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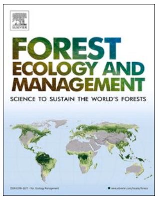

Defoliation frequency outweighs timing as a driver of tree mortality related to drought-defoliation interaction

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ABSTRACT

Climate change is expected to increase the frequency and severity of forest disturbance, making it more likely that multiple forms of disturbance will occur simultaneously. The resulting disturbance interactions could have compounding effects on tree mortality. Between 2016 and 2018, southern New England experienced both severe drought and spongy moth defoliation resulting in widespread tree mortality. The frequency and timing of defoliation varied substantially across the region, while drought conditions were relatively uniform. Our goal was to assess the influence of variable defoliation frequency and timing (relative to the preceding drought) on variation in tree mortality rates using a combination of remotely sensed data on defoliation patterns and field data on forest stand characteristics and tree mortality. Stand-level tree basal area mortality associated with the drought-defoliation interaction averaged 19 % across all study sites, with a maximum level of 50 %. Based on our analysis, mortality rates were most strongly explained by combinations of defoliation severity, frequency, and stand characteristics ($R^2 = 0.52$–0.60). Sites experiencing only drought but no defoliation or drought and a single year of defoliation had comparably low mortality rates, while sites experiencing drought and multi-year defoliation had higher mortality rates. Our research suggests that defoliation frequency was an important factor in predicting tree mortality, while defoliation timing and drought itself had less importance in this interaction.

1. Introduction

Forests are experiencing rapid alterations to disturbance regimes as global change introduces novel stressors and exacerbates the effects of existing disturbance agents (Trumbore et al., 2015). Climate change models project further increase in the frequency, severity, and scope of individual disturbances in the coming decades (IPCC, 2014). As individual disturbances become more frequent and greater in scope the potential for interacting disturbances with compounding effects increases (Seidl et al., 2017). In recent decades, disturbance interactions have contributed to significant widespread tree mortality events such as the loss of an estimated 100 million trees in California following an interaction of drought, wildfire, and bark beetle outbreaks (Millar and Delany, 2019). Tree mortality following such events has often exceeded historical patterns and predictions, possibly due to synergistic effects, where interacting disturbances have greater than additive impacts on ecosystems (Buma, 2015; Buma and Wessman, 2011). Such compounding effects may substantially increase tree mortality rates beyond what would be expected based on the effects of the individual disturbances acting alone (Paine et al., 1998; Dale et al., 2001; Kane et al., 2017).

The effects of interacting disturbances on ecosystem structure and function have become an important topic in recent ecological studies (e.g., Keane et al., 2015; Burton et al., 2020). Efforts to characterize

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disturbance interactions have focused on understanding mechanisms of specific interactions (e.g., Veblen et al., 1994; Anderegg et al., 2015), cross-scale interactions (e.g., Allen, 2007; Buma, 2015), and ecosystem resilience (e.g., Buma and Wessman, 2011). These studies have acknowledged that frequency and timing of disturbances can be influential on ecosystem response and resilience and the potential for synergistic effects (Johnstone et al., 2016; Burton et al., 2020), but the influence of variable temporal patterns among the individual disturbances that produce a disturbance interaction are less well understood.

Drought and insect defoliation are two important forest disturbance agents that are expected to increase in frequency and extent with projected climate change (Swanston et al., 2018). Drought depletes tree carbohydrate stores, limits leaf area production, and affects the production and resulting structure of wood (Bréda et al., 2006). Severe drought conditions may cause tree mortality directly or increase vulnerability to additional disturbances (Bréda et al., 2006). Drought has been shown to potentially have a time lagged effect, where tree mortality rates may increase in years following drought (Peterken and Mountford, 1996; Bigler et al., 2007). Defoliation similarly stresses trees by depleting leaf area and if defoliation occurs early in the growing season, trees often expend resources to refoliate mid-season (Kulman, 1971). Past studies of defoliation-only disturbance have found that single-year defoliation rarely results in substantial mortality, but that multi-year defoliation events contributes to higher tree mortality rates (Davidson et al., 1999). One of the most important tree defoliation agents in temperate North American deciduous forests is the spongy moth (*Lymantria dispar dispar*), a non-native insect that spread through northeastern North America during the early and mid-1900s and preferentially defoliates oaks (McManus and Csóka, 2007). Historically, spongy moth has been present throughout oak-dominated forests in eastern North America, but only periodically achieves outbreak status (i.e., when the population increases up to 100-fold; McManus and Csóka, 2007).

From 2016–2018, southern New England, USA was affected by a drought and concurrent and subsequent spongy moth defoliation. In 2016, up to 100 % of Connecticut and 98 % of Massachusetts experienced widespread drought conditions with approximately 90 % of the area experiencing “severe” drought based on US Drought Monitor criteria (NDMC, 2022). This time period represented the fourth and seventh driest March-November since 1895 for Connecticut and Massachusetts, respectively (NOAA, 2017). This drought coincided with the onset of a widespread spongy moth outbreak of a scale and severity unrivaled for many decades (USDA-FS, 2022). Drought conditions may have pre-disposed forests to defoliation and mortality in multiple ways, including suppressing the fungus (*Entomophaga maimaiga*) that has recently controlled spongy moth populations (Andreadis and Weseloh, 1990), as well as reducing tree vigor, defense mechanisms, and non-structural carbohydrate stores (Barker Plotkin et al., 2021). At the peak of spongy moth outbreak in 2017, approximately 825,000 ha were defoliated by spongy moth in oak-dominated New England forests (USDA–FS, 2022). Timing of the outbreak onset varied across the landscape, with the result that individual stands experienced between zero and three years of defoliation starting largely either in 2016 or 2017 (Pasquarella et al., 2017). Defoliation in 2016 coincided with severe drought conditions, while defoliation in 2017 occurred when drought conditions were subsiding. Following the interaction of these two disturbances, many affected stands experienced high rates of canopy tree mortality. Assessments from twenty-nine permanent study areas in Connecticut and Rhode Island identified plot-level tree mortality rates up to 79.4 % with an average of 36 % for plots experiencing severe defoliation (Ward et al., 2022). However, the role that the temporal juxtaposition of these disturbances played in stand-level mortality outcomes is not well understood.

