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Intermediate disturbances drive long-term fluctuation in old-growth forest biomass: an 84-yr temperate forest record

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Abstract. What are typical values and dynamic status of live-tree biomass pools in old-growth, mesic, cool temperate forests? A handful of biomass density estimates in eastern North American temperate forests show large biomass/carbon reserves on a per-area basis. However, it is less clear whether these ecosystems are, over multi-decade scales, typically steady-state or non-equilibrial carbon pools. Previous studies have suggested both possibilities, but claims are based on inferences from short-term studies or proxy data sets. An unusually long-term and extensive data set from repeatedly sampled permanent plots (84 yr, ca. 10 ha sample area, 6–8 measurements), from old-growth conifer-hardwood forest in northern Michigan, USA, allows direct estimation of multi-decade trends in aboveground live-tree biomass. Results confirm prior suggestions of high-biomass density for old-growth temperate forests (averaging >300 Mg/ha), but, despite significant decade-scale variation, show no overall, long-term directional change. Study plots typically show multi-decade trends of gradually increasing biomass density, interrupted by sharp declines attributed to intermediate-severity disturbances, with recovery of pre-disturbance biomass density requiring upwards of a half-century. At the stand scale, biomass dynamics are strongly historically contingent, and short-term studies may yield biased or misleading results. Disturbance legacies, through demographic and structural effects, can have multi-decade effects on vulnerability to further disturbance. While this study shows no general trend in aboveground biomass pools, it suggests that changes in disturbance regime may drive important feedbacks in biomass pool dynamics.

Key words: biomass pool; carbon cycle; ecosystem stability; hemlock-hardwood forests; late-successional forest; long-term study; old-growth; research natural area; stand development.

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INTRODUCTION

As large and active biomass pools, forests play a central role in the global carbon cycle. Forests of northeastern North America have acted as a significant carbon sink in recent decades, largely because of regional dominance by relatively young forests, following post-agricultural forest re-establishment and changes in forest management (Myneni et al. 2001, McKinley et al. 2011, Pan et al. 2011, Lu et al. 2017). There is little agreement, however, about likely trajectories of net ecosystem production as these forests age into later stages of stand development. Better understanding of biomass and carbon dynamics in older forests is important for modeling the carbon cycle and for management and monitoring of biomass/carbon pools and fluxes, but longitudinal studies of biomass density in late succession remain rare.

A long-held and influential model of biomass development over succession in temperate

forests of northeastern North America (Bormann and Likens 1979) predicts that forests more than 300 yr old should, over decadal scales, exhibit stable biomass density, or net ecosystem productivity near zero, following an earlier peak and decline. The spatial scale for this dynamic is implied, but it is usually taken to apply at the scale of the "stand"—perhaps several to hundreds of ha. The Bormann and Likens model, however, used empirical data only from relatively young, post-logging forests, inferring biomass dynamics for older stands from simulation models. Models assumed disturbance dynamics dominated by spatially scattered and temporally continuous single-tree mortality (i.e., "gap-phase" dynamics), creating a dynamically stable "shifting mosaic" of small patches the size of one or a few canopy trees (typically 10s of m^2). To date, only a few studies have directly quantified biomass density for old-growth forests of this region (Keeton et al. 2011, Woods 2014, Halpin and Lorimer 2016, D'Amato et al. 2017). While these studies show very high biomass/carbon reserves on a per-area basis, they generally do not directly assess multi-decade biomass dynamics.

Over the last two decades, empirical studies have suggested variations on and departures from the steady-state model of biomass in old-growth forests (Bormann and Likens 1979). Some retain the expectation of stand-scale steady-state biomass density in old-growth, but call for longer times for reaching this state (Tyrrell and Crow 1994, Fahey et al. 2005). Others raise the possibility of continuing (or very long-term) biomass increases, making older forests carbon sinks (Ziegler 2002, Pregitzer and Euskirchen 2004, Luyssaert et al. 2008, Keith et al. 2009, Foster et al. 2014, Gough et al. 2016), or even of old-growth forests acting as net carbon sources (e.g., Baccini et al. 2017, in tropical forests). Inconsistency in ideas about carbon storage and biomass dynamics over multiple decades or centuries may be attributed to differences in accounting for effects of natural disturbance, stand structure, or tree species composition.

In particular, researchers have questioned earlier assumptions, including those of the Bormann-Likens (1979) model, about disturbance regimes in old-growth forests. Several recent studies suggest an important role for intermediate disturbances—less frequent, but more intense and extensive than the gap-phase processes assumed by earlier models—in shaping community assembly and population structures in temperate old-growth forests (Millward and Kraft 2004, Woods 2004, 2007, Hanson and Lorimer 2007, Nagel et al. 2007, Firm et al. 2009, Stueve et al. 2011), However, studies focused on effects of intermediate disturbances have not addressed consequences for net ecosystem production and biomass accumulation. Researchers in other systems (e.g., Heinselman 1973 in subboreal forests) have extended the "shifting mosaic" concept to include much broader spatial scales and more severe disturbances, including stand-originating disturbances to predict dynamically stable ecosystems over large landscapes, while stand-scale dynamics remain generally non-equilibrial.

Definitions of intermediate disturbance vary and are often approximate. We follow the terminology of Stueve et al. (2011) who define intermediate disturbances as those causing ca. 30–60% canopy loss, at stand scales, in a single event. Such disturbances are not incorporated in the Bormann-Likens model, and we focus on their potential role in shaping biomass dynamics. Intermediate and larger disturbances may alter canopy structures in ways affecting efficiency of photosynthetic light capture (Hanson and Lorimer 2007, Hardiman et al. 2013, Fahey et al. 2015) as well as age distributions and species composition differently than single-tree "gap-phase" disturbance processes. Some researchers estimate return times for intermediate disturbances to be less than the typical lifetime or canopy residence time of trees in late-successional stands (Hanson and Lorimer 2007). Dominant tree species in conifer-hardwood forests of eastern North America have potential life-spans exceeding 300 yr and typical canopy residence times of 150–200 yr (Frelich and Graumlich 1994, Dahir and Lorimer 1996, Ziegler 2002). Consequently, it is important that models of old-growth dynamics include intermediate disturbance effects on biomass density.

Relationships between biomass density and species composition and size structure are also poorly documented for old-growth temperate forests. Stand-scale biomass density can be dominated by large stems of low frequency in

temperate coniferous forests of western North America (Lutz et al. 2012) and in a global network of forest plots (Lutz et al. 2018). In the latter study, however, study sites from eastern North America all exhibit 'large-tree' biomass proportions well below the global mean of ca. 50%, and most are not old-growth forests. Documentation of effects of canopy species composition on biomass density within old-growth hemlock-northern hardwoods is sparse and inconsistent. Differences in species composition are correlated with differences in maximum biomass across regions (Busing 1993, McGarvey et al. 2015). However, estimates for northeastern mesic forests have shown both conifer-dominated (Hoover et al. 2012) and hardwood-dominated (Woods 2014) stands with higher biomass density.

