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Beech bark disease does not reduce the long-term wood production of two forests contrasting in age, productivity, and structure

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ABSTRACT

The distribution of pests and pathogens is increasing in many forested regions, producing uncertainty for ecological functions, including aboveground wood net primary production (NPP). In North American deciduous forests, beech bark disease (BBD) is restructuring and modifying the composition of forest stands, producing gradients of *Fagus grandifolia* mortality at finer patch scales. We investigated the multi-decadal effects of BBD on the aboveground wood NPP of a moderately productive middle-successional stand positioned on a glacial outwash plain and a relatively high productivity late-successional stand located on a moraine. Despite average stand-scale basal area losses of ~ 21% from BBD, aboveground wood NPP increased over time in both the middle- and late- successional stands. At the patch scale, the initial magnitude of change in aboveground wood NPP following BBD infestation correlated with the extent of recovery in the late, but not middle, successional stand, suggesting early responses to disturbance sometimes – but not always – predict long-term production patterns. Patch-scale aboveground wood NPP during different stages of BBD infestation was associated with vegetation quantity and production efficiency, with the latter generally increasing in later stages of the BBD progression. We conclude that the aboveground wood NPP of two forest stands increased through late stages of BBD, despite differences in stand productivity, structure, and age, while patch-scale aboveground wood NPP responses were more variable.

1. Introduction

The temperate forests of eastern North America have been carbon (C) sinks for the last century (Pan et al., 2011), but changing disturbance regimes threaten the future of this critical ecosystem function (Williams et al., 2016). In particular, a region-wide increase in moderate severity disturbances (i.e., those killing only a fraction of trees) could affect rates of C accumulation in biomass, or net primary production (NPP) (Cohen et al., 2016; Edgar and Westfall, 2022; McDowell et al., 2020). In the upper Great Lakes basin, climate change and human-assisted introductions are accelerating the geographic expansion of insect pests and pathogens (Edgar and Westfall, 2022). Among these, beech bark disease (BBD) is particularly widespread, drastically altering the demography of a keystone species, American Beech (*Fagus grandifolia*), throughout its indigenous range (Garnas et al., 2011).

Beech bark disease and other wood-boring disturbances produce gradients of tree mortality within stands with variable effects on NPP at the "patch" scale, a discrete area with a relatively uniform level of BBD-impacted basal area at a common stage of disease progression (*sensu* Pickett and Thompson, 1978). For example, patch-scale NPP was negatively correlated with emerald ash borer tree mortality in a lower Great Lakes forest (Flower and Gonzalez-Meler, 2015). In contrast,

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patch-scale NPP in an upper Great Lakes forest was stable following the experimental removal of phloem tissue up to a threshold of ~ 60% basal area removal, beyond which production abruptly declined (Stuart-Haentjens et al., 2015). A study conducted across a gradient of BBD-induced tree mortality in eastern North American found that aboveground NPP was highest at moderate levels of infestation (Hancock et al., 2008). Such divergent patterns, could arise if NPP were recorded during different stages of disturbance progression or recovery. Alternatively or in addition, different climate, environmental, or ecological conditions along with variable wood-boring mechanisms and severities at each site could influence long-term carbon cycling responses to disturbance (Dorheim et al., 2022; Flower et al., 2013).

Among the suite of ecological and site factors thought to influence how forests respond to disturbance, the effects of BBD on NPP may partly depend on the successional stage during which infestation and peak mortality occur, along with site productivity and stand structure prior to disturbance (Fahey et al., 2015; Flower and Gonzalez-Meler, 2015; Gough, Atkins, et al., 2021). For example, middle- and late-successional stands generally contain different plant species assemblages and quantities of biomass prior to disturbance, variables that are linked to NPP's response to disturbance at our site and elsewhere (Gough, Atkins, et al., 2021; Gray et al., 2016). Moreover, intertwined site factors, including landform, soils, and productivity may influence the magnitude of initial change in NPP following disturbance and affect longer-term patterns of recovery (Kannenberg et al., 2020). Together, ecological and site factors may influence the amount of material legacies, such as nitrogen and residual healthy vegetation, available to offset growth lost to tree mortality(Johnstone et al., 2016; Niedermaier et al., 2022). While identifying the factors that differentiate forests' response to disturbance is challenging because of co-varying ecological and environmental variables, long-term concurrent observations from different stands are important to understanding the full range of responses over time to common disturbance sources (Hicke et al., 2012).

Quantitative metrics that describe the direction and relative magnitude of change – or stability – in ecosystem structure, composition, or processes over time can aid in the interpretation of disturbance responses and facilitate comparisons between sites (Hillebrand et al., 2018). While multiple disturbance response frameworks have been developed, all provide standardized and normalized quantitative summaries of ecological behavior at different stages of disturbance progression or response (Donohue et al., 2013; Hillebrand et al., 2018). Most measures of stability are expressed as ratios or effect sizes, allowing direct contrasts among sites with potentially different absolute (but similar relative) changes over time (Mathes et al., 2021). *Resistance* can be defined as the relative change in ecosystem functioning (e.g., NPP) at peak disturbance, *recovery* as the degree of functioning that follows peak disturbance, and *resilience* as the relative difference between functioning before and after peak disturbance. The derivation of multiple disturbance-response metrics can facilitate quantitative comparisons and hypothesis testing, including whether different stages of ecosystem response exhibit trade-offs or interactions (Mathes et al., 2021). For example, ecosystem processes displaying lower levels of resistance are hypothesized, but not broadly shown, to exhibit higher degrees of recovery (Anderegg et al., 2016; Hillebrand and Kunze, 2020). Such patterns, should they exist, could inform ecological forecasts and adaptive forest management (Seidl et al., 2011).