Our research aimed to evaluate potential drivers of tree mortality associated with a drought-spongy moth interaction with a focus on evaluating the specific influence of disturbance timing. We used a combination of field-based surveys, geospatial data layers, and remote sensing imagery to assess mortality patterns as a function of disturbance timing, defoliation frequency, and landscape characteristics. We hypothesized: 1) greater mortality in sites experiencing spongy moth defoliation and drought than those affected by drought alone, 2) greater mortality in sites experiencing repeated defoliation, with mortality rates increasing with defoliation frequency, and 3) greater mortality where defoliation was more temporally proximate to drought conditions due to the overlap in impacts and lack of potential recovery time between individual disturbances. We also evaluated a suite of stand characteristics, physiographic, and edaphic factors as potential additional drivers of mortality patterns.

2. Materials and methods

2.1. Study Area

The general study area for this analysis was southern New England, USA and specifically two areas encompassing pre-existing plot networks in eastern Connecticut and central Massachusetts. Use of these existing plot networks facilitated rapid response following disturbance and allowed us to leverage existing data on spongy moth abundance and damage (Fig. 1). The forests in the study areas are predominantly temperate mixed-hardwoods with oak-hickory dominated stands most common, but with stands of northern hardwood and hardwood-pine-hemlock mixtures also represented. Climate in this region in classified as cool, moist temperate, with annual precipitation averaging ~110–133 cm and average annual temperature of ~8–10 °C. Spongy moth populations have been established in the region since the late 1800s, with periodic spongy moth outbreaks including especially significant events in the late 1960’s and early 1980’s. We sampled plots that had been previously censused for spongy moth larva and egg mass abundance, and characterized plots based on the different defoliation timing categories that occurred in the dataset (none, 2017-only, 2018-only, 2016/2017, 2017/2018, and 2016/2017/2018; Table 1). In Connecticut, 25 study stands each sampled with 3 spatially non-independent 20 m x 20 m plots were selected from a network established by the Fragmented Ecological Networks Project (Bagchi et al., 2018, Anderson et al., 2019). In Massachusetts, ten study stands in and around Harvard Forest that were sampled in an equivalent fashion were also included.

2.2. Data Sources and Preparation

A combination of field surveys, remotely sensed data, and existing geospatial datasets were used to develop tree mortality-focused response variables and a set potential predictor variables related to disturbance characteristics (drought severity and defoliation frequency, timing, pattern, and severity), stand conditions (tree species composition and stem density), and landscape factors (soils and topography; Table 2). Data were processed in ArcMap 10.7.1 (ESRI, 2019) and Python 2.7.18 using the Integrated Development and Learning Environment (Python Software Foundation, 2022). All data products were projected to USA Contiguous Albers Equal Area Conic projection using the ArcMap ‘project’ and ‘project raster’ tools (ESRI, 2019). Raster data were aggregated to the plot level by averaging the values of all pixels intersecting the plot for all variables.

Field plots were surveyed during summer 2019 (leaf-on conditions) to assess tree mortality and characterize stand composition and structure. All canopy trees (defined as having a diameter at breast height (DBH) of at least 20 cm) were assessed for species, DBH, crown class, condition (live/dead – based on the presence or absence of green foliage in the canopy, basal sprouts were not considered live stems), and crown dieback (classified by severity using the approximate percent of affected tree crown volume). Field data were used to develop stand structure and composition variables including: total plot-level basal area, average tree basal area, relative basal area of oak species (*Quercus* spp.), tree species