Because of the multi-century timescale of forest development, variation in ecosystem properties over a few years or decades may not be representative of long-term dynamics, and is inadequate for the assessment of long-term stability in biomass. The risk of erroneous conclusions from data of inappropriate time-scale was defined by Magnuson (1990) as the 'invisible present' problem. Studies of ecosystem function in old-growth forests are few, and most are based on either short-term or proxy data, and so are particularly vulnerable to this source of error; relatively stable biomass over one or a few decades is weak evidence for long-term equilibrium. While planned long-term forest dynamics studies have been established recently in cool-temperate forests (Anderson-Teixeira et al. 2015), old-growth temperate forests are not well-represented in these systems. Consequently, claims about dynamic properties in old-growth forests are subject to severe data constraints and generally rely on extrapolations from conceptual models, stand simulations, or space-for-time substitution, all involving difficult-to-test assumptions.

We use a dense network of permanent plots from a mesic old-growth forest in Michigan, USA, established in 1935 and remeasured 6–8 times through 2019, to assess trends in biomass density and to assess competing models and predictions. This unique data set supports analysis of aboveground, living biomass at spatial scales from single plots (ca. 800 m^2) to about 50 ha, and for time intervals from 5 to >80 yr. While the full study period remains relatively short in terms of the intrinsic time-scale of these systems, this is one of the longest-term data sets for old-growth temperate forests (but see Brzeziecki et al. 2020), and the first in eastern North America to reach half the estimated typical canopy residence time for dominant species. We use this data set to address several related questions about biomass dynamics, specifically for old-growth, cool-temperate forests:

1. Are living biomass dynamics over >80 yr more consistent with expectations of stand-scale steady-state as suggested by the Bormann and Likens model, or non-equilibrium alternative models? Are short-term patterns indicative of longer-term trends?
2. How are biomass dynamics related to stand properties like species composition and stem-size distribution?
3. How do small-scale (gap-phase) and intermediate disturbance differ in effects on biomass dynamics, at plot and stand scales and at varying temporal scales?

Methods

Study site

The Dukes Research Natural Area (RNA) is a 100-ha parcel within the Dukes Experimental Forest of the Hiawatha National Forest, in northern Michigan, USA (approximately 46°02′ N 87°09′ W), about 14 km south of Lake Superior (Fig. 1). The RNA was established in 1974 (USDA Forest Service 1974) to preserve relatively undisturbed, mature hemlock (*Tsuga candensis*)-hardwood *forests that were once common in the region prior to European-American settlement. Increment cores (K.D. Woods, unpublished data*) from upland portions of the study area show mixed age structures with maximum ages of ca. 400 yr for dominant species in all portions of the stand. The RNA is buffered in the landscape by a continuous cover forest that was never clear-cut and has been managed with long cutting cycles and high stocking levels (high residual stand basal area).

Forests of northern Michigan are influenced by both fire and wind disturbances. However, mesic stands on fine-textured soils rarely show evidence of significant fire disturbance. Typical

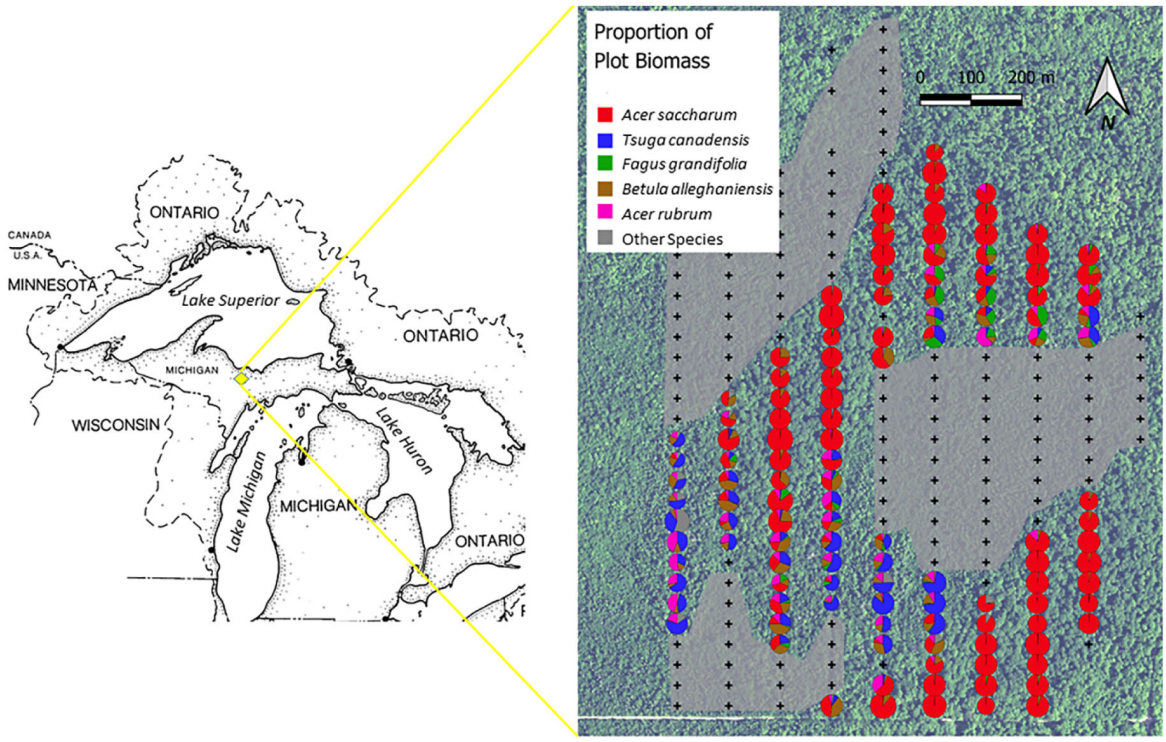

Fig. 1. (Left) Location of the Dukes Research Natural Area (RNA) study site in the western Great Lakes Region (map modified from NOAA Great Lakes Environmental Research Laboratory "Map of the Laurentian Great Lakes"). (Right) Map of Dukes RNA with upland sample plots indicated by pie-charts representing proportional biomass for dominant species for the 1997–1999 sampling period (prior to the 2002 windstorm). Plots in grayed areas (shown by crosses) are in peaty wetlands and dominated by swamp conifers. Size of each pie-chart is proportional to total biomass for the plot: Maximum plot biomass density for the 1998 sampling period was 548 Mg/ha. "Other species" with significant representation in some plots include *Pinus strobus*, *Thuja occidentalis*, *Tilia americana*, *Fraxinus nigra*, and *Ostrya virginiana*.

fire-dependent and fire-resistant species are lacking at the Dukes RNA. Soil charcoal, burnt stumps, and fire scars have not been observed. Return times for canopy-killing fire in such stands have been estimated at several millennia for the region (Frelich and Lorimer 1991, Zhang et al. 1999), several times the return interval for severe windthrow events. We assume wind to be the dominant cause of intermediate to major disturbance in upland portions of the Dukes RNA.

