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Carbon cycling across ecosystem succession in a north temperate forest: controls and management implications

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Abstract

Despite decades of progress, much remains unknown about successional trajectories of carbon (C) cycling in north temperate forests. Drivers and mechanisms of these changes, including the role of different types of disturbances, are particularly elusive. To address this gap, we synthesized decades of data from experimental chronosequences and long-term monitoring at a well-studied, regionally representative field site in northern Michigan, USA. Our study provides a comprehensive assessment of changes in above- and belowground ecosystem components over two centuries of succession, links temporal dynamics in C pools and fluxes with underlying drivers, and offers several conceptual insights to the field of forest ecology. Our first advance shows how temporal dynamics in some ecosystem components are consistent across severe disturbances that reset succession and partial disturbances that slightly modify it: both of these disturbance types increase soil N availability, alter fungal community composition, and alter growth and competitive interactions between short-lived pioneer and longer-lived tree taxa. These changes in turn affect soil C stocks, respiratory emissions, and other belowground processes. Second, we show that some other ecosystem components have effects on C cycling that are not consistent over the course of succession. For example, canopy structure does not influence C uptake early in succession, but becomes important as stands develop, and the importance of individual structural properties changes over the course of two centuries of stand development. Third, we show that in recent decades, climate change is masking or overriding the influence of community composition on C uptake, while respiratory emissions are sensitive to both climatic and compositional change. In synthesis, we emphasize that time is not a driver of C cycling; it is a dimension within which ecosystem drivers such as canopy structure, tree and microbial community composition change. Changes in those drivers, not in forest age, are what

control forest C trajectories, and those changes can happen quickly or slowly, through natural processes or deliberate intervention. Stemming from this view and a whole-ecosystem perspective on forest succession, we offer management applications from this work and assess its broader relevance to understanding long-term change in other north temperate forest ecosystems.

1. Introduction

The general trajectories of carbon (C) stocks and sequestration rates over the course of secondary succession in north temperate forests are well known. Rapid sequestration during the initial decades after disturbance begins to decline later in the first century of stand development, while standing C stocks continue to increase, potentially for centuries (Pan et al. 2011; Pregitzer and Euskirchen 2004). However, there is considerable variation in these trends, evidenced by large amounts of variance in age-C relationships within individual sites, sites that show the same general patterns over very different timescales, and sites that depart from general trends altogether (Birdsey et al. 2023; Bradford and Kastendick 2011; Keeton et al. 2011; Thom and Keeton 2019). This variation indicates that our understanding of the factors controlling forest C trajectories has room to grow; it also highlights the fact that forest age is far from the only thing that influences C cycling over decade to century timescales.

Because all approaches to studying ecosystem succession struggle with its long timescales, sites that combine multiple complementary approaches can make powerful contributions to our understanding of the topic. Chronosequences have limitations, but as yet they are the only way to empirically quantify C pools and fluxes over centuries (Wardle et al. 2012; Yanai et al. 2003). The other empirical approach—long-term monitoring—allows for longitudinal observation and evaluation of trends inferred through chronosequences, but even the longest-running of such studies cannot capture centuries-long trajectories of ecosystem succession (Eisen and Barker Plotkin 2015; Fahey et al. 2005; Hoover et al. 2011; Novick et al. 2018). In combination, these two approaches can identify patterns and mechanisms of successional change, but even still it can be challenging to place their results in the context of north temperate forests more broadly. Such context, however, is necessary to produce transferable insights based on mechanistic understanding.

Long-term studies indicate several factors likely to control C stocks and sequestration rates over successional timescales in north temperate forests. The importance of forest structure—particularly canopy structure—to C cycling has often been demonstrated, though typically not through a successional lens (Gough et al. 2019; Ishii et al 2004; Reich 2012). Where it has been investigated as an ecosystem property that develops over the course of succession, increasing canopy structural complexity has been shown to increase forest C uptake by increasing resource use efficiency (Gough et al. 2022; Hardiman et al. 2013; Pan et al. 2013; Scheuermann et al. 2018). However, canopy structural complexity is to some extent linked to another important driver of forest C: forest community composition (Pedro et al. 2017). Trees are the most readily observed aspect of forest biotic communities, and their compositional change over time is used almost synonymously with succession (although succession is a whole-ecosystem process). As a driver, the composition of the tree community determines canopy functional traits that influence many ecosystem processes, including C cycling (Fahey et al. 2019). Tree community composition also affects forest C in other ways, including interspecific variation in hydraulic strategies, wood density, aboveground vs. belowground C allocation, and interactions with the composition of other organismal communities, such as soil microbial communities (Abramoff and Finzi 2016; Davidson et al. 2002; Prescott and Grayston 2013, Woodcock and Shier 2002).

Soil microbial communities in turn connect to a third major driver of forest C pools and fluxes: soil biogeochemistry. Soil biogeochemistry in this sense encompasses successional changes in soil properties such as pH (Compton et al. 1998; Flinn and Marks 2007), as well as the microbial communities themselves and the C- and nutrient-transforming processes that they mediate (Goodale and Aber 2001; Knelman et al. 2017; Lewis et al. 2014; Lovett et al. 2018). Nitrogen (N) is particularly important among nutrients because it limits primary production in many north temperate forests, and the forms of it available for plant and microbial uptake change over the course of succession (Leduc and Rothstein 2010; Nave et al. 2009). Moreover, different microbial taxa play different roles in mineralizing organic matter and releasing soil N (Phillips et al. 2013). In acidic northern forest soils, ectomycorrhizal (EcM) fungi are major players in N cycling, and EcM taxa that explore larger volumes of soil or produce organic matter depolymerizing enzymes play more prominent roles as succession advances and a larger share of soil N pool is held in less accessible organic forms (Chen et al. 2019; Hobbie et al. 2013; Leduc et al. 2013). As yet, successional interactions between soil N availability, photobiont C supply, and mycobiont enzyme production and N foraging are better characterized in boreal forest soils, but are relevant to the N economy and C balance of temperate forest soils as well (Baldrian et al. 2023; Fosmark et al. 2024; Hay et al. 2015; Jorgensen et al. 2022). Research that places these biogeochemical processes in the context of aboveground ecosystem dynamics (e.g., tree community composition, canopy structure) is particularly needed to better understand succession as a whole-ecosystem process.

In working towards the goal of transferable, predictive science, enumerating the factors that influence forest C over succession is arguably less important than describing how these factors operate holistically in ecosystems. Inspired by recent multi-decadal C cycling assessments from intensively studied north temperate forests (Desai et al. 2022; Finzi et al 2020; Hollinger et al. 2021), we synthesize new data and past results from long-term monitoring and chronosequence experiments at a well-studied site, the University of Michigan Biological Station (UMBS), in northern Lower Michigan, U.S.A. Our analysis extends this body of work, investigating longer-term successional changes spanning decades to centuries, by: (1) identifying trends and drivers of major C pools and fluxes; (2) describing mechanisms by which they operate; (3) assessing relevance to the ecology and management of north temperate forests. These objectives are facilitated by several predictions that inform the C pools, fluxes, and drivers we focus on here. First, we predict that successional development of forest structure regulates vegetation growth and overall ecosystem C accumulation. Second, we predict that changes in aboveground (tree) and belowground (microbial) community composition are coupled through successional time, with corresponding influences on biogeochemical functioning. Third, we predict that concurrent changes in composition and environmental drivers have influenced trends in ecosystem C uptake and loss over recent decades.

