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INNOVATIVE VIEWPOINTS

Disturbance, complexity, and succession of net ecosystem production in North America's temperate deciduous forests

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Abstract. Century-old forests in the U.S. upper Midwest and Northeast power much of North America's terrestrial carbon (C) sink, but these forests' production and C sequestration capacity are expected to soon decline as fast-growing early successional species die and are replaced by slower growing late successional species. But will this really happen? Here we marshal empirical data and ecological theory to argue that substantial declines in net ecosystem production (NEP) owing to reduced forest growth, or net primary production (NPP), are not imminent in regrown temperate deciduous forests over the next several decades. Forest age and production data for temperate deciduous forests, synthesized from published literature, suggest slight declines in NEP and increasing or stable NPP during middle successional stages. We revisit long-held hypotheses by EP Odum and others that suggest low-severity, high-frequency disturbances occurring in the region's aging forests will, against intuition, maintain NEP at higher-than-expected rates by increasing ecosystem complexity, sustaining or enhancing NPP to a level that largely offsets rising C losses as heterotrophic respiration increases. This theoretical model is also supported by biological evidence and observations from the Forest Accelerated Succession Experiment in Michigan, USA. Ecosystems that experience high-severity disturbances that simplify ecosystem complexity can exhibit substantial declines in production during middle stages of succession. However, observations from these ecosystems have exerted a disproportionate influence on assumptions regarding the trajectory and magnitude of age-related declines in forest production. We conclude that there is a wide ecological space for forests to maintain NPP and, in doing so, lessens the declines in NEP, with significant implications for the future of the North American carbon sink. Our intellectual frameworks for understanding forest C cycle dynamics and resilience need to catch up to our more complex and nuanced understanding of ecological succession.

Key words: biodiversity; carbon storage; carbon uptake; complexity; disturbance; ecosystem development; forest age; net ecosystem production; net primary production; structure-function; succession; temperate deciduous forests.

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Aging Forests, Shifting Disturbance Regimes, and Uncertainty in Future Forest Production

The temperate forests of the United States absorbed 12% of national anthropogenic CO_2 emissions during the first decade of the 21st century, storing the resulting carbon (C) in biomass, soils, and dead plant material (Pan et al. 2011*b*). Notably, temperate deciduous forests in the upper Midwest and Northeast have, in aggregate, persisted as a century-long C sink since deforestation of the 19th and 20th centuries reset ecological succession, triggering regrowth and a refilling of C pools vacated by clear-cut harvesting and fire disturbance (Birdsey et al. 2006, Williams et al. 2012). Deforestation reshaped the physical and biological structure of these regions' forests, abruptly transforming structurally complex, uneven-aged ecosystems into younger, simpler ones (Fig. 1). As this cohort of regrown forests now approaches a mid-successional transition in which shorter lived tree species mature, die, and give way to longer lived species, tree community composition is changing and forests are gradually regaining aspects of complexity lost over a century ago (Rhemtulla et al. 2009), although with notable structural and compositional differences from pre-settlement climax old-growth forests (Stearns and Likens 2002, Wolter and White 2002, Thompson et al. 2013).

In this *Innovative Viewpoint*, we present a theoretical framework and empirical synthesis linking structural complexity of deciduous forests, arising from cumulative patchy disturbance, to higher-than-expected NEP during middle succession through its positive effects on primary production. Synthesizing empirical data and revisiting ecological theory, we ask whether age-related changes in deciduous forest structure are likely to alter stand-level C fluxes into the future. We focus on two separate but related measures of stand-scale C dynamics, net primary production (NPP) and net ecosystem production (NEP), and on the next 50 yr, a period in which many regional forests disturbed roughly a century ago will, in the absence of severe disturbance, undergo substantial structural changes during advancement to middle succession; this timeframe is also a duration relevant to forest managers and carbon markets (Hurteau et al. 2013). Net ecosystem production, or ecosystem C balance, can be quantified as the difference between C fixed and invested in new biomass production (i.e., NPP) and C released back to the atmosphere from heterotrophic respiration.

Our article is not intended to provide a comprehensive assessment of how and why NEP changes over the course of ecosystem development or in response to intensifying environmental change, and does not focus on heterotrophic respiratory C losses over successional timescales as prior hypothesis-focused papers have (Harmon et al. 2011). Rather, our goal is to contribute to the evolving discussion on how forest physical structure—a key ecosystem feature changing over long periods of time—affects NPP; this could provide one explanation for observations of higher-than-expected NEP in aging forests (Urbanski et al. 2007, Luyssaert et al. 2008). Several factors, including atmospheric nitrogen deposition, rising CO_2 and longer growing seasons, likely contribute to high NEP in aging forests, and are discussed elsewhere (White et al. 1999, Magnani et al. 2007, Richardson et al. 2010, Keenan et al. 2013). We conclude by discussing how recent findings may inform land-use and management decisions aimed at maintaining stand-scale C storage in aging temperate deciduous forests, while underscoring the need for future research to determine the universality, or not, of canopy structure-production relationships as they relate to shifting ecosystem successional dynamics and disturbance regimes.

Forecasting any future terrestrial C sink requires an understanding of how changing disturbance regimes will affect stand-scale forest development and structure in coming decades. Relative to other regions, disturbances in the upper Midwest and Northeast have transitioned from high-severity events, that historically caused complete forest stand replacement, to more moderate severity disturbances, characterized by partial canopy defoliation or loss of select species at the stand or ecosystem scale (Birdsey et al. 2006, Vanderwel et al. 2013, Cohen et al. 2016).