In the northwestern Great Lakes region, windthrow is typically associated with regional convection-driven systems—severe thunderstorms—producing localized, patchy blowdowns (Canham and Loucks 1984, Frelich and Lorimer 1991, Zhang et al. 1999, Schulte and Mladenoff 2005). Severe and extensive blowdowns associated with regional storm events like derechos are estimated to have return times of one to several millennia, and disturbance patterns within these events tend to be patchy (Fujita 1978, Jenkins 1995). In the absence of more severe disturbance, "background" mortality associated with gap-phase dynamics has been estimated to affect about 10% of the canopy per decade (Frelich and Lorimer 1991, Woods 2004). Moderate-severity disturbances, defined as dominated by blowdown patches of <1 ha and affecting 30–60% of the canopy (Stueve et al. 2011), are estimated to have local return times of 100–300 yr (Frelich and Lorimer 1991). The Dukes RNA has experienced two disturbances of intermediate scale, one documented and one undocumented but inferred, over the 84-yr

study period. The documented disturbance, a local thunderstorm in July 2002, with winds of ca. 150 km/h, caused mortality approximately equal to the previous decade of "background" gap-phase mortality over the entire stand. Storm-caused mortality was, however, patchy and substantially more intense in some parts of the stand (Woods 2004, 2007). The undocumented disturbance between 1935 and 1948 (hereafter "post-1935 disturbance," discussed below) is inferred from observations as reported below.

Annual mean temperature for 1935–2020 (the period of the data set), at the weather station nearest the RNA (at Marquette, MI, ca. 30 km NW) was 5.1°C (January average = –8.9°C, July average = 18.9°C) (NOAA Online Weather Data, https://w2.weather.gov/climate/xmacis.php?wfo=mqt). Annual precipitation averaged 858 mm with nearly half as snowfall (cumulative annual snowfall averages >4000 mm). Climate is moderated by proximity to Lake Superior. Elevation within the RNA varies by <10 m, with average elevation of ca. 330 m AMSL (about 100 m above Lake Superior). Upland soils are developed in thick glacial till over Paleozoic sedimentary deposits; some areas have well-developed hardpan, and there is significant variation in base cation availability (USDA Forest Service 1974, Woods 2000). Peaty, organic soils occur over about half the RNA.

Forest composition in the RNA varies with soil conditions. Peaty wetlands within the RNA are dominated by *Thuja occidentalis* L., *Picea mariana* (Mill.) Britton, Sterns & Poggenb., *Fraxinus nigra* Marshall, *Acer rubrum* L., and, formerly, *Ulmus americana* L. (Woods 2007), but these areas are not addressed in this paper. Uplands (sandy and silty loams of varying chemistry (Woods 2000, 2007)) support hemlock-hardwood forests with dominance varying among *Acer saccharum* Marshall, *Fagus grandifolia* Ehrh., and *Tsuga canadensis* (L.) Carrière. Subdominant species include *Betula alleghaniensis* Britten, *Acer rubrum*, *Ostrya virginiana* (Mill.) K. Koch (sub-canopy only) and several minor species (Woods 2000, 2007). *Fagus* arrived in the area only in latest Holocene, 500–1000 ybp (Davis et al. 1986, Woods and Davis 1989), and the RNA is within ca. 10 km of the species' main western range limit.

The RNA has never been managed or cleared for settlement; however, some early, undocumented removal of selected species may have occurred within the RNA boundaries (USDA Forest Service 1974). For example, logging of *Pinus strobus* L. from 1880–1900 and some cutting of *Ulmus* sp. and *Tilia americana* L. occurred in the vicinity of the RNA from 1900–1910. However, the cutting, if any, was likely light, because very large individual *Pinus strobus* are still present in the RNA, stand structures as early as 1935 do not suggest large-scale disturbance (particularly in upland areas), and no cut stumps were noted in sampled areas in the 1930s (data sheets) or 1970s (KW, Dr. Frederick Metzger, *personal communication*).

Sampling design

This study uses data from a network of permanent ("Continuous Forest Inventory") sample plots, established in 1935 on a uniform grid (2 × 5 chain—ca. 40 × 100 m—spacing) across the RNA. Plots are circular with area of 0.2 acre (ca. 809 m^2), and centers are marked with an iron pipe, allowing precise relocation. The network includes 246 plots in total, including upland and peatland areas. In 1935, stems were tallied by species and dbh to the nearest inch for 238 plots (some plots identified as "transitional" between mapped forest types were skipped). The minimum dbh recorded was 5 inch; assuming measurements were to nearest inch, the smallest stems recorded would have been about 11.5 cm dbh. In 1948, 123 plots (alternating along N-S grid lines) were remeasured using the same protocol. Between 1974 and 1980, remeasurements of 243 plots included all stems to minimum dbh of 0.5 inch (1.3 cm). From 1989 to 2019, 123 plots, in upland stands only, were remeasured on staggered 5-yr cycles, and stems >5 cm dbh were measured and mapped, to permit spatial and demographic analysis.

Data set

Analyses reported here use data from 123 plots in upland portions of the RNA (excluding plots in peatland areas) and include only stems >11.5 cm dbh for consistency across all measurement periods. For most comparisons, data were pooled for the 1974–1980 period (subsequently referred to as "1977 sampling period") and for measurements in 1992–1994 ("1993 sampling period") and subsequent five-year remeasurements (identified as "1998 sampling period"

through "2018 sampling period"). To visualize trends over time, data were simplified by pooling staggered sampling of plot subsets by "sampling periods" defined above. Not all plots were measured in each sampling period. See previous publications (Woods 2000, 2004, 2007, 2009) for additional details concerning sampling and data set.

To examine variation related to spatial and compositional patterns in the RNA, plots were assigned to previously defined forest "patches," defined by substrate and canopy composition (Woods 2000, 2007). Patches were categorized as "sugar maple-dominated" (canopy dominated by *A. saccharum*), "hemlock-dominated" (canopy dominated by *Tsuga canadensis*), and "mixed" (significant representation of *Acer* (including *A. rubrum*), *Tsuga*, and *Fagus*) (Fig. 1).