We characterized aboveground wood NPP before and after the introduction of BBD in separate low productivity middle and higher productivity late-successional forest stands to address two primary goals. Our first goal was to assess the multi-decadal trajectories of aboveground wood NPP before, during, and after BBD infestation in two stands that share a common climate but differ in age, soils, composition, and structure. A second goal was to characterize the resistance, recovery, and resilience of aboveground wood NPP at the patch-scale (i.e., within each stand), examining whether relationships (including trade-offs) exist among levels production across different stages of BBD progression. We hypothesized (H1) that relatively low overall tree mortality from BBD would have limited effects on the long-term aboveground wood NPP of middle- and late-successional stands. We further hypothesized (H2) that a trade-off would exist between aboveground wood NPP resistance and recovery at the patch-scale, with larger initial declines in production associated with greater long-term increases in aboveground wood NPP after peak BBD infestation (Fig. 1).

2. Methods

2.1. Study sites

Our study was conducted at the University of Michigan Biological Station in northern lower Michigan in two temperate deciduous forest stands within 10 km of one another that were concurrently affected by BBD: a 100-year-old middle-successional stand (45°33′35.1″N/ 84°42′49.5″W) and a 180-year-old late-successional stand (45°29′11.1″N/ 84°40′56.6″W) (Table 1). The middle-successional stand, which developed following region-wide clear-cut harvesting and wildfires in the early 20th century, contained a mixture of senescent early successional *Populus granidentata* (bigtooth aspen) and emergent later successional species, including *Quercus rubra* (northern red oak), *Acer rubrum* (red maple), *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech), and *Pinus strobus* (white pine). Canopy dominant species in the late-successional stand, which was never clear-cut but was selectively logged through the early 20th century, included *A. saccharum* (sugar maple), *F. grandifolia* (American beech), *Q. rubra* (red oak), *A. rubrum* (red maple), *P. strobus* (white pine), and *Tsuga canadensis* (eastern hemlock). The subcanopy, 1 to 7 m above the forest floor, in both stands was primarily *F. grandifolia* and *A. saccharum*, and also includes *A. rubrum*, *A. pensylvanicum*, *T. canadensis*, *Q.* rubra, and *P. strobus*. In addition to compositional differences, the two landscapes are positioned on different soils and landforms (Pearsall, 1995). The middle-successional forest is located on a glacial outwash plain with well-drained, sandy, and relatively low-productivity soils. The late-successional forest landscape is on a gently sloping moraine with more productive sandy-loam soils. Late-successional stands occupy a small proportion of the region's forested area relative to the more widespread middle-successional forest distributed throughout the upper Great Lakes (Frelich, 1995; Hanberry and He, 2015).

Because age, disturbance history, plant community composition, soils, productivity, and pre-disturbance structure vary between the middle- and late-successional stands, our study does not attempt to attribute a single site, environmental, or ecological factor to differences in long-term aboveground wood NPP. However, for the purpose of concision, we refer to "middle-successional" and "late-successional" stands, while acknowledging the stands differ in several ecologically relevant ways that are distinct from (e.g., landform) or intertwined with (e.g., pre-disturbance biomass) stand age (Table 1), and are known factors influencing wood NPP at our site and elsewhere (Gough et al., 2010; Nave et al., 2017).

Inventory plots were established in the late-successional stand between 1992 and 1994 (30, 0.045 ha plots) and in middle-successional stand between 1997 and 2003 (57, 0.08 ha circular plots) to characterize biomass stocks and forest composition in advance of BBD infestation. We selected 23 (14 late-successional, 9 middle-successional) of these original plots for resampling in 2013, 2015, 2016, and/or 2017, encompassing a gradient of total plot basal area affected by BBD infestation (i.e., here termed "disturbance severity", *sensu* Hicke et al., 2012). Specifically, we calculated plot-scale disturbance severity by dividing the basal area of BBD-infected American beech by the total plot basal area inclusive of all species, and then multiplying this ratio by 100 to express as a percent. Species composition and disturbance severity are inherently intertwined, but we sought to minimize non-beech species compositional differences across disturbance severities. The distribution of *F. grandifolia* across plots in late-successional and middle-successional

Fig. 1. Beech bark disease (BBD) in a relatively low productivity middle successional stand and higher productivity late-successional stand caused patchy tree mortality. Our study examined the aboveground wood NPP of these two stands differing substantially in age, productivity, and structure and composition over a period of nearly two decades, through a complete progression of BBD.

Table 1
Summary of pre-disturbance stand characteristics for the middle (MS) and late (LS) successional forest landscapes. The area experiences a mean annual temperature of 5.5 °C and receives a mean annual precipitation of 817 mm Values represent plot-based means with standard deviation in parentheses. NPP—net primary production, VAI—vegetation area index.