A recent U.S.-wide survey of forest disturbance type and severity by region showed that, on average, forests of the upper Midwest and Northeast are subjected to relatively low rates of high-severity harvesting and fire disturbance,

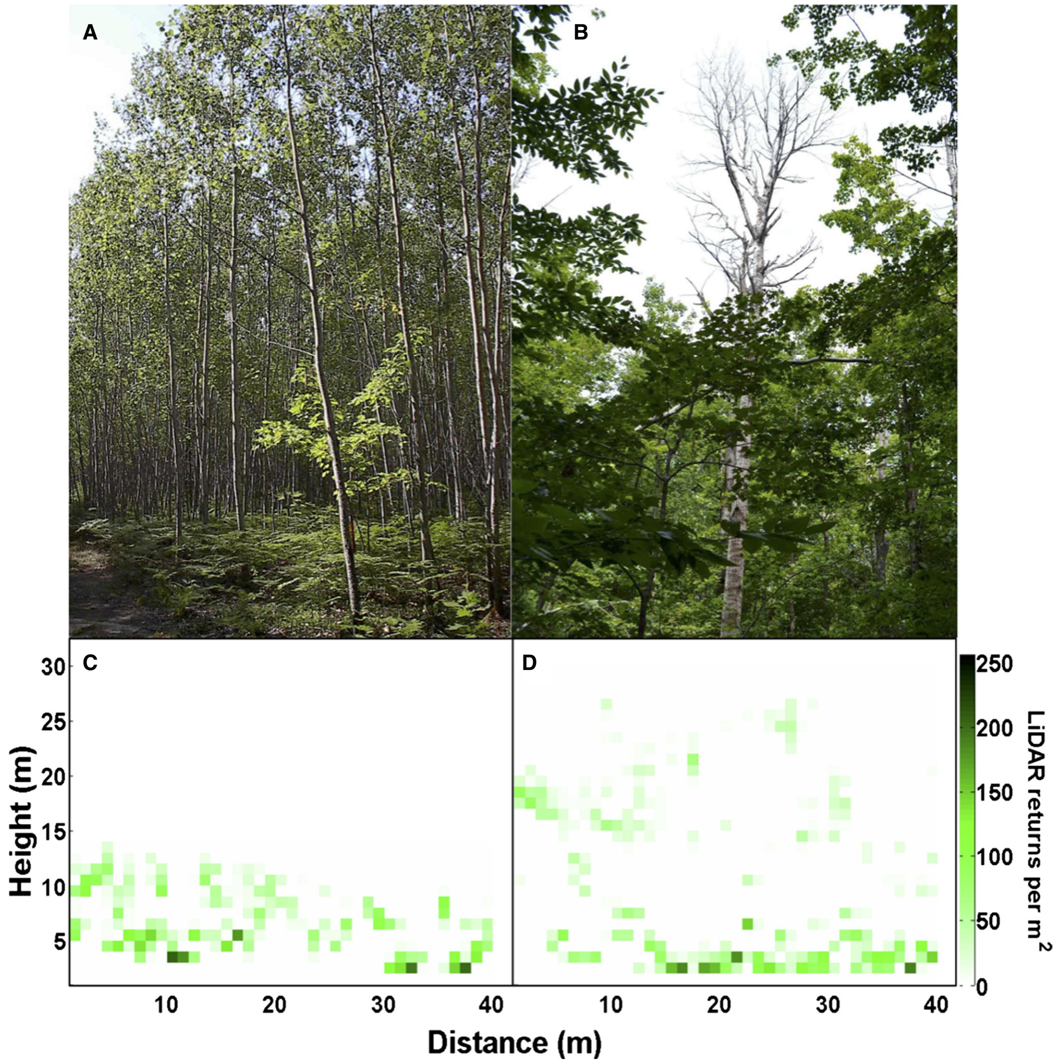

Fig. 1. Images, and vegetation density and distribution of a young (30 yr old) aspen-dominated canopy (A, C) and a more structurally complex, middle successional (100 yr old) forest following aspen decline (B, D). Vegetation density, which includes leaves and branches, is approximated from the number of LiDAR returns within a squared meter of canopy space along a 40-m transect, with dark green squares indicating dense foliage. The physical and biological structure of the young forest is characterized by more evenly distributed foliage contained within a short canopy, low canopy tree diversity, and low mortality. As short-lived aspen die, canopy gaps form producing a more multilayered, dispersed canopy comprised of longer lived species.

but are trending upward in total annual area disturbed as moderate and sometimes prolonged disturbances increase (Cohen et al. 2016). Sources of such moderate disturbances include partial harvests, extreme weather, pathogens, insects, diseases, and age-related senescence (e.g., Amiro et al. 2010, Hicke et al. 2012), which may recur periodically during forest development without resetting ecosystem succession back to stand initiation (cf. Runkle, 1985). These lower severity disturbances may be spatially and temporally diffuse, killing individuals or clusters of trees rather than all trees within a stand, and they sometimes induce mortality over years rather than hours or days (Dietze and Matthes 2014, Flower and Gonzalez-Meler 2015, Cohen et al. 2016).