Biomass calculations and analyses

Aboveground biomass was estimated for all living trees >11.5 cm dbh at each sampling period using allometric equations from Jenkins et al. (2004) and other sources (see Appendix S1 for full list of original equation sources and full species names). When multiple options were available, selection favored equations that were developed in the northwestern Great Lakes region, were based on larger sample sizes, and fitted on samples including larger diameter stems. However, no allometric equations were fitted using trees larger than about 70 cm dbh (less for several species). For all significant upland canopy species in the Dukes RNA, stems >70 cm dbh are present and can account for a large proportion of total biomass in individual plots (see *Results*). For species with multiple published equations, biomass estimates for stems up to about 60 cm dbh were generally quite similar, but estimates sometimes diverged for larger stems, differing by up to 30% in the 90–100 cm range (maximum sizes for most species in this study) (Woods 2014). Additionally, very few allometric equations include assessment of estimation error, although Woods et al. (1991) estimate coefficients of variation of 5–20% for plot-level biomass density estimates based on allometric equations for successional sub-boreal forests. Consequently, biomass estimates here include an unknown error and unknown potential bias with respect to contributions by the largest stems. Biomass for all stems was summed by plot and sampling period and converted to biomass density (Mg/ha).

Mean biomass density for each sampling period was taken as the average of plot-level biomass density calculated for all plots measured in the sampling period, and compared across sampling periods (question 1). Because plot-level biomass estimates within sampling periods were not normally distributed, 95% confidence intervals (CIs) for sampling-period means were bootstrapped ("mean_cl_boot" option for stat_summary operator, ggplot2 package in R (Wickham 2016)). We assess non-overlapping 95% CIs as indicating change in average stand biomass density between measurements. However, a strict interpretation of *P*-level is inappropriate because repeated measurements of the same stems and potential spatial autocorrelations among plots limit assumptions of independence.

To assess relationships between biomass dynamics and initial stand properties (question 2), we examined patterns of total and proportional biomass change as related to initial plot biomass density for each sampling period. For each sampling interval, we used linear relationships between initial and final plot biomass densities (fitted, with 95% CI, with "glm" option in ggplot2 package of R) to interpret both general biomass trends and effects of initial conditions on biomass dynamics. Equilibrial biomass at the plot scale (question 1) should generate a distribution of points around the 1:1 diagonal (slope = 1). Where the observed 95% CI for the relationship between initial and final biomass density does not include this diagonal, plot-level biomass equilibrium may be rejected for that interval in favor of general gains (relationship positioned generally above the diagonal) or losses (below the diagonal). Slopes <1 indicate greater absolute biomass growth for plots with initially lower biomass density and slopes >1 the reverse relationship. Patterns in proportional change in biomass density were examined using Spearman rank correlations between initial plot biomass and proportional change over succeeding measurement interval. For the five-year intervals from 1993 to 2018, analyses were also conducted for pooled intervals of 10–15 yr after the 2003 sampling period to obtain an interval more comparable with pre-1993 intervals, to

assess whether patterns observed are sensitive to temporal scale of observation (Magnuson 1990), and to examine biomass recovery following the 2002 windstorm. The 1999–2003 period was not pooled with other intervals because it contained the disturbance event.

To assess relationships between tree size distributions and biomass density dynamics (question 2), we calculated empirical cumulative distributions (ECDs) of biomass as a function of stem diameter for each sampling period. To focus on the relative contributions of larger stems, ECDs were calculated and plotted from the largest to smallest stems. Again, some intervals were pooled, allowing focus on longer periods bracketing the 2002 blowdown. Differences between ECDs were assessed by Kolmogorov-Smirnov tests ($P < 0.05$ interpreted as significant difference).

Maps of plot biomass density and biomass density changes for individual sampling periods and intervals were compared to assess stand-scale spatial patterns in biomass dynamics (question 3). Spatial patterns in biomass effects of the 2002 windstorm were compared to patterns in intervals without known significant disturbance events and to patterns related to the post-1935 inferred disturbance (see *Results*). We used simple chi-squared tests for post hoc comparisons of disturbance frequency between portions of the study area.

To focus on the effects of specific, intermediate disturbances (question 3), we contrasted sets of plots most affected by the two identified disturbances with comparable, nearby plots that experienced little or no mortality and biomass loss in the same intervals. Twenty plots lost >25% of pre-storm biomass in the 2002 windstorm. Twenty comparison plots that had little (<5%) or no biomass loss in the 2002 windstorm were selected from the nearest upland plots to each of the severely disturbed plots. Because blowdown disturbance patterns were quite patchy at the plot scale (Woods 2007), it was possible, in all cases, to select comparison plots within 100 m (and usually within 40 m) of "disturbed" plots. Fifteen plots experienced >25% biomass loss between 1935 and the next sampling period (1948 or 1977) (because of potential regrowth before remeasurement, initial loss of biomass may have been substantially greater), and a similar comparison set of plots was selected for these. It is impossible to be certain that this post-1935 biomass loss was due to a single event, and we found no documentation of a significant storm or blowdown for the relevant period, but clustered spatial distribution within the stand (see *Discussion*) is consistent with a single-disturbance interpretation. By contrast, only four, scattered plots showed >25% biomass loss during the 21-yr period 1977–1998, suggesting no intermediate to severe stand-scale disturbance in that interval.

All statistical analyses were performed in the R environment, versions 3.4 to 4.0 (R Core Team 2021), as reported in Appendix S2.

Results

General biomass trends (question 1)

Biomass density, averaged across all upland sample plots, varied by more than 20% over sampling periods, ranging from 294 Mg/ha in 1948 (for a smaller sample size) to 352 Mg/ha in the 1993 sampling period (1992–1994) (Table 1). Biomass density in individual plots frequently

Table 1. Average plot biomass densities at Dukes RNA by patch type and sampling period.