Site	Age (yr)	Basal Area (m^2 ha^{-1})	Density (stems ha^{-1})	Aboveground Biomass (Mg ha^{-1})	Aboveground wood NPP (Mg C ha^{-1} yr^{-1})	VAI	Landform	Soils
MS	100	24.8 (9.8)	743.1 (158.4)	171.6 (54.1)	1.9 (0.3)	7.0 (0.8)	high-level plain	sandy Haplorthrod
LS	180	44.2 (13.6)	547.6 (127.1)	330.6 (101.8)	2.6 (1.0)	7.7 (0.2)	gently sloping moraine	sandy over loamy Haplorthod

enabled the comparison of comparable disturbance severity gradients in both successional stages (1 to 53% in late-successional and 4 to 55 % in middle-successional). Mean plot disturbance severity and associated variances did not differ between sites ($p = 0.94$; Bartlett test, $p = 0.95$). However, the aboveground biomass of the more productive, late-successional stand before BBD infestation was nearly twice that of middle-successional stand. Hereafter, the "patch" scale references individual plot-level observations and "stand" scale is the mean of plot-level observations contained within the affected middle-successional or late-successional sampling areas. Because pre-disturbance tree community composition (and thus the distribution and abundance of beech) was uniform within a plot, each patch was a relatively homogenous unit of BBD infestation and, consequently, disturbance severity.

2.2. Progression of infection

Beech bark disease (BBD) is a disease complex resulting primarily from feeding by the introduced beech scale insect (*Cryptococcus fagisuga* Lind.) and subsequent infection by fungal pathogens (*Neonectria* spp.). The progression of BBD proceeds through three temporally and biologically distinct phases at the landscape scale: 1) the *advance front*, during which the scale-insect (*Cryptococcus fagisuga*) begins to inhabit trees but infection and visible damage or tree mortality by the fungal pathogen (*Neonectria spp.*) is rare; 2) the *killing front*, associated with prevalent BBD infection and host mortality, and 3) the *aftermath*, at which point the density of surviving host trees is low (Cale et al., 2017). The timing and duration of the advance front is variable, generally lasting four to five (but up to ten) years while the beech scale-insect proliferates but maintains relatively low population densities (Houston et al., 2005). During the killing front phase, the timing from infection to mortality varies between two to six years post-onset depending on forest community composition and soils, individual tree resistance, age, and size, with larger and older trees more vulnerable to BBD mortality (Busby and Canham, 2011; Ouimet et al., 2015; Van Leaven and Evans, 2004).

To determine the infection stage of trees within each plot, we applied a ranking system developed by Griffin et al. (2003). Stage 1 – very little or no habitation of scale insect and 100 % crown foliage; Stage 2 – scale insect present, small cracks in bark, and > 75 % crown foliage intact; Stage 3 – bark heavily cracked, significant cankering, and some crown damage or limb loss with canopy foliage 25–75 % intact; Stage 4 – bark severely cracked, large girdling cankers, and significant crown loss with < 25 % canopy foliage intact; Stage 5 – snag or fallen tree.

2.3. Net primary production and reference sites

We quantified aboveground wood net primary production (NPP) from repeated inventories of stem diameter at breast height (dbh, 1.37 m height). Within all 23 plots, the species and dbh of each individual tree ≥ 8 cm dbh were recorded each census year. Trees < 8 cm were grouped in sapling dbh classes one (0.1–1.9 cm), two (2.0–3.9 cm), three (4.0–5.9 cm), and four (6.0–7.9 cm). Site -or region- and species-specific allometric equations were used to estimate individual tree aboveground wood mass from dbh (Gough et al., 2008). Aboveground wood NPP was calculated as the annual change in summed aboveground wood carbon mass (derived from all stem diameter classes) within late-successional and middle-successional plots. Census years in late-successional were 1992 or 1994 (depending on year of plot establishment), 2014, 2016, 2017, and 2018, and in middle-successional stands were 1997, 1998, 2001, 2010, 2015, and 2018. Even following wood-boring disturbance (stimulated via stem-girdling), NPP estimates at our site are made with high certainty following disturbance (95 % C.I. of estimated total NPP averages ± 16 %) (Gough et al., 2013; Gough et al., 2010; Gough et al., 2008), and closely parallel independent meteorological tower estimates of net ecosystem production (NEP) (Gough et al., 2008).

Because our study is opportunistic rather than experimental (in the sense that a BBD invasion was not planned), robust paired controls were not possible; instead, we report concurrently collected "reference" aboveground wood NPP and NEP data published for an undisturbed site within the same forested landscape. Annual aboveground wood NPP, 1999–2012, for a middle-successional stand without BBD was derived using the methods described (Gough et al., 2013; Gough et al., 2010). We also report independently derived NEP values for the undisturbed forest, 2012–2019, estimated from a nearby meteorological carbon flux tower (Gough, Bohrer, et al., 2021). The reference forest adjoined and was similar in prior disturbance history, age, composition, and soils to the BBD-infested middle successional stand. Because the methods, timing, and frequency of observations differ among BBD-affected and reference sites, we limit our comparisons of changes in production over time to directionality (positive or negative) rather than magnitude or slope.