Moderate severity disturbances of this nature impose structural changes considerably different from those caused by high severity, stand-replacing disturbance, and potentially enhance, rather than simplify, forest structural complexity (Seymour et al. 2002). For example, patchy (as opposed to catastrophic) tree senescence within a stand produces small canopy gaps on the order of meters rather than hundreds of meters or more wide and more evenly distributes foliage vertically within the canopy (Dyer et al. 2010, Gough et al. 2013, Hardiman et al. 2013, Fahey et al. 2015), both structural features characteristic of later successional forests (Lorimer 1980, Spies 1998). Similarly, wind damage to the upper forest canopy may be spatially localized and produce small gaps, prompting the competitive release of lower canopy vegetation (Cooper-Ellis et al. 1999, Allen et al. 2012, Forrester et al. 2014). In this way, the diffuse distribution and small spatial scale of moderate disturbance may have functionally distinct consequences from more severe disturbance, with close neighbors of senescent canopy trees poised to acquire newly liberated growth-limiting resources unavailable to distant vegetation (Carlton and Bazzaz 1998, Coates 2002, Gravel et al. 2010).

An assessment of the region's forest type cover and age distribution highlights how declines in the extent of clear-cut harvesting are leading to a broad emergence of aging and largely middle successional deciduous and mixed forests (Fig. 2). Forests of all types, including those dominated by conifers, covered 42% or 71 million hectares of the total land area in 2011 within the 20-state USDA Forest Service Eastern Region (USDA 2013), the area encompassing forests of the upper Midwest and Northeast. Over nearly a century, from 1920 through 2012, the forested area in the region increased by 18%, which was more than Southern (+11%) and Western regions (−2%, Oswalt and Smith 2014). In 2011, deciduous-dominated forests, including deciduous and mixed forests with a dominant deciduous canopy, were 84% of the total forested area and had a median age of 70 yr, an age coinciding with middle stages of ecosystem development based on the dominant canopy taxa of many forests with published NPP and NEP values (Appendix S1: Tables S1, S2). The most abundant forest types in the Eastern Region in

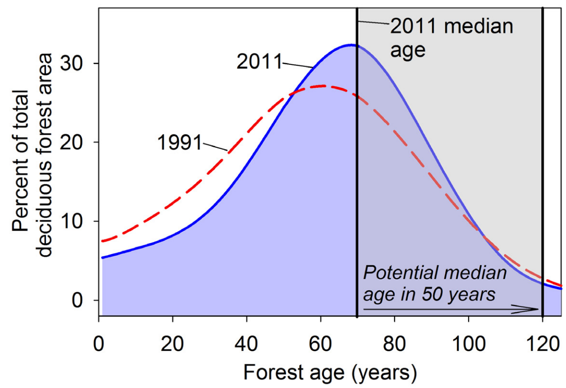

Fig. 2. The age distribution of deciduous forests in the 20-state U.S. upper Midwest and Northeast regions in 1991 (red dashed line) and 2011 (solid blue line) (USDA 2013). The gray-shaded area illustrates the potential median age of the region's deciduous forests if land-use change and stand-replacing disturbance are minimized during the next 50 yr.

2011 were overwhelmingly deciduous and, given canopy taxa, in middle stages of ecological succession: oak-hickory (*Quercus-Carya*; 25.7 million hectares), maple-beech-birch (*Acer-Fagus-Betula*; 18.4 million hectares), and aspen-birch (*Populus-Betula;* 6.8 million hectares). Middle successional oak-hickory and maple-beech-birch communities comprised nearly two-thirds of the entire forested land area in the region. Average age of all deciduous forest types in the region is increasing: the area that was > 60 yr old increased 9% from 1991 to 2011, while the area < 40 yr old declined by a similar percentage. Projections of land-use change through mid-century predict stability in the region's forested area (Radeloff et al. 2012), suggesting that many of these deciduous-dominated forests will continue to age.

A regional decline in the extent of clear-cut harvesting is thus enabling the cohort of forest stands established following broad deforestation decades ago to advance into middle succession—a transitional stage of ecosystem development in which later successional species gradually replace shorter lived trees—while accruing structural complexity arising from periodic moderate severity disturbances. These regional declines in clear-cut harvesting stand in stark contrast to present and forecasted disturbance regimes in the forested U.S. Pacific Northwest and Southeast, where intensive management for wood products favors younger, structurally simple forests with low tree diversity (Alig et al. 2003, Pan et al. 2011*a*, Cohen et al. 2016). Recognizing that an immediate repeat of deforestation throughout the upper Midwest and Northeast is unlikely raises the following question relevant to ecologists, land managers, and climate policy makers: are age-related declines in production imminent for the region's temperate deciduous forests over the next several decades?

Ecological Theory and Contemporary Observations

Understanding how NEP changes over the course of ecosystem development is a longstanding focus of forest ecologists. Underpinning decades of research (see Goulden et al. 2011) in this area is an ecological theory (Kira and Shedei 1967, Odum 1969) predicting a rapid rise in NEP during the early stages of ecological succession as primary producers re-populate an area following disturbance, followed by a gradual NEP decline before C neutrality is reached in steady-state, old-growth forests. At this stage, the C taken up and invested in new plant growth (NPP) is balanced by C losses from heterotrophic respiration (Fig. 3A). In this longheld theoretical model, NPP declines during the transitional period of middle succession because fast-growing short-lived early successional trees are replaced by slower growing later successional species; heterotrophic respiration increases as dying or dead early successional trees increase detritus-fueled microbial decomposition, which cycles C back to the atmosphere. This generalized pattern of NEP decline as forest stands transition from early to middle succession is supported by several recent syntheses, including one published by some authors of this review (Pregitzer and Euskirchen 2004, Gough et al. 2008, Luyssaert et al. 2008, Goulden et al. 2011, Coursolle et al. 2012).

