Evaluating forest subcanopy response to moderate severity disturbance and contribution to ecosystem-level productivity and resilience

Robert T. Fahey[1]*, Ellen J. Stuart-Haëntjens[2], Christopher M. Gough[2], Aubrie De La Cruz[3], Elizabeth Stockton[3], Christoph S. Vogel[3], and Peter S. Curtis[4]

[1]University of Connecticut, Department of Natural Resources and the Environment & Center for Environmental Sciences and Engineering

[2]Virginia Commonwealth University, Department of Biology

[3]University of Michigan Biological Station

[4]Ohio State University, Department of Evolution, Ecology and Organismal Biology

*Corresponding author

1376 Storrs Rd. Unit 4087

Storrs, CT 06269-4087

robert.fahey@uconn.edu

(860) 486-4169

Abstract

North American temperate forests have functioned as a terrestrial carbon (C) sink for more than a century, but the future of this sink is highly uncertain as disturbance frequency increases and regrown forests approach maturity. The subcanopy is integral to the functional recovery of forests, supporting short-term resilience of primary production and longer-term shifts in tree species composition and diversity. However, the factors that contribute to variation in forest subcanopy response to disturbance are not well understood. In this study, we investigated subcanopy shifts in aboveground wood net primary productivity ($ANPP_w$) and composition following experimental moderate severity disturbance emulating natural canopy mortality from age-related senescence. We assessed the importance of variation in disturbance severity, site fertility, and community composition on subcanopy disturbance response and contribution to total (canopy and subcanopy) $ANPP_w$ response. We also assessed the effect of the moderate severity disturbance on species composition and diversity, and competitive patterns within the subcanopy layer. Subcanopy aboveground biomass and $ANPP_w$ increased substantially relative to pre-disturbance levels by a factor of 1.4 and 22.7, respectively. The subcanopy (stems < 8cm DBH) made up a large component of overall (canopy plus subcanopy) post disturbance $ANPP_w$ (16.2%) and disturbance response (post-disturbance $ANPP_w$ /pre-disturbance $ANPP_w$; 54.1%). Subcanopy $ANPP_w$, subcanopy post-disturbance $ANPP_w$ response, and subcanopy contribution to total post-disturbance $ANPP_w$ response were all most strongly predicted by subcanopy community composition in combination with canopy composition and site fertility. Variation in disturbance severity was not a strong predictor of subcanopy $ANPP_w$ response to disturbance. Subcanopy compositional trends and growth patterns both indicate likely increased heterogeneity in canopy composition (greater β diversity) and a potential shift toward greater dominance by mid-tolerant *Quercus rubra* (northern red oak). Our results illustrate the importance of the subcanopy in the response of forest productivity to moderate severity disturbance and illustrate that composition of the subcanopy layer exerts a strong influence on the growth response both of the subcanopy and the forest as a whole. Our findings highlight the unique role of moderate severity disturbance, relative to more severe disturbances, in promoting biological and structural heterogeneity in forest ecosystems and favoring underrepresented mid-tolerant species.

Keywords: intermediate disturbance; northern hardwood; ecological silviculture; *Quercus rubra, Acer rubrum*; Great Lakes region

Highlights:

- Subcanopy contributed substantially to forest growth response to moderate disturbance
- Variable subcanopy response was mediated by composition not disturbance severity
- Moderate severity disturbance promoted growth of mid-tolerant northern red oak

1. Introduction

For more than a century, secondary forests of eastern North America have represented an important global carbon (C) sink during their regrowth following widespread harvesting and agricultural clearing more than a century ago (Houghton *et al.*, 1999; Caspersen *et al.*, 2000; Birdsey *et al.*, 2006). However, the sustainability of this C sink is in doubt because of changes in disturbance frequency and intensity, advancing forest age, and land management and global wood product markets (Birdsey *et al.*, 2006). Agricultural abandonment and resulting afforestation has slowed considerably, such that the area of forest cover is no longer increasing in eastern North America (Drummond and Loveland, 2010). In addition, decreased utilization of northern forests for wood products has led increasing proportions of these forests to attain mid-late-successional status (Birdsey *et al.*, 2006; Gough *et al.*, 2016). The transition of forests from early to middle and late-successional communities will have implications for both short- and long-term C dynamics (Gough *et al.*, 2013) as well as longer-term composition of the regional forest and resilience to stressors such as global climate change and exotic pest introductions (Duveneck *et al.*, 2014b). However, the effect that ongoing changes in land management, disturbance regimes, and successional transitions will have on C sequestration and community composition in eastern North American forests remains uncertain (Caspersen *et al.*, 2000; Hurtt *et al.*, 2002; Duveneck *et al.*, 2014a; Gough *et al.*, 2016).

An important feature of the regional transition from early to late-successional canopy dominance will be widespread senescence of canopy dominant early-successional trees and subcanopy response to this disturbance (Birdsey *et al.*, 2006; Gough *et al.*, 2010). This transition will likely affect C dynamics in these forests (Bond-Lamberty *et al.*, 2004; Gough *et al.*, 2007; Amiro *et al.*, 2010). Forest productivity has been shown to be highly resistant to this type of moderate (i.e., non-stand replacing) disturbance, and thus this transition may have limited near-term effects on C dynamics (Gough *et al.*, 2013). Subcanopy tree response may be an important factor in forest primary production resilience, helping maintain productivity through the transition from an early to mid-late successional stage (Stuart-Haëntjens *et al.*, 2015). However, subcanopy responsiveness to disturbance varies greatly with disturbance severity and among forest types and the factors associated with this variability are not always clear (Frelich, 2002). Pre-existing differences in subcanopy community composition and structure may be an important factor underlying variability in the resistance of ecosystem productivity to disturbance (Frelich, 2002; Papaik and Canham, 2006).

Subcanopy community composition and the growth response of its constituents to successional transition will also affect the composition and structure of future forest stands (e.g., Henry and Swan, 1974; Frelich, 2002; Halpin and Lorimer, 2016a). Future species composition will greatly affect the resilience of the region’s forest to threats such as climate change and introduced pests and pathogens (Duveneck *et al.*, 2014b). For example, in many forests in northeastern North America the dominance of maples (*Acer spp.*) is increasing greatly relative to historical conditions due to loss of fire and resulting “mesophication” in the landscape, and much of this shift has come at the expense of oak (*Quercus*) species (Nowacki and Abrams, 2008). Reduced diversity and extreme dominance of forest stands and landscapes by maples could reduce the resilience of these ecosystems to climate change (Stoy *et al.*, 2008) and could make the landscape especially vulnerable to the exotic pest Asian Longhorned Beetle (Haack *et al.*, 2010). In addition, there has also been a trend toward reduced tree functional diversity in many forested landscapes, which is due in part to the shift to maple dominance (Rhemtulla *et al.*, 2009). Coniferous species, which often have important functional roles in northern mixed hardwood forests (e.g., wildlife habitat and unique structural elements; DeGraaf *et al.*, 1993; Fahey and Lorimer, 2014b), have declined greatly in importance relative to historic conditions in some areas (Schulte *et al.*, 2007; Fahey and Lorimer, 2014a). Also, many shade intolerant/mid-tolerant species are underrepresented in modern northern hardwood forests, in part due to reliance on single-tree selection management which favors shade tolerant, late-successional species (Neuendorff *et al.*, 2007). This trend toward reduced diversity of species and functional groups may become even more pronounced in the future if the landscape transitions to increased late-successional community dominance (Duveneck *et al.*, 2014a).

The transition from early to mid-late succession can happen rapidly and produce a somewhat abrupt moderate severity canopy disturbance, especially if mediated by environmental factors (e.g., drought) or pest/pathogen outbreaks (Allen *et al.*, 2010; Flower *et al.*, 2013)**.** Such disturbances can promote shade intolerant and mid-tolerant species and maintain or increase overall species diversity (Frelich and Reich, 1999), but may also lead to accelerated succession (Allen *et al.*, 2012)**.** Due to potential positive impacts on species diversity, size and age structure, productivity, and structural complexity, management approaches modeled after moderate severity disturbance have been advocated for use in ecological forest management (Hanson and Lorimer, 2007). Assessing the impact of moderate severity disturbances, whether related to natural canopy senescence or management, on ecosystem functioning and species composition will be important to predicting future conditions in forested landscapes (Halpin and Lorimer, 2016b). However, although many studies have addressed the response of the subcanopy layer to gap creation (e.g., Canham, 1988; Lorimer and Frelich, 1989; Runkle, 1990), few have assessed the response of the subcanopy to moderate severity disturbance or its contribution to overall ecosystem resilience (Dyer *et al.*, 2010; Stuart-Haëntjens *et al.*, 2015).

The primary objective of this research was to better understand how the composition and structure of the forest subcanopy affect its response to canopy senescence and its role in overall forest resilience to moderate disturbance. We address this topic using an experimental forest canopy senescence experiment and focus on the following specific research objectives: 1) Evaluate how moderate severity disturbance affected characteristics of the subcanopy including biomass, stem density, species composition, and compositional trajectories, 2) Assess the effect of community composition and structure on individual species' growth responses following moderate severity disturbance, 3) Assess the effect of community composition and structure on subcanopy productivity following moderate severity disturbance, and 4) Evaluate how variation in subcanopy community composition and structure affect its relative contribution to overall forest productivity response to moderate severity disturbance.

2. Methods

2.1 Study Site

The study was conducted at the University of Michigan Biological Station (UMBS) in northern Michigan, USA (45^{o} 35N 84^{o} 43W). The location has a mean annual temperature of 5.5^{o} C and a mean annual precipitation of 817 mm. The forests of the area are primarily ~100 year old aspen-dominated stands resulting from intense clear-cut harvesting and wildfires in the early 20th century (Gough *et al.*, 2007). Short-lived early successional species such as bigtooth aspen (*Populus grandidentata*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) have dominated the upper canopy, but are now beginning to reach the limit of their natural life-spans (Gough *et al.*, 2013). Many stands in the region are undergoing gradual transition to dominance by mid- or late-successional species such as northern red oak (*Quercus* *rubra*), eastern white pine (*Pinus strobus*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*). At UMBS these species dominate the subcanopy layer, defined in this forest as stems < 8cm in diameter at breast height (DBH, 1.37 m), based on relationships between DBH and canopy position (Gough *et al.*, 2008). However, other species that are primarily confined to the subcanopy layer are also present, such as serviceberry (*Amelanchier arborea*), striped maple (*Acer pensylvanicum*), and ironwood (*Ostrya virginiana*).

The ecosystem-scale study used in this analysis was the UMBS Forest Accelerated Succession Experiment (FASET), which was designed to examine how the senescence of early successional tree species (aspen and birch) affects C cycling in a regionally representative forest ecosystem (Nave *et al.*, 2011). All aspen and birch trees within a 39 ha treatment area (>6700 stems) were mechanically stem girdled in Spring 2008. These species comprised 39% of total pre-treatment basal area within the experimental treatment area. Peak disturbance (expressed as loss of leaf area) occurred in 2010, when 97% of all girdled trees within the treatment area had senesced and leaf area index (LAI) was 44% lower than pre-disturbance values (Gough *et al.*, 2013). This experimental disturbance is similar in severity and extent to moderate natural disturbances related to wind or pest/pathogen outbreaks (Amiro *et al.*, 2010; Fahey *et al.*, 2015). The experimental area has canopy density of 700-800 stems per hectare, approximately 25 m^2/ha basal area, and leaf area index of ~3.5 (Gough *et al.*, 2013)

2.2 Data collection and preparation

We assessed subcanopy response at three spatial scales, with the expectation that growth response to disturbance varies depending on mechanisms operating at neighborhood to landscape scales: landscape (entire 39 ha manipulated area); plot (0.08 ha plots, n = 21); and neighborhood (5 m radius subplots within a subset of 8 plots). Within the treatment area, 21 circular 0.08 ha plots (16 m radius) were established at 100 m intervals along seven transects radiating from the base of a meteorological tower (Gough *et al.*, 2013). All canopy trees (≥ 8cm DBH) in each plot were tagged and had DBH measured in 2006, 2010, and 2012, encompassing pre- (2006-2010) and post-peak (2010-2012) disturbance periods. For the subcanopy (< 8 cm DBH), stems were tallied by species and diameter classes: <2 cm, 2-3.9 cm, 4-5.9 cm, and 6-7.9 cm in 2006, 2010, and 2012. Species and site or region-specific allometric equations were used to estimate aboveground biomass from DBH (Gough *et al.*, 2008) and biomass was converted to carbon based on a site specific conversion of 0.48 g of C per g of biomass (Gough *et al.*, 2013). For the subcanopy, the midpoint DBH for each diameter class (e.g., 3.0 cm for the 2 – 3.9 cm class) was used to estimate biomass for all stems. Mean annual aboveground wood net primary productivity ($ANPP_w$) was calculated as the absolute change in total aboveground wood biomass between census years divided by the number of years in the interval, providing a production value leading up to (2006-2010) and following (2010-2012) peak disturbance (Stuart-Haëntjens *et al.*, 2015).