2.4. Stability measures: Resistance, resilience, and recovery of production

We calculated three disturbance stability metrics from plot-scale aboveground wood NPP time-series coinciding with different stages of BBD infection. While variously defined in the literature (see Hillebrand et al., 2018), our approach is similar to that of other studies evaluating changes in plant growth during different phases of drought (Lloret et al., 2011; Pretzsch et al., 2013; Stuart-Haentjens et al., 2018). We use the following definitions: 1) *resistance* is the ratio of aboveground wood NPP at peak (i.e., aboveground wood NPP_{peak}) and pre- (aboveground wood NPP_{pre}) phases of BBD progression, aboveground wood NPP_{peak}/ aboveground wood NPP_{pre}; 2) *recovery* is the ratio of aboveground wood NPP after (i.e., aboveground wood NPP_{post}) and during peak phases of BBD progression, aboveground wood NPP_{post}/aboveground wood NPP_{peak}; and 3) *resilience* is the extent to which ANPP post-disturbance returns to its pre-disturbance value, or aboveground wood NPP_{post} /aboveground wood NPP_{pre}. The phases of plot-scale BBD progression were defined as the basal area of > 8 cm dbh *Fagus* with the following conditions: "pre" – stage 1, no BBD detected; "peak" – 80% of *Fagus* in stages 4 or 5; "post" – 100 % of *Fagus* in stage 5, complete mortality of beech (Fig. 2).

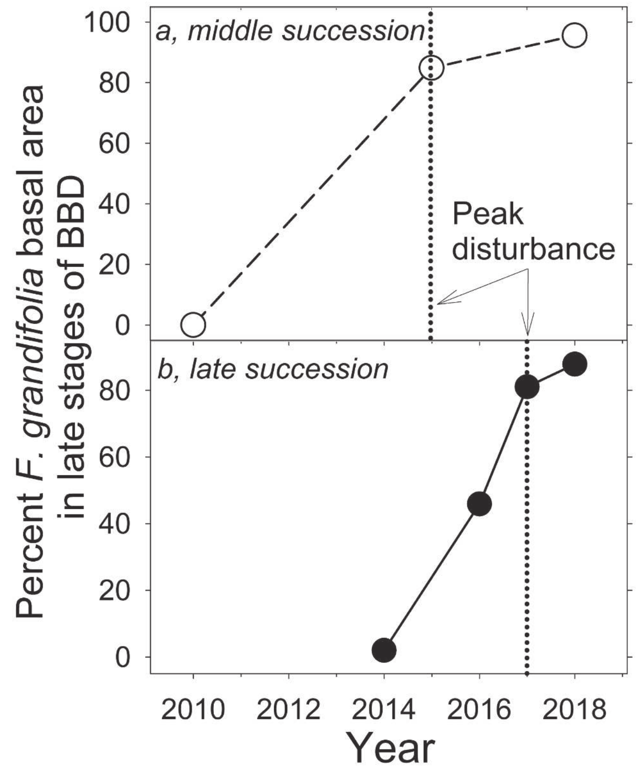

Fig. 2. The percentage of *Fagus grandifolia* basal area in stages 4 or 5 of Beech Bark Disease (BBD) in middle-successional and late-successional and forest stands (circles). Vertical lines illustrate the timing of peak disturbance, when > 80 % of the infected basal area had either senesced or advanced to late infestation BBD stages.

2.5. Production efficiency

Moderate severity disturbance may increase resource-use efficiency by redistributing limiting resources, "releasing" vegetation growth (Gough, Bohrer, et al., 2021), and thereby stabilize production. Therefore, we assessed production efficiency across gradients of disturbance severity in both the middle-successional and late-successional landscapes. We calculated plot-level production efficiency at each time interval coinciding with the stability measures. Production efficiency was estimated as the ratio of aboveground wood NPP to vegetation area index (VAI) (Atkins et al., 2021). We used ground-based Portable Canopy LiDAR (PCL) to estimate VAI, processing raw data using the *forestr* package in R (Atkins et al., 2018). There were no pre-existing relationships between disturbance severity and VAI or production efficiency at either site (middle-successional: $p = 0.92$; late-successional: $p = 0.87$).

2.6. Statistical analysis

We used simple linear regression to examine how aboveground wood NPPresistance, resilience, recovery, and production efficiency were related to disturbance severity. We used ANCOVA to test for differences in regression parameters (i.e. slopes and intercepts) between the middle-successional and late-successional landscapes.

All statistical analyses used R 3.4.4 (R Development Core Team 2018) statistical software or SYSTAT software (SYSTAT 2019). Relationships were considered significant when $p \leq 0.10$. For continuity among figures, we illustrate late-successional plots with filled symbols and solid lines and middle-successional plots with open symbols and dashed lines.

3. Results

3.1. Beech bark disease progression

Traces of the scale insect during the advance front were observed in both middle-successional and late-successional stands between 2008 and 2010, though widespread infection (i.e., the killing front) commenced in middle-successional between 2011 and 2013 and in late-successional between 2014 and 2015. Peak disturbance, defined as the census year that > 80% *F. grandifolia* basal area ≥ 8 cm diameter at breast height (dbh) had either died or advanced to late infection stages, occurred in 2015 in middle-successional plots and between 2016 and 2017 in late-successional plots (Fig. 2). Thus, for the purpose of deriving resistance, resilience, and recovery from aboveground wood NPP, pre-disturbance production was estimated using dbh data from 2001–2010 in middle-successional and 2014–2016 in late-successional plots; peak-disturbance dbh data were from as 2010–2015 in middle-successional and 2016–2017 in late-successional plots; and post-disturbance dbh data were from 2015 to 2018 in middle-successional and 2017–2018 in late-successional. Mean basal area morality at peak disturbance (relative to total, irrespective of species) was 20.5 % (+/- 16.2 %) and 21.0 % (+/- 15.9 %) in middle- and late-successional stands, respectively.