2. Methods

2.1 Study site- UMBS (45.56°, -84.72°) is in northern Lower Michigan, in the southeastern 1/3 of the 261,000 km^2 Laurentian Mixed Forest Province of the USDA Forest Service ecosystem classification framework (Cleland et al. 1997; McNab et al. 2007). The province has a humid continental climate with cold winters and warm summers; at UMBS, mean annual temperature (MAT; 6.9°) and mean annual precipitation (MAP; 893 mm, including 284 cm snowfall; 1991-

2020 for all parameters) fosters mixtures of warmer-temperate (*e.g.,* oak, maple) and cold-tolerant boreal (*e.g.,* spruce, fir, birch) forest types. Land use and disturbance history is broadly consistent throughout the province, where millennia of Native American ecosystem management activities were displaced by clearcutting and uncontrolled wildfires beginning with Euro-American colonization in the late 1800s and extending into the early 1900s (Lorimer 2001; Rhemtulla et al. 2009; Whitney 1987). Modern forest management began in the mid-20th century, and is more extensive than intensive: early-successional deciduous and mixed forests are clearcut and regrown over 40-80 year rotations, longer-lived deciduous cover types experience partial harvests at 10-20 year intervals, and upland conifers (mostly pines) are managed with periodic thinning followed by regeneration harvests at 60-100 years of age (Bates et al. 1993; Gahagan et al. 2015; Gerlach et al. 2002; Palik et al. 2003; Stone 2002).

A detailed description of the landscape setting and experimental design of UMBS (Nave et al. 2017) is summarized here. The regional Silurian and Devonian sedimentary bedrock lays buried beneath 100-200 m of glacial and lacustrine sediments deposited during the late Pleistocene. The highest elevations on the landscape are moraines of poorly-sorted till deposited directly by the continental ice mass; these are exceeded in area by lower-lying outwash plains, which were deposited by meltwater flowing away from ice margins. These landforms were modified during regional glacial re-advances 12,600 -10,500 years before present, and, at the lowest elevations, by lacustrine processes 4,300 - 3,000 years before present (Schaetzl et al. 2002; Nave et al. 2017b). Soils formed in till are mostly coarse-loamy Lamellic and Alfic Haplorthods (USDA Subgroups), outwash soils are predominantly sandy Entic Haplorthods, and soils in the lowest positions are predominantly Endoaquods, Endoaquents, and Haplosaprists (USDA Great Groups) formed in lake-modified outwash sediments and Holocene organic deposits.

Current vegetation at UMBS is the local result of the land use history that occurred across the wider ecological province. Namely, clearcutting and wildfires between 1870-1923 replaced pre-exploitation forests of long-lived species including red pine (*Pinus resinosa*), white pine (*P. strobus*), eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and red oak (*Quercus rubra*) with mixed deciduous-conifer forests dominated by early-successional taxa such as bigtooth aspen (*Populus grandidentata*) and paper birch (*Betula papyrifera*) in xeric to mesic settings, and trembling aspen (*P. tremuloides)* and balsam fir (*Abies balsamea*) in mesic to hydric settings. Most UMBS forestland is dominated by early-successional taxa, which have been increasingly replaced by longer-lived species in the last 20-30 years, due to lack of disturbances or management (Gough et al. 2010). Isolated portions of UMBS property were cut partially, or not at all, or were burned before cutting could occur and therefore serve as older reference forests, with composition and structure that might be more extensive today if not for the widespread disturbances of a century ago. Upland forests at UMBS are broadly representative of the wider Laurentian Mixed Forest Province in terms of their composition, growth rates, and disturbance history (Gough et al. 2007; Nave et al. 2017).

2.2 Experimental design- This study is based upon data collected through 2020 from several long-term experimental designs at UMBS (Fig. 1), with unique aspects detailed below.

2.2.1. Chronosequences and old reference forests- Two experimental chronosequences, differing in the type of stand-replacing disturbance, allow for the observation of stands ranging in age from 22 – 109 years. All chronosequence stands are on sandy outwash plains and have similar inherent soil properties. Individual chronosequence stands were established either by clearcut + residue burning (known as the Burn Plots; Scheiner and Teeri 1981), or by a clearcut not followed by an intentional residue fire. Because nearly all of the UMBS landscape experienced clearcutting and fire ~100 years ago, the difference between the two chronosequences is whether they have experienced one stand-replacing cut-and-burn disturbance (hereafter 1x cut+burn) or two stand-replacing cut-and-burn disturbances (2x cut+burn). In 2020, stand ages in the 1x cut+burn chronosequence were 33, 48, 68, and 109 years old (reflecting clearcutting in 1987, 1972, 1952, and 1911, respectively); 2x cut+burn stands were 22, 40, 66, 72, and 84 years old (clearcut + residue burning in 1998, 1980, 1954, 1948, and 1936, respectively).

The experimental chronosequences are complemented by observations of older reference stands, some of which have been monitored since the 1940s (Fig. 1). The oldest of the three reference stands reported here, Indian Point, is a hemlock-northern hardwoods forest with a long history of Native American management (Albert and Minc 1987); it is uneven-aged, but in the area that has been intensively monitored, dominant trees date to *ca.* 1830 (i.e., stand age = 190 years). The two other old reference stands are pine-dominated, with canopy dominants dating to 1885 – 1890 (stand age = 130 years). One of these stands was partially cut and lightly burned; the best available records (and site evidence) suggest the other was initiated after a stand-replacing fire. Due to their unique disturbance histories and differences in soils, landforms, and topoclimate, none of the three reference stands is an ideal representation of conditions that would be expected on the paired chronosequences after additional decades of development (Nave et al. 2019).

In both the experimental chronosequences and the old reference stands, individual stands range from just over 1 ha to more than 10 ha in size; in each stand, most data collection occurs within 3 plots, each 0.1 ha in size (except for 2 plots, 0.07 and 0.14 ha, in the 22-year-old “Burn Plot”). Throughout the remainder of this paper, we use the term “stand” to describe an area of forest of a known common age, composition, and disturbance, from one to several hectares in size. We distinguish stands from plots, which are sampling units of logistical convenience, but note that in many stands, individual plots were arrayed to sample across measurable or visually apparent spatial variation in ecosystem structure, disturbance severity, or to minimize edge effects. The sole exception to the "stand" vs. "plot" terminology is the Burn Plots, which by this definition consist of stands differing in ages, but whose name we reference (with capitalization) owing to their immediate recognition for generations of UMBS researchers.

2.2.2 Flux towers- The other experimental design that we draw upon for this analysis consists of paired reference and treatment flux towers known in the AmeriFlux Network as the US-UMB (reference) and US-UMd (disturbed) core sites (Fig. 1). The reference tower has a ~100 ha footprint and is supported by ground-based monitoring of ecosystem properties, C pools and fluxes across an array of 81 permanent plots since 1997. The treatment tower, erected in 2006, has a ~30 ha footprint where all of the aging, early-successional trees (aspen and birch) were stem girdled in 2008 to accelerate an incipient successional transition to longer-lived taxa- a process that has slowly unfolded in the reference footprint since that time. The treatment footprint holds 22 permanent sampling plots. In each footprint, a single 1.1 ha plot surrounds the flux tower, and the remainder of the plots (0.08 ha each) are located at 100 m intervals along transects that radiate away from the tower. Within the scientific literature, comparisons of ecosystem processes and C cycling between the reference and treatment footprints have occasionally been reported as results of the Forest Accelerated Succession ExperimenT (FASET; Nave et al. 2011). In this paper, we refer to the reference vs. treatment towers explicitly when differentiating between slower natural background succession vs. experimentally accelerated succession, or to FASET (as a paired design) when drawing inferences from the two footprints collectively. Like the paired chronosequences, the footprints of both flux towers are located principally on sandy, high-level outwash plains.

2.3 Data collection methods- This paper synthesizes existing and presents previously unpublished data collected over the last 40 years on the experimental designs described in section 2.2. The following subsections provide overview descriptions; details are provided in references cited here and in Appendix S1.

