related structural change at large spatial scales.

Acknowledgments

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DATA AVAILABILITY STATEMENT

Code and analysis are available at https://github.com/atkinsjeff/csc_disturbance

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3156/full