	Acer-dominated			*Tsuga*-dominated			Mixed, with *Fagus*			Overall		
Census	Mg/ha	N plots	SE	Mg/ha	N plots	SE	Mg/ha	N plots	SE	Mg/ha	N plots	SE
1935	331.0	66	9.5	273.9	18	20.9	290.5	32	11.6	310.9	116	7.3
1948	327.9	32	13.8	244.1	12	17.0	266.5	17	15.0	294.3	61	10.0
1977	359.6	65	9.1	260.9	24	15.0	316.5	33	13.1	328.5	122	7.5
1993	370.3	66	9.6	304.9	22	18.1	347.5	34	10.0	352.1	122	7.0
1998	377.1	66	10.0	313.1	22	18.4	356.2	34	10.1	360.9	120	7.2
2003	336.9	66	11.6	309.1	21	15.9	324.7	33	13.1	328.0	122	7.7
2008	335.5	66	11.7	309.4	22	14.2	314.5	34	15.0	325.0	122	8.0
2013	334.1	66	11.4	299.0	23	16.6	310.6	34	15.2	320.9	123	8.0
2018	350.2	66	11.5	322.4	21	16.7	316.7	34	14.6	336.0	121	8.1

varied by more than twofold over the study period, and by as much as 10-fold for plots severely affected by the 2002 windstorm (Figs. 2, 3). While mean biomass varied substantially between sampling periods, often with non-overlapping 95% confidence intervals (Fig. 2), overall mean biomass density at the final measurement period (2018) was not significantly

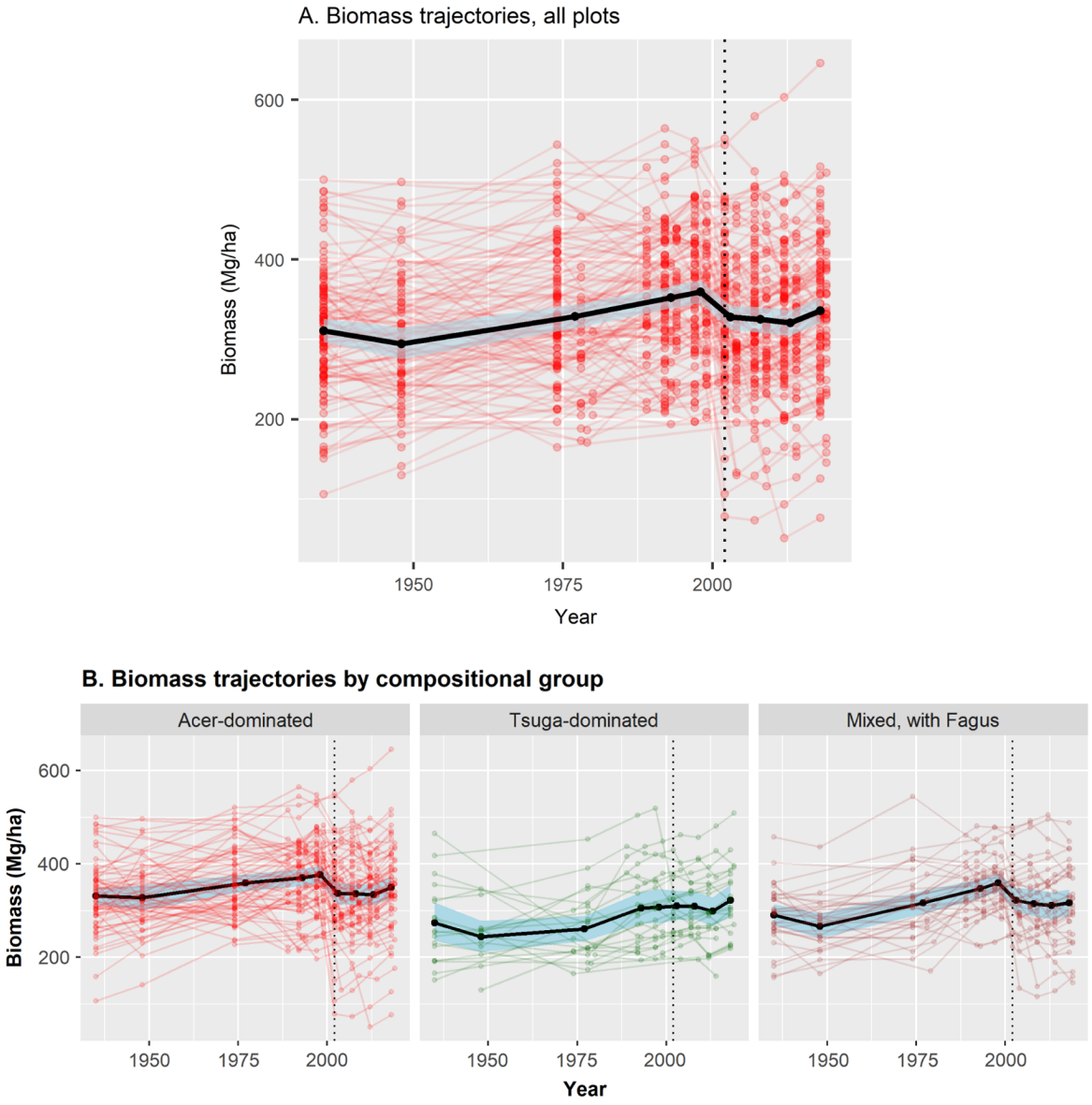

Fig. 2. Trajectories of biomass density over time by plot and means over an 84-yr study period at the Dukes Research Natural Area, Michigan, USA. Vertical dashed lines indicate the 2002 blowdown. (A) Red lines connect dots for each sample year for individual sample plots (Not all plots were sampled in all sampling periods). Heavy black line connects mean biomass density for each "sampling period" grouping; light blue shading shows bootstrapped 95% confidence intervals. (B) Similar representation for forest "patches" or plot groups of similar canopy composition and substrate. For each grouping, number of plots varies over sample periods (Table 1).