2.3.1 Ecosystem C stocks- Inventories supporting the estimation of aboveground live tree, standing dead tree, and coarse down woody debris C stocks are typically completed at 5-year intervals in the experimental designs reported in this paper. At each census, permanent plots are inventoried for all trees ≥1.37 m in height, which are identified to species and measured for diameter at breast height. Aboveground biomass C stocks are calculated from these inventory data using a combination of site-specific and generalized allometric equations (Nave et al. 2017) and appropriate plot area expansion factors. For presentation and discussion, live trees are grouped into short-lived deciduous (aspen, paper birch), long-lived deciduous (all other deciduous taxa), and long-lived coniferous functional groups (all coniferous species found in these plots are long-lived). Coarse down woody debris (DWD) is censused for dimensions, density, and species on 3 subplots per 0.1 ha permanent plot, and scaled up using expansion factors (Clay et al. 2022). Soil, coarse and fine root C stocks were inventoried in 2014 to a depth of 1 m, as described in Nave et al. (2019). All data are publicly available (Nave et al. 2024).

2.3.2 Canopy structure- In this paper we report canopy structural parameters collected using ground-based portable canopy LiDAR in the individual plots located in each chronosequence and old reference forest stand. These parameters were collected along two perpendicular transects (40 m each) in each plot (Fahey et al. 2019; Scheuermann et al. 2018). From the raw LiDAR returns, we used the *forestr* package to compute three canopy structural parameters for analysis, including leaf area index (LAI), mean maximum canopy height, and canopy rugosity (Hardiman et al. 2013; Atkins et al. 2018). These canopy structural data have been previously published (Atkins 2002; Fahey et al. 2019; Scheuermann et al. 2018), but not used to address the specific questions of the present synthesis.

2.3.3 Biometric C flux measurements- This paper reports four major C fluxes derived from plot-based biometric measurements: wood net primary production (NPP_W), soil respiration (Rs), fine root production, and leaf litterfall. Wood NPP was calculated for all experimental chronosequence and old reference forest stands as the change in woody biomass C between 2019 and 2014 census intervals, divided by the 5-year remeasurement interval. Soil respiration measurements were made on *in situ* collars across a range of dates and soil temperatures each year in the experimental chronosequence and old reference forest stands from 2014-2021, and from 1998-2020 and 2008-2017 in the UMB and UMd tower footprints, respectively. Detailed description of data collection and scaling to stand-level means is available in Clay et al. (2022) and Appendix S1. Fine root production, measured in chronosequence and old reference stands during the 2016-2019 growing seasons, is also described in Clay et al. (2022). Briefly, we used plastic mesh cores packed with freshly sieved, root-free native soil in each stand to quantify growing season root production (5-6 month) each year, averaged across all years within each stand. Soil respiration and fine root production data are publicly available (Nave et al. 2024).

Leaf litterfall fluxes reported in this paper come from a temporally consistent subset of the 0.08 ha permanent plots in the reference (n=12, 1997-2019) and treatment (n=14, 2006-2019) flux tower footprints. In each plot, the contents of individual traps (n=3) were aggregated into plot-level total leaf litterfall, which was sorted by species and component, and used to calculate annual means according to Gough et al. (2008).

2.3.4 Tower-based CO_2 and water vapor fluxes- In this paper, we report annual values of gross ecosystem C uptake (as gross primary production; GPP), gross ecosystem C emission (as ecosystem respiration; R_{eco}), and net ecosystem C uptake (as net ecosystem exchange; NEE) from publicly available AmeriFlux data for the US-UMB (2000-2020) and US-UMd (2008-2020) towers using the AmeriFlux-FLUXNET processed version of the data (Gough et al 2023a; 2023b). Annual values have been screened, gap-filled, and computed from the raw flux data collected on the two towers according to FLUXNET methods described in Pastorello et al. (2020). We also present growing season, midday (1100 – 1400 local time) ecosystem water use efficiency (WUE) for reference (2001-2020) and treatment (2007-2020) towers (calculated from the same AmeriFlux-FLUXNET data sources), computed only for non-gap-filled periods.

2.3.5 Soil C dynamics- We examine changes in soil C using two distinct datasets and approaches to address two distinct questions. First, to assess soil C trajectories over a century of stand development, we compiled data from five known sampling campaigns on the Burn Plots. Across these campaigns, only O horizons were sampled consistently. Assuming differences in individual judgment and specific sampling techniques, we used unweighted effect-size meta-analysis to quantify the magnitude and temporal patterns of O horizon C stocks following cut+burn disturbance. Statistical methods follow Nave et al. (2021). Second, to assess how soil C stocks have changed in recent decades, we report results from a longitudinal re-sampling of an unmanipulated reference area adjacent to the Burn Plots. This area of 1911-origin (clearcut + unintentional residue fire) forestland was sampled in 1980, and again in 2009, providing an opportunity to compare mineral soil C stocks by genetic horizon over a 29-year period, independent of any disturbances other than the original region-wide cut+burn disturbance.

2.3.6 Soil biogeochemistry and microbial communities- In this paper, we report results from a systematic 2015 biogeochemical and microbial characterization of Burn Plots topsoils (A horizons). These samples allowed for comparison of fungal communities, extracellular enzyme activity, root biomass, microbial biomass C, soil N availability, soil C and N concentrations, pH, and soil moisture across the 5 experimental stands comprising the 2x cut+burn Burn Plots (data published in Nave et al. 2024). All preparation and most analysis steps were completed in the UMBS Analytical Laboratory, with sequencing at the Microbial Systems Molecular Biology Laboratory at the University of Michigan. Detailed methods are provided in Appendix S1. To inform fungal N cycling aspects of these measurements, we collected fungal sporocarps in 2022 from paired plots (n=6 plots) in the reference and treatment flux tower footprints that received ^{15}N tracer additions in 2010 (Nave et al. 2013). We analyzed these fungal samples by isotope ratio mass spectrometry in the UMBS Analytical Laboratory in order to assess long-term N foraging of several ectomycorrhizal (EcM) fungal taxa, using ^{15}N-enrichment as an indicator.

2.3.7 Climatology and atmospheric deposition- Daily climatology and weekly atmospheric deposition have been monitored since the late 1970s on the main campus of UMBS on the south shore of 1,700 ha Douglas Lake (Fig. 1). We present MAT as the average of daily maximum and minimum values and MAP as the sum of daily water-equivalent values (UMBS 2024). For atmospheric deposition, we present annual total inorganic N deposition values, as obtained from the National Atmospheric Deposition Program, of which UMBS is site MI09.