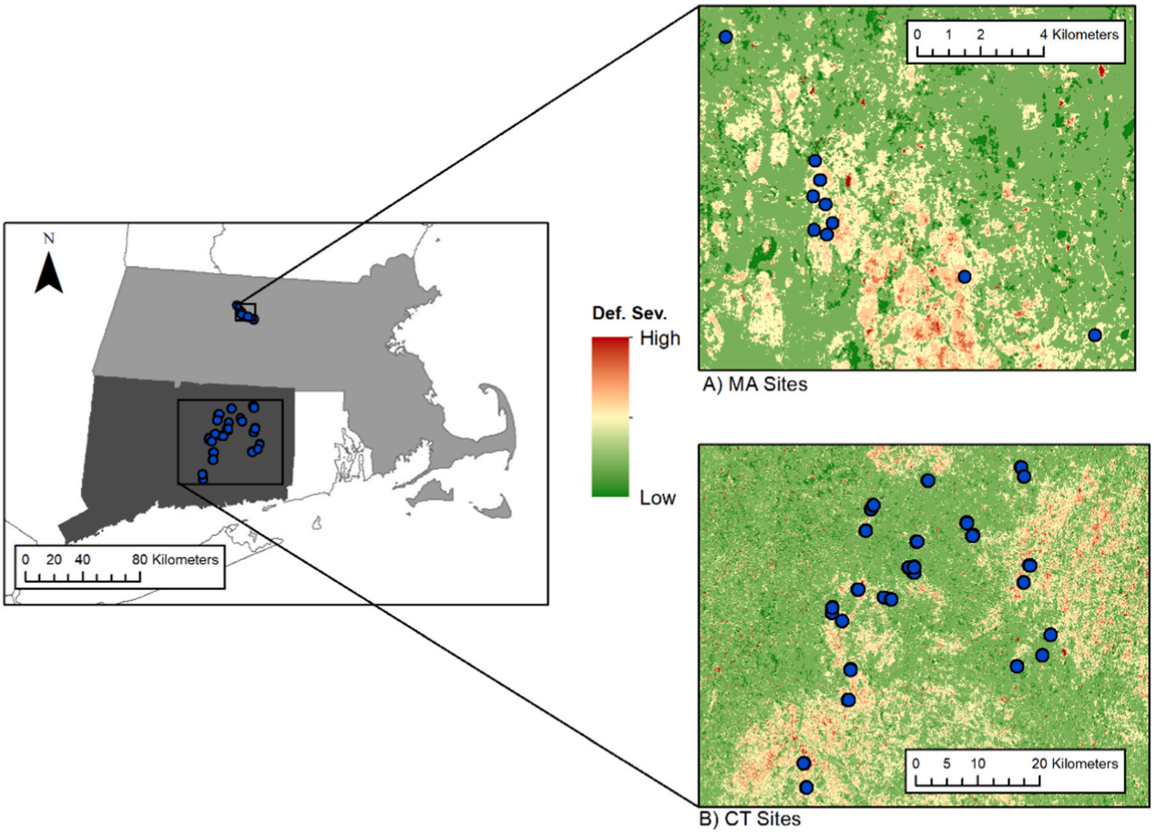

Fig. 1. Depiction of the study stands located within state-owned forest properties throughout eastern Connecticut and central Massachusetts, USA. A) Massachusetts study sites and B) Connecticut sites are overlaid on the 2017 Spongy Moth Annual Defoliation Severity Assessment (Pasquarella et al., 2017).

Table 1
Site characteristics, defoliation patterns, and mortality outcomes for study locations. Sites consisted of multiple stands which were the individual sampling units and were sampled with three non-independent 20 x 20 m sampling plots (0.12 ha per stand). Numbers are means across stands within sites.

Site	Number of Stands	Basal Area (m^2/ha)	Relative Basal Area Oak	Prop. Basal Area Mortality	Prop. Oak Basal Area Mortality	Mean Defoliation (2016–18)	# Years Defoliated	Defoliation Patterns	Mean PDSI 2016
Beaver Brook	2	20.20	0.86	0.50	0.54	−2.98	3	All	−3.41
Bolton	3	24.73	0.34	0.19	0.35	−1.15	1	17	−2.95
Bishop Swamp	2	29.71	0.51	0.15	0.38	−2.18	0,1,3	17, All	−3.12
Cockaponset	2	14.68	0.31	0.05	0.04	−1.68	1,2	16/17, 17	−4.28
Coventry	2	22.24	0.49	0.00	0.00	−0.63	1,2	17, 17/18	−3.40
Meshomasic	3	25.94	0.63	0.20	0.35	−1.75	1,2	16/17, 17	−2.76
Natchaug	1	27.21	0.15	0.01	0.00	−0.68	0,1	17	−2.24
Nye Holman	1	20.01	0.84	0.00	0.00	−0.70	1	17	−2.72
Quabbin	8	31.53	0.64	0.31	0.38	−1.90	0,1,2,3	17, 18, 17/18, All	−3.70
Harvard Forest	2	36.80	0.63	0.24	0.31	−1.97	1,2	17, 17/18	−3.89
Scotland	2	21.34	0.66	0.22	0.46	−1.34	0,1	17	−4.14
Salmon River	2	23.49	0.64	0.16	0.26	−1.94	1,2	16/17, 17	−3.89
Storrs	2	28.80	0.26	0.02	0.00	−0.96	1	17	−3.35

Table 2
Summary of linear model input predictor and response variables, including sources and dates of data coverage or acquisition.

Category	**Variables**	**Source Data**	**Dates**
Response			
Mortality	Canopy Oak Mortality (Stem-Based, Basal-Area Based), Canopy Non-oak Mortality	Field Surveys	2019
Predictors			
Vegetation	Relative Oak Basal Area, Tree Species Richness	Field Surveys	2019
Physiography	Potential Annual Direct Incident Radiation, Topographic Position Index	CT ECO; MassGIS	2016; 2005
Soil Characteristics	Available Water Supply (for depths of 0–50 cm)	WebSoilSurvey	2021
Defoliation	Mean Defoliation Severity, Defoliation Frequency, Defoliation Timing, Defoliation Pattern	Pasquarella et al.; Landsat	2016–2018
Drought	Mean 2016 Palmer Drought Severity Index	Climate Engine – gridMET (PDSI)	2016–2018

richness, and tree density (Table 1). Field surveys were also used to develop tree mortality-focused response variables including the proportion of dead trees (stem count-based) and the proportion of dead tree basal area (Table 1 & 2). Mortality proportions were also calculated specifically for oak and non-oak species (e.g., proportion of oak stems or basal area that was dead) for comparison between overall tree mortality rates and rates for preferred and non-preferred host species for spongy moth.