3.2. Aboveground wood net primary production and vegetation area index

Neither stand exhibited declines in aboveground wood NPP following BBD infestation, despite mean net reductions in VAI of 4% and 19% in middle- and late-successional stands, respectively. Instead, aboveground wood NPP increased significantly following BBD introduction in both stands (middle-successional: $r^2 = 0.89$, $p = 0.058$, $m = 21.51$; late-successional: $r^2 = 0.84$, $p = 0.084$, $m = 90.70$). The rate of increasing aboveground wood NPP over time was nearly six times greater in late-successional (124.4 +/- 80.2 [95% C.I.] kg C ha^{-1} yr^{-1}) than in middle-successional (21.5 +/- 10.6 kg C ha^{-1} yr^{-1}) forest stand (ANCOVA: $F = 8.2431$, $p = 0.063$). By comparison, the aboveground NPP of a nearby undisturbed reference site declined significantly from 1999 through 2012. Conversely, the annual NEP of the reference stand increased significantly from 2012 to 2019. (Fig. 3).

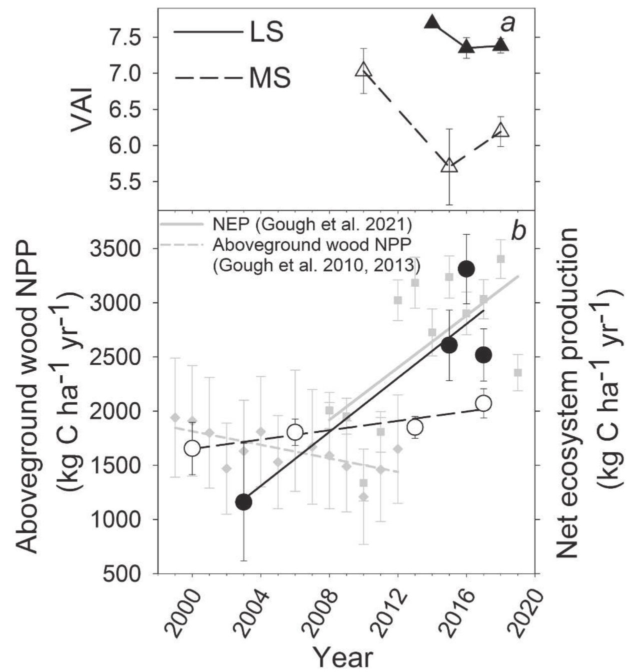

Fig. 3. Mean (+/- 1 S.E.) aboveground wood net primary production (NPP) (panel b, circles) and vegetation area index (VAI) (panel a, triangles) in middle (open symbols and dashed line) and late (filled symbols and solid line) successional forest stands. Values are plot averages ($n = 9$ in middle-successional, $n = 14$ in late-successional), derived from changes in wood mass between census years and error bars represent standard error of the mean. Gray-shaded diamonds and dashed line are aboveground wood NPP and trendline, respectively (Gough et al.; 2010; Gough et al., 2013), and gray-shaded squares and solid line are net ecosystem production (NEP) data (Gough et al., 2021) for a nearby undisturbed reference site.

3.3. Production stability across the disturbance severity gradient

Within each stand, plots exhibited different patterns of aboveground wood NPP resistance, recovery, and resilience across the BBD-associated disturbance severity gradient (Fig. 4). As disturbance severity increased, patch-scale aboveground wood NPP resistance did not change significantly in middle-successional stands but declined in late-successional stands ($r^2 = 0.44$, $p = 0.010$; Fig. 4a). In contrast, aboveground wood NPP recovery increased significantly with rising disturbance severity in both late-successional ($r^2 = 0.56$, $p = 0.002$) and middle-successional plots ($r^2 = 0.58$, $p = 0.018$; Fig. 4b). Resilience increased with disturbance severity only in middle-successional plots ($r^2 = 0.45$, $p = 0.048$; Fig. 4c), though this pattern was driven by the high leverage of the most severely disturbed plot. Resilience was more variable among late-successional plots, displaying no significant trend with increasing disturbance severity.

3.4. Production efficiency and vegetation area index across the disturbance gradient

Relationships between patch-scale production efficiency, VAI, and disturbance severity differed among successional stages and periods of BBD progression. With the exception of the middle-successional recovery, VAI declined in response to increasing disturbance severity during the different disturbance progression periods (Fig. 5a-c). During the resistance phase of disturbance progression, production efficiency increased with disturbance severity in middle-successional and decreased in late-successional plots. In contrast, during recovery, production efficiency increased with rising disturbance severity in late-successional plots and did not change significantly in middle-successional plots (Fig. 5d-f).