2.4 Data analysis- This paper is intended to provide a holistic view of interactions between ecosystem components over time, and how they influence C cycling. This required synthesizing and analyzing many different types of data according to a range of approaches and techniques. Analytical details are provided here, in Appendix S1, and in figure captions. The following narrative enumerates the specific statistical tests used to address each topic of interest; parenthetical references to figures are provided to aid in connecting these statistical tests to the results we present and the inferences we draw from them. To test for differences in total ecosystem C stocks (and in individual pools) over succession (Fig. 2a), we treated each plot in each chronosequence and old reference stand as an experimental unit, binned plots into 40-year age classes, and used one-way ANOVAs with Fisher's Least Significant Difference post-hoc tests to identify significant differences between age classes. Changes in composition over the same 40-year age classes (Fig. 2b) are expressed as the proportion of aboveground live tree biomass in each of three functional groups (short-lived deciduous, long-lived deciduous, long-lived coniferous); these data are presented for visualization but are not analyzed statistically. To test relationships between canopy structure and C uptake over succession (Fig. 3), we treated each plot in each chronosequence and old reference stand as an experimental unit, selected NPP_w as the response variable, and used multiple linear regression to determine the predictive capacity (as partial r^2) of leaf area index (LAI), maximum canopy height, and rugosity. We conducted separate regressions for young (22-48 years; n=11), middle-aged (66-84 years; n=6), and old (>100 years; n=12) stands. We standardized the values for the three structural parameters by subtracting their means and dividing by their standard deviations. To examine successional trajectories of growth and canopy production in taxonomic detail in recent decades (Fig. 4), we treated individual plots in the reference and treatment tower footprints as experimental units, selected leaf litterfall mass as the response variable, and used year as the predictor variable in simple linear regressions to predict temporal trajectories in leaf production (total across all species), and for individual species (red oak), genera (red +sugar maples), and functional groups (early-successional species, i.e., aspen and birch). To test for successional trends in soil respiration (Fig. 5), we treated each chronosequence and old reference stand as an experimental unit, and used simple linear regression to test for temporal trends (i.e., as a function of stand age) in Rs fluxes and proportions. We ran separate regressions for annual vs. growing-season-only trends, for each of the following fluxes and proportions: 1) total soil respiration [Rst], 2) autotrophic soil respiration [Rsa], 3) heterotrophic soil respiration [Rsh], and 4) heterotrophic proportion [Rsh/Rst]. To examine relationships between stand age, fine root production, and soil respiration (Fig. 6), we conducted two regressions: first, stand age vs. mean growing season fine root production (averaged to the stand level across all available years of ingrowth core incubation); second, mean growing season fine root production vs. annual total soil respiration. To examine long-term successional patterns in O horizon C stocks on the Burn Plots (section 3.2 narrative), we used unweighted effect size meta-analysis to test (1) for a significant effect of past disturbance on C stocks using categorical meta-analysis and (2) whether O horizon C stock changes vary significantly with time since disturbance using continuous meta-analysis. To test for long-term changes in soil properties across the Burn Plots (Fig. 7a), we treated individual stands as experimental units, selected A horizon %C, pH, and microbial biomass C as response variables, and used stand age as the predictor variable in simple linear regressions. To test for relationships between soil properties and biogeochemical function (Figs. 7b, c), we treated individual Burn Plot stands as experimental units, selected α-glucosidase activity rate as the response variable, and regressed it against %C and pH as predictor variables (respectively) using simple linear regressions. To test for changes in fungal community composition over succession on the Burn Plots (Fig. 8), we treated individual soil samples from each stand as experimental units. In QIIME, we (1) identified fungal families driving community dissimilarity across stands using ANCOM, (2) visualized fungal communities with a PCoA biplot, and (3) tested for statistical significance of community dissimilarity along a Bray-Curtis dissimilarity matrix. To identify soil properties driving community dissimilarity (Fig. 9), we again selected individual Burn Plots soil samples as experimental units and used a (1) dbRDA biplot to visualize dissimilarity in soil properties across stand ages, and (2) forward stepwise regression, including α-glucosidase activity, microbial biomass C and N, soil NH_4-N availability, soil C and N concentrations, pH, and water content as predictor variables, to identify statistically significant predictors of variation in community dissimilarity. To test for significant differences in competition for N among different EcM fungal families (Fig. 10), we treated individual plots in the reference and treatment tower footprints as experimental units, selected the ^{15}N value of bulk fungal sporocarps from each family as the response variable, and used family as the predictor variable in a one-way ANOVA. To test for significant changes in mineral C stocks in recent decades (Fig. 11), we treated individual soil profiles as experimental units, selected total C stock as the response variable, and used a two-way ANOVA to test for significant effects of horizon (A, E, B), sampling year (1980, 2009), and their interaction on C stocks. To test for significant temporal trends in GPP, R_{eco}, NEE, and WUE (Figs. 12a-c), we used multiple linear regressions. For each response variable, we ran a multiple regression model with year (continuous) and treatment (dummy variable, coded relative to the reference footprint) to test for significant temporal trajectories and significant differences between footprints. Flux timeseries were 2000-2020 for the reference tower and 2008-2020 for the treatment tower. We used a paired t-test to determine whether mean cumulative growing season soil respiration efflux differed in reference vs. treatment tower footprints over the long-term timeseries. To test for significant temporal changes in MAT and MAP (Figs. 12d, 12e) we ran simple linear regressions with year as the predictor, for a 1980-2020 climatology period. To test for significant changes in atmospheric N deposition, we used piecewise regression to examine break-point timing and slope for annual total inorganic N deposition values from the UMBS NADP station, 1980-2020.

In the case of all tests, we used data transformations as necessary to mitigate non-normality or unequal variances, and set $P<0.05$ as the threshold for accepting test results as statistically significant. In a limited number of cases and in the context of results significant at $P<0.05$, we discuss several results with $P>0.05$ but $P<.0.10$ as marginal trends. We completed t-tests, ANOVAs, and regressions in SigmaPlot 14.0 (SYSTAT Software, San Jose, CA US). We used MetaWin 3.0 (Rosenberg 2022) to analyze Burn Plots soil C data. Data processing and analyses of fungal community composition were completed in R and QIIME.

3. Results

3.1 Ecosystem C stocks and aboveground dynamics over succession- Total ecosystem C stocks in UMBS upland forests increase over 200 years of succession ($P<0.001$), largely due to increases in aboveground biomass ($P<0.001$), which exceed soil as the largest C pool by ~50 years of stand development (Fig. 2a). Smaller C pools also show significant temporal dynamics, including larger standing dead tree C stocks in the 40-80 and 80-120 year age classes ($P<0.001$), larger O+A horizon C stocks in 120-160 and >160 year old stands, and larger DWD ($P<0.001$) and smaller fine root ($P=0.05$) C stocks in >160 year old stands (Appendix S1). As this successional increase in total ecosystem C unfolds, forest composition changes, with short-lived pioneer species giving way to longer-lived deciduous or coniferous taxa (Figure 2b).

Rates of biomass increase (as NPP_w) also vary over succession, with the aspects of canopy structure influencing NPP_w shifting over time (Fig. 3). Early in succession (plots in stands that are 22-48 years old), NPP_w varies nearly four-fold between plots, but this variation is unrelated to structural parameters (multiple regression $P>0.05$). In middle-aged stands (66-84 years old) NPP_w is less variable among plots, and is significantly related (multiple regression $P=0.03$) to canopy height (partial $r^2=0.72$), leaf area index (partial $r^2=0.21$), and, to a lesser extent, canopy rugosity (partial $r^2=0.04$). Old stands (>100 years old) possess the widest between-plot variance in NPP_w, which is significantly related (multiple regression $P=0.02$) to leaf area index ($r^2=0.60$), and to a lesser extent canopy height and rugosity (both partial $r^2<0.05$).

Leaf litterfall data from the flux tower footprints detail the changes in forest composition that occur as pioneer species give way to longer-lived taxa at the close of the first century of succession. In the reference tower footprint where background natural succession is ongoing, a 23-year decline in leaf production by early-successional aspen and birch (Fig. 4a; regression $P<0.001$) has been offset by a significant increase by red oak (Fig. 4b; $P<0.001$), maintaining whole-canopy leaf production at the same level (Fig. 4a; regression $P>0.05$). Leaf production by maple (primarily *A. rubrum,* secondarily *A. saccharum*) has remained unchanged over this interval (Fig. 4b; regression $P>0.05$). The 14-year litterfall record for the treatment tower footprint reveals a pattern of compositional change that is functionally similar, but greater in rate and magnitude. There, where the mortality of early-successional taxa was accelerated by stem girdling (Fig. 4a), leaf production by oak and maple both increased significantly (Fig. 4c; $P<0.001$ and $P=0.03$, respectively), albeit threefold more rapidly for oak, based on slope coefficients for the two taxa. Indeed, oak transitioned from being subdominant to maple during the first 5 years of litterfall collections in the treatment footprint, to consistently being the canopy dominant in more recent years.

3.2 Belowground C, soil biogeochemistry, and microbial dynamics over succession- Soil respiration is the largest loss term in the UMBS C budget, and is dominated by emissions during the growing season (Fig. 5). On an annual basis, total soil respiration (Rst) does not vary with successional stage (P=0.29), but marginal decreases in autotrophic (Rsa; P=0.07) and increases in heterotrophic (Rsh; P=0.06) components lead to an overall increase in the proportion of total emissions that are heterotrophic (Figs. 5a, 5b). During the growing season, successional trends in soil respiration are more evident, with Rst (P=0.04) and Rsa (P=0.03) declining with stand age, and Rsh/Rst increasing with stand age (Figs. 5c, 5d). Growing season fine root production, which is unrelated to stand age (Fig. 6a, P=0.22), is in fact a stronger predictor of Rst than stand age itself (Fig. 6b; P<0.01).