Digital elevation models (DEM) provided by CT ECO (https://maps.cteco.uconn.edu/map-services/#elevation; 2 ft resolution) and MassGIS (https://www.mass.gov/info-details/massgis-data-lidar-dem-and-shaded-relief; 1 m resolution) were used to calculate all topography variables except landform. Slope and aspect were calculated using the respective tools from the Spatial Analyst (Surface) toolbox in ArcGIS 10.7.1 (ESRI, 2019). Predicted annual direct incident radiation was calculated for each plot location based on slope aspect and angle and latitude of the plot (McCune and Keon, 2002). The Topographic Wetness Index was calculated using ArcMap ModelBuilder with the tools 'flow direction', 'flow accumulation', and 'slope' from the Hydrology and Surface toolboxes (Beven and Kirkby, 1979; ESRI, 2019). The topographic wetness index is derived using the natural log of the catchment area to slope and quantifies water flow and accumulation throughout the landscape. Topographic Position Index, which represents the comparative altitude of a location in relation to its surroundings, was calculated in Python 2.7.18 using a moving window technique to calculate the difference between local slope height and average neighborhood height (Gallant and Wilson, 2000; Weiss, 2001). Landform classifications were derived at 10-meter resolution using DEMs and a pattern recognition technique to create a categorical representation of local topography (Jasiewicz and Stepinski, 2013). Landform was classified twice – by individual landform categories (e.g., ridges, footslopes) and by broader categories grouping several similar landform classes (e.g., slopes, flats), plots were assigned to the landform category that was most common in the plot area.

Soils data were prepared by the Natural Resources Conservation Service and included available water supply (AWS) at depths of 0–50 cm, 0–100 cm, and 50–100 cm and a ratio of AWS from 50–100 cm to AWS from 0 to 100 cm (USDA, 2021). AWS summarizes plant available water holding capacity for a given depth range (USDA, 2021). Each depth range is assigned one value based on the available water content of each soil layer at field capacity and the thickness of the layers within the depth range. This product was then aggregated at 10 m resolution. AWS is a function of soil properties including soil texture, soil organic matter, and coarse fragment content and incorporates soil depth to water restriction. Available water influences tree response to drought (Phillips et al., 2016) and AWS provides a modeled estimate of relative field capacity of available water supply across plots.

Spongy moth defoliation severity and timing from 2016 through 2018 were assessed by characterizing plots based on the overlapping pixel(s) from a 30m-resolution annual defoliation condition score product (Pasquarella et al., 2017). This product uses harmonic modeling of historic Landsat data to predict Tasseled Cap Greenness (TCG) with synthetic Landsat imagery. Defoliation is assessed by the difference in TCG observed in the corresponding Landsat image and TCG as predicted for the synthetic image normalized by root mean squared error of the regression model (Pasquarella et al., 2017). Pasquarella et al. (2021) showed that this condition change product explained 60 % of the variance in ground-based observations of defoliation, based on field surveys in 2017 (Pasquarella et al., 2021). For assessing frequency, timing, and pattern of defoliation, we used a threshold of > 0.5 reduction in TCG to denote defoliation occurrence in for each plot in each year (Pasquarella et al., 2021). While the condition change values are deviations from a baseline and cannot be interpreted directly as percent defoliation, more-negative values for the Landsat based product were correlated with more severe defoliation based on field surveys. Temporal patterns of spongy moth defoliation were assessed as defoliation frequency (the number of years of defoliation), timing of defoliation relative to 2016 drought (number of years between 2016 and initial defoliation), and pattern of defoliation on an annual basis (e.g., defoliation in 2016 and 2017 vs. 2017 and 2018).

Drought severity and timing were assessed with a 4-km modeled Palmer Drought Severity Index (PDSI) using gridMET precipitation data from ClimateEngine (climateengine.org; Huntington et al., 2017). PDSI is modeled for daily products and was aggregated to a monthly product. We used the monthly product to calculate the average and maximum PDSI values recorded across the growing season (April through October) from 2016 to 2018, as well as the duration of drought. Drought duration (number of months) was assessed using a categorical interpretation of PDSI (low (d0), mild (d1), moderate (d2), and severe (d3) drought conditions) and reflected the number of months a site experienced drought severity that met or exceeded the given severity level. PDSI represents trends of drought and water availability per site. While drought was primarily present in 2016, data from 2017 and 2018 were also evaluated as potential predictors.

2.3. Statistical Methods

To evaluate how defoliation, drought, stand characteristics, soil characteristics, and landscape factors affected tree mortality outcomes, we related mortality response variables (proportions of basal area and stems that died) to predictor variables using generalized linear models with a beta link function (using the *betareg* package in *R* v.4.4.2), which is appropriate for use with proportion data such as the mortality data analyzed here (Cribari-Neto and Zeileis, 2010). Prior to model building, predictor variables were tested for multicollinearity and strongly colinear variables were not included together in models (full correlation matrix included in Supplemental Materials, Fig. S5). Based on correlation results and pre-determined relationships of interest we defined an *a priori* model set to relate mortality to general categories of predictors and their combinations (Table 2, full model set depicted in Supplemental Material, Table S1). Categories included defoliation parameters and combinations, defoliation interaction with drought severity, defoliation combined with site/stand characteristics, and full and null models (Table S1). Models were evaluated based on Akaike's Information Criterion (AIC) and compared based on ΔAIC and Akaike weights and pseudoR^2 values were also calculated to assess model fit.

3. Results

3.1. Defoliation, drought, and mortality patterns

There was substantial variation among sites in patterns of defoliation, both in terms of defoliation severity, frequency, and timing. The Landsat-based condition change metric (Pasquarella et al., 2017) varied from 0.63 to −2.98, with the largest negative values occurring in most sites in 2017. (Table 1). All sites experienced at least one year of defoliation, while seven sites had two years of defoliation, and one site (Beaver Brook) had defoliation in all three years (Table 1). The pattern of defoliation timing varied across sites, such that 2 stands had two years between the drought and max defoliation, 23 had one year between, and 6 stands had max defoliation concurrent with the drought (Table 1). Drought severity in 2016 based on PDSI only varied slightly among sites with most values between −3 and −4 (indicating "severe" drought conditions), with a maximum modeled severity of −4.14 at the Scotland site and minimum of −2.24 at the Natchaug site (Table 1).

