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# Forest aging, disturbance and the carbon cycle

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## Summary

Large areas of forestland in temperate North America, as well as in other parts of the world, are growing older and will soon transition into middle and then late successional stages exceeding 100 yr in age. These ecosystems have been important regional carbon sinks as they recovered from prior anthropogenic and natural disturbance, but their future sink strength, or annual rate of carbon storage, is in question. Ecosystem development theory predicts a steady decline in annual carbon storage as forests age, but newly available, direct measurements of forest net $CO_2$ exchange challenge that prediction. In temperate deciduous forests, where moderate severity disturbance regimes now often prevail, there is little evidence for any marked decline in carbon storage rate during mid-succession. Rather, an increase in physical and biological complexity under these disturbance regimes may drive increases in resource-use efficiency and resource availability that help to maintain significant carbon storage in these forests well past the century mark. Conservation of aging deciduous forests may therefore sustain the terrestrial carbon sink, whilst providing other goods and services afforded by these biologically and structurally complex ecosystems.

## I. Introduction

In the late 19th century, rapidly expanding logging operations and slash-fueled wildfires resulted in the near-complete destruction of the original forests of the Great Lakes States in North America. In the ecological blink of an eye, 36 million hectares of old-growth forest were converted to tree seedlings or non-forest cover. Over the past century, trees have regrown across half of their former range in the upper Midwest, and these forests now contain on the order of 2000 Tg carbon in plant biomass (USDA, 2008). The forests of New England, having undergone a similar if less cataclysmic transformation, hold another 1500 Tg of nonsoil carbon. The development of this regional carbon pool, a consequence of logging, fire and agricultural abandonment, has been an important component of the contemporary North American carbon sink (Amiro *et al.*, 2010; McKinley *et al.*, 2011; Pan *et al.*, 2011; Hicke *et al.*, 2012).

Although logging continues in the American upper Midwest and Northeast, harvest rates are well below replacement levels, meaning that these northern deciduous forests are steadily growing older. Barring a major increase in forest cutting, average stand age will exceed 100 yr in many areas in a few decades. Will these aging forests continue to contribute to the region's terrestrial carbon sink or will they functionally retire, relegating that ecosystem service to the shrinking area of young forests, long assumed to be superior carbon sinks relative to their older counterparts? New instrumentation and the coordinated, interdisciplinary efforts of biogeoscientists around the world, together with the open data they supply, now allow a critical appraisal of this important question.

## II. Forest aging and carbon storage

The annual rate of forest carbon storage (hereafter 'annual carbon storage') is dominated by two large and opposing fluxes: carbon uptake, or gross primary production (GPP), driven by photosynthesis, and carbon loss or ecosystem respiration ($R_e$), the sum of plant and microbial respiration. When GPP exceeds $R_e$, carbon accumulates in biomass and soils (positive net ecosystem production, or NEP), whereas the reverse occurs when $R_e$ exceeds GPP (negative NEP). Both fluxes are sensitive to environmental factors, such as temperature, soil moisture, and atmospheric or soil chemistry, as well as to organismal factors, such as tree height, tissue nutrient content, and plant and microbial species identity, all of which can be modified to varying degrees by disturbance and slowly change along a forest age or successional continuum (Ryan *et al.*, 1997; Law *et al.*, 2002; Irvine *et al.*, 2004).

In the absence of major disturbance, ecosystem theory dating to the seminal work of E. P. Odum (Odum, 1969) predicts increasing annual forest carbon storage, or NEP, early in ecological succession, followed by a plateau during mid-succession when rising tree mortality causes $R_e$ to increase relative to GPP, and then a sharp drop as the two fluxes come into rough balance during late succession when annual carbon storage approaches zero (Fig. 1). The prediction of rapidly declining forest annual carbon storage beginning in mid-succession has been included in carbon management policy documents and features prominently in standard ecology textbooks.

The high-intensity, 'stand replacing' disturbances that regularly occurred during the logging era in the upper Midwest resulted in an initial large loss of carbon through biomass combustion and elevated $R_e$, after which these ecosystems became strong carbon sinks as GPP of the young, re-growing forests greatly exceeded $R_e$ (Gough *et al.*, 2007). In drought-prone ecosystems, such as many Western US coniferous forests, this remains a typical natural disturbance and recovery cycle (Kashian *et al.*, 2006). In the wetter eastern deciduous forests, large stand-replacing disturbances are now rare, surpassed in importance by more frequent, moderate-intensity disturbances caused by insects or pathogens, localized environmental stress and age-related mortality of individual trees (Cohen *et al.*, 2016).