Soils data from the Burn Plots chronosequence reveal changes in C, biogeochemical, and microbial properties over the course of succession. Categorical meta-analysis of the 5 known sampling campaigns shows that O horizon C stocks were diminished by the clearcut+burn that established these stands (-29%, bootstrapped confidence interval -14% to -42%), with no temporal trend to imply recovery over the duration of the chronosequence (meta-regression, P=0.74). In contrast to O horizons, topsoils appear to be recovering as stands develop over the course of the chronosequence. Successional trends (Fig. 7a) include increased soil %C (P=0.03) and microbial biomass C (P<0.01), and decreased pH (P=0.03). These trends have biogeochemical consequences, with higher %C and lower pH being linked to higher rates of cellulose-degrading enzyme activity (α-glucosidase; Figs. 7b, 7c; P=0.03).

Across the Burn Plots, successional changes in soil pH, %C, microbial biomass, and α-glucosidase activity are accompanied by significant changes in fungal community composition (Fig. 8; P=0.025). During the initial decades after disturbance, taxa in the EcM Amanitaceae and mixed saprotrophic/EcM Clavariaceae dominate. Stand development progresses through stages dominated by EcM taxa in the Tricholomataceae and Russulaceae, and by a century of succession, the fungal community is dominated by EcM taxa in the Cortinariaceae (Fig. 8; see Appendix S1 for specific taxa). This long-term fungal community shift is accompanied by the topsoil property changes in Fig. 7, as well as increased moisture and root biomass, and a successional decline in soil NH_4-N availability (Fig. 9; $P<0.05$). Of all these soil properties, pH, moisture, α-glucosidase activity, root biomass, and NH_4-N availability are most strongly related to shifts in the fungal community over the course of succession on the Burn Plots (Fig. 9).

Patterns from the Burn Plots are informed by two results from other experimental designs that address fungal N cycling and soil C stocks. First, fungal sporocarp analyses from the decadal ^{15}N tracer experiment in the ~110 year old forests of the flux tower footprints reveal that of the four most frequently observed EcM families, sporocarps of taxa in the Cortinariaceae have significantly higher ^{15}N enrichment (Fig. 10; $P=0.01$). Second, multidecadal soil monitoring in the 1911-origin reference stand adjacent to the Burn Plots demonstrates significant declines in A and E horizon C stocks in the last 30 years in this ~110 year old reference stand (Fig. 11; 1980 vs. 2009).

3.3 Ecosystem C fluxes and climate forcings- Two decades of flux tower observations reveal significant changes in whole-ecosystem C fluxes and their environmental drivers (Fig. 12). Ecosystem C uptake (GPP, negative=uptake) has become significantly more negative with time, with no difference in the rate of change between reference and experimentally accelerated succession footprints (Fig. 12a, lower portion). Concurrently, R_{eco} has increased significantly in the reference footprint, but not in the treatment footprint (Fig. 12a, upper portion). In both footprints, WUE has increased concurrently with GPP, with no difference in the rate of increase between footprints (Fig. 12b). In terms of net C balance, NEE has become more negative with time in both footprints, but this increase in C sequestration has been significantly weaker in the background natural succession footprint due to the long-term increase in R_{eco} (Fig. 12c). Over the common period of record, cumulative mean growing season Rst has been significantly larger in the reference footprint than the treatment footprint ($P<0.001$, Appendix S1).

Changes in C and water fluxes observed in the past 10-20 years have been accompanied by ongoing changes in climate and atmospheric deposition over the past 40 years. From 1980 to 2020, UMBS became significantly warmer (Fig. 12d) and wetter (Fig. 12e), with increases of +0.25° MAT and +5.0 cm MAP per decade. Over the same period, wet inorganic N deposition declined significantly (-25%; Fig. 12f), primarily since the year 2000.

4. Discussion

4.1 Synthesis of ecosystem changes over succession

Our synthesis illustration (Fig. 13) integrates this multitude of ecosystem components, their changes and interactions over the range of timescales and experimental designs at UMBS. This illustration is a simplified representation of results reported above, which are parenthetically referenced in the text below and complemented with UMBS-relevant citations.

Following stand-replacing disturbance on the sandy outwash plains of UMBS, aboveground biomass accumulation is initially rapid and unrelated to canopy structural development (Figs. 2a, 3b, 13a). As stands approach mid-succession, vertical canopy development drives the accumulation of aboveground biomass, which soon exceeds soil as the largest ecosystem C pool (Figs. 2a, 3b). Increases in aboveground biomass C continue later into succession, where between-stand variation in leaf area explains rates of continued increase (Figs. 2a, 3b, 13c).

Stand-replacing disturbance diminishes organic horizon C stocks (section 3.2, meta-analysis) for 100 years, but mineral soil C and related soil physicochemical, biogeochemical, and microbial properties begin to recover during the first century of succession. Recovery encompasses increases in A horizon moisture, exchangeable acidity, root and microbial biomass, and Bs horizon pedogenic iron concentrations, and decreases in A horizon pH, base cations, cation exchange capacity, and soil N availability (Figs. 7a, 9, 13a; Nave et al. 2019; White et al. 2004). These soil property changes have functional consequences including increased rates of α-glucosidase activity and a successional increase in the heterotrophic fraction of soil respiration (Figs. 7b, 7c, 5a, 5c, 13a), and are accompanied by long-term shifts in fungal and tree community composition (Figs. 13a, 13b). Over this 100-year timescale, communities shift from being dominated by short-lived aspen and birch with mixed saprotrophic/enzymatically weak EcM fungal communities, to increased representation of longer-lived deciduous trees and fungal communities dominated by EcM taxa in the Cortinariaceae, with known organic matter decomposition abilities (Figs. 2b, 8, 13a, 13b; Bödeker et al. 2014; Kyaschenko et al. 2017). As these compositional shifts unfold over decades, the heterotrophic fraction of total soil respiration increases (Figs. 5a, 5c). After a century of succession, combined O + A horizon C stocks recover from stand-replacing disturbance (Fig. 13c).

By 100 years of succession after stand-replacing disturbance, aspen and birch have begun to die out, at rates that naturally vary according to soil and landform properties, and in the case of the experimental girdling disturbance, have been deliberately accelerated (Figs. 2b, 4a, 13b; Nave et al. 2014). Similar to the Burn Plots but over a shorter timescale, accelerated aspen-birch mortality in the treatment flux tower footprint causes a temporary increase in soil N and an excursion from EcM to saprotrophic fungal taxa (Fig. 13b; Castillo et al. 2018; Nave et al. 2011a; 2013; 2014). Subsequently, oak outcompetes maple for canopy gaps and N, especially in the treatment tower footprint, with its EcM associates in the Cortinariaceae proving highly competitive for N (Figs. 4a, 4b, 10, 13ab; Nave et al. 2013). In reference forests where gradual background mortality of aspen and birch is ongoing (i.e., the reference flux tower footprint and the 1911-origin reference stand adjacent to the Burn Plots), soil and total ecosystem respiration increase as surface soil C stocks decline, weakening the C sink strength compared to the experimentally accelerated succession footprint (Figs. 11, 12a top, 13b). In both footprints, GPP and WUE exhibit ongoing increases with mean annual temperature and precipitation (Figs. 12a bottom, 12b, 12d, 12e).

Predictions of C cycling and its drivers through the end of a second century of succession are hindered by the prospects of continued climate change and the unique conditions on which the three old reference forests in our experimental design are found (Fig. 13c). While some of the more robust chronosequence trends may hold into the future, such as long-term aboveground biomass increases, (Fig. 2a), others are less clear. For example, differences in LAI and NPP_w between the ~130 year old pine-dominated stands on outwash and the ~190 year old hemlock-hardwoods on moraine may be successional trends, or results of unique landform and soil properties (Fig. 13c, Albert and Minc 1987; Nave et al. 2017; 2019; Scheuermann et al. 2018).