Why revisit a long-held theory supported by observation? First, because the underlying theory was based on "dense pure stands" (Kira and Shedei 1967) and laboratory microcosms (Odum 1969), far simpler and different ecosystems than the multispecies, structurally complex deciduous forests emerging in the U.S. upper Midwest and Northeast. Odum (1969) himself cautioned against extrapolating too readily from these simpler systems, while noting that spatially and temporally diffuse minor forest disturbances could "set back" the successional clock, at least to some degree, by increasing the resource availability. Second, earlier syntheses reporting declines in NEP during middle succession of >50% from peak values were driven by observations of older, mostly arid, coniferous evergreen forests (Pregitzer and Euskirchen 2004, Luyssaert et al. 2008, Coursolle et al. 2012), which may not mirror trajectories of NEP in temperate deciduous forests. These syntheses aggregated deciduous and coniferous evergreen forests because few NEP observations were available at the time for deciduous forests older than 100 yr (Pregitzer and Euskirchen 2004, Gough et al. 2008, Luyssaert et al. 2008). Consequently, substantial declines in NEP during middle succession were generally assumed to be universal among temperate and boreal forests. This assumption has been included in policy documents intended to inform ecosystem carbon management and land-use policy (e.g., see Birdsey et al. 2007, *State of the Carbon Cycle Report*), and features prominently in standard ecology textbooks (Chapin et al. 2002).

More data from 100+ year-old deciduous forests are now available. To evaluate whether observations support a generalized NEP decline in temperate deciduous forests comparable in magnitude to that reported in aggregated deciduous-coniferous evergreen syntheses, we conducted a new age-NEP synthesis solely of deciduous forests, incorporating recently published data for middle and late successional deciduous forests in North America, Asia, and Europe. We focus on a 50-yr age window (approximately the middle stages of succession) that many U.S. deciduous forests, in the absence of stand-replacing disturbance, will occupy in coming decades. Our site-level "space-for-time" substitution, or chronosequence, approach follows that of several prior age-NEP syntheses (Pregitzer and Euskirchen 2004, Gough et al. 2008, Luyssaert et al. 2008, Goulden et al. 2011, Coursolle et al. 2012), but is more conservative in that it focuses on a single forest biome: the temperate deciduous forest. Nonetheless, the results should be interpreted with caution, given the large variation among sites in climate, productivity, and plant community composition (Appendix S1: Table S1).

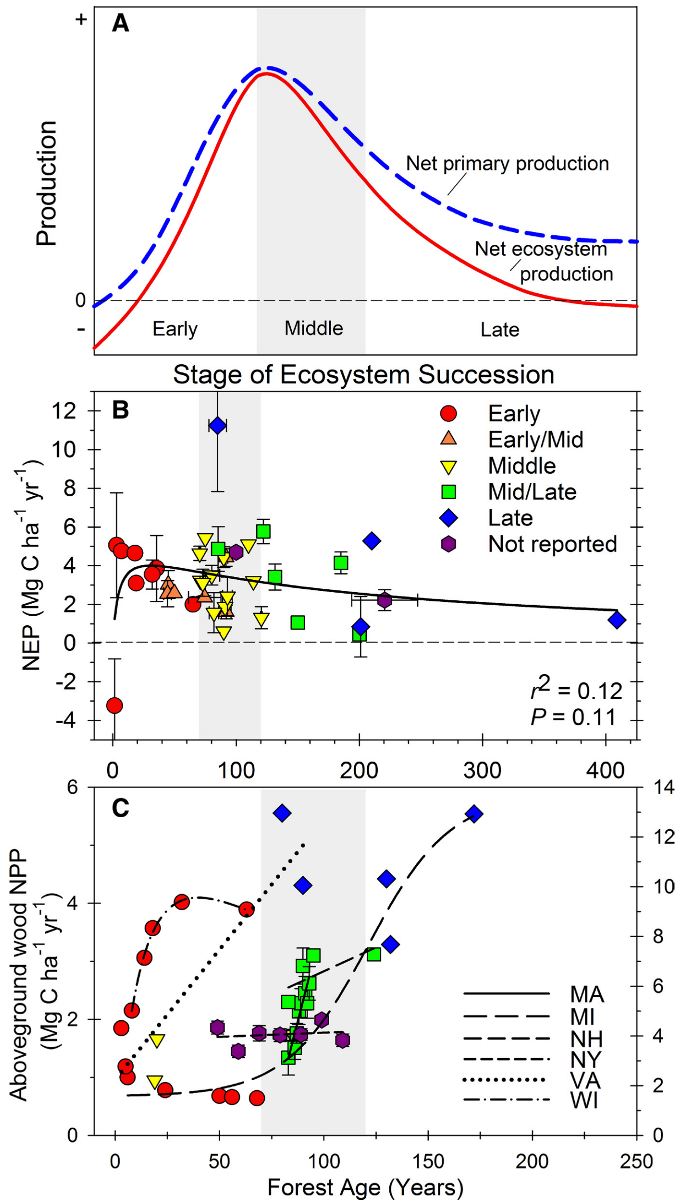

Fig. 3. Predictions of net ecosystem production (NEP) and aboveground wood net primary production (NPP) over the course of ecological succession (after Odum 1969). NEP, the annual rate of C uptake and storage in biomass, soils and, dead plant material, is equal to total NPP, the rate of new plant biomass accumulation, minus C losses from heterotrophic respiration, primarily via microbial decomposition of detritus (A). Observed NEP in relation to age, defined as time since stand initiation, and successional stage (see legend and Appendix S1) for 39 deciduous-dominated (deciduous-only and mixed deciduous-conifer) forest sites from three continents. Mean annual NEP and age (± 1 SD) for each site is shown (B). Aboveground wood (+ leaf for VA only) NPP in relation to age and successional stage plotted separately for six U.S. deciduous-dominated forest sites reporting long-term (> 10 yr) time series or chronosequence data (C). The location of each site is indicated using U.S. state abbreviations, with trendlines shown separately for each site. The right y-axis applies to the VA site (dotted line) only. The legend in panel b indicating successional stage applies to panels b and c. See Appendix S1 for age-NEP synthesis methods and the sources of NEP and NPP data.