Do temperate deciduous and coniferous forests, with different prevailing disturbance regimes, share similar age-annual carbon storage relationships? As recently as a decade ago, few NEP observations were available for temperate deciduous forests older than 100 yr. Consequently, the generalized pattern of NEP decline as forest stands transition from early to middle and then late succession, supported by a considerable body of work (Pregitzer & Euskirchen, 2004), was disproportionately influenced by more numerous observations from older coniferous forests and assumed to be shared by temperate deciduous forests. More data from 100+-yr-old deciduous forests are now available, many of them obtained from the growing global network of carbon 'flux towers' using modern, eddy covariance methods to derive NEP (Box 1; Fig. 2). This expanding network and its open data policy are offering unprecedented opportunities to investigate carbon cycling processes at large spatial scales and across biomes, including the evaluation of NEP dynamics in older deciduous forests.

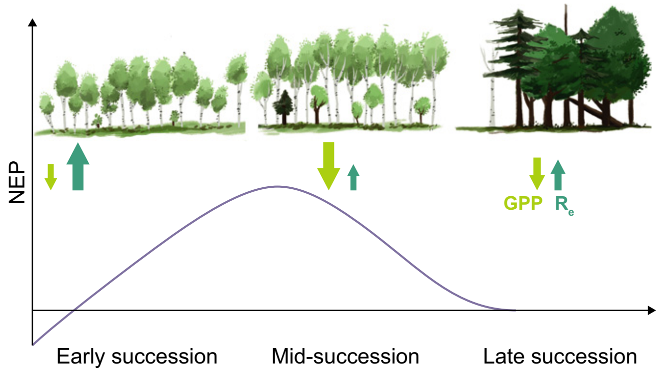


**Fig. 1** Odum's hypothesis of ecosystem development posits an initial rapid increase in net ecosystem production (NEP) during early succession, as carbon gains from gross primary production (GPP) increasingly outweigh carbon losses from ecosystem respiration ($R_e$). During mid-succession, as competition intensifies and short-lived plants senesce, Odum predicted a gradual decline in NEP that would extend into late succession, when GPP and $R_e$, equal in magnitude and operating in steady state, offset one another and NEP is reduced to zero.

**Box 1** The eddy covariance method for the calculation of net ecosystem $CO_2$ exchange

The term 'eddy covariance' is shorthand for the statistical method used to compute fluxes of $CO_2$, water vapor, energy and other atmospheric components within a turbulent boundary layer, as often exists over forest canopies. As air passes over the canopy, it can be conceptualized as consisting of many rotating eddies of different sizes, each with a vertical component (Fig. 2; after Burba & Anderson, 2007). For ideal terrain, the $CO_2$ flux ($F_c$) is calculated as the mean covariance between deviations in instantaneous vertical wind speed ($w'$) and density of $CO_2$ in the air ($\rho'_c$):

$$F_c = \overline{w'\rho'_c}$$

There is an array of site and instrumentation requirements necessary for this method to yield robust estimates of forest $CO_2$ exchange. Important among them are that the terrain is relatively horizontal and of uniform vegetation height, there is sufficient turbulent flow from wind, measurements are made within the boundary layer of interest and the instruments being used can detect very small changes at very high frequency. Data processing can be complex and, in many instances, results in significant gaps in the data record, for example during night-time periods of low turbulence or in winter due to bad weather or power outages. The calculation of forest annual carbon storage requires the summation of continuous flux estimates, and a number of strategies for filling the inevitable data gaps have been proposed (Aubinet *et al.*, 2012). Strict attention to all facets of instrument deployment, maintenance and data processing is necessary to obtain valid $CO_2$ exchange estimates.

The eddy covariance method is the only approach available for the direct measurement of forest net ecosystem $CO_2$ exchange with the atmosphere, and is now conducted on all continents spanning much of the world's climate space and representative biomes. Progress is steadily being made in the application of eddy covariance methods in non-ideal terrains in which underlying assumptions may not be met and from non-tower-based platforms, such as manned or unmanned aircraft. Eddy covariance sites are often coordinated in regional networks, such as AmeriFlux (http://ameriflux.lbl.gov/), and globally within FLUXNET (http://fluxnet.fluxdata.org/), which includes > 800 active and historic sites, many of which provide open carbon flux data to the public.