4.2 Detailed discussion of ecosystem components

4.2.1 Aboveground wood production and canopy structure- Our finding that the canopy metrics that drive aboveground growth change over the course of succession (Fig. 2) addresses the first of the predictions enumerated at the close of the Introduction. In young stands, canopy structural complexity does increase with age, but it is not the driving force for aboveground growth. Instead, the severity of the stand-establishing disturbance may be a more important determinant of between-stand variation in NPP_w (Scheuermann at al. 2018). Canopy structural control of NPP_w becomes stronger in middle aged stands, evidenced by low residual variance in the structure – NPP_w relationship, and suggests that the rate at which a deeper canopy develops fundamentally constrains NPP_w during this period of rapid vertical growth, possibly involving a tradeoff between vertical growth and lateral crown expansion (i.e., increased LAI). Beyond a century of development, variation in LAI explains the majority of the variance in NPP_w. This may indicate that as rates of overstory tree vertical growth begin to slow with succession, canopy stratification (including the developing understory) becomes more important to whole-canopy photosynthetic C fixation (Murphy et al. 2023).

4.2.2 Soil C – microbial interactions over succession- Soil C stocks and microbial communities were profoundly altered by region-wide stand-replacing disturbances a century ago, but have begun to recover during the century of succession that has unfolded since. The meta-analytic reduction in O horizon C stocks that we report (-29%, section 3.2) falls in the range of losses reported in meta-analyses of harvest and fire for temperate forest soils generally (Nave et al. 2010; 2011b), but is larger than typical in the Lake States (Nave et al. 2021). This may reflect a compound effect of the second (experimental) cut-and-burn disturbance applied to create each Burn Plot (i.e., chronosequence stand) throughout the 20th century, which is in addition to the landscape-wide cutting and fires that occurred in the latter 19th through early 20th centuries (Gough et al. 2007). In contrast to persistently diminished O horizons, A horizons across the Burn Plots appear to be recovering, with %C, microbial biomass C, and pH showing significant relationships with stand age (Fig. 7a). These results independently confirm a previously reported decrease in topsoil pH across the Burn Plots (Nave et al. 2019), and add mechanistic insight by revealing that as topsoils begin their post-disturbance recovery of acidity and organic matter, the microbial community and its enzymatic functions (Fig. 7b, 7c) follow suit.

4.2.3 Coupled tree-fungal compositional-functional changes- Our synthesis of results from the Burn Plots and FASET reveals that stand-replacing and partial disturbances induce microbial and N cycling responses that are similar in pattern, but different in timescale and magnitude. On the Burn Plots, clearcutting + fire causes soil N availability and nitrophilic fungi (EcM and saprotrophs) to increase abruptly, then decline over 100 years as N-foraging EcM decomposers in the Cortinariaceae rise in dominance (Figs. 8, 9; Birkebak et al. 2013; Bödeker et al. 2014; Chen et al. 2019; Kyaschenko et al. 2017; Nave et al. 2019; White et al. 2004). Similarly, in FASET, the pulse of aspen and birch mortality in the treatment footprint led to a 2-4 year increase in soil N availability relative to the reference footprint, accompanied by a decline in EcM and an increase in saprotrophic fungi (Castillo et al. 2018; Nave et al. 2011a; 2013; 2014). Since that time, EcM fungi and their N uptake have recovered, with taxa in the Cortinariaceae outcompeting taxa in the Amanitaceae, Boletaceae, and Russulaceae for the ecosystem ^{15}N tracer that was applied during the disturbance period (Fig. 10). Based on their strong decomposing enzyme production, the shift in the fungal community towards the Cortinariaceae would seem to favor increased rates of soil C mineralization and CO_2 emission.

Successional changes in microbial communities and their functions go hand-in-hand with changes in tree community composition and functioning, addressing our second prediction (coupled aboveground-belowground compositional-functional linkages). Increases in the enzymatically proficient Cortinariaceae may mean that these EcM taxa are increasing the ability of longer-lived hosts (primarily red oak) to access less available forms of soil N (Jorgensen et al. 2022; Leduc et al. 2013; Lindahl et al. 2021). Indeed, red oak has outcompeted red maple for soil N during the successional transition out of aspen-birch dominance (Nave et al. 2013), has higher foliar N concentrations (Nave et al. 2009), rates of stomatal conductance, photosynthesis, and sap flux (Gough et al. 2021; Matheny et al. 2017). These acquisitive vs. conservative traits may underpin the multi-decadal trends in canopy production by the two species. Over this period, oak has had the clear competitive advantage (Fig. 4), especially in the treatment footprint, where water and N availability were elevated for 2-4 years following experimentally accelerated aspen mortality (He et al. 2014; Nave et al. 2014). Compared to the aspen they are replacing, however, oak and maple both have lower rates of photosynthesis and stomatal conductance, and lower foliar N concentrations (Gough et al. 2021; Nave et al. 2009). Thus, this successional transition to longer-lived species may have longer-term consequences for functions such as water use, C uptake and respiratory emissions at the ecosystem scale.

4.2.4 Ecosystem C fluxes, net balance, and environmental drivers- Over the course of succession, compositional change from aspen to longer-lived tree taxa with lower photosynthetic rates would seem to favor reduced whole-canopy GPP. Decades of monitoring in the flux tower footprints shows that the opposite has occurred (Fig. 12). This addresses our third prediction and implies that external forcings, such as warming and wetting, are overriding compositional influences on successional trajectories of C cycling, at least on the uptake side. On the emissions side, the picture is more complex. Respiratory emissions should be decreasing with succession in the tower footprints, because the longer-lived taxa replacing aspen and birch have higher C use efficiency (less C respired per unit C fixed; Gough et al. 2021), and the chronosequences suggest long-term declines in Rst and Rsa with age (Fig. 5). Counter to that prediction, R_{eco} has remained stable in the treatment footprint where composition has changed rapidly over the last decade, and increased in the reference footprint. Some of this increase in R_{eco} in the reference footprint has been due to increased Rst emissions, which have been larger than in the treatment footprint in the last 1-2 decades (section 3.3 and Appendix S1). These elevated respiratory losses are consistent with surface soil C stock declines observed over recent decades in the 110 year old Burn Plot reference stand, which is in all regards similar to the UMB reference footprint (Fig. 11). Collectively, these patterns imply an overarching, climate-driven increase in respiratory emissions, which is being canceled out in the treatment footprint by rapid successional change to tree taxa with lower specific respiration rates.

Though it is unclear whether climate or composition has the stronger influence on its constituent fluxes, the increasing C sink strength (NEE) over time in both footprints indicates that GPP has increased more rapidly than R_{eco} (Fig. 12). This strengthening C sink over the past 1-2 decades of succession has been concurrent with increased WUE in both footprints, due in part to the replacement of aspen and birch with oak and maple, which have higher WUE (Matheny et al. 2014). However, similar trends in NEE and WUE are occurring in other humid north temperate forests where compositional change is less likely to be a substantial mechanism, implying a role for broader environmental drivers such as warming, wetting, CO_2 fertilization, and N oligotrophication (Finzi et al. 2020; Groffman et al. 2018; Hollinger et al. 2021; Keenan et al. 2013). The key takeaway from this trend is thus much the same as for respiratory emissions: there is evidence for a broader climatic influence on ecosystem C balance and water use, and an influence of successional change in composition. Unfortunately, our experimental design cannot parse these factors as independent drivers.