Data from 39 deciduous-dominated forest stands on three continents suggest a considerably smaller postpeak reduction in NEP relative to syntheses aggregating deciduous and coniferous evergreen forest types, and biomes. Inclusion of a 400-yr-old deciduous forest increased the significance of the age-NEP relationship (Fig. 3B; $r^2 = 0.12$, $P = 0.11$ as shown), but trends were the same (statistically indistinguishable) when this very old forest site was removed from the analysis ($r^2 = 0.10$, $P = 0.16$ when oldest site removed). Eighteen forest sites, broadly distributed across the three continents, were within the projected median age range of future North American deciduous-dominated forests, with all but two sites in middle successional stages of ecosystem development, based on published tree canopy composition data or self-reported stage of ecosystem development (Appendix S1: Table S1).

These empirical data support Odum's hypothesized trend of rapidly increasing NEP in young forests but, when compared with other syntheses combining deciduous and coniferous evergreen forests (e.g., Luyssaert et al. 2008), suggest differences among these forest types in age-NEP trajectories after NEP peaks. Our deciduous-only age-NEP relationship shows a 16% decline in NEP following its peak at 30 yr through the century mark, a more gradual decline than that reported in syntheses combining forest types or biomes (Pregitzer and Euskirchen 2004, Luyssaert et al. 2008, Coursolle et al. 2012). For example, an aggregated synthesis of Canadian forests showed NEP declining to zero at ~100 yr (Coursolle et al. 2012); other syntheses grouping temperate deciduous and coniferous evergreen forests (Pregitzer and Euskirchen 2004) or multiple forest biomes (Luyssaert et al. 2008) suggest NEP reductions of 50% or more by an age of 100 yr. By comparison, in our synthesis of temperate deciduous forests only, NEP did not decline to half its peak value until 315 yr—far beyond any current management or carbon-sequestration planning horizon.

A notable limitation of the data set is that only one North American forest with published NEP values is older than a century (at 122 yr), a consequence of the history of mass deforestation in the region a century ago and the concentration of carbon flux towers in these regrown forests; therefore, our inference of NEP in forests greater than 100 yr old draws mostly from European and Asian forests. Relatively high NEP in older deciduous forests, however, is consistent with decadal NEP time series from several individual North American sites that show stable, or in some cases rising, NEP in temperate deciduous forests approaching the century mark (Urbanski et al. 2007, Dragoni et al. 2011, Gough et al. 2013, Keenan et al. 2013).

One explanation for higher-than-expected NEP in century-old deciduous forests may be sustained or increasing NPP, particularly of long-lived biomass such as wood, during and beyond middle successional stages of ecosystem development; another is that heterotrophic respiration may increase less than expected in older forests (cf. Amiro et al. 2010). Focusing on wood primary production, we found that age-aboveground wood NPP observations from multiple U.S. deciduous forests do not indicate a strong decline in the rate of C sequestration in wood within the age range projected for many regional forests over the next half-century, assuming severe disturbance is avoided (Fig. 3C, Appendix S1: Table S2). With the exception of one site for which data were not available, our analysis focused on *wood* primary production since this pool is measured with high confidence and its slow turnover, relative to more ephemeral pools like leaves, is closely coupled with NEP (Clark et al. 2001, Giardina and Ryan 2002, Gough et al. 2013); trends for total aboveground NPP, which include leaf production, and wood-only NPP were comparable (data not shown). We included single-site deciduous forest chronosequences and sites with published long-term continuous (> 10 yr) records of aboveground wood NPP to minimize spatial changes in soils and climate that may co-vary with stand age. Among the forests evaluated, four showed significant increases and one exhibited no significant change in aboveground wood NPP within the age range expected for many of the region's deciduous forests.

Other recent assessments of age-NPP relationships used nation-wide forest inventories for the United States and China to compare forest biomes (Pan et al. 2011*a*, Wang et al. 2011, He et al. 2012), and global databases combining deciduous and coniferous evergreen forests to examine patterns of total NPP into old-growth