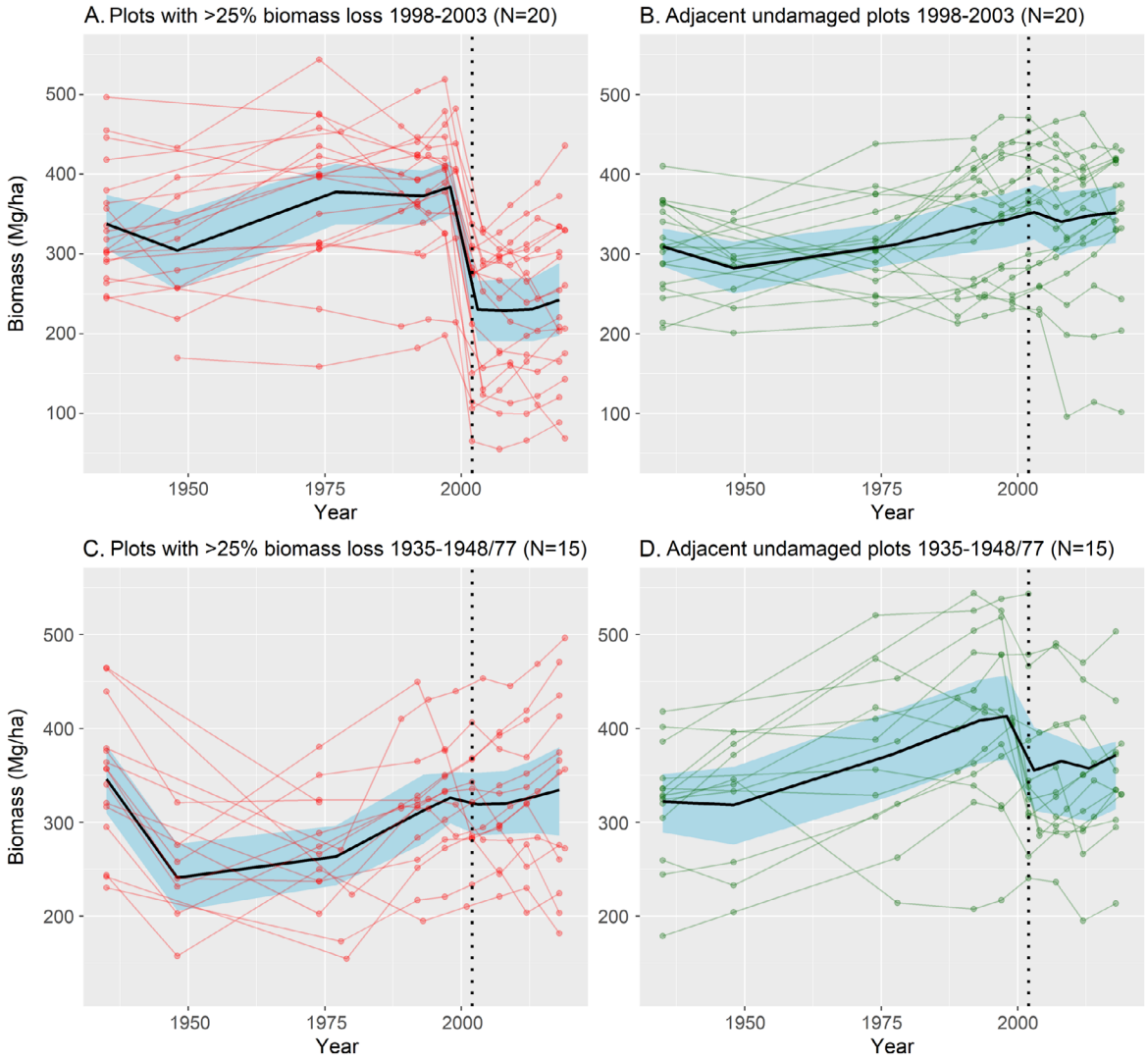

Fig. 3. Biomass trajectories associated with two intermediate disturbances during study period. Representation by lines and colors is the same as in Fig. 2, but for subsets of plots experiencing >25% biomass loss in the 2002 windstorm (A) and in inferred post-1935 disturbance (C), compared to subsets of adjacent and similar plots that were not significantly influenced by these events (B for the 2002 windstorm, D for the post-1935 inferred disturbance). See "*Biomass calculations and analyses*" for explanation of comparisons.

different from that for the initial (1935) sampling period (Fig. 2).

Even though average biomass density did not differ between the initial and most recent sampling periods, averages increased over the majority of intervals between sampling periods. Mean biomass density increased during intervals from 1948–1977, 1977–1993, 1993–1998, and 2008–2018, totaling 60 yr, or more than two-thirds of the 84-yr study period. Rates of increase for the first three of these intervals were nearly constant. Stand-averaged biomass density decreased over intervals (1935–1948 and 1998–2008) totaling less than half as long as increasing intervals, but these shorter-term losses approximately balanced long-term gains.

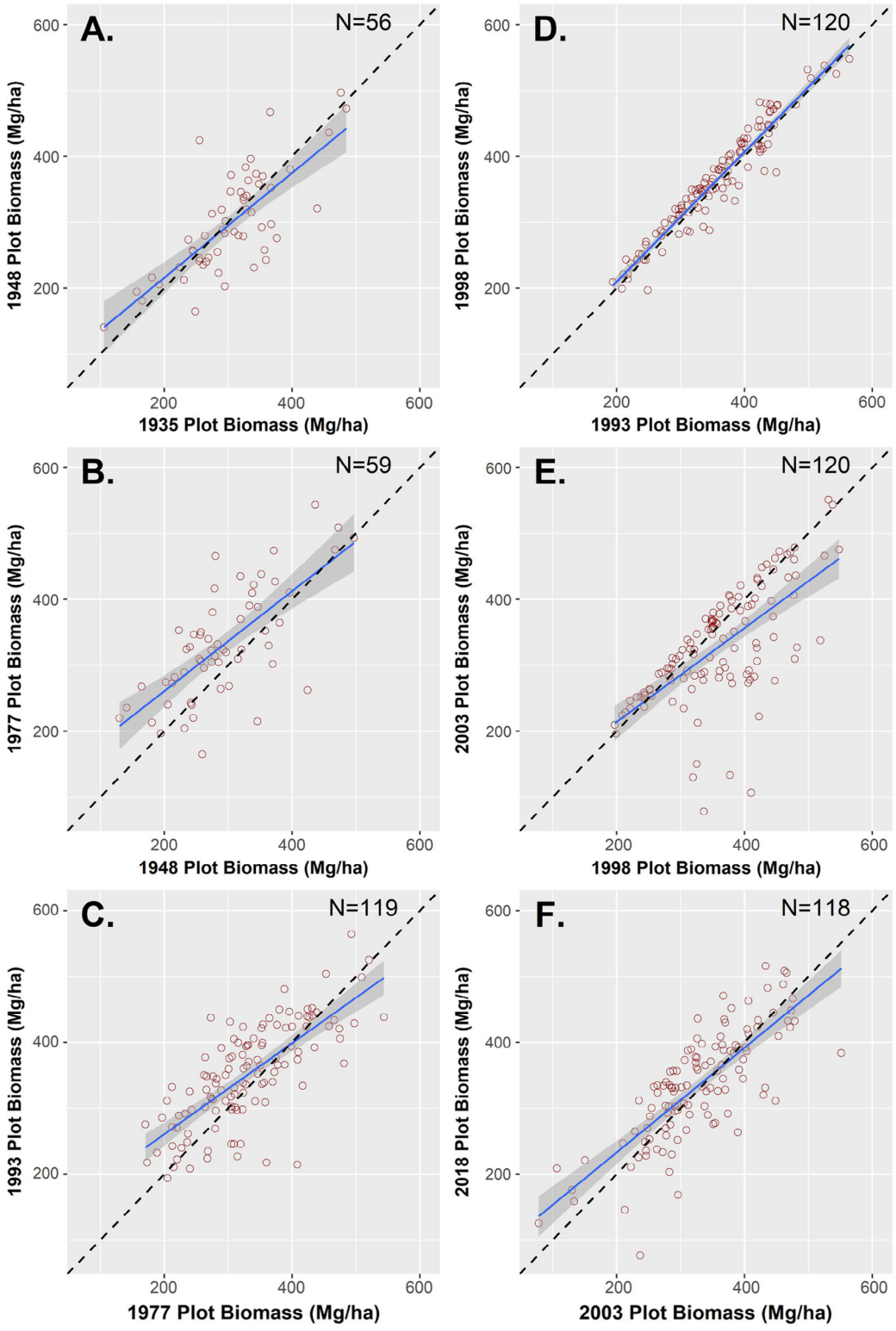

Fig. 4. Stability of biomass density over sampling intervals within the 84-yr study period. Symbols show