One factor that may be influencing respiratory emissions at UMBS is non-native earthworms. Most of the earthworm taxa present at UMBS in recent decades have been present since the early- to mid-1900s, but changes in their spatial distribution and community composition have occurred (Crumsey et al. 2014). One of the more notable changes has been the expansion of *Lumbricus terrestris*, which directly consumes and vertically redistributes larger quantities of surface leaf litter than other taxa (Crumsey et al. 2015). On balance, *L. terrestris* and other taxa, including those that consume and redistribute mineral soil organic matter, have a small negative effect on soil C at UMBS (Crumsey et al. 2013). This implies that declining soil C stocks and increasing soil and ecosystem respiration is due, in some part, to the activity of these organisms. Overall, earthworm spatial distribution and community structural will likely continue to change over time at UMBS, in a patch dynamic influenced by factors such as road proximity, soil texture, and tree community composition (Crumsey et al. 2014). As these changes unfold, earthworm dietary preferences may interact with forest successional dynamics to affect C cycling outcomes, as maple leaf litter is much preferred, and more quickly consumed, than oak litter (Crumsey et al. 2013).

4.3 Context and broader relevance to north temperate forest ecosystems and their management- Our study is both representative and unique, in ways that help to understand its relevance to C cycling in other north temperate forests. In composition, UMBS is broadly representative, as the aspen-birch cover type is the most extensive at the site and across the broader Laurentian Mixed Forest Province (Nave et al. 2017; Ruefenacht et al. 2008). In age, UMBS is unique: regionally, aspen-birch forests tend to be younger, because their persistence depends on large-scale disturbance or management that has not occurred at UMBS (Carson et al. 2023; Friedman and Reich 2005). In terms of broader relevance, many general patterns we report here are similar to other empirical studies across the U.S. Lake States, Northeast, and adjacent Canada. These include a strengthening C sink in a maturing forest over recent decades (Finzi et al. 2020; Hollinger et al. 2021), successional increases in ecosystem C stocks that are driven by aboveground biomass (Alban and Perala 1992; Keeton et al. 2011), and long-term recovery of soil properties following disturbance (Poirier et al. 2016; Roy et al. 2021). However, for every one of these general patterns, there are studies in the same region that show divergent or more nuanced trends (Arain et al. 2022; Desai et al. 2023; Gao et al. 2018; Prest et al. 2014; Wang et al. 2014). This highlights that site specifics such as disturbance and management history can obscure or override generally predictable successional trends and drivers (Ford and Keeton 2017; Hoover 2011; Kern et al. 2021; Latty et al. 2004).

In the north temperate forest literature, the lack of any one consistent successional C trajectory or set of drivers reflects diversity in forest ecosystems, including in the ways that they have been managed or otherwise altered by people. Accepting this diversity and the uncertainty that it introduces into future forest functioning is part of forest management. In this context, the many drivers that influence C cycling can then become explicit targets for manipulation when C is a management objective. Managing forests means much more than managing their age, e.g., by clearcutting to restart, or allowing to "mature" by leaving them untouched. Directly and indirectly, managing forests means manipulating structure (above and belowground), composition (plants and microbes), and relationships between ecosystem components, including their functional and biogeochemical outcomes. Taking this ecological view of forest management, and setting aside the notion that forest age is a driver itself, we offer several management applications relevant to north temperate forests.

The most timely management application of our results emerges from the decadal trends in C uptake and emissions in the two flux tower footprints. In the treatment footprint, the intentional killing of over one-third of the live trees has had a paradoxical effect: an increase in C sequestration. There, altering forest composition redistributed resources (access to light, soil N) from resource-demanding to resource-efficient taxa. This action decreased canopy structural complexity—a driver usually positively associated with C sequestration (Gough et al. 2021;

Hardiman et al. 2011; Thom and Keeton 2020)—and nonetheless increased C sequestration, implying a greater role for N than light limitation of C uptake. In contrast, in the reference footprint, natural succession towards an older and more structurally complex condition has been accompanied by a weaker increase in C sink strength, due to a concurrent increase in respiratory losses. Collectively, this difference between footprints implies that partial harvests to manipulate composition may be a way to simultaneously increase within-forest C sequestration, while removing C that would otherwise be respired and instead storing it in harvested wood products (Gahagan et al. 2015; Powers et al. 2011). Our results suggest such treatments will be most effective where there is a wide difference in resource efficiency between the dominant trees that are removed, and the codominant or suppressed trees that are released, with greater trait diversity in released species facilitating climate adaptation and C mitigation (Clark and D'Amato 2021; Thom et al. 2021; Wiechmann et al. 2022).

Our findings provide a belowground view on the typically aboveground-focused work of managing forests. We show that predictable tree community composition changes over succession are linked to concurrent changes in soil properties and microbial communities. Whether severe and stand-replacing or partial and patchy, disturbances that kill trees accelerate the N cycle and shift the fungal community from low-N EcM fungi that are strong decomposers, to more nitrophilic EcM and saprotrophic fungi. These shifts can be subtle and short-lived, as in the experimental girdling that accelerated succession in FASET, or more persistent, as in the clearcut harvest + fire of the Burn Plots, where fundamental soil properties are still changing many decades later. In both cases, aboveground dynamics (tree growth, community composition) have successional implications for belowground processes, including root production, soil CO_2 emissions, and long-term soil C stock changes.

The final management consideration of our synthesis emerges from its landscape context. At 4,000 ha, UMBS is large enough to host multiple experimental designs on the same kind of "site"—sandy outwash plains—yet also large enough that its landscape holds other ecosystem types where findings from these study sites do not apply. Thus across UMBS and other humid temperate glaciated landscapes with mosaics of mixed hardwood-conifer forests, our results will be most relevant on drier landforms and soils with lower nutrient availability. On more productive landforms and soils, successional patterns and C cycle trajectories may be different, or similar but for different underlying reasons. Drawing management applications from this and other long-term studies will therefore be most effective when disturbances and succession are seen as whole-ecosystem processes, with bottom-up and belowground factors given equal weight to the plant communities that usually capture the most attention (Barnes et al. 1982). Vegetation treatments to achieve C cycle objectives can then be optimized to the kinds of ecosystems where they are most likely to be effective. For example, our results imply that partial harvests to release codominant or overtopped oak can increase ecosystem C sequestration, but that this outcome is most likely on drought-prone, low-nutrient soils where its water- and N-acquisitive traits make it best suited to capitalizing on release from competition. On more mesic, productive soils, treatments to release maple and capitalize on its high levels of water and C use efficiency may be more effective at increasing C sequestration. Still other management strategies, approaches, and tactics may be needed to balance C with other objectives in other settings. In this way, moving beyond stand-level thinking to landscape management mosaics can diversify the composition, structure, connectivity, climate adaptation capacity, and C management strategies of larger forested areas (Ontl et al. 2020; Thom and Keeton 2020). Ultimately, as climate, disturbance regimes, and species distributions continue to change, management must be conducted in this larger context in order to maintain forest functions- and in some areas, forests at all.

4.4 Key unknowns- Our work struggles with several limitations, and also highlights several areas in need of future research. Its most significant limitation emerges from its greatest strength, in the sense that so many experimental designs and datasets can be brought to bear on so many aspects of the ecosystem at a single site. While this allows for a holistic view of C cycling and its drivers, the lack of consistency in individual studies precludes an elegant, balanced synthetic analysis. The resulting narrative synthesis is as complex as the ecosystem itself, and in simplifying this complexity for clearer communication, we have minimized attention to potential issues such as stand-level variation in disturbance histories and the disconnect between inferences from a 20-year flux record vs. a 200-year chronosequence. The spatial and temporal distribution of past clearcutting and fire at UMBS is more nuanced than we communicate here, and in focusing on what is consistent across disturbance types, we overlook the potential that localized past events may be influencing the results we report (Cooper 1981; D'Amato et al. 2017; Farmer 1958; Kilburn 1957). Similarly, we emphasize consistencies, rather than differences between the decadal patterns of succession in the flux tower footprints and the centuries-long continuum of chronosequence and old reference stands. Notably, our NEP estimates over these longer timescales indicate that only one of these stands is definitively a C sink (Clay et al. 2022), a result which is at odds with tower-based observations showing a consistent C sink over time.