Across all sites the average mortality across all species was 19 % (in terms of basal area loss) and for oak species specifically 28 %. However, mortality patterns varied substantially within and among sites, with 11 of 13 study areas exhibiting some tree mortality. The maximum stand-level mortality across all tree species was 69 % and the maximum mean mortality across stands at the site level was 50 %, both at the Beaver Brook site (Table 1). For oak species the maximum stand-level mortality was 95 % at one of the Quabbin plots, but the maximum across all stands within a site was 54 % at Beaver Brook, which was also the site with the highest relative basal area of oak species (86 %; Table 1).

Mean oak basal area mortality was 60 % in stands that had 3 years of defoliation, 30 % in stands defoliated 2 times, 17 % in stands defoliated once, and 2 % in stands without significant defoliation (Fig. 2). Among sites that had 2 years of defoliation mean oak basal area mortality was 36 % in sites that had initial defoliation in 2016 and 24 % for sites with defoliation starting in 2017 (Fig. 2). Among sites with a single year of defoliation those that had defoliation in 2017 had mean oak basal area mortality of 17 % while the one site that had defoliation in 2018 had 9 % mortality (Fig. 2). Relationships with frequency and timing patterns were similar for oak stem-based mortality.

3.2. Predictors of mortality

Model selection for beta regression modeling resulted in multiple highly supported models (based on a criteria of ΔAIC <2) being identified for percent oak basal area mortality and percent oak stem mortality (Table 3). Each of the highly supported models for oak basal area mortality included defoliation frequency as a predictor and the two highest weighted models included stand characteristics and defoliation severity as additional predictors (Table 3). In the oak mortality model sets the null models (including only the intercept term) were the least supported models in the entire set (Table 3, Tables S2–4). In the models with non-oak mortality as the response there were no models that were more highly supported than the null model (Table 3).

Based on pseudo R^2 from beta regression, the selected models explained ~52–60 % of the variance in oak basal area mortality response (Table 4). Mortality increased with greater defoliation severity

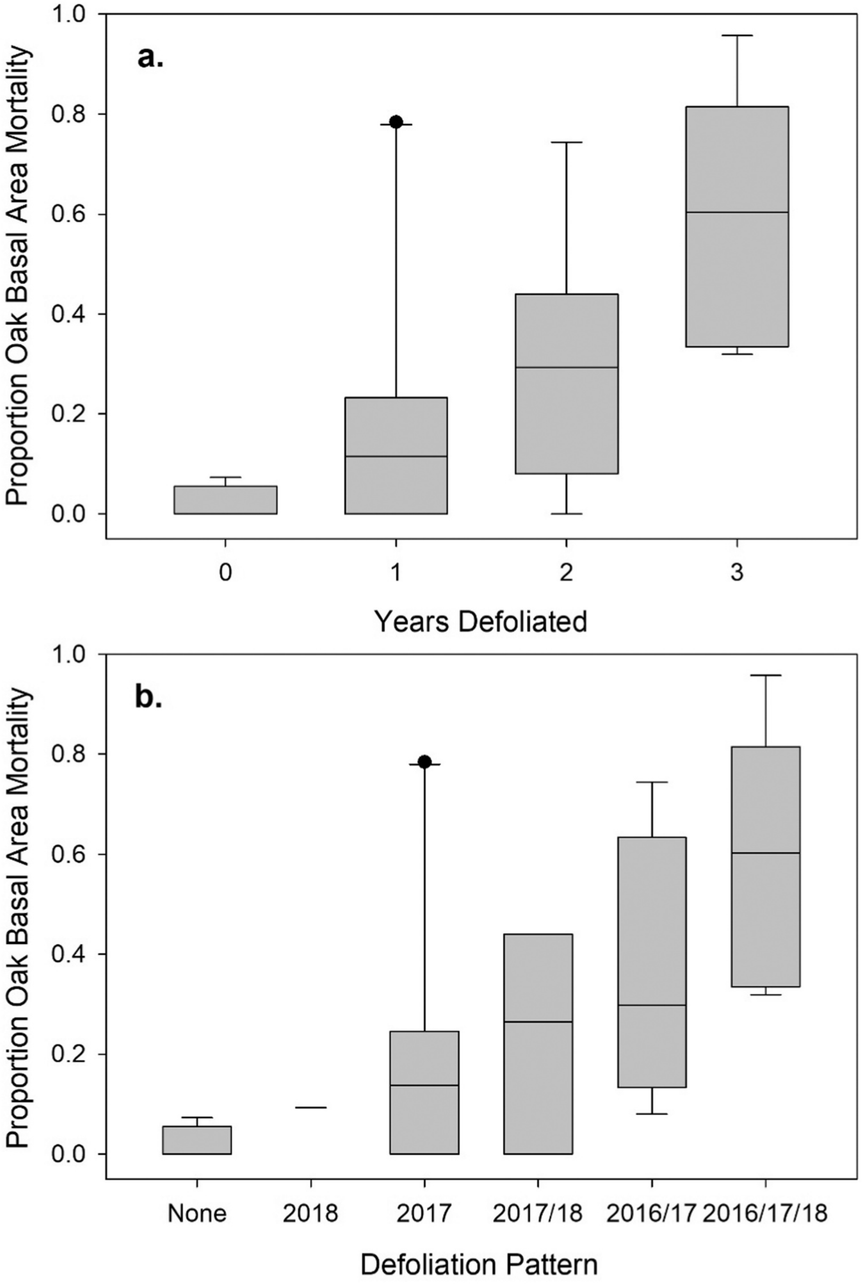

Fig. 2. Box plot illustrating proportion of oak basal area mortality in relation to a) defoliation frequency and b) defoliation pattern categories.

Table 3
Partial model list from beta regression of mortality response with top models (those with ΔAIC < 2) and null model for oak basal area mortality and non-oak stem mortality. Results for oak stem mortality were similar and can be found in Supplemental Material. Full model lists are included in the Supplemental Material (Tables S3-5).