## III. Successional trends of NEP in northern deciduous forests

To evaluate whether empirical evidence points to declining NEP in temperate deciduous forests during mid-succession, we examined published data from 39 temperate deciduous forests on three continents (Gough *et al.*, 2016). All stands older than 2 yr were net carbon sinks, including 12 forests > 100 yr old, and we found little evidence of declining carbon storage during mid-succession (100–200 yr) and more gradual declines than expected in late succession (> 200 yr, Fig. 3). On average, NEP was lower in very old forests, but the decline from peak annual carbon storage was gradual, falling to half the maximum value at 315 yr, well within late succession. This slow and modest reduction in NEP as deciduous forests advance in age is considerably less than that of coniferous forests (Pregitzer & Euskirchen, 2004; Luyssaert *et al.*, 2008; Coursolle *et al.*, 2012). However, one consequence of North America's relatively recent logging history is that our analysis included only one NEP observation from forests on this continent older than a century, and our inference of NEP trends in older forests is thus drawn largely from observations at European and Asian sites.

An immensely important resource provided by FLUXNET, and other *in situ* monitoring networks, is a growing abundance of open-access eddy covariance-based NEP estimates derived using

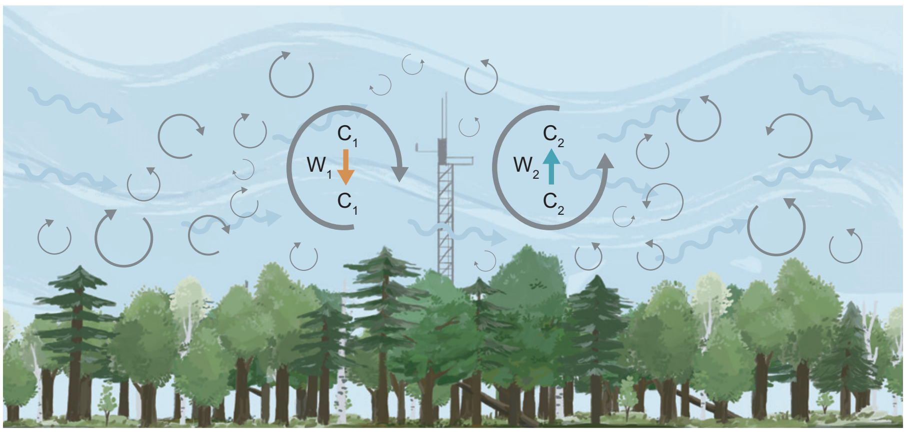


**Fig. 2** Measurement of $CO_2$ fluxes within the boundary layer above a forest canopy. At a single measurement point, an eddy at time 1 moves a parcel of air ($c_1$) downwards with velocity ($w_1$), whilst the next eddy at time 2 moves a parcel of air ($c_2$) upwards with velocity ($w_2$). The flux of $CO_2$ into or out of the canopy can be understood as a covariance of the air parcel's vertical velocity and $CO_2$ concentration.

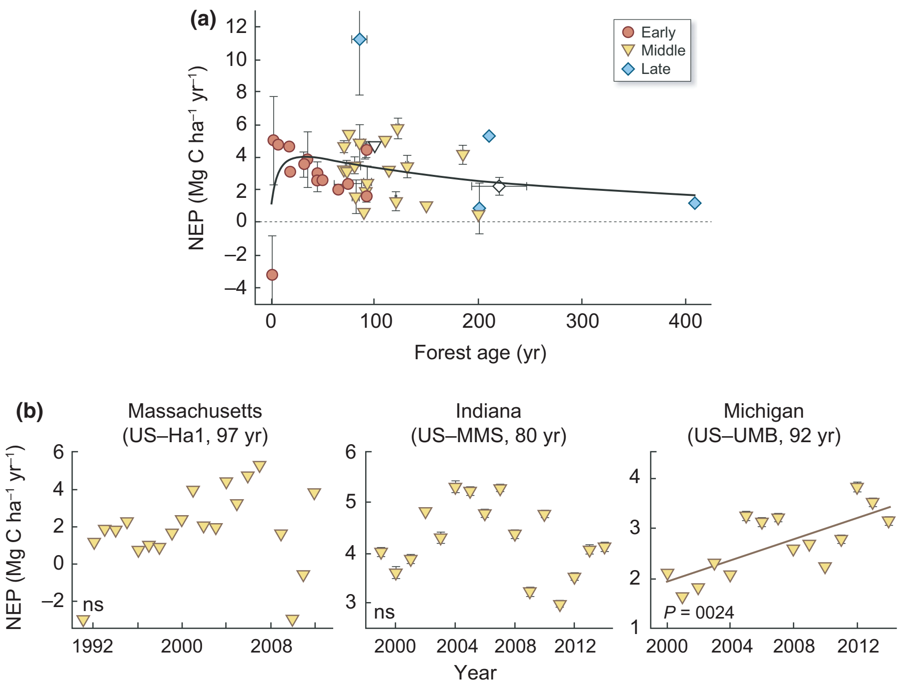


**Fig. 3** A survey of published net ecosystem production (NEP) data for temperate deciduous forests on three continents and spanning multiple stages of ecosystem development (a) yielded no evidence for a steep decline in NEP during mid-succession (after Gough *et al.*, 2016; mean annual NEP and age ± 1 SD for each site is shown, successional stage self-reported by individual study authors). Similarly, long-term eddy covariance data from three mid-successional North American temperate forests revealed either no change or increasing NEP (b, with location, FLUXNET Site ID and stand age in 2010).