To assess neighborhood scale responses, four non-overlapping 5 m radius (0.008ha) subplots were established along each cardinal axis at randomly selected distances (but far enough from plot center to avoid overlap) within a subset of 8 plots (Table 1) that spanned a range of disturbance severities (13 to 67% canopy tree basal area loss). For all small subcanopy stems (0-3.9 cm DBH) in these subplots we measured height growth increment based on visual analysis of growth whorls and terminal bud scars. For all large subcanopy stems (4-7.9 cm DBH) we collected increment cores using an increment hammer to assess recent basal area (BA) growth. Increment cores were mounted on grooved wood blocks and sanded with progressively finer sand paper to distinguish rings. Annual growth increments were measured to 0.001 mm using a Velmex stage micrometer and Metronics Quick-Check 4100. Current DBH and annual growth increments were used to calculate tree diameter in each year, which was then converted to basal area. Annual basal area increment (BAI) was then calculated based on change in basal area between years, and total BAI for pre- and post-peak disturbance periods was calculated based on these increments.

For each plot and subplot we quantified disturbance severity as the fraction of total pre-treatment BA (for stems $\geq$8 cm DBH) that senesced due to stem girdling (Stuart-Haëntjens *et al.*, 2015). Due to the patchy distribution of aspen and birch across the site, disturbance severity varied greatly with the treatment area, with plot-level BA senescence (across all 21 plots) varying from 9 to 69%. We also used pre-disturbance canopy layer NPP_w as a proxy for plot-scale variation in site fertility (hereafter "pre-disturbance canopy productivity"). Importantly, pre-disturbance canopy productivity and disturbance severity were not correlated ($r = 0.21$, $p = 0.35$), indicating the lack of a pre-existing relationship between forest production and disturbance severity (Stuart-Haëntjens *et al.*, 2015). In addition, total subcanopy biomass prior to disturbance in 2006 varied greatly among plots (750 to 3267 kg C ha^{-1}), but did not differ systematically with pre-disturbance canopy productivity ($r = -0.07$) or disturbance severity ($r = -0.30$).

Hemispherical canopy images and light data were collected in subplots at peak LAI in 2013 to examine how disturbance affected canopy structure and light distribution through the canopy. Images were taken under diffuse sky conditions in each subplot at ground level, 1 m, and 5 m using a leveled camera with an 180^o fisheye lens facing skyward. We derived estimates of canopy openness at each level using Gap Light Analyzer (GLA Version 2.0) software with the automatic optimal threshold algorithm applied (Nobis and Hunziker, 2005). We quantified the fraction of absorbed photosynthetically active radiation (fAPAR) in each subplot as percent of above canopy PAR available at 5 m, 1m, and ground level. A BF2 sunshine sensor (Delta-T Devices, Cambridge, UK) on a meteorological tower measured total and diffuse PAR above the canopy. Separate PAR sensors (SQ-110 Quantum Sensor, Apogee Instruments, Logan, Utah USA) were stationed at ground level and 5 m above the forest floor in all subplots and connected to a central datalogger. To minimize the influence of sunflecks, we quantified fAPAR based over >4 hours when light was >85% diffuse (e.g., Tobin and Reich, 2009) and to reduce the influence of solar angle, the PAR time-series from each sensor was averaged. Because of poor diffuse conditions or sensor failure, we report results from 20 subplots.

2.3 Data analysis

Characteristics of the subcanopy layer (including biomass, stem density, and biomass increment) were compared between pre-disturbance and post-disturbance periods using two-tailed t-tests in Sigmaplot v. 13 (SYSTAT Software Inc. 2014). Correlations of these variables with disturbance severity, pre-disturbance primary production (~site fertility), and community composition (from ordination, see below) were tested using Pearson Product Moment Correlation statistics using Sigmaplot. Differences among years in biomass and relative dominance for subcanopy tree species were tested for using repeated measures Analysis of Variance (ANOVA) and individual comparisons were made using Holm-Sidak multiple comparison correction using Sigmaplot. Plot-level biomass and tree species distribution data for both canopy (≥ 8cm DBH) and subcanopy (0-7.9cm DBH) were used to assess community composition and species diversity (richness, evenness, Shannon diversity index, and Beta diversity; McCune and Grace, 2002). Compositional patterns were extracted using nonmetric multidimensional scaling (NMS) ordination on matrices of species biomass by plot for both the canopy and subcanopy layers. NMS was performed using PC-ORD v.5.31 (McCune and Mefford, 2006) with the “slow-and-thorough” auto-pilot setting, using 250 runs of real data and 250 Monte Carlo randomizations to assess the robustness of the solution. Axes from the resulting ordination solutions were used as predictors representing the major compositional gradients in both layers. Variables relating to subcanopy production and response were overlayed on ordination graphs to visually assess their relationship with species composition.

To analyze compositional trajectories (Obj. 1), NMS ordination was performed (as above) on a combined matrix of relative biomass by species in the canopy and subcanopy layers in each plot. Compositional differences at the time of measurements and potential future community composition trajectories were illustrated using overlayed transitional vectors (McCune and Grace, 2002). To assess the effect of disturbance severity and pre-disturbance canopy productivity on variation in compositional differences between canopy layers, vectors were translated to the origin and the position of subcanopy points was regressed against these factors. Differences in subcanopy tree growth (height and BAI) and growth response among species (Obj. 2) were tested for with ANOVA and Kruskal-Wallis Rank ANOVA (where data were non-normal) using Sigmaplot.

To evaluate factors associated with subcanopy tree growth (Obj. 2), community-level productivity and resilience (Obj. 3) and the relative contribution of subcanopy to overall productivity response (Obj. 4) we used multiple linear regression in an information-theoretic framework (Burnham and Anderson, 2002) using PROC MIXED in SAS v. 9.2 (SAS-Institute-Inc., 2005). We tested a set of *a priori* models regarding the effect of a suite of stand and site characteristics (see below) on the following response variables: 1) post-disturbance subcanopy productivity (2010-2012 subcanopy $ANPP_w$), 2) absolute difference in pre- vs. post-disturbance subcanopy productivity (2010-2012 subcanopy $ANPP_w$ – 2006-2009 subcanopy $ANPP_w$), 3) relative change in pre- vs. post disturbance subcanopy $ANPP_w$ ((2010-2012 subcanopy $ANPP_w$ – 2006-2009 subcanopy $ANPP_w$)/2006-2009 subcanopy $ANPP_w$)) , 4) proportion of total (canopy + subcanopy) post-disturbance productivity contributed by subcanopy (2010-2012 subcanopy $ANPP_w$/2010-2012 total $ANPP_w$), 5) ratio of subcanopy response to total response ((2010-2012 subcanopy $ANPP_w$ – 2006-2009 subcanopy $ANPP_w$)/(2010-2012 total $ANPP_w$ – 2006-2009 total $ANPP_w$)), 6) post-disturbance subcanopy growth of large subcanopy stems (4-7.9 cm DBH) (2010-2013 subcanopy BAI), and 7) post-disturbance growth response of large subcanopy stems (2010-2013 subcanopy BAI – 2006-2009 subcanopy BAI).

Potential predictors of plot-level subcanopy productivity and disturbance response (variables #1-5 above) included tree species composition (NMS ordination axes, percent late-successional hardwood or oak dominance) and diversity (Shannon index) in the canopy and subcanopy layers, as well as disturbance severity (based on percent of canopy basal area girdled) and site fertility (based on pre-disturbance canopy NPP). Predictors of subplot-level BA growth (variables #6 & 7 above) included these factors and also pre-disturbance subcanopy basal area, canopy openness, and fAPAR at 5m. For both plot and subplot-level analyses a matrix plot was constructed with all predictors and response variables to assess linearity of relationships and check for co-linearity among predictors. For the subplot-level analysis plot identity was included as a random effect in the model to incorporate the nested design into the analysis. A set of plausible models (Appendix C) stemming from our understanding of factors likely to be related to subcanopy response (Gough *et al.*, 2013; Stuart-Haëntjens *et al.*, 2015) were evaluated using the corrected Akaike Information Criterion (AICc; Burnham and Anderson, 2002). AIC_c is derived from the maximum log-likelihood estimate and number of parameters in a given model, penalizing models for lack of fit and the addition of parameters (lower values indicate better models). Models were ranked by the difference between the AIC_c value for the model and the lowest value in the full model set (ΔAIC_c), which included the null model. This method allows for comparison of the strength of evidence among the models, with increasing ΔAIC_c values indicating decreasing probability of the fitted model being the best model in the set. Models with $\Delta AIC_c < 2$ are considered to have substantial support and models above this threshold are generally not interpreted (Burnham and Anderson, 2002). To approximate the probability of a model being the best in a given set, ΔAIC_c values were used to calculate Akaike weights (w_i).

3. Results

3.1 Landscape-level patterns in subcanopy layer characteristics – Objective 1

There were major shifts in characteristics of the subcanopy layer, but landscape scale patterns in subcanopy stem density, biomass, and productivity ($ANPP_w$) were not related to differences among plots in disturbance severity or site fertility (based on pre-disturbance canopy productivity). Subcanopy stem density five years following disturbance, in 2012, varied greatly among plots (1175 to 5788 stems ha^{-1}) but was not correlated with pre-disturbance canopy productivity ($r = 0.03$) or disturbance severity ($r = -0.08$). Subcanopy biomass in 2012 was significantly greater than pre-disturbance levels (2542 vs 1800 kg C ha^{-1}; $t = 2.56$, $p = 0.014$; Table 1), but variation among plots was not explained by plot disturbance severity ($r = -0.06$) or pre-disturbance canopy productivity ($r = -0.21$). There was a relatively strong correlation between pre-disturbance and post-disturbance subcanopy biomass at the plot scale ($r = 0.79$). However, total subcanopy productivity across the study period was not related to pre-disturbance subcanopy biomass (r = -0.12), indicating that greater response was not associated with greater initial biomass. Subcanopy productivity was significantly greater following peak disturbance (341 kg C ha^{-1} yr^{-1} in 2010-2012) relative to the period leading up to peak disturbance (15 kg C ha^{-1} yr^{-1} in 2006-2009; t = 7.48, p < 0.001; Table 1).

Patterns in species composition at the landscape scale (across all plots covering the large manipulated area), were similar before and after the disturbance with the same five species making up the majority of subcanopy biomass: beech, sugar maple, red maple, white pine, and northern red oak (Fig. 1). Although species biomass varied among years (species by year interaction - $F_{24,480}$ = 5.28, p < 0.001) for a number of species in the subcanopy (Fig. 1), relative dominance only changed substantially following the disturbance for northern red oak (species by year interaction - $F_{24,480}$ = 2.00, p = 0.004; Appendix A). The major shift was that northern red oak increased in biomass and dominance (from 9.5 to 17.6% relative dominance) while the other major species increased in biomass but declined in dominance, especially sugar maple (from 21.1 to 15.1% relative dominance). Northern red oak had the greatest increase in landscape-scale subcanopy biomass across the study period, but was still only 4th most abundant overall in 2012.

Following the disturbance (in 2012) there was strong plot-level variation in subcanopy species composition, with groups characterized by northern red oak/serviceberry, sugar maple/ironwood, beech/striped maple, and pine dominance (Fig. 2a). NMS ordination of subcanopy composition resulted in a three-dimensional solution which was significant based on Monte Carle test (Stress = 9.7, p = 0.036). The 3D solution explained 85.7% of the variation in the original data matrix. Each of the three axes explained a large component of the variation: Axis 1 = 21.9%, Axis 2 = 40.9%, and Axis 3 = 22.9%. Subcanopy species composition in 2012 was not strongly related to pre-disturbance canopy productivity (Axis 1 – r = -0.35, Axis 2 – r =

0.27, Axis 3 – r = -0.15) or disturbance severity (canopy BA loss; Axis 1 – r = 0.35, Axis 2 – r = -0.33, Axis 3 – r = -0.37).