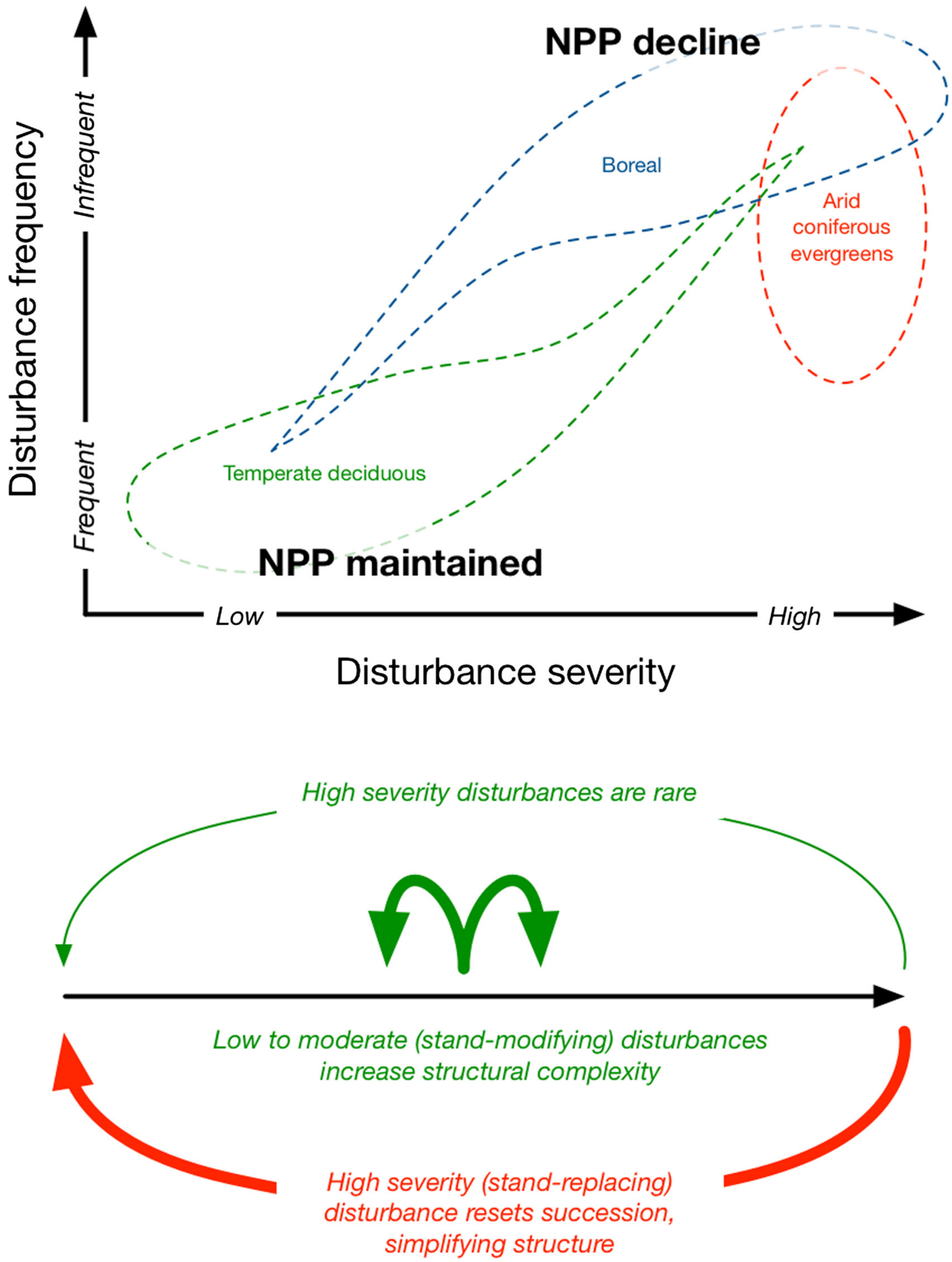

Fig. 4. Hypothesized relationships between disturbance frequency and severity, and trajectories of net primary production, a primary determinant of net ecosystem production, during middle succession, and the space occupied by different forest biomes (top panel). Temperate deciduous forests are increasingly positioned along the disturbance frequency-severity continuum in a space dominated by repeated low to moderate severity disturbances that enhance forest structure (bottom panel, green); boreal and arid coniferous evergreen forests are more likely to experience stand-replacing disturbances that reset ecosystem succession and simplify forest structure (bottom panel, red). Disturbance-related modifications to forest structure, and associated changes in canopy physiology and resource distribution, may account, in part, for different age-production trajectories among forest biomes.

stages of development (Michaletz et al. 2014, Tang et al. 2014). The national studies demonstrate, through aggregated analyses of many stands, that total NPP of temperate deciduous forests is sustained or declines only slightly during middle succession, a trajectory that notably contrasts with more pronounced age-related reductions in coniferous evergreen forests. In the United States, the total NPP of deciduous and mixed deciduous-coniferous forest stands slowly falls 10–15% from peak levels as age approaches 100 yr, while coniferous evergreen forest biomass production declines by 50% (He et al. 2012). Similarly, a global analysis of total NPP and age combining forest types suggests minimal change in primary production during middle succession, with significant declines occurring only in very old forests (Tang et al. 2014). If these age-NPP relationships are broadly indicative of how primary production trajectories differ among forest biomes, then NEP during middle succession may decline only gradually in many temperate deciduous forests, even as C losses from heterotrophic respiration increase with age.

Ecological Intersections of Disturbance, Succession, and NEP in Deciduous Forests

In summary, the ecological theory that gave rise to assumptions about age-related forest NEP declines was derived from simple, single-species ecosystems; Odum (1969) suggested that some types of disturbances could rewind succession to some degree, and recent empirical evidence suggests that disturbance severity, frequency, and source broadly vary among forest types and biomes, with implications for successional trajectories of NEP (Amiro et al. 2010). Neither theory nor observation gives us particular reason, then, to expect that deciduous (characterized by low to moderate severity, high-frequency disturbances) and arid coniferous evergreen or boreal (high-severity, low frequency disturbances) forests will exhibit the same age-NEP trajectories. Rather, deciduous forests tend to inhabit a different part of the disturbance severity vs. frequency space (Fig. 4), allowing them to maintain relatively high levels of NPP and, consequently, NEP as forest age advances.