(Fig. 4. *Continued*)

individual plot biomass density at the end of a sampling interval graphed against biomass density at beginning of interval for all plots sampled in both sampling periods: (A) 1935–1948, (B) 1948–1977, (C) 1977–1993, (D) 1993–1998, (E) 1998–2003 (including 2002 windstorm), and (F) 2003–2018. Dashed line of slope = 1.0 indicates no change tendency or stable biomass over the sampling interval. Linear regressions (95% confidence interval shaded in gray) have slopes significantly <1.0 ($P < 0.01$) except for the 1993–1998 interval (D).

Biomass trends related to local stand properties (question 2)

For individual plots, absolute biomass density change over individual measurement intervals was significantly negatively related to biomass density at the beginning of the interval. For all intervals >10 yr in duration (1935–1948, 1948–1977, 1977–1993, and the pooled interval from 2003–2018: Fig. 4), linear regressions of end-interval biomass density against initial biomass density had slopes significantly less than one ($P < 0.01$ in all cases). In most cases, regression lines crossed the $x = y$ locus indicating biomass loss for high-biomass plots (Fig. 4). Among the five 5-yr intervals between 1993 and 2018, three yielded regressions with slopes indistinguishable from 1.0 (1993–1998, 2003–2008, and 2013–2018), but when pooled to produce intervals of 10 yr or more, all slopes were <1. Assumptions of linear regression were generally met, except for significant skewness of residual distributions for 1977–1993 and 2003–2018, and significant kurtosis, skewness, and heteroscedasticity for 1993–2003 (encompassing the 2002 windstorm). All cases of violated assumptions were due to "outlying" plots with large biomass loss (mortality).

Compositional patches (Woods 2000) differed consistently in mean biomass density; sugar maple-dominated areas had highest biomass, followed by "mixed" patches with *Fagus*, and lowest biomass in hemlock-dominated areas (Table 1). Plot mean biomass density for sugar maple-dominated patches was significantly greater than for either of the other patches (Mann-Whitney *U*, $P < 0.05$ with correction for multiple tests) for all sampling periods except 2003 (immediately following the 2002 windstorm).

Tree size distributions and biomass dynamics

Empirical cumulative distributions (ECDs) of biomass with respect to tree size (dbh) showed strong tendencies over most sampling intervals toward increasing dominance of the living biomass pool by large trees. Comparisons of six sampling periods showed significant difference between the 1998 (just prior to the 2002 windstorm) ECD and all previous sampling periods (Fig. 5; Kolmogorov-Smirnov tests, $P < 0.05$ after adjustment for multiple tests). The 2003 (post-blowdown) ECD was different from those for 1935 through 1977, but was not different from 1998 (pre-blowdown). The 2018 ECD differed from all pre-blowdown (1935–1998) ECDs. Differences between curves appeared most evident in the relative importance of large stems. For example, stems >60 cm dbh accounted for just over 25% of all biomass in 1935 and 1948 (Fig. 5), with this proportion increasing to 40% in 1998 and decreasing slightly after the 2002 windstorm. Stems >75 cm dbh decreased from ca. 10% of total biomass in 1935 to less than 5% in 1948, but more than tripled in cumulative proportion to 17–18% in 1998–2018.

Effects of disturbance

Empirical cumulative distributions for the "disturbed" plot subset differed from those for "comparison" plot subset for the 2002 blowdown, showing distinct size structure dynamics, both before and following disturbance. Proportional contributions of larger stems increased consistently over the entire study period for the (undisturbed) "comparison" subset (Fig. 5B, C), and ECDs for 1998–2018 differed significantly from the 1935 curve (Kolmogorov-Smirnov tests, $P < 0.05$ after adjustment for multiple tests). The "disturbed" subset showed similar trends from 1935 through 1998 but, following the 2002 windstorm, ECDs for 2003 and 2018 showed large decreases in the contributions of large stems (Fig. 5C). Kolmogorov-Smirnov tests for the 'disturbed' group identified significant differences between the 1998 (pre-blowdown) ECD and