Differences in canopy and subcanopy composition following disturbance indicate a potential future shift from relatively homogenous canopy to the 3 or 4 much more differentiated species assemblages mentioned above (based on subcanopy dominance; Fig. 3, Fig. 2a). Species richness was higher in the subcanopy (mean = 6.6) than the canopy (4.4), but species diversity (Simpson's diversity index) was very similar between the two layers (0.54 and 0.55 respectively). Composition was more differentiated among plots in the subcanopy than the canopy layer, with greater beta diversity (B_d) evident in the subcanopy (1.6) versus the canopy (1.1). Combined NMS ordination of canopy and subcanopy composition (relative dominance) resulted in a three-dimensional solution which was highly significant based on Monte Carle test (Stress = 10.7, p = 0.004). The 3D solution explained 89.7% of the variation in the original data matrix. The first two axes explained the majority of the variation – Axis 1 = 44.9% and Axis 2 = 29.2%. The direction and magnitude of canopy-subcanopy trajectories were somewhat related to disturbance severity (Axis 1 - r = 0.47) and pre-disturbance canopy productivity (Axis 2 - r = 0.41; Fig. 3).

3.2 Species-level subcanopy growth patterns – Objective 2

Height growth response of smaller subcanopy trees (<4cm dbh) varied greatly among species (based on Kruskal-Wallis rank ANOVA; H = 107.30, df = 6, p < 0.001). Among smaller subcanopy trees , the species with by far the greatest average individual height growth response (post vs. pre-disturbance growth increment) was beech, which also ended the study period with the fastest average growth rate (Fig. 4a; H = 184.74; df = 6, p < 0.001). Although beech was most responsive, red maple dominated basal area among these small subcanopy trees and also had the greatest overall population-level height increment, despite a relatively minor response in total height increment following the disturbance (Fig. 4b).

Basal area growth response of larger subcanopy trees (4-8cm dbh) also varied greatly among species (based on Kruskal-Wallis rank ANOVA; H = 30.12, df = 5, $p < 0.001$). For larger subcanopy stems northern red oak was dominant in both total population and average individual stem growth (Fig. 5). Northern red oak also had the largest response to disturbance in terms of average individual basal area increment (BAI) and especially total BAI across the entire population (Fig. 5). Prior to peak LAI loss in 2010, northern red oaks were already growing fastest on a per-BA basis (BA growth relative to total BA) among the canopy tree species in the system (Fig. 6; behind only ironwood – a subcanopy-only species which had very low total BA; ANOVA $F_{7,137} = 2.34$, $p = 0.03$). In the period following peak disturbance (2010-2013), northern red oak BAI per unit BA was much greater than that of any of the other canopy dominant species ($F_{7,137} = 7.96$, $p < 0.001$) and had also increased much more than any other species relative to pre-disturbance growth rates (Fig. 6; $F_{7,137} = 5.21$, $p < 0.001$).

Neighborhood scale (5m radius subplot) analysis of the predictors of BAI for large subcanopy stems (≥4 cm DBH) indicated that species composition and structural/environmental conditions (i.e., canopy openness and light transmittance) combined to predict the response of the subcanopy to moderate severity disturbance. Specific response variables are defined in section *2.3 Data analysis* above and referenced by corresponding numbers. Full lists of all potential candidate models are included in Appendix C. Post-disturbance growth rates (response variable #6) were most strongly predicted by subcanopy oak dominance and pre-disturbance subcanopy BA (Table 2). The model containing subcanopy oak dominance and pre-disturbance subcanopy BA as predictors was the most highly supported and accounted for a large proportion of the weighting in the model set (70%). Growth of subcanopy trees was higher in locations with high oak dominance and high pre-disturbance subcanopy BA (Fig. 7). The post-disturbance response of subcanopy BA growth (response variable #7) at the neighborhood scale was most strongly predicted by subcanopy oak dominance and the fraction of above-canopy photosythetically active radiation (fAPAR) available at 5m above the ground surface (Table 2). The model containing these two predictors was more highly supported than any other model in the set (all $\Delta AICc > 2.0$) and accounted for 59% of the weighting in the model set. Growth response in subcanopy trees was highest with greater oak dominance and greater transmittance of PAR into the upper part of the subcanopy (Fig. 7).

3.3 Community-level subcanopy biomass and productivity – Objective 3

In general, subcanopy productivity and response to disturbance at the plot scale were predicted by subcanopy community composition and not disturbance severity. By far the strongest predictor of post-disturbance subcanopy productivity (response variable #1) was subcanopy community composition (Axis 1 from NMS ordination; $r = 0.74$; Appendix B). Post-disturbance subcanopy productivity was not related to disturbance severity ($r = 0.24$; Appendix B), but was somewhat negatively correlated with pre-disturbance canopy productivity ($r = -0.57$; Appendix B), indicating that the subcanopy was less productive in highly productive sites, presumably because of greater competition from canopy trees (Fig.7). The most highly supported models from multiple regression of post-disturbance subcanopy productivity included combinations of pre-disturbance canopy productivity, subcanopy composition, and canopy oak dominance (Table 3, full model lists in Appendix C). The three most highly supported models that included combinations of these predictors accounted for 14-32% of the weighting in the full set of models. Post-disturbance subcanopy productivity was highest in plots with northern red oak dominance in the subcanopy and in areas with lower pre-disturbance canopy productivity and lower canopy dominance by northern red oak (Fig. 7).

Absolute response in subcanopy productivity following disturbance (response variable #2) was most strongly predicted by a combination of subcanopy species composition (Axis 2 from NMS ordination; r = -0.75; Appendix B), pre-disturbance canopy productivity (r = -0.56), and canopy dominance by oaks (r = -0.59) and late-successional hardwoods (r = 0.74). The model containing these predictors was more highly supported than any other model in the set (all $\Delta AICc > 2.0$) and accounted for 60% of the weighting in the model set (Table 3). Relative response in subcanopy productivity (response variable #3) was most strongly predicted by subcanopy composition (Axis 2 from NMS ordination; r = -0.51) and late-successional hardwood dominance in the canopy layer (r = 0.42). The model containing these predictors was more highly supported than any other model in the set (all $\Delta AICc > 2.0$) and accounted for 47% of the weighting in the model set (Table 3). Both absolute and relative responsiveness were much lower in locations with subcanopy dominance by pines (Fig. 2b) and canopy dominance by oaks relative to late-successional hardwoods (Fig. 7).

3.4 Subcanopy contribution to overall productivity and disturbance response – Objective 4

The subcanopy made a significant contribution to overall (subcanopy + canopy) wood production in the period following peak disturbance (from 2010-2012) averaging 16.2% across all plots within the moderately disturbed landscape. At the plot scale, subcanopy contribution to total wood production ranged between 5.3% in plot D3 and 28.8% in plot C2, which had low pre-disturbance canopy productivity and high disturbance severity (Table 1). Subcanopy contribution to productivity (response variable #4) was most strongly predicted by a combination of subcanopy species composition (Axis 1 from NMS ordination; r = 0.68; Appendix B), canopy species composition (Axis 2 from NMS ordination; r = 0.64), pre-disturbance canopy productivity (r = -0.64), and subcanopy species diversity (r = 0.14). The model containing these predictors was more highly supported than any other model in the set (all $\Delta AICc > 2.0$) and accounted for 67% of the weighting in the model set (Table 4). Subcanopy contribution to total productivity was greater in areas with low pre-disturbance canopy productivity where the canopy was dominated by sugar maple and basswood and the subcanopy by northern red oak.

The contribution of the subcanopy to overall productivity response (response variable #5) was substantial, averaging 54.1% across all plots. At the plot level, this contribution varied between 17% in plot F2 and 100% in the 6 plots which had a decline in canopy layer productivity (Table 1). Subcanopy contribution to plot scale growth response was most strongly predicted by pre-disturbance canopy productivity (r = -0.54; Appendix B) and subcanopy composition (Axis 2 from NMS ordination; r = -0.52). The models including combinations of these predictors were all more highly supported than other models in the set (all $\Delta AICc > 2.0$) and accounted for 18-28% of the weighting in the model set (Table 4). Subcanopy contribution to response was greater in areas with low pre-disturbance canopy productivity and where the subcanopy was pine dominated.

4. Discussion

4.1 Subcanopy composition and ecosystem resilience

The subcanopy played a central role in forest ecosystem wood productivity response to moderate severity disturbance, and this role was strongly mediated by subcanopy community composition and the local light environment. Enhanced productivity in forest subcanopies has been shown to contribute significantly to overall ecosystem productivity response following disturbance (Romme *et al.*, 1986; Veblen *et al.*, 1989; Foster *et al.*, 1997; Dyer *et al.*, 2010). This was the case in the FASET disturbance as well, as subcanopy productivity was stimulated by the disturbance and associated redistribution of growth-limiting resources to undisturbed vegetation (Gough *et al.*, 2013; Stuart-Haëntjens *et al.*, 2015). In our analysis, the subcanopy accounted for greater than half of the total wood production response (change in productivity relative to pre-disturbance levels) following disturbance.

Although productivity response in the subcanopy was generally positive across the experimental disturbance (in 20 of 21 plots; Table 1), there was considerable variation among plots in both production and relative growth response following disturbance (approximately one order of magnitude in both cases) owing to subcanopy composition and environmental variation. The neighborhood-scale effects of moderate severity disturbance on resource distribution can be highly heterogeneous (Woods, 2004), and variation in the contribution of the subcanopy to ecosystem response has been associated with spatial variation in disturbance severity (Stuart-Haëntjens *et al.*, 2015). However, in this analysis subcanopy species composition outweighed disturbance severity and pre-disturbance canopy productivity (i.e., site fertility) as factors predicting responsiveness of growth to disturbance at the plot-scale. Community composition and diversity in vegetated ecosystems have previously been shown to be strong drivers of productivity (Chapin *et al.*, 1997; Tilman *et al.*, 2012) and response to disturbance (Spies and Franklin, 1989; Frelich and Reich, 1999), including at our study site (Gough *et al.*, 2010). Our results illustrate how fine-scale variation in community composition and resource availability within a disturbed area can affect the response of forest ecosystems to disturbance, specifically through variable subcanopy response.

At a neighborhood scale, subcanopy light availability, which is associated with disturbance severity (Stuart-Haëntjens *et al.*, 2015), interacted strongly with species composition to drive growth response following moderate disturbance severity. Neighborhood disturbance severity, expressed as canopy basal area loss at the 5 m radius subplot-scale, was not strongly related to growth response in subcanopy trees. However, we found that variation in subcanopy light availability, specifically the proportion of photosynthetically active radiation that was transmitted (fAPAR) to the approximate top of the subcanopy layer (5 m height), was related to patterns in subcanopy tree growth at a neighborhood-scale. Subcanopy light availability is related to variation in canopy structure, which was driven partially by substantial fine-scale variation in disturbance severity (Stuart-Haëntjens *et al.*, 2015). The growth response of subcanopy trees was not mediated by light transmittance alone, though, as species composition was a strong and independent predictor of post-disturbance growth response. However, the response of species was not straightforwardly linked to perceived shade tolerance. Northern red oak, which is mid-tolerant of shade (Crow, 1988), was able to respond across a wide range of light environments and across the gradient in disturbance severity, not just in the most open sites.