4. Discussion

In our study, aboveground wood NPP increased in forest stands differing in age, soils, landform, and disturbance history during a multi-decadal progression from early to late stages of BBD. In contrast, the production values (as aboveground wood NPP or NEP) of a nearby undisturbed reference site decreased initially and then increased over the same two-decade period, suggesting BBD’s effects on long-term production were limited. Plot aboveground wood NPP resistance, recovery, and resilience metrics revealed that substantial spatio-temporal variation in patch-scale production often, but not always, correlated with the amount of total basal area affected by BBD. Our results align with those showing initial changes in patch-scale NPP are influenced by the quantity and extent of tree mortality from pests and pathogens (Flower and Gonzalez-Meler, 2015; Flower et al., 2013). However, our findings depart from those of Hancock et al. (2008), who observed no systematic change in aboveground wood NPP at the stand- or plot-scales as BBD-related mortality increased. Moreover, our results do not mirror the findings of a nearby stem-girdling experiment showing early successional tree species mortality uniformly increased patch-scale aboveground wood NPP until a threshold of 60% basal area killed was exceeded (Stuart-Haentjens et al., 2015). Collectively, these variable outcomes underscore how similar disturbance mechanisms can impart different effects on ecosystem processes (Hicke et al., 2012), and they

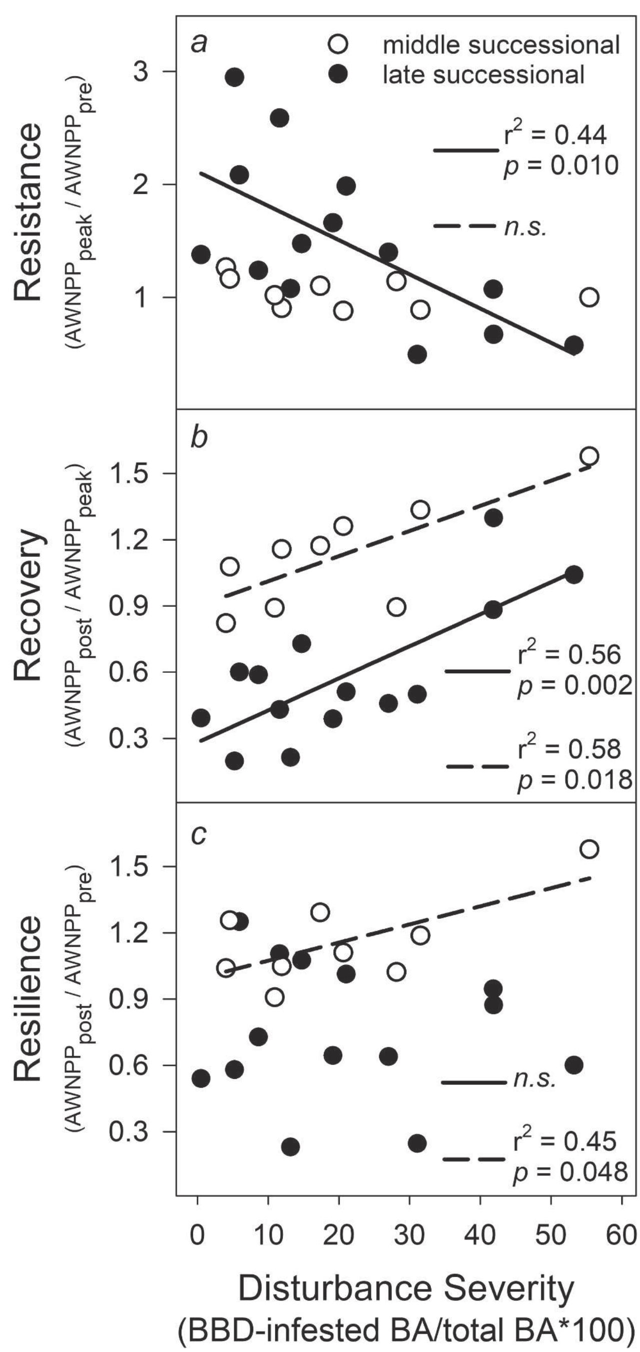

Fig. 4. Resistance (*a*), recovery (*b*), and resilience (*c*) of aboveground wood net primary production (AWNPP) in middle- open circles and dashed line) and late- (filled circles and solid line) successional forests across a gradient of Beech Bark Disease (BBD) disturbance severity (plot BBD-infested basal area [BA] divided by total plot basal area). $AWNPP_{pre}$ refers to annual aboveground wood NPP prior to widespread BBD onset, $AWNPP_{peak}$ describes annual NPP during peak disturbance mortality, and $AWNPP_{post}$ refers to annual NPP in the year(s) immediately following peak disturbance. The absence of a line indicates no significant relationship ($p \geq 0.1$).

reinforce evidence that disturbance severity-production relationships lack global uniformity.

Although both BBD-infected stands exhibited long-term increases in aboveground wood NPP, the production of the late-successional forest increased nearly 6-times more rapidly than that of middle-successional forest. While our study design cannot elucidate the underlying cause, disturbance interactions with site and ecological factors jointly shape long-term carbon cycling processes (Fahey et al., 2015; Gough, Bohrer, et al., 2021; Jentsch and White, 2019; Shure et al., 2006). While the mean basal area affected by BBD (~21%) was similar in middle- and late-successional stands, VAI declined more precipitously in the younger forest, reflecting differences between stands in the rate of compensatory growth as the disease progressed. In our study, moderate levels of canopy tree mortality may have stimulated production more vigorously in the biomass-rich and productive late-successional stand, if undergoing retrogression (Peltzer et al., 2010), by redistributing growth limiting-resources and releasing subcanopy vegetation (Abrams and Orwig, 1996; Fraver et al., 2009). Subcanopy light availability may have increased more in the late-successional stand where beech occupy the upper canopy and BBD-related mortality of dominant and codominant beech forms large gaps. In contrast, beech's sub- and mid-canopy position in middle-successional forests may result in its removal having a more limited effect on subcanopy light levels. In addition, the trajectory of aboveground wood NPP could be lower in the middle- successional stand because of compounding (i.e., sequential) disturbances (*sensu* Buma and Wessman, 2011) associated with BBD and rapid age-related senescence of maturing aspen and birch, which are declining at a rate of > 40% per decade (Gough et al., 2010).