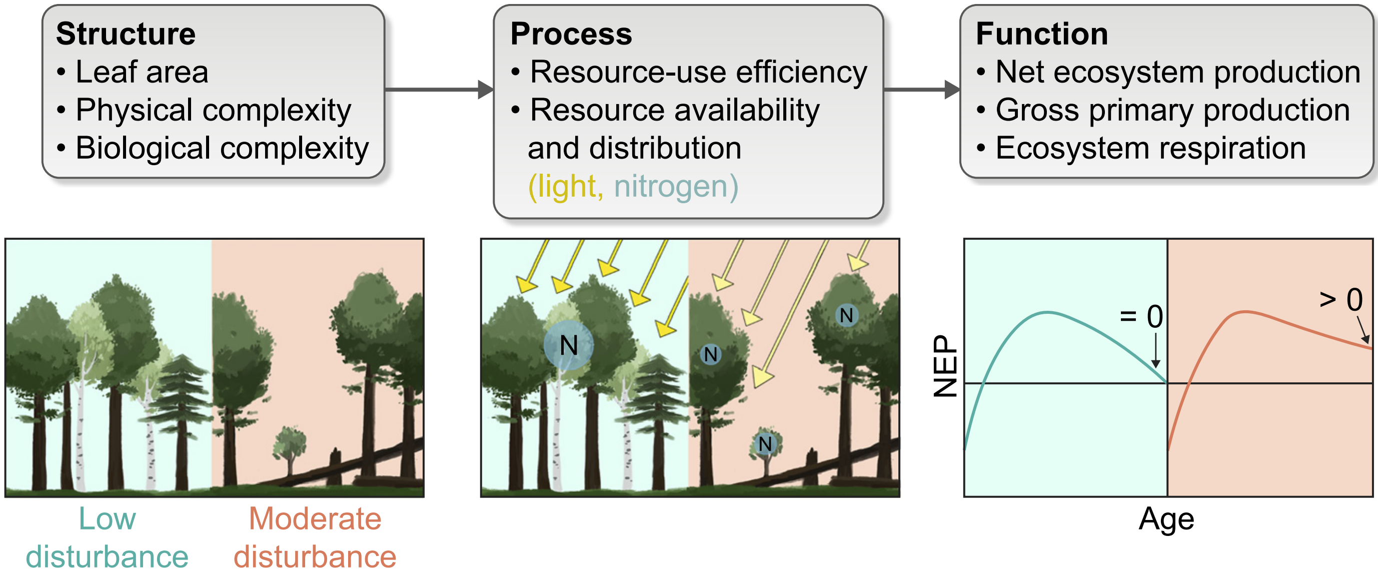


**Fig. 4** Moderate-severity disturbance may sustain net ecosystem production (NEP) at higher than expected rates in aging forests by the introduction of physical and biological complexity as the leaf area recovers, which, in turn, may result in the redistribution of growth-limiting resources and enhance resource-use efficiency. Canopies made more complex and physiologically efficient through periodic moderate disturbance may sustain NEP later into ecosystem development.

systematic, peer-reviewed data processing protocols (FLUXNET, 2015) containing NEP values for hundreds of sites (Mahecha *et al.*, 2017; Marcolla *et al.*, 2017). Through FLUXNET's published data, multi-decadal records are now available for three temperate North American deciduous forests approaching or exceeding the century mark (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/). Consistent with our cross-continent analysis, we found no evidence for declining NEP in these aging forests as they near the century mark. Instead, decadal carbon storage of a Michigan forest was trending upward and, in Massachusetts and Indiana, annual carbon storage exhibited no long-term trend (Fig. 3).

These observations yield two insights that challenge long-held ecological theory and depart from conclusions drawn from syntheses leaning heavily on coniferous forests. First, our multi-continent assessment of NEP, like other studies (Luyssaert *et al.*, 2008), does not support Odum's theoretical assumption of carbon neutrality in old-growth forests. Second, our findings, when contrasted with those of other syntheses, suggest that the timing and magnitude of NEP decline vary among forest ecosystems, and we suggest that the prevailing disturbance regime may be one key distinguishing variable (Gough *et al.*, 2008; Amiro *et al.*, 2010; Pan *et al.*, 2011).