The factors most strongly associated with spatial variation in subcanopy response to the landscape-scale moderate severity disturbance depended on the scale of the analysis and the proxies that were used to quantify disturbance severity. The ecological correlates of response to heterogeneous disturbance may vary across spatial scales (e.g., light transmittance vs. basal area), but some of our findings may also be explained by methodological factors associated with analysis scales. Plot-scale results suggested that the variable effects of moderate severity disturbance on productivity were more strongly associated with pre-existing variation in subcanopy and canopy species assemblages and site fertility than the direct effects of differing disturbance severity (Frelich and Reich, 1999; Reyes and Kneeshaw, 2008). However, at the neighborhood scale the effect of disturbance-associated heterogeneity in resource conditions was apparent (in this case light transmittance, although other resources and edaphic factors such as N, water availability, and temperature may also be important; Nave *et al.*, 2011; Matheny *et al.*, 2014). This may be a more appropriate scale at which to assess subcanopy tree growth response to such a fine-grained heterogeneous disturbance (Frelich and Reich, 1999). However, although light transmittance may have a stronger direct functional link to subcanopy tree growth than basal area loss, light transmittance was not directly correlated with disturbance severity (correlation between BA loss and fAPAR was $r = 0.59$ at the subplot scale) and is less meaningful when averaged across subplots to the plot scale. Basal area loss can be a useful proxy for disturbance severity at the plot or stand scale (Stuart-Haëntjens *et al.*, 2015), but may not be as suitable at the neighborhood scale, due to the high weighting to individual trees in such a small area (0.008ha). The emphasis given to basal area loss and light transmittance at the plot and neighborhood scale reflects that they are likely the best proxies at these scales for matching data availability and ecological processes driving subcanopy growth/productivity response (Canham *et al.*, 2006).

The specifics of ecosystem response to moderate severity disturbance are likely to depend greatly on pre-disturbance forest structure and disturbance type (Turner *et al.*, 1997; Millward and Kraft, 2004; Cohen *et al.*, 2016). In forests with more homogenous species composition the relative effects of resource and environmental heterogeneity on disturbance growth response may be much more pronounced (Romme *et al.*, 1986; Veblen *et al.*, 1989). Similarly, in more patchy moderate severity disturbances (e.g., with different spatial grain of disturbance patches) gradients in disturbance severity and therefore resource redistribution may be even more pronounced and may, thus, have a greater effect on community response (Woods, 2004; Reyes *et al.*, 2010; Fahey *et al.*, 2015). Our findings illustrate the need to understand the specific compositional and structural characteristics of forests to predict ecosystem response to disturbance (Hicke *et al.*, 2012). However, our results also suggest that the response of forest ecosystems to moderate disturbance is likely to be an interactive relationship between site, community, and disturbance patterns, which may affect growth responses to disturbance differently at different spatial scales.

4.2 Subcanopy compositional trajectories

Our results support the view that moderate severity disturbance, including those related to senescence of early-successional species, could play an important role in maintaining northern red oak in eastern deciduous forests (Hibbs, 1983; Crow, 1988). Patterns of species-level productivity and individual tree growth rates suggest greater future importance of northern red oak as a component of the FASET ecosystem following disturbance, matching results from studies on other natural and anthropogenic moderate severity disturbances (Oliver and Stephens, 1977; Lorimer, 1983; Buckley *et al.*, 1998; Kaelke *et al.*, 2001; Parker and Dey, 2008). Northern red oak is generally described as mid-tolerant of shade and is associated with post-disturbance environments and edges (Crow, 1988). However, the trend toward oak dominance was not limited to areas with higher disturbance severity, as there was a very strong response from this species across the disturbance gradient. In this study, northern red oak appeared to be competitive with red maple in locations where the species co-occurred. This result may be considered somewhat surprising given the widespread and ongoing replacement of oaks by maples and other mesophytic species across eastern North America (Lorimer, 1984; Nowacki *et al.*, 1990; Nowacki and Abrams, 2008), as well as previous work indicating that northern red oak is outcompeted by red maple in all but the most open conditions and even under oak canopy (Hibbs, 1982; Hartman *et al.*, 2005). However, the specific site conditions represented in the FASET experiment are also likely to have affected these patterns. For example, the UMBS area has sandy soils and relatively low N deposition and is fairly representative of the Upper Great Lakes region (Nave *et al.*, 2009). Previous studies have indicated that northern red oak can have a competitive advantage over shade tolerant species under such conditions (Kim *et al.*, 1996; Kaelke *et al.*, 2001). Ecosystems that do not have these characteristics may not be as suitable for northern red oak even with the influence of moderate severity disturbance (Crow, 1988).

The FASET disturbance appears to have created a patchy mosaic lacking widespread dominance by shade-tolerant, late-successional species. This finding matches predictions of theoretic and mechanistic models (Roxburgh *et al.*, 2004; Papaik and Canham, 2006) and patterns shown for other forests following moderate severity disturbance (Woods, 2004; Reyes *et al.*, 2010). Early results from this site do not indicate a trend toward accelerated dominance by shade-tolerant, late-successional species as has been illustrated elsewhere (Webb and Scanga, 2001; Allen *et al.*, 2012). Overall, compositional trajectories suggest a potential "tri-furcation" of the community from uniform pre-disturbance aspen dominance to northern red oak, sugar maple, and beech dominated patches (Fig. 3). There was greater variation in species composition among plots (higher β diversity) in the subcanopy than the canopy layer, suggesting that the future canopy may be even more heterogeneous. However, within the disturbance area variation among plots in compositional trajectory was not related to variable disturbance severity but rather to differences in pre-disturbance canopy productivity. This finding suggests that compositional transitions related to the FASET disturbance are being mediated by variation in site fertility, rather than directly by variable disturbance impacts (Reyes and Kneeshaw, 2008). The patterns presented here support the potential for moderate severity disturbance to maintain species diversity and create spatial heterogeneity in species composition (Hanson and Lorimer, 2007), but suggest that these effects may be limited to certain site conditions (e.g., heterogeneous sites, diverse communities) (Webb and Scanga, 2001; Reyes and Kneeshaw, 2008).

4.3 Management Implications and Conclusion

Emulating moderate severity disturbances has been a major focus of ecological forestry in recent decades (Franklin *et al.*, 2002; Seymour and White, 2002; Puettmann *et al.*, 2009). The results of the FASET experiment provide some support for the utility of moderate severity disturbance in managing for biological diversity and structural heterogeneity, but also some insight on the potential limitations of such treatments. One primary goal of ecological forestry has been creation of structural complexity in forest stands and landscapes (Puettmann *et al.*, 2009) and moderate severity disturbances have been shown to be highly effective at producing such conditions (Hanson and Lorimer, 2007; Fahey *et al.*, 2015). The structural complexity produced by the FASET disturbance has been strongly implicated in the resistance of the system to declines in productivity (Hardiman *et al.*, 2011; Gough *et al.*, 2013). The development of a robust subcanopy appears to be an important component of this current complexity and will also affect the future structure of the forest.

Another major goal of ecological forestry is to promote species and functional diversity, often through management focused on under-represented mid-tolerant species (Poznanovic *et al.*, 2013). The FASET disturbance has promoted some species that are considered mid-tolerant and under-represented at a regional scale (e.g., northern red oak). However, pines were not positively affected by the disturbance and community trajectories indicate a potential reduction in pine importance in the future at our site. Such a shift, if widespread, would represent a decrease in the primary conifer component in the system and the further reduction of an important component of functional diversity that has already declined at a regional scale following broad deforestation more than a century ago (Schulte *et al.*, 2007). The effects of moderate severity disturbances in promoting diversity are highly dependent on pre-existing conditions, as newly established seedlings are unlikely to be competitive with advance regeneration or sprouts (Webster and Lorimer, 2005; Dietze and Clark, 2008). Thus reintroduction or enrichment plantings focused on mid-tolerant species (possibly in combination with understory management) may be needed to take advantage of canopy disturbance in some cases (Dey *et al.*, 2012; Fahey and Lorimer, 2013). Also, relying on moderate severity disturbance *per se* may not be sufficient to promote some species or functional types that require conditions associated with specific disturbance types. For example, to maintain a pine component, a combination of prescribed surface fire and moderate canopy disturbance may be needed (Frelich, 2002).

Our findings highlight the fundamental linkages between community composition and ecosystem structural and functional response to disturbance (Chapin *et al.*, 1997; Tilman *et al.*, 2012). Efforts to predict the resilience of forest ecosystems to broad-scale, emerging threats such as global climate change and exotic pest outbreaks must account for the interaction of communities and ecosystem processes (Flower and Gonzalez-Meler, 2015; Thom and Seidl, 2015). In addition to illustrating the potential response of forest ecosystems to canopy senescence related to successional transition, the results of this study could be applicable to understanding the response of forest ecosystems to ongoing exotic pest and pathogen outbreaks

(Flower *et al.*, 2013). Our work also illustrates the potential for diverse and heterogeneous forest communities to promote resilience to forest disturbance or successional change (Tilman *et al.*, 2012). Understanding specific community responses to disturbance and landscape change will be essential to effectively modeling future forest landscapes and their ecological functioning (Duveneck *et al.*, 2014b).

Acknowledgements

Funding for the UMBS AmeriFlux core site was provided by the U.S. Department of Energy's (DOE) Office of Science and by the DOE Climate and Environmental Sciences Division, Office of Science (Award Nos. DE-SC0006708, DE-SC0006708) with additional support from the National Oceanic and Atmospheric Administration [NA11OAR4310190]. A. De La Cruz and E. Stockton were supported by the UMBS Summer Research Experience for Undergraduates (REU) program through NSF [AGS-0851421]. We acknowledge the University of Michigan Biological Station for facilities and material support and specifically J. Tallant for assistance with data management and spatial data layers.

References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.T., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660-684.

Allen, M.S., Thapa, V., Arévalo, J.R., Palmer, M.W., 2012. Windstorm damage and forest recovery: accelerated succession, stand structure, and spatial pattern over 25 years in two Minnesota forests. Plant Ecol. 213, 1833-1842.

Amiro, B., Barr, A., Barr, J., Black, T., Bracho, R., Brown, M., Chen, J., Clark, K., Davis, K., Desai, A., 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. J. Geophys. Res.-Biogeo. 115.

Birdsey, R., Pregitzer, K., Lucier, A., 2006. Forest carbon management in the United States. J. Environ. Qual. 35, 1461-1469.

Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob. Change Biol. 10, 473-487.

Buckley, D.S., Sharik, T.L., Isebrands, J., 1998. Regeneration of northern red oak: positive and negative effects of competitor removal. Ecology 79, 65-78.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York.

Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69, 786-795.

Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecol. Appl. 16, 540-554.

Caspersen, J.P., Pacala, S.W., Jenkins, J.C., Hurtt, G.C., Moorcroft, P.R., Birdsey, R.A., 2000. Contributions of land-use history to carbon accumulation in US forests. Science 290, 1148-1151.

Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., Tilman, D., 1997. Biotic control over the functioning of ecosystems. Science 277, 500-504.

Cohen, W.B., Yang, Z., Stehman, S.V., Schroeder, T.A., Bell, D.M., Masek, J.G., Huang, C., Meigs, G.W., 2016. Forest disturbance across the conterminous United States from 1985–2012: The emerging dominance of forest decline. For. Ecol. Manage. 360, 242-252.

Crow, T., 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)-a review. For. Sci. 34, 19-40.

DeGraaf, R.M., Yamasaki, M., Leak, W.B., 1993. Management of New England northern hardwoods, spruce-fir, and eastern white pine for neotropical migratory birds. In: Finch, Deborah M.; Stangel, Peter W. (eds.). Status and management of neotropical migratory birds: September 21-25, 1992, Estes Park, Colorado. Gen. Tech. Rep. RM-229. Fort Collins, Colo.: Rocky Mountain Forest and Range Experiment Station, U.S. Dept. of Agriculture, Forest Service: 363-373.

Dey, D.C., Gardiner, E.S., Schweitzer, C.J., Kabrick, J.M., Jacobs, D.F., 2012. Underplanting to sustain future stocking of oak (*Quercus*) in temperate deciduous forests. New Forest. 43, 955-978.

Dietze, M.C., Clark, J.S., 2008. Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. Ecol. Monogr. 78, 331-347.

Drummond, M.A., Loveland, T.R., 2010. Land-use pressure and a transition to forest-cover loss in the eastern United States. BioScience 60, 286-298.

Duveneck, M.J., Scheller, R.M., White, M.A., 2014a. Effects of alternative forest management on biomass and species diversity in the face of climate change in the northern Great Lakes region (USA). Can. J. For. Res. 44, 700-710.

Duveneck, M.J., Scheller, R.M., White, M.A., Handler, S.D., Ravenscroft, C., 2014b. Climate change effects on northern Great Lake (USA) forests: a case for preserving diversity. Ecosphere 5, art23.

Dyer, J.H., Gower, S.T., Forrester, J.A., Lorimer, C.G., Mladenoff, D.J., Burton, J.I., 2010. Effects of selective tree harvests on aboveground biomass and net primary productivity of a second-growth northern hardwood forest. Can. J. For. Res. 40, 2360-2369.