Percent Oak Basal Area Mortality	**df**	**AIC**	**ΔAIC**	**Weight**
Frequency, Species richness, Rel. BA Oak	5	−46.80	0.00	0.24
Severity, Frequency	4	−46.68	0.11	0.23
Frequency	3	−46.37	0.43	0.20
Frequency, Soil	4	−45.12	1.68	0.10
Null model	2	−27.84	18.95	< 0.001
Percent Non-oak Mortality	**df**	**AIC**	**ΔAIC**	**Weight**
Null model	2	−136.90	0.00	0.19
Severity	3	−135.67	1.23	0.10
Frequency	3	−135.19	1.71	0.08
Timing	3	−134.99	1.91	0.07

(mean across 2016–2018 based on change in tasseled-cap greenness; Pasquarella et al., 2017) and with defoliation frequency (the number of years defoliated based on change in tasseled-cap greenness; Pasquarella et al., 2021) as illustrated in Fig. 3a. Mortality also decreased with higher species richness (Table 3, Fig. 3b). Neither defoliation timing (number of years between drought and defoliation) nor pattern (categories of defoliation sequencing) was included in the most highly supported models, although the strong correlation of these variables with defoliation frequency precluded their inclusion in models with this most influential predictor. Drought severity (as mean 2016 PDSI) was also not included in any highly supported models, either as a main effect or as an interaction with defoliation variables. Soil available water content was included in a model with ΔAIC< 2, but the nested model including only defoliation frequency was more highly supported and the AIC weight for the soil + defoliation frequency model was substantially lower than the top 3 models, thus this model was not interpreted. The models for oak stem-based mortality were similar (Table S3).

The most supported models for non-oak mortality had very low explanatory power (explaining only 1–3 % of the variance based on pseudo R^2). These models included only defoliation characteristics, but were not more highly supported than the null model and thus not interpreted.

4. Discussion

4.1. *Defoliation severity, frequency, and drought-defoliation interactions*

Prior work on defoliation-only events has indicated that trees and stands experiencing single-year defoliation outbreaks often recover by refoliating and temporarily limiting wood production (Kulman, 1971; Davidson et al., 1999). However, in a disturbance interaction such as that here between drought and a spongy moth outbreak, there is the potential for synergistic or compounding effects associated with the dual loss of leaf area and depletion of carbohydrate stores (Bréda et al., 2006). However, contrary to expectations, stands in our study experiencing a single year of defoliation during or soon after a drought had similar mortality rates to stands without defoliation (Fig. 2). In our study system, increasing severity of the preceding drought does not appear to have reduced the survival of trees in stands affected only by a single defoliation event, suggesting that individual trees were able to initially recover from the interaction between severe drought and single-year defoliation. Trees experiencing only a single year defoliation, even with drought-defoliation interaction, may be able to recover before non-structural carbohydrate stores fall below a critical threshold for potential recovery (Barker Plotkin et al., 2021).

Repeated defoliation, which further depletes resources and prolongs the recovery period (Johnstone et al., 2016), has been shown to strongly increase the potential for mortality, including through increased vulnerability to secondary mortality factors (Kulman, 1971; Davidson et al., 1999). Such an effect was supported in our analysis, which illustrated no substantial increase in mortality with one year of defoliation, but greatly increased mortality rates for stands experiencing multiple years of defoliation (Fig. 2 & 3). There was also a substantial additional increase in mortality as defoliation frequency increased beyond two years, as stands experiencing drought and three years of defoliation had double the average mortality of twice defoliated stands (Fig. 2). Within this disturbance interaction, two years of defoliation may be enough to deplete resources to a point where trees are unable to recover and three years of defoliation appeared to frequently push stands into high mortality. While this study did not assess individual tree responses, a recent assessment of tree mortality following the same multi-year defoliation linked defoliation with decreased levels of non-structural carbohydrates (NSC) and identified a threshold below which tree mortality occurs (Barker Plotkin et al., 2021). NSC depletion is linked to carbon starvation and may also influence tree response to drought (e.g., Sapes et al., 2021). The combination of two or more years of defoliation within a drought-defoliation interaction may deplete NSC stores beyond this critical threshold, but further experimental work may be required to test the generality of this finding.

Within the interaction between drought and multiyear defoliation that we studied, landscape patterns of defoliation varied such that stands experienced different temporal patterns of disturbance (Pasquarella et al., 2017). In stands where peak defoliation occurred in 2016, there was significant overlap between severe drought conditions and spongy moth defoliation, but in stands where defoliation began in 2017, defoliation began at the end of the drought period and the final year of defoliation occurred following the drought. However, despite variation among sites in timing of initial defoliation, this factor was not an important predictor of mortality outcomes. We had expected that stands experiencing two years of defoliation with outbreak onset in 2016 would have higher mortality rates than those with defoliation outbreak onset in 2017, due to the potential recovery between individual disturbances in the latter case (Johnstone et al., 2016). However, our results were not consistent with these expectations as mortality rates were similar in sites that experienced defoliation in 2016 and 2017 to those with defoliation in 2017 and 2018. This suggests that the specific timing of defoliation relative to drought was less important than whether the forest experienced multiyear defoliation. One factor that could have contributed to this lack of effect is that the overall duration of the combined disturbance differed between these categories (i.e., 2016 through 2017 versus 2016 through 2018), which could have also impacted tree mortality rates and could be a focus of future research.

Table 4
Coefficients for beta regression models of oak basal area mortality, model numbers correspond to model ranking in Table 3. AIC = Akaike Information Criteria, w = Akaike weighting, pR^2 = pseudo R^2.