What biological mechanisms, consistent with our ecological knowledge and empirical observations, could maintain NPP and, by extension, support higher-than-expected NEP in deciduous forests advancing from early to middle succession? We suggest that one strong candidate for such an NPP-sustaining mechanism is canopy complexity, in particular increasing stand structural (i.e., physical) and biological complexity as minor disturbances accumulate with age. More complex leaf arrangements arise from small, spatially and temporally diffuse disturbances that occur repeatedly within a forest stand during development. These low to moderate severity disturbances cumulatively increase structural complexity as canopy gaps form and a more multilayered canopy emerges. Complexity increases rapidly during middle succession as shorter lived tree species gradually die and is also a function of disturbance regime. Canopy complexity theoretically plateaus when canopy gap formation is balanced by ingrowth during late stages of forest development (Parker and Russ 2004).

Our recent findings from a deciduous forest stand in Michigan indicate that increasing NPP during middle succession is associated with the accrual over time of canopy structural complexity (Hardiman et al. 2013), a mechanism consistent with several studies citing high levels of both complexity and production in older forests (Knohl et al. 2003, Schulze et al. 2009, Kane et al. 2010, Seidl et al. 2012, Bolton et al. 2013). This contrasts with the early stages of ecosystem development, during which rising leaf area index (LAI) is strongly correlated with NPP (He et al. 2012, Reich 2012). In young forests, leaf *quantity* is therefore broadly recognized as a primary driver of ecosystem production. But, at our site, after maximum stand leaf area was achieved, continued increases in NPP were instead correlated with rising heterogeneity in the distribution of canopy leaves (Hardiman et al. 2013), a finding that suggests leaf *arrangement* emerged as increasingly important to rising NPP.

Changes in canopy complexity may unleash a cascade of effects that influence forest NPP and NEP. Perhaps most importantly, mid-successional complexity gains may improve both *the amount of resources* acquired and *how efficiently* resources such as light and nitrogen are harnessed to drive

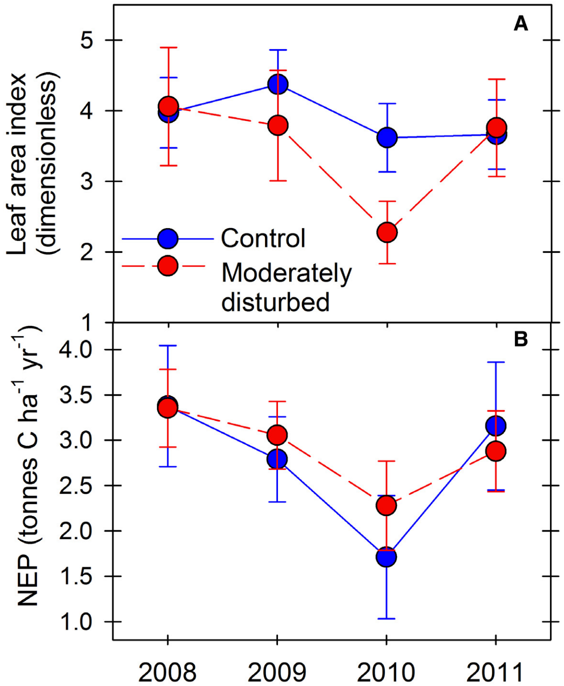

Fig. 5. Changes over time in leaf area index (LAI, A) and net ecosystem production (NEP, B) in century-old unmanipulated control and nearby experimentally disturbed deciduous forests. In the disturbed forest, one-third of canopy dominant trees, all maturing early successional *Populus and Betula*, senesced within 3 yr and were left standing following stem girdling, producing a canopy structure similar to that which is expected to emerge more broadly in the U.S. upper Midwest. Low NEP occurred in 2010 in both control and moderately disturbed forests, indicating that climate rather than disturbance caused low C uptake in both forests; however, NEP of the moderately disturbed forest was comparable to that of the control forest despite having lower LAI in 2010, with the disturbed forest exhibiting higher canopy light-use efficiency 3 out of 4 yr following disturbance while trending upward in canopy structural heterogeneity as diffuse and patchy mortality occurred across the disturbed landscape over time (Gough et al. 2013). Error bars are ±95% confidence intervals (data from Gough et al. 2013).

growth (i.e., resource-use efficiency). The hypothesis that complexity enhances ecosystem production was experimentally tested over a decade ago in constructed grasslands, which stored more C in biomass when a collection of structurally and physiologically diverse plant species co-existed within the same constructed ecosystem (Tilman et al. 1997), although this is not universal (Adler et al. 2011). Several forest modeling experiments similarly suggest linkages between canopy complexity and production, with plant functional diversity positively correlated with forest growth (Falster et al. 2011, Coomes et al. 2014, Duveneck et al. 2014, Shanin et al. 2014, Pedro et al. 2015). In addition, observational experiments suggest forest complexity is coupled with NPP and other ecosystem functions (Stoy et al. 2008, Bradford 2011, Gamfeldt et al. 2013, Gillman et al. 2015).

A simple example offers insight into the potential relationship between ecosystem structure and production: two plant species with different structural features, one with a shallow and the other with a deep root system, will extract more growth-limiting soil nutrients together than individually. Similarly, a structurally diverse, multilayered forest canopy containing functionally different tree species or individuals of the same species, some with leaves optimized for C fixation in high light and others in lower light, may capture light more completely and also use this resource more efficiently to drive primary production under a range of light conditions (Stoy et al. 2008, Niinemets 2010, Hardiman et al. 2013). In this way, middle successional temperate deciduous forest canopies—with a broadening array of tree heights, a variety of crown architectures, and a mix of sun and shade optimized plant species and foliage—may have higher rates of canopy C fixation and consequently NPP than younger, structurally simple forests containing plant species that perform optimally under high light.