Fahey, R.T., Fotis, A.T., Woods, K.D., 2015. Quantifying canopy complexity and effects on productivity and resilience in late-successional hemlock-hardwood forests. Ecol. Appl. 25, 834-847.

Fahey, R.T., Lorimer, C.G., 2013. Restoring a midtolerant pine species as a component of late-successional forests: Results of gap-based planting trials. For. Ecol. Manage. 292, 139-149.

Fahey, R.T., Lorimer, C.G., 2014a. Habitat associations and 150 years of compositional change in white pine-hemlock-hardwood forests based on resurvey of public land survey corners. J. Torr. Bot. Soc. 141, 277-293.

Fahey, R.T., Lorimer, C.G., 2014b. Persistence of pine species in late-successional forests: evidence from habitat-related variation in stand age structure. J. Veg. Sci. 25, 584-600.

Flower, C.E., Gonzalez-Meler, M.A., 2015. Responses of temperate forest productivity to insect and pathogen disturbances. Ann. Rev. Plant Biol. 66, 547-569.

Flower, C.E., Knight, K.S., Gonzalez-Meler, M.A., 2013. Impacts of the emerald ash borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biol. Invasions 15, 931-944.

Foster, D.R., Aber, J.D., Melillo, J.M., Bowden, R.D., Bazzaz, F.A., 1997. Forest response to disturbance and anthropogenic stress. BioScience, 437-445.

Franklin, J., F. , Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399-423.

Frelich, L.E., 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press.

Frelich, L.E., Reich, P.B., 1999. Minireviews: neighborhood effects, disturbance severity, and community stability in forests. Ecosystems 2, 151-166.

Gough, C., Vogel, C., Schmid, H., Su, H.-B., Curtis, P., 2008. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. Agr. Forest Meteorol. 148, 158-170.

Gough, C.M., Curtis, P.S., Hardiman, B.S., Scheuermann, C.M., Bond-Lamberty, B., 2016. Disturbance, complexity, and succession of net ecosystem production in North America's temperate deciduous forests. Ecosphere.

Gough, C.M., Hardiman, B.S., Nave, L., Bohrer, G., Maurer, K.D., Vogel, C.S., Nadelhoffer, K.J., Curtis, P.S., 2013. Sustained carbon uptake and storage following moderate disturbance in a Great Lakes forest. Ecol. Appl. 23, 1202-1215.

Gough, C.M., Vogel, C.S., Hardiman, B., Curtis, P.S., 2010. Wood net primary production resilience in an unmanaged forest transitioning from early to middle succession. For. Ecol. Manage. 260, 36-41.

Gough, C.M., Vogel, C.S., Harrold, K.H., George, K., Curtis, P.S., 2007. The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. Glob. Change Biol. 13, 1935-1949.

Haack, R.A., Hérard, F., Sun, J., Turgeon, J.J., 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: a worldwide perspective. Annu. Rev. Entomol. 55, 521-546.

Halpin, C.R., Lorimer, C.G., 2016a. Long-term trends in biomass and tree demography in northern hardwoods: An integrated field and simulation study. Ecology 86, 78-93.

Halpin, C.R., Lorimer, C.G., 2016b. Trajectories and resilience of stand structure in response to variable disturbance severities in northern hardwoods. For. Ecol. Manage. 365, 69-82.

Hanson, J.J., Lorimer, C.G., 2007. Forest structure and light regimes following moderate wind storms: implications for multi-cohort management. Ecol. Appl. 17, 1325-1340.

Hardiman, B.S., Bohrer, G., Gough, C.M., Vogel, C.S., Curtis, P.S., 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology 92, 1818-1827.

Hartman, J.P., Buckley, D.S., Sharik, T.L., 2005. Differential success of oak and red maple regeneration in oak and pine stands on intermediate-quality sites in northern Lower Michigan. For. Ecol. Manage. 216, 77-90.

Henry, J., Swan, J., 1974. Reconstructing forest history from live and dead plant material--an approach to the study of forest succession in southwest New Hampshire. Ecology 55, 772-783.

Hibbs, D.E., 1982. Gap dynamics in a hemlock-hardwood forest. Can. J. For. Res. 12, 522-527.

Hibbs, D.E., 1983. Forty years of forest succession in central New England. Ecology, 1394-1401.

Hicke, J.A., Allen, C.D., Desai, A.R., Dietze, M.C., Hall, R.J., Kashian, D.M., Moore, D., Raffa, K.F., Sturrock, R.N., Vogelmann, J., 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Glob. Change Biol. 18, 7-34.

Houghton, R., Hackler, J., Lawrence, K., 1999. The US carbon budget: contributions from land-use change. Science 285, 574-578.

Hurtt, G., Pacala, S., Moorcroft, P., Caspersen, J., Shevliakova, E., Houghton, R., Moore, B., 2002. Projecting the future of the US carbon sink. P. Natl. Acad. Sci. 99, 1389-1394.

Kaelke, C.M., Kruger, E.L., Reich, P.B., 2001. Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light-availability gradient. Can. J. For. Res. 31, 1602-1616.

Kim, C., Sharik, T.L., Jurgensen, M.F., Buckley, D.S., Dickson, R.E., 1996. Effects of nitrogen availability on northern red oak seedling growth in oak and pine stands in northern Lower Michigan. Can. J. For. Res. 26, 1103-1111.

Lorimer, C.G., 1983. Eighty-year development of northern red oak after partial cutting in a mixed-species Wisconsin forest. For. Sci. 29, 371-383.

Lorimer, C.G., 1984. Development of the red maple understory in northeastern oak forests. For. Sci. 30, 3-22.

Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can. J. For. Res. 19, 651-663.

Matheny, A.M., Bohrer, G., Vogel, C.S., Morin, T.H., He, L., Frasson, R.P.d.M., Mirfenderesgi, G., Schäfer, K.V., Gough, C.M., Ivanov, V.Y., 2014. Species-specific transpiration responses to intermediate disturbance in a northern hardwood forest. J. Geophys. Res.-Biogeo. 119, 2292-2311.

McCune, B., Grace, J.B., 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR, US.

McCune, B., Mefford, M.J., 2006. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software Design. Gleneden Beach, Oregon, USA. Version 5.2.

Millward, A.A., Kraft, C.E., 2004. Physical influences of landscape on a large-extent ecological disturbance: the northeastern North American ice storm of 1998. Landscape Ecol. 19, 99-111.

Nave, L., Gough, C., Maurer, K., Bohrer, G., Hardiman, B., Le Moine, J., Munoz, A., Nadelhoffer, K., Sparks, J., Strahm, B., 2011. Disturbance and the resilience of coupled carbon and nitrogen cycling in a north temperate forest. J. Geophys. Res.-Biogeo. 116.

Nave, L.E., Vogel, C.S., Gough, C.M., Curtis, P.S., 2009. Contribution of atmospheric nitrogen deposition to net primary productivity in a northern hardwood forest. Can. J. For. Res. 39, 1108-1118.

Neuendorff, J.K., Nagel, L.M., Webster, C.R., Janowiak, M.K., 2007. Stand structure and composition in a northern hardwood forest after 40 years of single-tree selection. North. J. Appl. For. 24, 197-202.

Nobis, M., Hunziker, U., 2005. Automatic thresholding for hemispherical canopy-photographs based on edge detection. Agr. Forest Meteorol. 128, 243-250.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the eastern United States. BioScience 58, 123-138.

Nowacki, G.J., Abrams, M.D., Lorimer, C.G., 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. For. Sci. 36, 276-292.

Oliver, C.D., Stephens, E.P., 1977. Reconstruction of a mixed-species forest in central New England. Ecology, 562-572.

Papaik, M., Canham, C., 2006. Species resistance and community response to wind disturbance regimes in northern temperate forests. J. Ecol. 94, 1011-1026.

Parker, W.C., Dey, D.C., 2008. Influence of overstory density on ecophysiology of red oak (*Quercus rubra*) and sugar maple (*Acer saccharum*) seedlings in central Ontario shelterwoods. Tree Physiol. 28, 797-804.

Poznanovic, S.K., Webster, C.R., Bump, J.K., 2013. Maintaining mid-tolerant tree species with uneven-aged forest management: 9-year results from a novel group-selection experiment. Forestry 86, 555-567.

Puettmann, K.J., Coates, K.D., Messier, C.C., 2009. A critique of silviculture: managing for complexity. Island Press, Washington, DC, USA.

Reyes, G.P., Kneeshaw, D., 2008. Moderate-severity disturbance dynamics in *Abies balsamea-Betula* spp. forests: the relative importance of disturbance type and local stand and site characteristics on woody vegetation response. Ecoscience 15, 241-249.

Reyes, G.P., Kneeshaw, D., De Grandpre, L., Leduc, A., 2010. Changes in woody vegetation abundance and diversity after natural disturbances causing different levels of mortality. J. Veg. Sci. 21, 406-417.

Rhemtulla, J.M., Mladenoff, D.J., Clayton, M.K., 2009. Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s-1930s-2000s). Ecol. Appl. 19, 1061-1078.

Romme, W.H., Knight, D.H., Yavitt, J.B., 1986. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? Am. Nat. 127, 484-494.

Roxburgh, S.H., Shea, K., Wilson, J.B., 2004. The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. Ecology 85, 359-371.

Runkle, J.R., 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. Can. J. For. Res. 20, 632-641.

SAS-Institute-Inc., 2005. SAS v. 9.2. SAS Institute Inc., Durham, NC, US.

Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L.C., Cleland, D.T., 2007. Homogenization of northern US Great Lakes forests due to land use. Landscape Ecol. 22, 1089-1103.

Seymour, R.S., White, A.S., 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. For. Ecol. Manage. 155, 357-367.

Spies, T.A., Franklin, J.F., 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology 70, 543-545.

Stoy, P.C., Katul, G.G., Siqueira, M.B.S., Juang, J.Y., Novick, K.A., McCarthy, H.R., Oishi, A.C., Oren, R., 2008. Role of vegetation in determining carbon sequestration along ecological succession in the southeastern United States. Glob. Change Biol. 14, 1409-1427.

Stuart-Haëntjens, E., Curtis, P.S., Fahey, R.T., Vogel, C.S., Gough, C.M., 2015. Net primary production of a temperate deciduous forest exhibits a threshold response to increasing disturbance severity. Ecology 96, 2478-2487.

Thom, D., Seidl, R., 2015. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol. Rev., doi: 10.1111/brv.12193.

Tilman, D., Reich, P.B., Isbell, F., 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. P. Natl. Acad. Sci. 109, 10394-10397.

Tobin, M.F., Reich, P.B., 2009. Comparing indices of understory light availability between hemlock and hardwood forest patches. Can. J. For. Res. 39, 1949-1957.

Turner, M.G., Dale, V.H., Everham, E.H., 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. BioScience 47, 758-768.

Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1989. Blowdown and stand development in a Colorado subalpine forest. Can. J. For. Res. 19, 1218-1225.

Webb, S.L., Scanga, S.E., 2001. Windstorm disturbance without patch dynamics: Twelve years of change in a Minnesota forest. Ecology 82, 893-897.

Webster, C.R., Lorimer, C.G., 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. Ecol. Appl. 15, 1245-1262.

Woods, K.D., 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. J. Ecol. 92, 464-476.

Table 1. Characteristics of sample plots within the FASET treatment area, including proportion of basal area lost to girdling, which is used as a proxy for disturbance severity, and pre-disturbance ANPP$_w$, which was used as a proxy for site fertility.