Model	**Intercept**	**Explanatory Variables**				**Evaluation Criteria**		
		Defoliation Severity	*Defoliation Frequency*	*Relative Oak BA*	*Species richness*	*AIC*	*w*	*pR^2*
1	−1.86*		0.85***	0.58	−0.15*	−46.80	0.24	0.60
2	−3.09***	−0.37*	0.80***			−46.68	0.23	0.56
3	−2.78***		0.95***			−46.37	0.20	0.52

* $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$

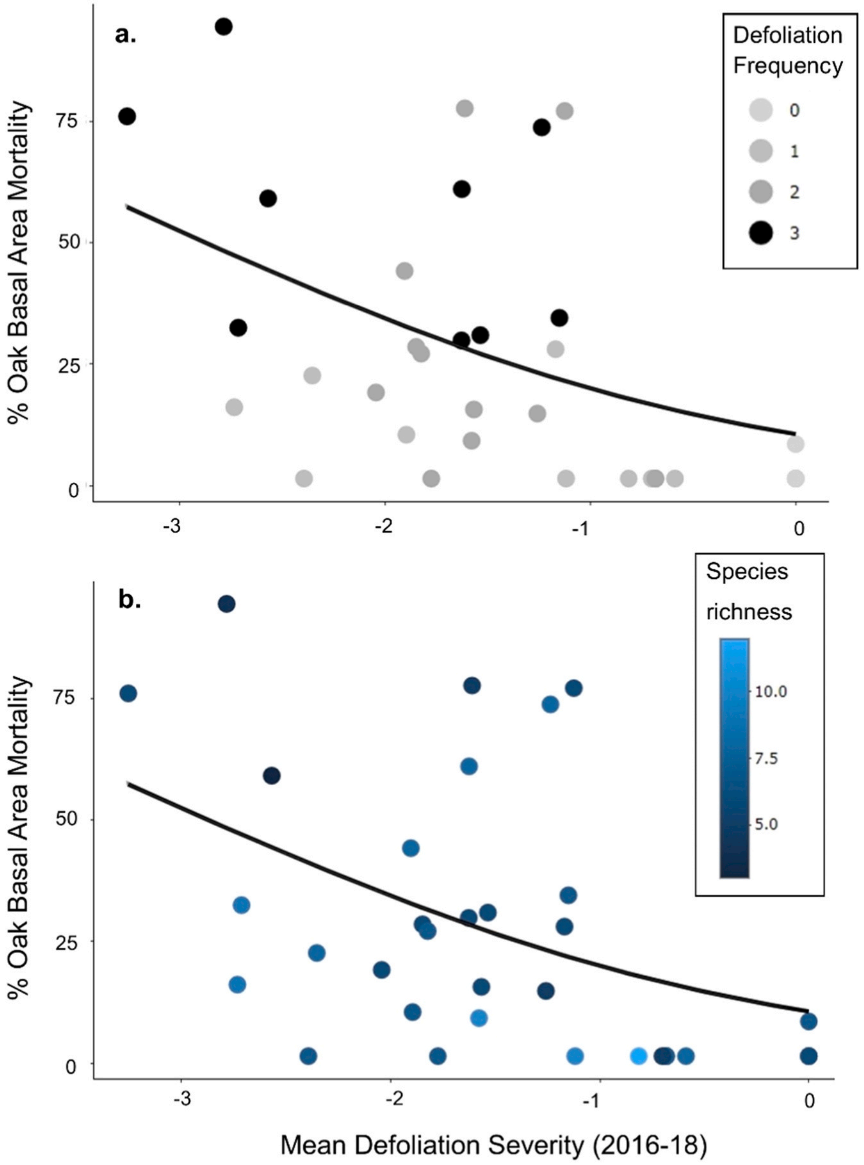

Fig. 3. Relationships between oak basal area mortality response and predictor variables from beta regression modeling with two top models (based on AIC weights) illustrated. Relationships for stem-based oak mortality were very similar and are illustrated in Supplemental Material, Fig. S6.

4.2. Drought severity

While defoliation frequency was a strong driver of tree mortality, spatial variation in drought severity appeared to be less influential. The apparent lack of a drought severity effect could be associated with a variety of factors, including the relatively small differences in drought severity and timing across the landscape, scale mismatch between stand-level mortality and the use of modeled Palmer Drought Severity Index (PDSI) as an indicator of drought severity, and potential lag effects associated with drought impacts. The regional drought that was studied here was similar in magnitude across our study area, which may have limited our ability to discern how drought severity interacts with defoliation. Additionally, PDSI is a modeled product and has limited capacity to reflect fine-scale variation in drought conditions (Mishra and Singh, 2010). These modeled data may not capture site-scale trends of soil moisture and plant water stress in forested systems. Without direct soil moisture monitoring tools implemented prior to or during the disturbance interactions, it is not possible to assess the true *in-situ* soil moisture content response related to the drought. Even with such direct monitoring soil moisture may still not fully capture plant water stress (Calvet et al., 2004). In addition, our research covered a period of three years, which may be too short of a period capture lag effects of drought on mortality, which have been observed, but are not well understood (Innes, 1998; Bigler et al., 2007). Future mortality patterns may still be influenced by drought legacies or compounded effects with single-year or multi-year defoliation (Innes, 1998; Bigler et al., 2007).

4.3. Stand and site characteristics

In addition to disturbance factors, site characteristics, including edaphic factors and physiographic features, have been shown to influence tree mortality patterns following disturbances (e.g., Davidson et al., 1999). Our results generally did not support physiographic variation as a driver of forest mortality patterns, which could be related to the similarity of sites included in this study or to the confounding effects of stand composition and associated variation in defoliation patterns. We expected higher mortality rates in drier, upland sites; an effect that has been indicated in drought-only studies (Anderegg and Trugman, 2019), through effects on soil water dynamics (Rosenberg et al., 1983; Pachepsky et al., 2001; Geroy et al., 2011) and stand characteristics such as tree species composition and growth rates (Fekedulegn et al., 2003; Frey et al., 2007). However, topography was not an important driver of mortality outcomes and was also not correlated with defoliation severity or frequency ($r < 0.01$; Fig. S5), which may have limited its influence on mortality outcomes.