The different site productivities and pre-disturbance structures of middle and late-successional forest stands also may have influenced long-term aboveground wood NPP and its response to BBD. The late-successional stand was positioned on relatively productive sandy-loam moraine soils, while the middle-successional forest overlays poorer sandy, well-drained soils on an outwash plain (Pearsall 1995). Such physiographic differences drive substantial variation in successional patterns of primary production in Great Lakes forests (Nave et al., 2017). In our observational study, physiographic provenance and successional stage were confounded and, consequently, their effects cannot be disentangled. While determining the influence of these multiple interacting factors on long-term aboveground wood NPP was not possible, the increase in production observed in both stands through late stages of BBD suggests a high level of sustained functioning in both ecosystems despite large differences in site productivity, age, composition, and structure. Experimental studies that control for co-varying ecological and environmental factors are important to separating the effects of multiple drivers on long-term production.

As hypothesized, we observed relationships, including apparent trade-offs, between some periods of disturbance response at the patch-scale. For example, resistance decreased and recovery increased with rising BBD infestation in late-successional plots, demonstrating that forest patches exhibiting steeper initial declines in aboveground wood NPP regrew more vigorously following peak disturbance. Moreover, these dynamic changes in late-successional plot aboveground wood NPP resistance were coupled with production efficiency, indicating that the amount of biomass produced per unit vegetation area initially decreased and then increased. While trade-offs between initial carbon cycling responses to disturbance and rates of recovery are hypothesized, they are rarely evaluated empirically in forests (Donohue et al., 2013; Downing et al., 2020; Radchuk et al., 2019) because disturbance studies are often short-term, or focus on a single disturbance source, severity, frequency, or ecosystem type (Buma and Schultz, 2020). Although our study does not provide an exhaustive mechanistic basis for such trade-offs, the initial resistance-phase following disturbance can be a period of ecological disorganization, with tree mortality reducing the efficiency in which resources are used to drive biomass production (Gough, Bohrer, et al., 2021). However, following compensatory regrowth, the reorganization and optimization of vegetation structure, and associated gains in resource-use efficiency, aboveground wood NPP may recover rapidly, with the magnitude of recovery proportional to how much production declined initially (Anderegg et al., 2016). Identifying conserved relationships, including tradeoffs, between different stages of disturbance response – should they exist – could enhance forecasts of functional recovery and support evidence-based adaptive management (Gough,

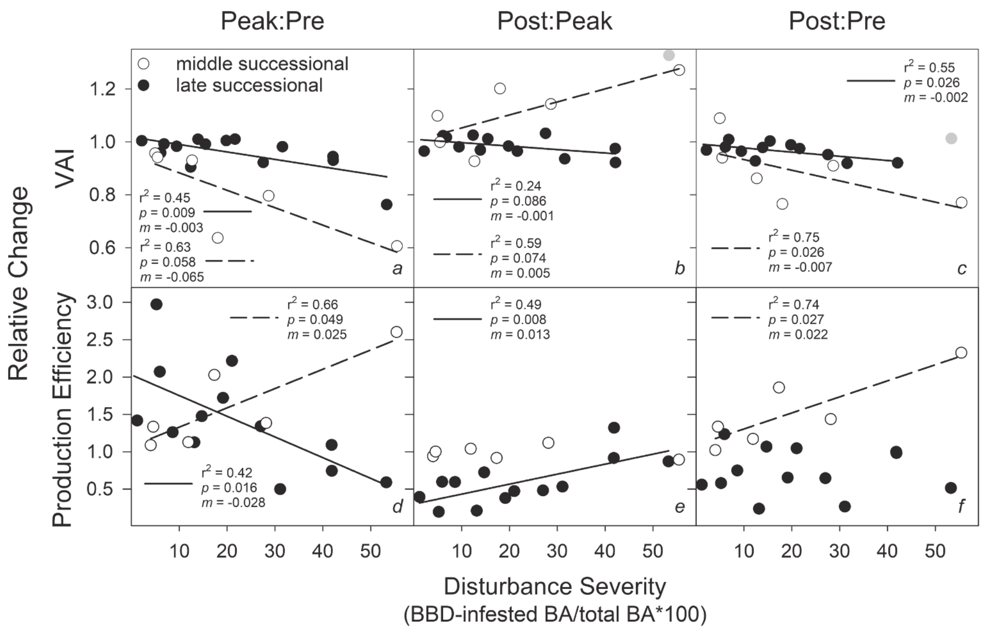

Fig. 5. Relative changes in vegetation area index (VAI) (a-c) and in production efficiency (d-f) across the gradient of disturbance severity (plot BBD-infested basal area [BA] divided by total plot basal area) in middle- (open circles) and late- (filled circles) successional forest plots. Calculation periods correspond to the time intervals associated with resistance, recovery, and resilience. The absence of a line indicates no significant relationship ($p \geq 0.1$). Gray circles indicate statistical outliers in the dataset that were not included in the regression analysis.