	Basal area	Pre-disturbance	Subcanopy biomass (kg C ha^{-1})			Subcanopy ANPP$_w$ (kg C ha^{-1} yr^{-1})				Prod.	Resp.
Plot	loss#	canopy ANPP$_w$	2006	2010	2012	Pre	Post	All	Response	ratio^	ratio^
A1*	0.58	1369.9	1822.8	2196.4	3309.5	93.4	556.6	247.8	463.2	22.6	46.4
A2*	0.54	1286.1	1685.3	2116.3	3383.2	107.8	633.4	283.0	525.7	25.3	47.6
A3	0.37	1250.0	2430.9	1654.8	2746.2	-194.0	545.7	52.5	739.7	26.5	73.7
B1*	0.47	1722.6	1408.2	2559.5	3750.7	287.8	595.6	390.4	307.7	22.8	50.9
B2	0.38	1011.8	1745.3	1945.2	2998.4	50.0	526.6	208.8	476.6	27.7	56.9
B3	0.23	1766.9	3267.3	2499.9	3231.1	-191.8	365.6	-6.0	557.4	10.7	30.3
C1*	0.64	2546.5	2416.9	2758.5	3663.5	85.4	452.5	207.8	367.1	21.2	100
C2	0.64	852.0	906.5	1195.4	2054.5	72.2	429.5	191.3	357.3	28.8	62.9
C3	0.30	1486.4	3198.3	2631.3	3295.3	-141.8	332.0	16.2	473.7	15.2	56.5
D1*	0.38	1900.8	863.2	992.7	1666.6	32.4	336.9	133.9	304.6	17.5	100
D2*	0.67	1634.3	750.2	719.7	1200.0	-7.6	240.1	75.0	247.7	18.7	100
D3	0.45	2099.0	844.9	918.8	1129.2	18.5	105.2	47.4	86.7	5.3	100
E1	0.49	1790.0	3242.3	3352.9	4008.5	27.6	327.8	127.7	300.1	15.4	97.3
E2	0.10	1411.9	3223.0	3062.8	3737.5	-40.0	337.3	85.7	377.4	17.0	62.2
E3	0.22	2394.7	2232.6	2963.0	3277.1	182.6	157.0	174.1	-25.6	7.3	6.2
F1*	0.13	1627.3	1405.0	1144.6	1720.2	-65.1	287.8	52.5	352.9	13.7	66.1
F2	0.09	1702.7	1126.2	1085.7	1377.0	-10.1	145.6	41.8	155.7	5.6	17.3
F3	0.12	1729.5	1798.8	2075.0	2520.6	69.0	222.8	120.3	153.8	8.9	22.1
G1	0.69	3214.1	1338.4	1075.3	1335.2	-65.8	129.9	-0.5	195.7	8.3	100
G2	0.19	1431.9	1289.1	1197.2	1754.8	-23.0	278.8	77.6	301.8	14.5	59.2
G3	0.53	2180.3	798.5	928.9	1224.4	32.6	147.8	71.0	115.2	6.9	100

Proportion of total pre-disturbance basal area that was removed by stem girdling treatment

* Plots where measurements of subcanopy tree height and diameter growth were made on nested subplots.

^ Prod. ratio = post-disturbance subcanopy $ANPP_w$/total post-disturbance $ANPP_w$, Resp. ratio = post-disturbance subcanopy $ANPP_w$ response/total post-disturbance $ANPP_w$ response.

Table 2. Model lists for multiple regression modeling of basal area growth of large subcanopy stems at the subplot scale.

Model*	**k**	***AIC_c***	***ΔAIC_c***	***w_i***
Post-peak BAI				
SCPreBA SCOakDom[%]	4	-271.8	0.0	0.70
SCPreBA SCNMS1	4	-269.4	2.4	0.21
SCPreBA SCNMS1 OpennessGround	5	-267.6	4.2	0.09
SCOakDom	3	-261.7	10.1	0.00
SCOakDom OpennessGround	5	-260.2	11.6	0.00
BAI Response				
SCOakDom FracfAPAR5m[&]	4	12.1	0.0	0.59
SCNMS1 FracfAPAR5m	4	14.1	2.0	0.22
SPDistBA SCOakDom FracfAPAR5m	5	15.8	3.7	0.09
SPDistBA SCNMS1 FracfAPAR5m	5	17.8	5.7	0.03
SPDistBA FracfAPAR5m	4	18.3	6.2	0.03

* SCNMS1 = axis from ordination of subcanopy composition at the subplot-scale, SCOakDom = relative basal area of northern red oak in subcanopy layer, FracfAPAR5m = fraction of above canopy photosynthetically active radiation at 5m above ground, SPDistBA = basal area removed by experimental disturbance at the subplot level, OpennessGround = percent canopy openness at ground level, SCPreBA = pre-disturbance subcanopy basal area at the subplot scale.

[%] Model parameters and standard errors: Intercept -0.0008 (0.0005), SCPreBA 0.23 (0.03), SCOakDom 0.00004 (0.000001).

[&] Model parameters and standard errors: Intercept -0.0008 (0.0005), SCOakDom 0.008 (0.002), FracfAPAR5m 1.15 (0.48).

Table 3. Model lists for multiple regression modeling of subcanopy productivity and productivity response at the plot scale.

Model*	**k**	***AIC$_c$***	***ΔAIC$_c$***	***w_i***
Post-peak Productivity				
CanPreNPP SubCanNMS1 CanOakDom[%]	5	185.1	0.0	0.32
CanPreNPP SubCanNMS1	4	185.5	0.4	0.26
SubCanNMS1 CanOakDom	4	186.7	1.6	0.14
SubCanNMS1	3	188.2	3.1	0.07
CanPreNPP SubCanNMS1 CanOakDom CanNMS2	6	188.6	3.5	0.05
Absolute change in productivity				
CanPreNPP SubCanNMS2 CanOakDom CanLSHDom[&]	6	180.5	0.0	0.60
SubCanNMS2 CanOakDom CanLSHDom	5	183.5	3.0	0.13
CanPreNPP CanOakDom CanLSHDom	5	184.6	4.1	0.08
CanPreNPP SubCanNMS2 CanOakDom CanLSHDom SubCanD	7	184.8	4.3	0.07
CanPreNPP SubCanNMS2	4	186.5	6.0	0.03
Relative change in productivity				
SubCanNMS2 CanD[$]	4	14.1	0.0	0.47
SubCanNMS2 CanNMS2 CanD	5	17.5	3.4	0.09
SubCanNMS2 CanD CanLSHDom	4	17.6	3.5	0.08
CanNMS2 CanD	4	17.9	3.8	0.07
SubCanNMS2	3	18.3	4.2	0.06

* CanPreNPP = pre-disturbance ANPP$_w$ for canopy, SubCanNMS1 & 2 = axes from ordination of subcanopy composition at the plot-scale, CanNMS1 & 2 = axes from ordination of canopy composition at the plot-scale, CanOakDom & CanLSHDom = relative basal area of northern red oak and late-successional hardwoods (sugar maple, basswood, beech) in canopy layer, CanD = canopy species diversity (Simpson's diversity index).

[%] Model parameters and standard errors: Intercept 94.97 (13.21), CanPreNPP -0.015 (0.007), SubCanNMS1 22.39 (7.04), CanOakDom -31.23 (16.88).

[&] Model parameters and standard errors: Intercept 88.09 (11.22), CanPreNPP -0.015 (0.006), SubCanNMS2 -17.99 (6.52), CanOakDom -34.68 (13.14), CanLSHDom 47.00 (18.89)

[$] Model parameters and standard errors: Intercept 0.44 (0.20), SubCanNMS2 -0.31 (0.10), CanD 0.93 (0.34).

Table 4. Model lists for multiple regression modeling of subcanopy contribution to total productivity and response of productivity to disturbance.

Model*	**k**	***AIC_c***	***ΔAIC_c***	***w_i***
Subcanopy contribution to overall productivity				
CanPreNPP SubCanNMS1 CanNMS2 SubCanD[%]	6	58.4	0.0	0.67
CanPreNPP SubCanNMS1 CanOakDom CanNMS2 SubCanD	7	60.5	2.1	0.23
CanPreNPP CanOakDom CanNMS2 SubCanD	6	64.0	5.6	0.04
CanPreNPP SubCanNMS1 CanNMS2	5	65.0	6.6	0.02
CanPreNPP CanNMS2 SubCanD	5	66.9	8.5	0.01
Subcanopy contribution to overall response				
CanPreNPP	3	191.9	0.0	0.28
SubCanNMS2	3	192.1	0.2	0.25
CanPreNPP SubCanNMS2[&]	4	192.8	0.9	0.18
SubCanNMS2 CanNMS2	4	194.4	2.5	0.08
CanNMS2	3	194.5	2.6	0.08

* CanPreNPP = pre-disturbance $ANPP_w$ for canopy, SCNMS1 & 2 = axes from ordination of subcanopy composition at the plot-scale, CanNMS2 = axis from ordination of canopy composition at the plot-scale, CanOakDom = relative basal area of northern red oak in canopy layer, SubCanD – species diversity (Simpson's diversity index) of subcanopy layer.

[%] Model parameters and standard errors: Intercept 3.24 (0.78), CanPreNPP -0.001 (0.0002), SubCanNMS1 0.85 (0.27), CanNMS2 1.12 (0.22), SubCanD 4.35 (1.08).

[&] Model parameters and standard errors: Intercept 33.4 (14.44), CanPreNPP -0.013 (0.008), SubCanNMS2 -10.73 (7.04).

Figure Captions

Figure 1. Mean plot-level subcanopy biomass by species in 2006, 2010, and 2012 – error bars indicate standard error. Letters indicate significant differences among years for species based on repeated measures ANOVA ($F_{24,480} = 5.283$, $p < 0.001$). Species acronyms as follows: ACPE – *Acer pensylvanicum*, ACRU - *Acer rubrum*, ACSA - *Acer saccharum*, AMEL - *Amelanchier spp.*, BEPA - *Betula papyrifera*, FAGR - *Fagus grandifolia*, OSVI - *Ostrya virginiana*, PIRE – *Pinus resinosa*, PIST - *Pinus strobus*, POGR - *Populus grandidentata*, POTR - *Populus tremuloides*, QURU - *Quercus rubra*.

Figure 2. Non-metric multidimensional scaling ordination of subcanopy composition with (a) species centroids and (b) plot symbols scaled by post-disturbance subcanopy productivity ($ANPP_w$). Species acronyms can be found in Fig. 1 caption.

Figure 3. Non-metric multidimensional scaling ordination for combined canopy and subcanopy in 2012 showing difference in composition between layers in each plot. Species acronyms can be found in Fig. 1 caption.

Figure 4. Height increment trend by species for small saplings (< 4cm dbh) showing (a) mean individual height increment (error bars indicate standard error) and (b) total height increment summed across all individuals. Species acronyms can be found in Fig. 1 caption.

Figure 5. Basal area increment trends over study period by species for large saplings (> 4cm dbh) showing (a) mean individual basal area increment (error bars indicate standard error) and (b) total basal area increment summed across all individuals. Species acronyms can be found in Fig. 1 caption.

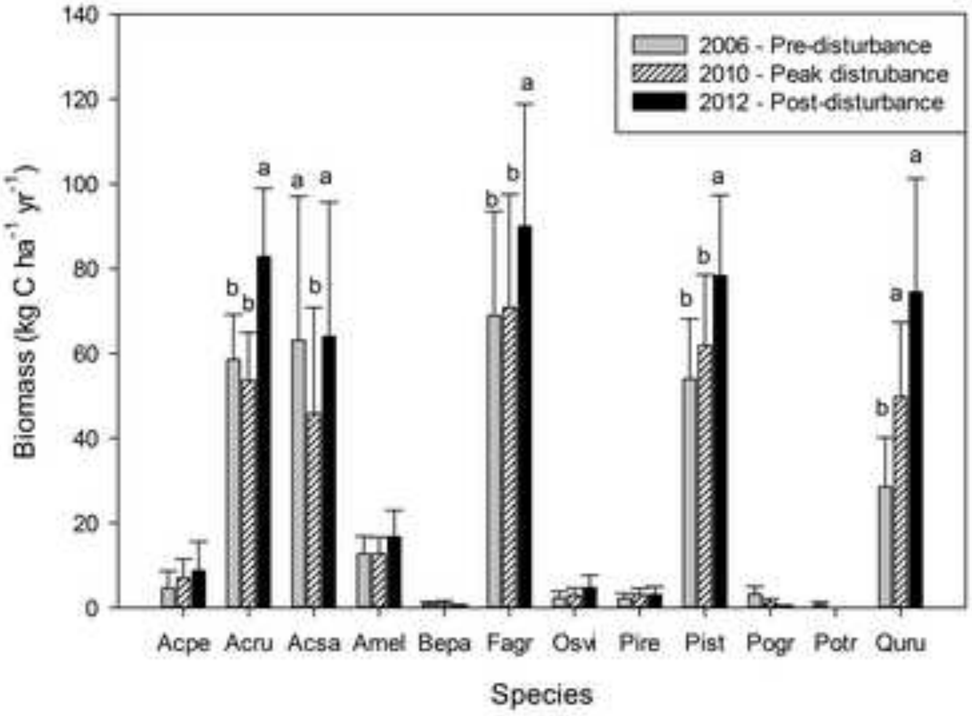
Figure 6. Relative growth (total basal area increment divided by total basal area) of subcanopy tree species before and after peak disturbance in 2010. Error bars represent standard error. Species acronyms can be found in Fig. 1 caption.