Soil properties, especially water holding capacity, can also reflect the relative overall influence of drought on a site level and could contribute to variation in mortality across sites with trees experiencing drier conditions having increased risk of mortality (Anderegg and Trugman, 2019; Trugman et al., 2021) due to hydraulic failure resulting in cavitation and the formation of embolisms that block the flow of water through the xylem, leading to cell dehydration (Bréda et al., 2006; McDowell et al., 2008; Sevanto et al., 2014). Trees may also respond to drought conditions by closing stomata to prevent water loss, which decreases rates of photosynthesis and may contribute to carbon starvation (Bréda et al., 2006; McDowell et al., 2008; Sevanto et al., 2014). Our results did not indicate a strong influence of estimated soil available water content on mortality outcomes. The use of modeled soil moisture could have limited our ability to isolate its effect, as spatial variability in soil moisture can be difficult to assess without direct measurements due to the influence of multiple factors like soil properties, topography, previous patterns of precipitation, and individual tree water use (e.g., Svetlitchnyi et al., 2003; Tromp-van Meerveld and McDonnell, 2006; Williams et al., 2009; Hu and Cheng Si, 2014; Gimbel et al., 2016) that can influence soil moisture non-linearly. In addition, inferred soil properties likely do not fully capture soil moisture and variation in plant available water across sites (Tromp-van Meerveld and McDonnell, 2006). Finally, species and their water use and acquisition traits and strategies vary across sites with varying soil properties, which can affect stand-level response to drought (Bréda et al., 2006).

Our analysis also evaluated the potential effect of stand characteristics which have been shown to influence the spatial distribution and severity of spongy moth defoliation outbreaks (Foster et al., 2013) and resilience to drought (Bréda et al., 2006). For example, high tree stem density at the stand scale has been positively related to tree mortality rates (Bottero et al., 2017), and reductions in stem density can positively impact drought resilience (D'Amato et al., 2013). The stand characteristics we assessed here (relative oak basal area and species richness) appeared to have some influence on oak mortality. Species richness was negatively associated with mortality, indicating that sites with more species had less mortality, likely because of the greater diversity of non-target species in these sites and possibly due to associational resistance (Jactel et al., 2021). The dominance of oaks (as primary host species for spongy moth) was a low influence driver of mortality at the stand-level, reflecting the death of large canopy oak trees, which are preferentially defoliated by spongy moth (McManus and Csóka, 2007, Barker Plotkin et al., 2025), but this effect was likely also associated with defoliation characteristics (which were somewhat correlated with oak dominance, $r = 0.28–0.48$, Fig. S5). However, stand characteristics also may not capture the specific drought and defoliation resistance of individual trees, which can be influenced by physiological traits. For example, a study considering individual tree mortality following multiyear defoliation found that mortality rates varied across individual oak species (Ward et al., 2022).

4.4. Conclusion

With increasingly rapid and substantial alteration of disturbance regimes, there is an urgent need to understand disturbance interactions and their potential for synergistic and compounding effects (Paine et al., 1998; Trumbore et al., 2015). Recent studies on disturbance interactions and resulting tree mortality have suggested that future research should focus on disturbance frequency and timing as potential drivers of variation in outcomes (Johnstone et al., 2016; Burton et al., 2020). Our research suggests that individual disturbance frequency within a disturbance interaction can impact resulting canopy tree mortality. However, our study also indicated that timing was not strongly associated with mortality outcomes, but there are timing components such as longer-term lag effects and overall disturbance duration that may be influential but were not possible to separate in this observational study. Further experimental and modeling work is needed to address these aspects of disturbance interactions. Understanding temporal influences and incorporating them in disturbance prediction models may increase our ability to predict and plan for disturbance interactions as they likely become more common with changing disturbance regimes (Seidl et al., 2017).

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Data Availability Statement

Data generated or analyzed during this study are available from the following sources:

Barker Plotkin A. 2022. Oak Forest Response to *Lymantria dispar* Defoliation in Central Massachusetts since 2019. Harvard Forest Data Archive: HF424 (v.1). Environmental Data Initiative: https://doi.org/10.6073/pasta/7955f18f43a3dba4638063264e69c557.

Pasquarella, Valerie J. (2018). Landsat-based Gypsy Moth Defoliation Assessment (Southern New England) (Version 3.0) [Data set]. Zenodo. https://doi.org/10.5281/zenodo.1493

FEN Lymantria larval and egg mass count data can be accessed at: https://github.com/BagchiLab-Uconn/Forest-Condition-Assessment

CRediT authorship contribution statement

Danielle N. Tanzer: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Fahey Robert:** Writing – original draft, Visualization, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Maya Sagarin:** Writing – review & editing, Visualization, Formal analysis. **Keenan J. Rivers:** Writing – review & editing, Investigation, Data curation. **James Mickley:** Writing – review & editing, Supervision, Investigation, Data curation. **Audrey Barker Plotkin:** Writing – review & editing, Supervision, Investigation, Data curation. **Robert Bagchi:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Data curation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Robert T Fahey reports financial support was provided by National Science Foundation. Robert Bagchi reports financial support was provided by National Science Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122859.

Data availability

Link to data repositories shared in Attach files step

Oak Forest Response to Lymantria dispar Defoliation in Central Massachusetts since 2019 (EDI)

Forest Condition Assessment (Github)

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