One of the key unknowns in this study is the degree to which several unaddressed belowground processes and C fluxes vary over successional time. In this work, we are limited to relatively coarse metrics of belowground C cycling, such as soil respiration and fine root production. More detailed investigations of processes such as root exudation, fungal hyphal production, and bacterially-mediated C and nutrient transformations would result in more mechanistic inferences into microbial and biogeochemical drivers of belowground C cycling over succession. This is particularly true for N cycling processes, given the likelihood that this site's strong N limitation will only increase with CO_2 fertilization and N oligotrophication (Groffman et al. 2018).

Another key unknown in our study is the broader spatial (and longer-term temporal) relevance of our results pertaining to the ecophysiology and growth trajectories of red oak. The similarity of oak's increase at UMBS and the long-term Harvard Forest AmeriFlux site (Finzi et al. 2020), concurrent with the increasing C sink strength at both sites, implies a potential connection between composition and C cycling functions, not to mention a bright future for oak. In contrast, a recent synthesis of oaks in the context of climate change indicates more complex, and likely negative prospects for the genus. Namely, the same acquisitive traits that have facilitated oak's competitive rise at these humid sites predispose them to decline as warming continues and vapor pressure deficit increases (Novick et al. 2022). Here, there are clear management implications for how drought, pests and pathogens, and C cycling interact in oak forests throughout the East. As climate change and other pressures continue to increase, management interventions such as thinning and prescribed fire may be necessary to support oak persistence, while accepting novel structures, reduced densities, and increased mortality as inevitable (Clark et al. 2022, Isaacson et al. 2023; Refsland et al. 2020). As conditions continue to change, further research will be needed to examine the ecological mechanisms by which management affects composition and C cycling, across a range of structures and successional stages, in oak and other forest types.

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Figure Captions

Figure 1. The UMBS landscape. Map shows the locations of plots within the paired chronosequence stands (1x cut+burn and 2x cut+burn) and old reference forests, as well as the US-UMB (reference, to west) and US-UMd (treatment, to east) flux tower plot networks. Shading indicates landscape-level physiography. Inset: UMBS' regional location.

Figure 2. Panel A: Total ecosystem C stocks and their distribution among pools, for plots in both chronosequences and the three old reference forests. Individual plots have been binned into 40-year age classes. Bars are means, errors are standard deviations, and letters denote significant differences between means (Fisher's L.S.D.; overall ANOVA $P<0.001$). See Appendix S1 for statistical test results. **Panel B:** Proportions of total aboveground live tree biomass for three functional tree groups, by 40-year age class (presented for qualitative patterns but not statistically analyzed).

Figure 3. Panel A: NPP_w (mean and standard error) vs. stand age for young (22-48 years), middle-aged (66-84 years), and old (>100 years) stands. **Panel B:** For a multiple regression model for each age category, the proportion of variance in NPP_w explained by individual structural parameters, including leaf area index (LAI; blue), mean maximum canopy height (Max Height; orange), and canopy rugosity as variance of combined vertical and horizontal leaf distributions throughout the canopy (Rugosity; green). The residual (unexplained) variance in each regression model (young, mid, old) is plotted in gray. **Panel C:** Standardized structural parameter values and NPP_w rates for individual plots in young, middle-aged, and old stands. Structural parameters significantly related to NPP_w are indicated with enlarged points and best-fit lines.

Figure 4. Long-term annual leaf litter production in reference and treatment (accelerated succession) tower footprints. Leaf litter production is shown for all vs. only early-successional species (panel A), and for *Q. rubra* vs. *Acer* spp. (panels B, C). Points plotted are means and standard errors for litterfall collections in 10-14 plots per footprint. Best fit lines indicate statistically significant relationships between year and leaf litterfall flux. Note differences in the period of record for reference (1997-2019) vs. treatment (2006-2019) footprints.

Figure 5. Soil CO_2 emissions as a function of stand age. **Panel A:** Annual total soil respiration (RstA) flux and the proportion of the total from heterotrophic sources (Rsh/Rst). **Panel B:** Annual autotrophic (RsaA) and heterotrophic (RshA) soil respiration fluxes. **Panel C:** Growing season total soil respiration (RstGS) flux and the proportion of the total from heterotrophic sources. **Panel D:** Growing season autotrophic (RsaGS) and heterotrophic (RshGS) soil respiration fluxes. Values presented are stand-level means across the 2014-2021 growing seasons. Statistics are for simple linear regression, with best-fit lines added for statistically significant relationships with stand age. In panels A and C, filled circles are Rst fluxes and open circles are Rsh/Rst proportions. In panels B and D, green triangles are Rsa fluxes and purple squares are Rsh fluxes.

Figure 6. Panel A: Growing season fine root production as a function of stand age. **Panel B:** Growing season fine root production vs. annual total soil respiration. Points plotted are stand-level means across all available years of observation; P and r^2 values are for simple linear regression.

Figure 7. Panel A: Relationships between stand age and A horizon properties including total C (%, filled triangles) and microbial biomass C (mg kg^{-1}, open triangles) concentrations, and pH (filled circles). **Panel B:** relationship between A horizon %C and pH. **Panel C:** Relationship

between A horizon pH and α-glucosidase activity. In each panel, r^2 and P values are presented for simple linear regressions relating the individual variables.

Figure 8. Principal coordinates analysis biplot of fungal community dissimilarity across A horizon soil samples from the Burn Plots. Points and ellipses are color-coded according to stand ages (in years, as of 2015 when samples were collected). Ellipses represent 95% confidence intervals for each stand, and vectors represent the top 5 families responsible for community dissimilarity.

Figure 9. Distance based redundancy analysis biplot of fungal community and soil property dissimilarity across A horizon soil samples from the Burn Plots. Points and ellipses are color-coded according to stand ages (in years, as of 2015 when samples were collected). Ellipses represent 95% confidence intervals for each stand, and vectors represent the soil properties that were significantly related to community dissimilarity in a forward stepwise regression model.

Figure 10. ^{15}N signatures of sporocarps collected from ^{15}N-labeled plots in reference and treatment footprints. Plots were labeled with $^{15}NH_4Cl$ in 2010; sporocarps were collected in 2022. Plotted are means and standard errors for 5-15 sporocarps per family, with significant differences ($P<0.05$; Fisher's LSD) between families indicated with letters.

Figure 11. Mineral soil carbon stocks, by genetic horizon, for soil profiles sampled in 1980 and 2009 in an area of unmanipulated 1911-origin reference forest adjacent to the Burn Plots. Plots show means and standard errors; difference of means is significant ($P<0.05$) for A and E horizons.

Figure 12. Panels A-C: Ecosystem C fluxes and water use efficiency, for reference (filled circles) and treatment (open circles) footprints. C fluxes follow eddy-covariance sign

conventions, such that uptake is negative (GPP, NEE) and emissions are positive (R_{eco}). To aid in visualization, timeseries lines connect individual annual values in each plot. Significance of year and treatment are denoted in each panel, with r^2 values provided when only year is significant, and the adjusted R^2 provided when year and treatment are both significant. **Panels D-F:** Mean annual temperature (D), precipitation (E), and bulk inorganic N deposition (F) at UMBS, 1980-2020, with regression P and r^2 values. Climatologic variables are averaged from daily observations from a weather station on the main campus, adjacent to Douglas Lake. Atmospheric deposition data are from the National Atmospheric Deposition Program (UMBS site ID MI09).

Figure 13. Synthesis of ecosystem changes over successional time. The three columns (A, B, C) correspond to the three experimental designs described in section 2.2, which correspond to three semi-discrete developmental phases that collectively span 200 years of succession. Column A shows trends inferred through the paired chronosequences (particularly the Burn Plots) over the first century of stand development. Column B corresponds to FASET, the paired comparison of background reference vs. experimentally accelerated succession footprints, over a 2-decade period from stand age ~90-100. Column C highlights the three old reference forests, with ages ranging from 130 years for the two pine-dominated stands to approximately 200 years in the uneven-aged hemlock-northern hardwoods stand. See section 4.1 for accompanying narrative. Illustration by Jennifer Kalejs.