Figure 7. Relationships of subcanopy (a) productivity (post-disturbance $\mathrm{ANPP_w}$ in kg C $\mathrm{ha^{-1}}$ yr), (b) productivity response ((post-disturbance $\mathrm{ANPP_w}$ – pre-disturbance $\mathrm{ANPP_w}$)/pre-disturbance $\mathrm{ANPP_w}$)), (c) post-disturbance basal area increment (in $\mathrm{m^2\ ha^{-1}}$ yr), and (d) response in basal area increment ((post-disturbance BAI – pre-disturbance BAI)/pre-disturbance BAI)) with strongest predictors from multiple regression analysis.

Highlights:

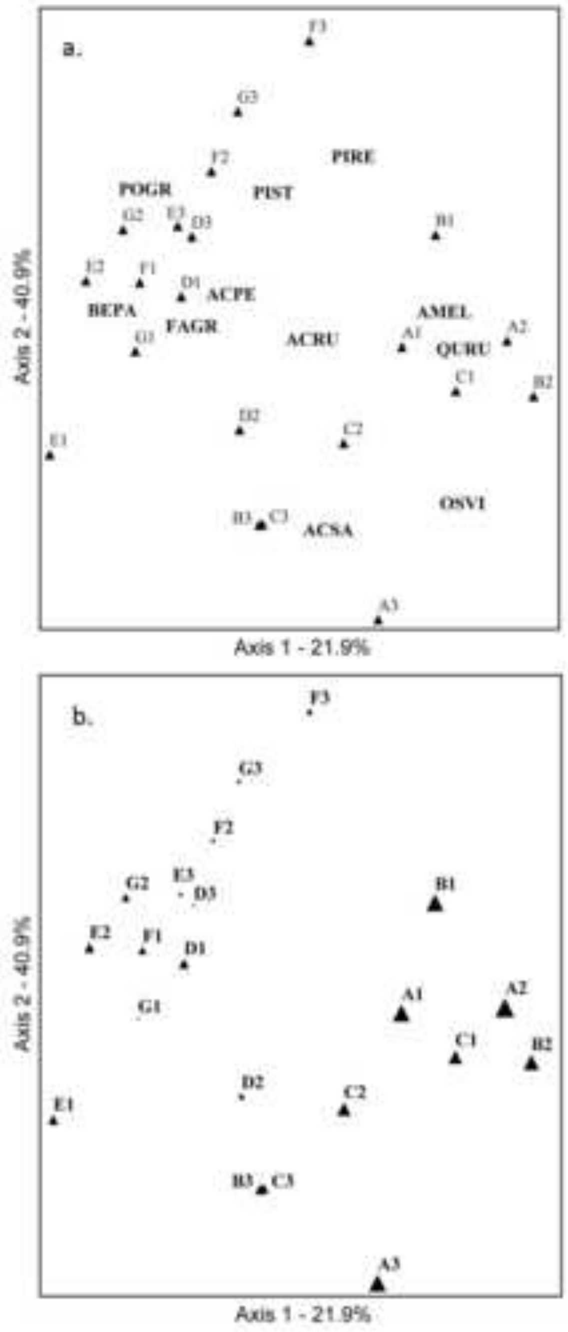
- Subcanopy contributed substantially to forest growth response to moderate disturbance
- Variable subcanopy response was mediated by composition not disturbance severity
- Moderate severity disturbance promoted growth of mid-tolerant northern red oak

Figure

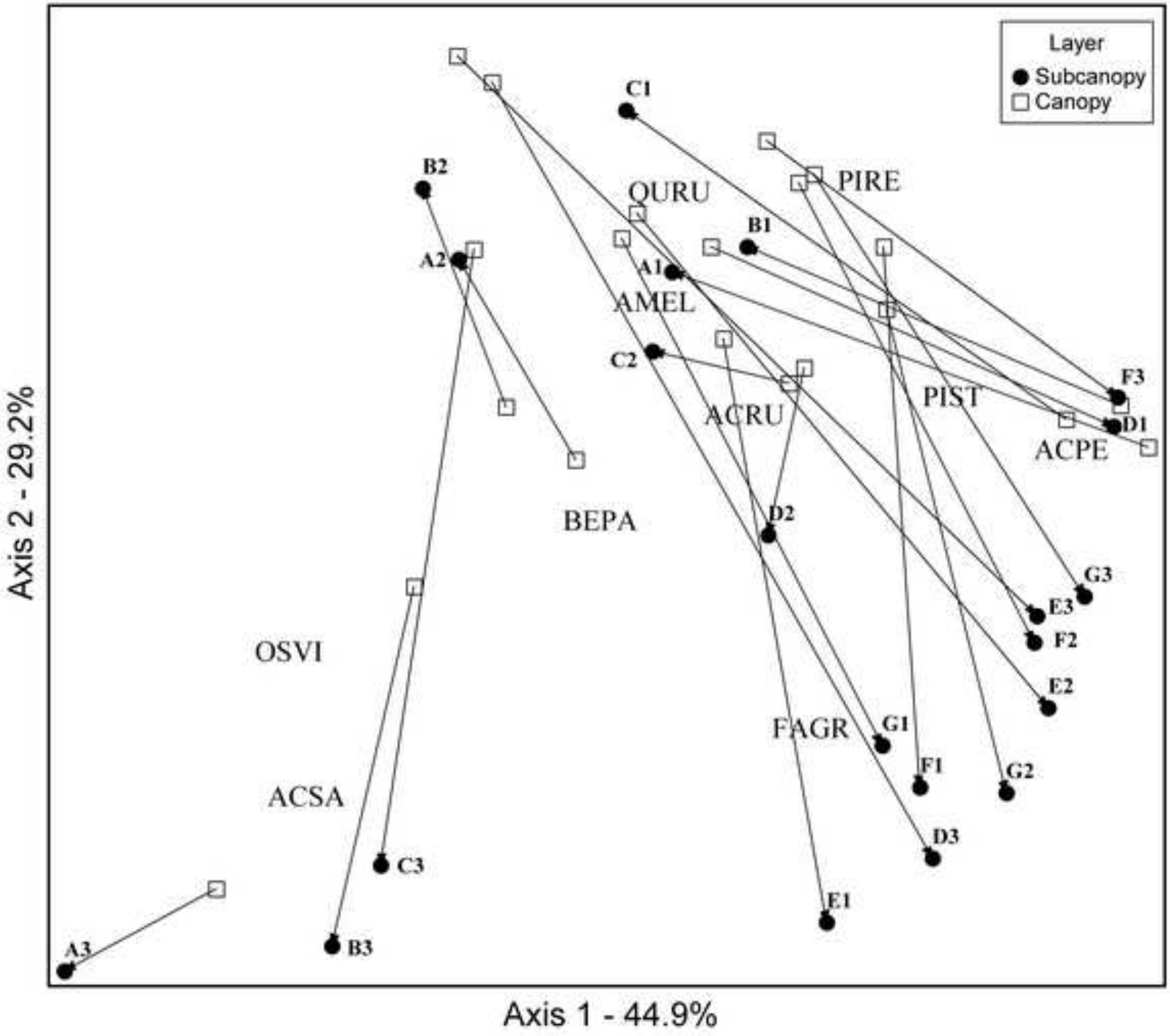


2006 - Pre-disturbance
2010 - Peak distrubance
2012 - Post-disturbance
Biomass (kg C ha^{-1} yr^{-1})
140
120
100
80
60
40
20
0
a
a
b
b
a
b
b
b
a
b
b
a
a
b
Acpe
Acru
Acsa
Amel
Bepa
Fagr
Osvi
Pire
Pist
Pogr
Potr
Quru
Species

Figure

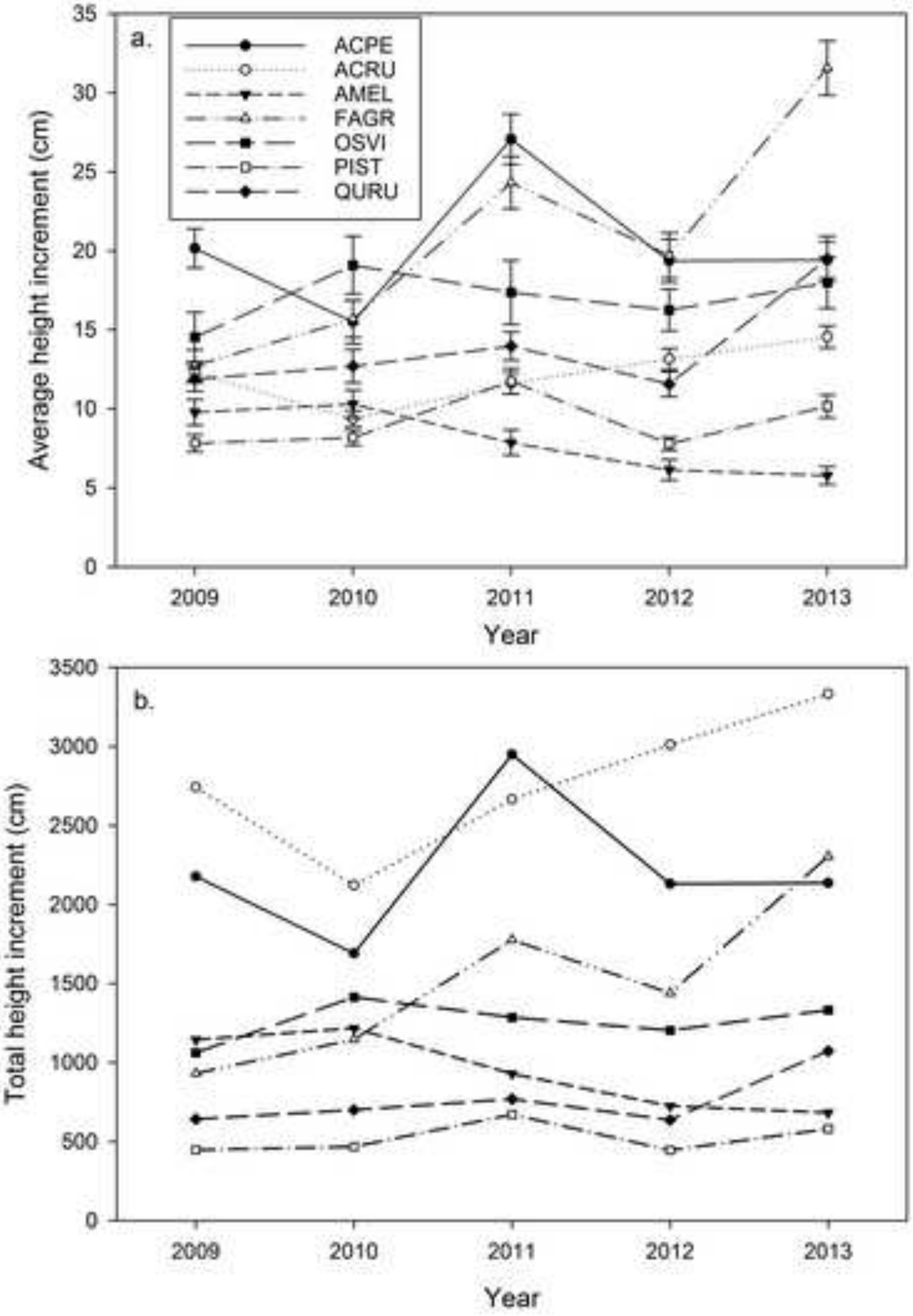

a.
F3
G3
F2
PIRE
POGR
PIST
G2
E3
D3
B1
E2
F1
D1
ACPE
BEPA
FAGR
AMEL
A2
G1
ACRU
A1
QURU
C1
B2
D2
E1
C2
OSVI
B3
C3
ACSA
A3
Axis 2 - 40.9%
Axis 1 - 21.9%
b.
F3
G3
F2
G2
E3
D3
B1
E2
F1
D1
A1
A2
G1
C1
B2
D2
C2
E1
B3
C3
A3
Axis 2 - 40.9%
Axis 1 - 21.9%