Improved resource-use efficiency may compensate for episodic declines in leaf area and increases in heterotrophic respiratory C losses from senescing and dead short-lived trees, providing the biological link that moves back the successional clock in a manner akin to that predicted by Odum (1969). For example, we found at our site that experimentally induced mortality of mature early successional trees (Fig. 1B image) did not reduce NEP (Fig. 5) or aboveground wood NPP, although leaf area temporarily declined by nearly half of its maximum (Gough et al. 2013, Stuart-Haentjens et al. 2015). Instead, NEP was stable because undisturbed vegetation, helped by improved access to light and nutrients, rapidly increased its C fixation and consequently NPP, and offset growth declines by dying trees, despite a brief decline in leaf quantity (during 2010). In a nearby unmanipulated century-old forest, we similarly found that NPP was stable as early successional trees naturally senesced because a biologically diverse tree canopy was in place to compensate for the declining growth of senescent individuals (Gough et al. 2010). Moreover, we observed a positive correlation among forest age, structural complexity, aboveground NPP, and resource-use efficiency across a 200-yr chronosequence, implying a causal, mechanistic linkage between rising structural complexity with age and sustained high NPP into late stages of succession (Hardiman et al. 2013).

Findings from these studies should be cautiously extrapolated since they derive from a single site, but they point to a common mechanism underlying higher-than-expected NEP in this deciduous temperate forest, in which the accumulation of structural complexity from repeated low-severity disturbance increased stand-level resource-use efficiency and, therefore, NPP, after LAI reached a maximum value or temporarily declined. Whether such a mechanism extends broadly to other deciduous forests as they age is the subject of ongoing work by these authors and others (Stark et al. 2012, Fahey et al. 2015).

Conclusions: Application and Future Directions

We have argued that although large declines across forest biomes in forest production during middle stages of ecosystem succession are frequently assumed to be universal, this is not supported by ecological theory, extant empirical data, or our biological understanding of temperate deciduous forests. This conclusion, informed by the data available from North American forests, suggests that forest C management and ecosystem models may thus substantially underestimate the region's future terrestrial C sink strength as deciduous forests advance in age. We suggest that, given mounting evidence highlighting the different disturbance regimes and biogeochemical responses exhibited among forests, ecologists, managers, and modelers should not assume a common age-NEP trajectory across forest biomes. In contrast to boreal and arid coniferous evergreen forests that have driven our generalized understanding of age-NEP relationships, in deciduous forests frequent and more minor disturbances accumulate, providing physical and ecological space for a more structurally complex canopy that uses resources more efficiently than expected.

Rather than being revolutionary, this hypothesis, and its distinction among forest biomes, draws from ideas within the foundational ecological theories. It does, however, argue against some prior studies implying that a landscape mosaic dominated by young, ostensibly more productive forest stands was critical to maintaining the land C sink over the next several decades (e.g., Birdsey et al. 2006). More generally, it suggests that our intellectual frameworks for understanding forest carbon-cycle trajectories and resilience need to catch up to our more complex and nuanced empirical understanding of ecological succession and its interaction with disturbance. The consequences are significant, as the trajectory of NEP in U.S. temperate deciduous forests progressing through middle succession will strongly influence the region's ability to offset future CO_2 emissions (Hurteau et al. 2013). Finally, we suggest that conservation of century-old deciduous forests in middle stages of succession may minimally reduce C uptake, while providing other ecological goods and services supplied by structurally complex forests, including pollination, seed dispersal, maintenance of biodiversity, and water and nutrient retention (Thompson et al. 2011).

We caution that many uncertainties in future land-use and climate, and in the rates of old-growth deciduous forest production, limit long-term projections of terrestrial C uptake. The region's terrestrial C sink could decline if clear-cut harvesting increases to meet demands for biofuels (Peckham et al. 2013), for example, or if extreme weather and fires increase stand-replacing disturbance (Gustafson and Sturtevant 2013). In addition, multiple forms of global change, including rising atmospheric CO_2 and the deposition of reactive nitrogen, may interact to modify future trajectories of forest NEP over stand development (Magnani et al. 2007, Luyssaert et al. 2008, Luo and Weng 2011, Keenan et al. 2013). We also stress that our *Viewpoint* is based on middle successional deciduous forests that have not yet reached old-growth stages of development; a deficiency of data for old-growth temperate deciduous forests limits understanding of NEP in very old forests. Similarly, some older coniferous evergreen ecosystems are underrepresented in age-NEP syntheses, including coniferous forests with high precipitation and low disturbance severity; such forests can be extremely complex and productive (Saunders et al. 2012, 2014, Raymond and McKenzie 2013).

Finally, we recognize that sustained rates of NPP from early to middle succession are not universal among deciduous forests. The explanation for significant age-related NPP declines in some forests has been the subject of many reviews (e.g., Gower et al. 1996, Ryan et al. 2006, DeLucia et al. 2007), which together suggest multiple mechanisms regulate NPP and NEP over stand development. To what degree these mechanistic linkages between disturbance, complexity, and production apply across ecosystems is a critical question as we move forward with future field experiments and sophisticated cross-site syntheses and meta-analyses. Ongoing and emerging multidecadal ecosystem observatory networks, such as FLUXNET and the National Ecological Observatory Network (NEON) will be essential to advancing understanding of long-term C cycling processes for a variety of ecosystems against the backdrop of global change, and to provide forest managers and policy makers with robust predictions about the future dynamics of forests.

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Supporting Information

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