## IV. Mechanisms sustaining NEP in aging deciduous forests

The clarification of the mechanisms by which disturbance could sustain, or conversely reduce, forest production is an important research frontier (Amiro *et al.*, 2010; Hicke *et al.*, 2012; Anderegg *et al.*, 2015; Hartmann *et al.*, 2018). One possible set of mechanisms lies at the confluence of two emergent ecosystem properties: first, that moderate-severity disturbance, through the introduction of canopy gaps, can increase ecosystem physical and biological complexity (Hardiman *et al.*, 2013; Pedro *et al.*, 2015; Meigs *et al.*, 2017; Trammell *et al.*, 2017) and, second, that there may be a positive relationship between ecosystem physical and biological complexity, and carbon uptake (Hardiman *et al.*, 2011; Pedro *et al.*, 2015; Danescu *et al.*, 2016; Glatthorn *et al.*, 2017; Tang *et al.*, 2017). Thus, in forest ecosystems experiencing moderate levels of disturbance, a corresponding increase in ecosystem complexity may initiate a cascade of process and functional changes that moderates the decline or even sustains NEP into late succession. Specifically, the formation of small, patchy gaps shifts light and nitrogen distribution downward in canopies (Stuart-Haentjens *et al.*, 2015; Helm *et al.*, 2017; Taylor *et al.*, 2017; Forrester *et al.*, 2018), which may increase how thoroughly and efficiently these resources are used to drive production, and consequently attenuate the rate of NEP decline as forests age (Fig. 4). This resource reallocation may increase light- and nitrogen-use efficiency (Niinemets, 2012) because, unlike the nitrogen-rich, light-saturated leaves of the upper canopy, photosynthetic rates of subcanopy leaves typically operate below their maximum capacity, and therefore are highly responsive to supplemental resources.

On the opposing side of the ledger, carbon losses from rising $R_e$ may be less than anticipated for aging and moderately disturbed forests. Severe disturbances that abruptly transfer carbon from live to dead pools substantially enhance emissions from decomposition, tipping the balance in favor of net carbon losses or 'negative' carbon storage (Harmon *et al.*, 2011). The principal substrate fueling this carbon loss is woody debris, which constitutes a particularly large pool in severely disturbed forests (Woodall *et al.*, 2013; Russell *et al.*, 2014). Following moderate disturbance, the influx of woody debris and corresponding release of carbon from decomposition are generally much less, and not sufficient to drive NEP below zero

(Schmid *et al.*, 2016; Clark *et al.*, 2018). Instead, increases in carbon uptake by aging and moderately disturbed forests may fully offset or even outpace relatively small and drawn out increases in carbon losses from decomposition, a hypothesis grounded in theory (Harmon *et al.*, 2011), supported by limited observations (Clark *et al.*, 2018) and deserving of further investigation.

Linkages between disturbance-driven changes in ecosystem physical structure, resource distribution and use, and, ultimately, function are consistent with Odum's original hypothesis. Odum, too, believed that moderate-severity disturbances, such as those that are increasingly prevalent in temperate deciduous forests, could partially rewind the successional clock and, in doing so, counter-intuitively stabilize NEP. Following this theoretical thread, one would expect a substantially different NEP trajectory for ecosystems, including Western US conifers, that are subject to much more severe stand-replacing disturbances in which succession is reset to its starting point.

In conclusion, new observations, ecological theory and our emerging biological understanding of temperate forest ecosystems point to sustained NEP in aging temperate deciduous forests. Recent evidence from meteorological carbon flux towers demonstrates that a one-size-fits-all forest age–annual carbon storage relationship is overly simplistic, arguing for a more nuanced empirical understanding of carbon storage successional dynamics. These findings have critical implications for fundamental ecological principles and their application, suggesting that ecologists, forest managers and modelers should not assume an imminent decline in the North American terrestrial carbon sink as deciduous forests transition into middle and eventually late succession. Open data networks, such as FLUXNET and the National Ecological Observatory Network, which combine tower-based carbon flux observations with remote sensing and plant inventory data, offer complementary platforms for the investigation of the mechanisms underpinning the timing and magnitude of NEP change as forests age. Our current knowledge suggests that the conservation of these aging forests into late stages of ecosystem development is likely to result in nominal reductions in the land carbon sink, whilst maintaining an immense store of terrestrial carbon, and restoring the many ecosystem services afforded by the resurgence of biologically and physically complex forest ecosystems in eastern North America.

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