Figure

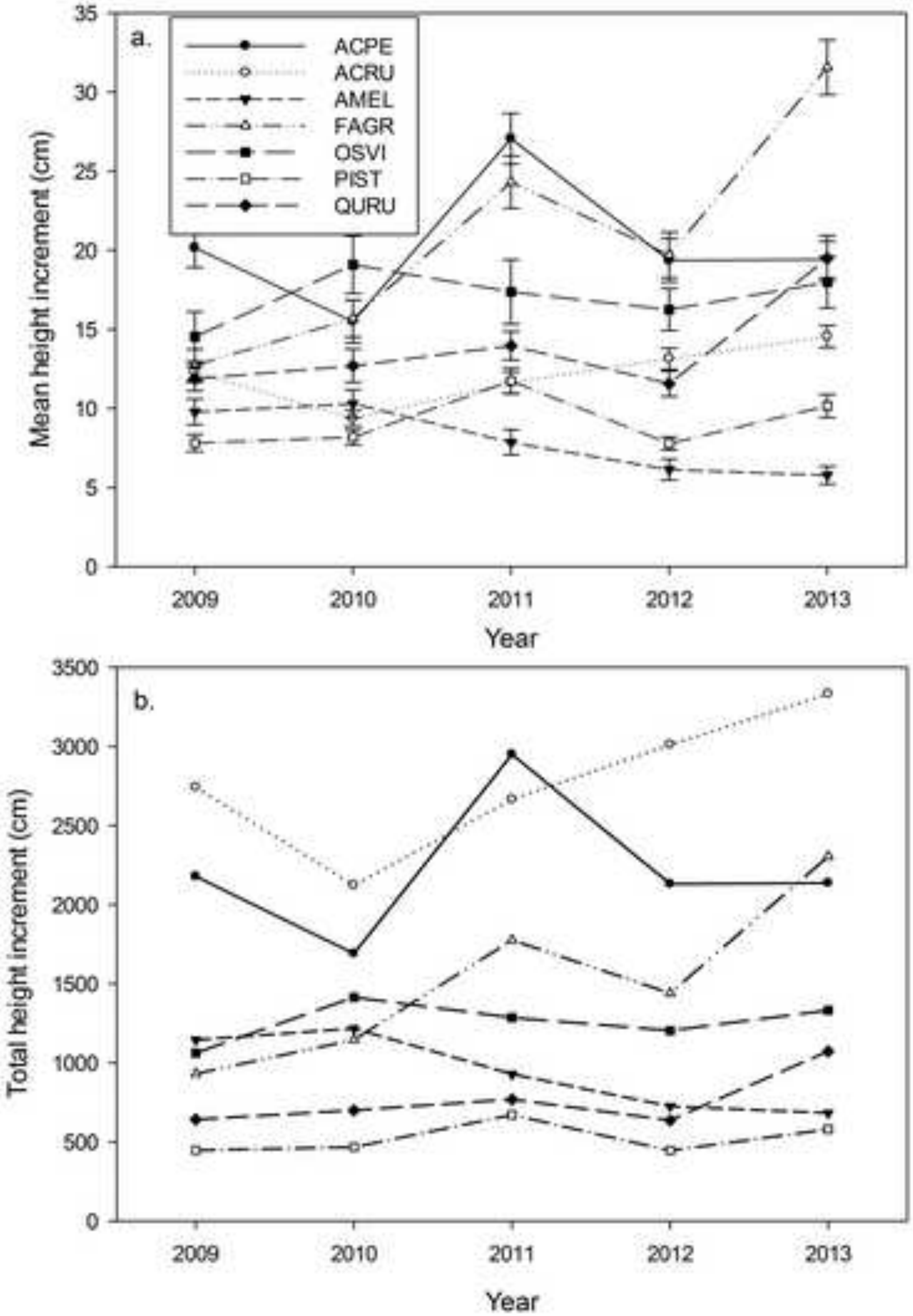


Layer
● Subcanopy
☐ Canopy
C1
B2
QURU
PIRE
B1
A2
A1
AMEL
C2
ACRU
PIST
F3
D1
ACPE
BEPA
D2
G3
E3
F2
OSVI
E2
FAGR
G1
F1
G2
ACSA
D3
C3
E1
A3
B3
Axis 1 - 44.9%
Axis 2 - 29.2%

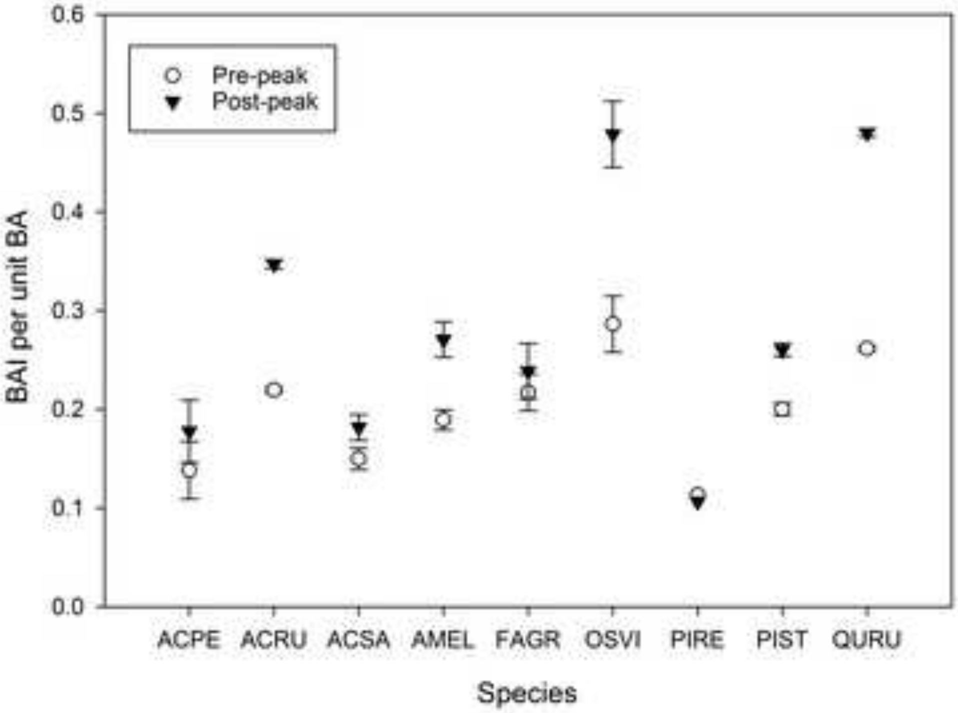
Figure


a.
ACPE
ACRU
AMEL
FAGR
OSVI
PIST
QURU
Average height increment (cm)
0
5
10
15
20
25
30
35
2009
2010
2011
2012
2013
Year
b.
Total height increment (cm)
0
500
1000
1500
2000
2500
3000
3500
2009
2010
2011
2012
2013
Year

Figure

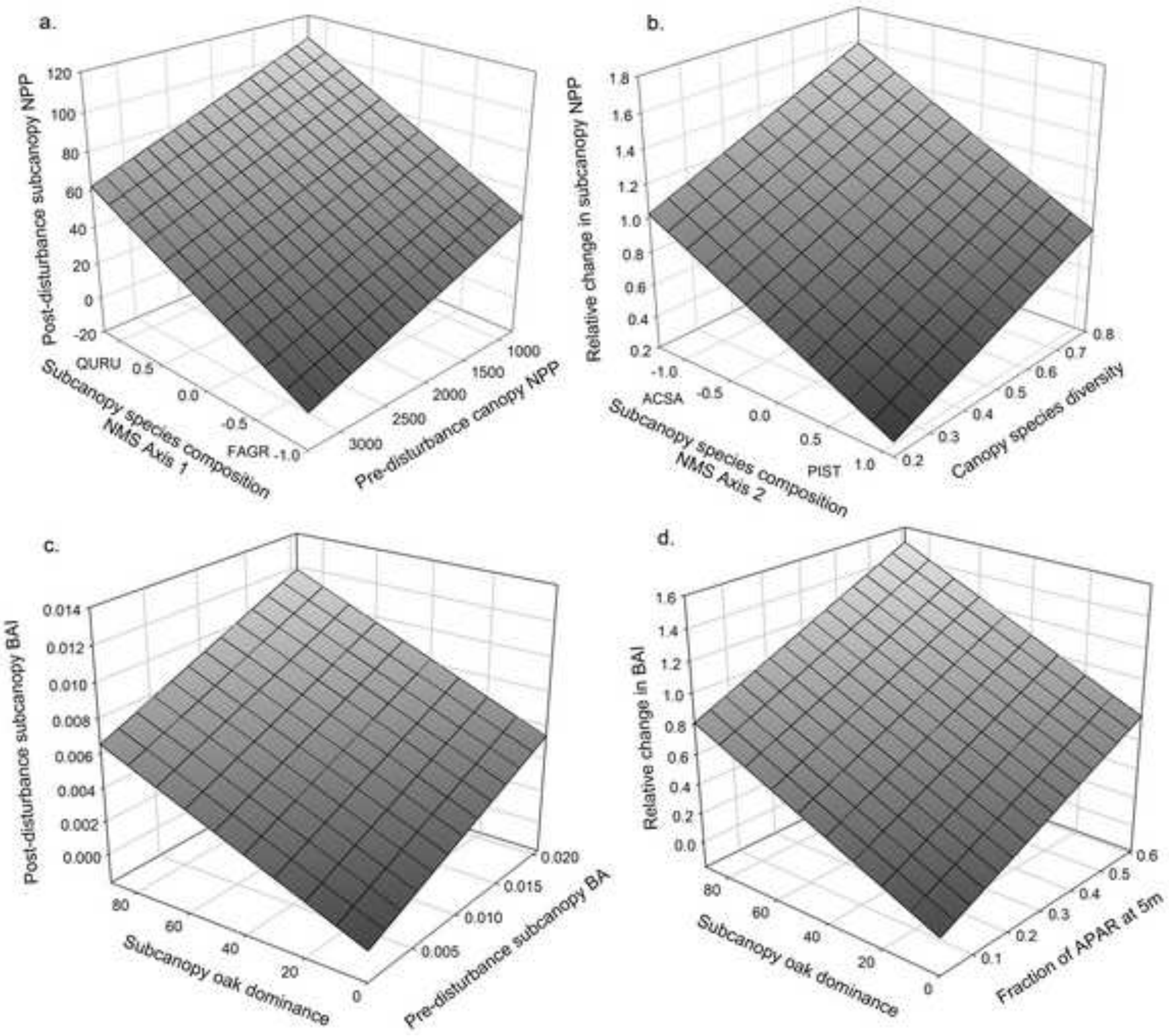

a.
ACPE
ACRU
AMEL
FAGR
OSVI
PIST
QURU
Mean height increment (cm)
0
5
10
15
20
25
30
35
2009
2010
2011
2012
2013
Year
b.
Total height increment (cm)
0
500
1000
1500
2000
2500
3000
3500
2009
2010
2011
2012
2013
Year

Figure



0.6
0.5
0.4
0.3
0.2
0.1
0.0
BAI per unit BA
○ Pre-peak
▼ Post-peak
ACPE
ACRU
ACSA
AMEL
FAGR
OSVI
PIRE
PIST
QURU
Species

Figure


a.
Post-disturbance subcanopy NPP
120
100
80
60
40
20
0
-20
QURU
0.5
0.0
-0.5
FAGR -1.0
Subcanopy species composition
NMS Axis 1
1000
1500
2000
2500
3000
Pre-disturbance canopy NPP
b.
Relative change in subcanopy NPP
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
-1.0
ACSA -0.5
0.0
0.5
PIST 1.0
Subcanopy species composition
NMS Axis 2
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Canopy species diversity
c.
Post-disturbance subcanopy BAI
0.014
0.012
0.010
0.008
0.006
0.004
0.002
0.000
80
60
40
20
0
Subcanopy oak dominance
0.005
0.010
0.015
0.020
Pre-disturbance subcanopy BA
d.
Relative change in BAI
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
80
60
40
20
0
Subcanopy oak dominance
0.1
0.2
0.3
0.4
0.5
0.6
Fraction of APAR at 5m