Atkins, et al., 2021; Mathes et al., 2021). However, additional work is needed to understand whether such relationships among different periods of disturbance response extend to other forest types and disturbance sources (Mathes et al., 2021).

Given the variety of ecological responses to insects and pathogens (Hicke et al., 2012), a key question remains: why do ecosystems respond differently to the same source of disturbance? While neither comprehensive nor conclusive, our study provides some clues. First, our separate patch- and stand-scale analyses reinforce the sensitivity of disturbance-related process change to spatial scale, and the timing and frequency of observations (Amiro et al., 2010; Sanchez-Pinillos et al., 2019; Sommerfeld et al., 2018). The differences we observed in aboveground wood NPP's response to BBD over time and between patch- and stand-scales highlights how one-time and single-scale assessments may fail to capture spatio-temporally variable dynamics arising from disturbance. These findings align with theory and observations showing that finer-scale responses to patchy disturbance, while variable, may offset one another, thereby stabilizing larger spatial-scale processes (Turner, 2010). Secondly, differences in pre-disturbance plant biomass in middle- and late-successional stands suggest material legacies influenced aboveground wood NPP's response to disturbance by affecting the quantity of healthy vegetation available to compensate for tree mortality (Johnstone et al., 2016). Alternatively, or in addition, pre-disturbance biomass may signal differences in site quality, with higher productivity in the late-successional forest stand conferring more rapid rates of tree growth before and after BBD (Gough, Atkins, et al., 2021; Nagy et al., 2017). Similarly, increasing production efficiency across the BBD mortality gradient at multiple stages of progression suggests limiting resources such as nitrogen were retained, rather than leached, and may have supported an overall upward trajectory of stand aboveground wood NPP (Nave et al., 2014), even through the progression of BBD. Lastly, when compared with disturbances from fire or wind that kill or fell trees immediately, the more gradual and staggered rate of tree mortality resulting from wood-boring disturbances could provide more time for the retention and redistribution of limiting resources to residual live vegetation, and ultimately support the compensatory growth required to stabilize and sustain stand-scale production (Gough, Bohrer, et al., 2021).

Our study of BBD's effects on aboveground wood NPP has several limitations. First, we evaluated only the first few years after BBD infestation and our analysis is confined to a single production pool. The response of other components of primary and ecosystem production, such as leaves and roots, may not parallel that of aboveground wood and could explain why increases in aboveground wood NPP in the middle-successional forest were lower than those of reference-site NEP, since net ecosystem production is a measure of total NPP minus heterotrophic respiration (Clay et al., 2022). Moreover, our study does not account for lags between BBD infestation and the large imminent influx of detritus, which will likely increase future carbon losses from heterotrophic respiration and could cause both forest stands to become net carbon sources (Harmon et al., 2011). In addition, the relative stability of forest stand aboveground wood NPP during BBD progression may not extend to other systems, particularly if already degraded or deficient in material legacies (Buma, 2015). Determining which biotic and abiotic characteristics confer high initial resistance to disturbance remains an important frontier. Finally, numerous factors other than disturbance shape long-term changes in production. While the upward trend in aboveground wood NPP through the BBD progression suggests disturbance did not drastically redirect the successional dynamics of production, long-term increases in production over time could be attributed to climatic variables or forest compositional and structural changes not considered in our study (Curtis and Gough, 2018).

5. Conclusions

Our findings generally support our hypotheses: BBD had minimal initial effects on stand-scale aboveground wood NPP and while smaller patch-scale responses were variable and sensitive to the degree of tree mortality, trade-offs between aboveground wood NPP resistance and recovery were present among late-successional plots. In an applied context, our results add to a growing literature that suggests adaptive forest management may confer greater resistance to slow-acting, moderate severity disturbances (Kosiba et al., 2018; Seidl et al., 2014). Management activities enhancing stand-level ecological resistance to disturbance include the cultivation of an established subcanopy and the retention of growth-limiting resources (De Grandpre et al., 2011), and possibly adaptive practices that slow the disease progression and allow for compensatory growth to offset declines in real-time. At the finer patch-scale, our findings suggest that initial responses to disturbance could be used to forecast longer-term changes. However, the lack of uniformity among resistance, recovery, and resilience components of disturbance response in middle- and late-successional forest stands underscores the ongoing need to identify the factors that regulate fine spatial-scale responses to a common disturbance (Hicke et al., 2012).

6. Data and code

Data, statical analyses, and figures from this manuscript are freely available via figshare: https://doi.org/10.6084/m9.figshare.22795688.

CRediT authorship contribution statement

Ellen Stuart-Haëntjens: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Jeff W. Atkins:** Investigation, Writing – review & editing. **Alexander T. Fotis:** Investigation, Writing – review & editing. **Robert T. Fahey:** Investigation, Writing – review & editing. **Brady S. Hardiman:** Investigation, Writing – review & editing. **Brandon C. Alveshere:** Investigation, Writing – review & editing. **Christoph Vogel:** Investigation, Writing – review & editing. **Christopher M. Gough:** Funding acquisition, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Christopher M. Gough reports financial support was provided by National Science Foundation.

Data availability

Our data will be publicly available via: 10.6084/m9.figshare.22795688

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