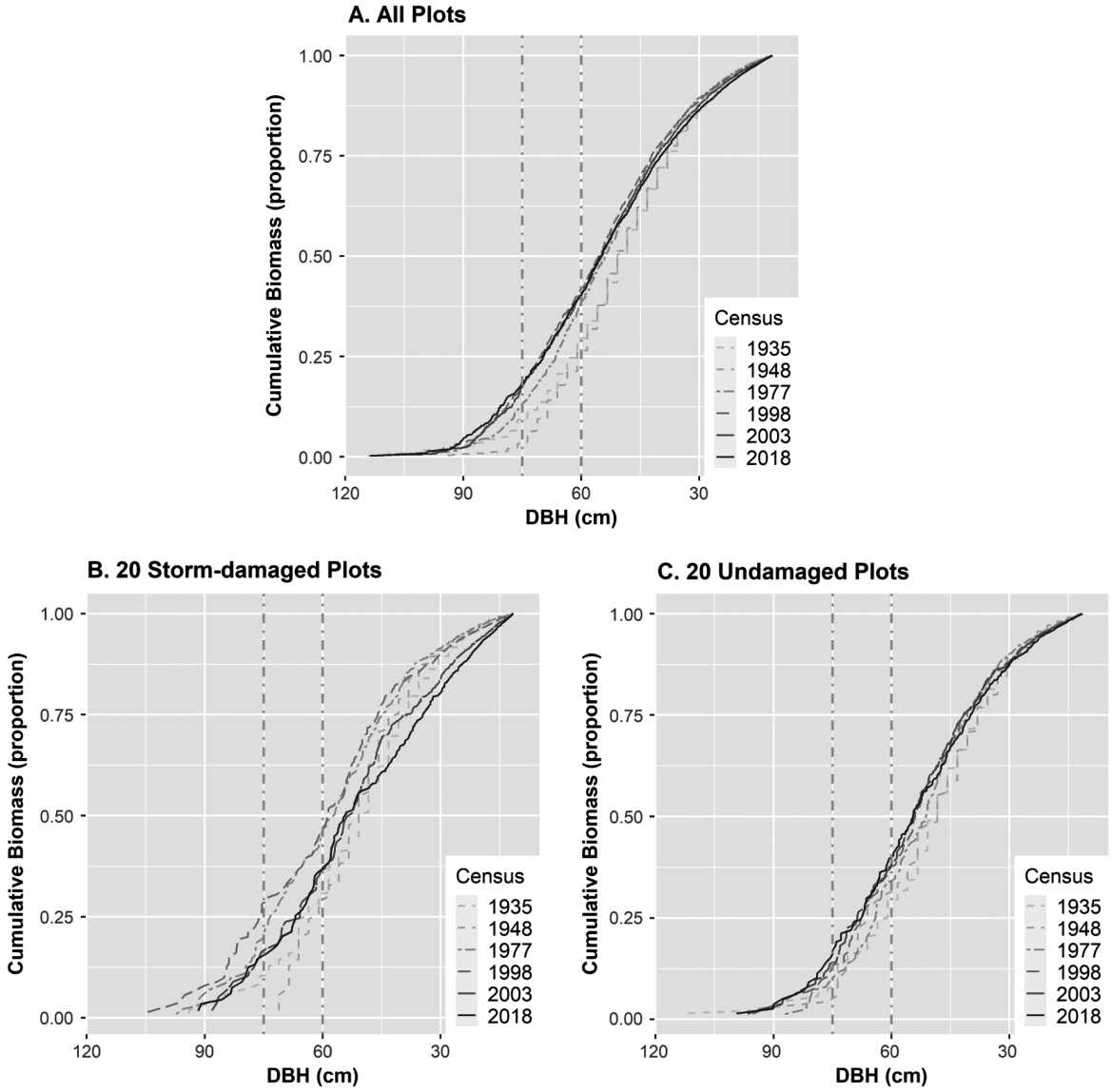

Fig. 5. Empirical cumulative distributions (ECDs) of biomass as a function of tree diameter (dbh) for selected sample periods and plot groups. ECDs are compiled from largest to smallest dbh. Sampling periods are represented by separate curves, with earlier samples indicated by lighter, more discontinuous curves. Vertical dashed lines for dbh = 60 and 75 cm help visualize proportion of biomass in larger stems. ECDs for all upland plots (A) show consistent increases in contributions of large trees, especially from 1935 to 1998 (proportion of biomass in trees >60 cm increases from ca. 25% to ca. 40%). Twenty plots with >25% biomass loss in the 2002 windstorm (B) show greater accumulation in large trees prior to the 2002 windstorm, and a reversal of this trend in later sampling periods, but 20 "comparison" plots little influenced by the storm (C) do not. For all plots pooled (A), total number of stems included ranges from 3449–3998 except for 1948 with 1735 stems. For plots most damaged in 2002 storm (B), comparable values are 444–544 and 198. For comparison plots (C), comparable values are 485–608 and 216.

ECDs for 1935 and 1948, and for the 2003 and 2018 (post-blowdown) ECDs compared to 1998 and 1977. Prior to the 2002 windstorm, stems >60 cm dbh accounted for ca. 45% of total biomass in the "disturbed" plots, compared to ca. 32% for the "comparison" set and ca. 40% for the full data set (Fig. 5). This is consistent with high-biomass plots, dominated by large trees, being over-represented among plots experiencing substantial disturbance from the 2002 windstorm (Fig. 4).

Empirical cumulative distributions for the full data set and for the "disturbed" subset for the post-1935 inferred disturbance showed decreased dominance of large stems between 1935 and the next measurement. Average biomass density for plots experiencing large post-1935 biomass loss had recovered to levels similar to those measured in 1935 by ca. 2000 (Fig. 3).

Plots with large biomass losses in either disturbance episode (post-1935 inferred disturbance or 2002 windstorm) showed distinct spatial distributions (Fig. 6). Of 25 plots with >20% biomass loss in 2002, 20 were in the eastern/northeastern portion of the stand. Of 18 plots with >20% biomass loss following the 1935 sampling period, 14 were in the southwestern portion of the stand, non-overlapping with the area most affected by the 2002 windstorm. Only two plots experienced >20% biomass loss in both periods. Distributions of plots with >20% biomass loss for post-1935 inferred disturbance and 2002 windstorm events depart significantly from an expectation of random distribution across a post hoc arbitrary division of the stand into NE and SW portions (Fig. 6) (chi-square test, $P < 0.001$). By comparison, in the 21-yr period, 1977–1999, only five plots experienced biomass declines >20%, and a large majority increased, some by nearly 50%. Between 2003 and 2018, biomass in 12 widely scattered plots experienced >20% loss in biomass density due to delayed mortality of trees uprooted but not immediately killed in the 2002 storm (unpublished field notes).

Discussion

Forests play a major role in global carbon cycling. However, the carbon status of very late-successional or old-growth forests, over decadal scales, remains debated, largely because of the absence of long-term data sets. This study uses a rare plot-based, longitudinal study spanning 84 yr—on the order of one half of typical canopy residence times for dominant tree species (Frelich and Graumlich 1994, Dahir and Lorimer 1996, Ziegler 2002)—to assess dynamics of aboveground living biomass in an old-growth northern hardwood forest. Despite large decade-scale fluctuations and spatial variation in biomass density, related to two intermediate disturbances, aboveground biomass pools at the end of the study period were similar to initial values. Legacy effects of intermediate disturbances include multi-decade increasing trends in biomass at plot scales, but, over longer periods, this study shows no significant change in aboveground biomass density for old-growth hemlock-hardwoods at the scale of the 100-ha study area.

Temporal patterns: Do old-growth forests exhibit equilibrial biomass?

Consistent with influential models that suggest approximately equilibrial biomass density in old-growth forests (Bormann and Likens 1979), the 84 yr of observations at the Dukes RNA show no significant difference in biomass density between the first sample in 1935 and the most recent in 2018–2019 (Table 1, Fig. 2). However, there are more complex dynamics at higher spatial and temporal resolutions. Biomass trajectories exhibit overall increasing trends over sampling intervals totaling more than 2/3 of the total study period. During the 50-yr interval from 1948 to 1998, overall average biomass densities increased by 15–30% (about 1–2 $Mg{\cdot}ha^{-1}{\cdot}yr^{-1}$), varying across sections of the RNA (Table 1, Fig. 2). These increases, however, were approximately balanced by relatively brief declines in biomass concentrated in spatially localized plot groups in 1935–1948 and 1998–2003, associated with windstorm disturbances (inferred for the post-1935 decline). A similar pattern of gradually increasing biomass with briefer episodes of biomass loss was described for permanent plots over ca. 50 yr in old-growth forests of the Huron Mts., <100 km northwest of the Dukes site (Woods 2014). Association of biomass dynamics with infrequent, intermediate disturbances suggests that equilibrial models based on gap-phase disturbance are not adequate descriptors of the system.

Over the stand, average biomass density varied significantly among sampling periods,

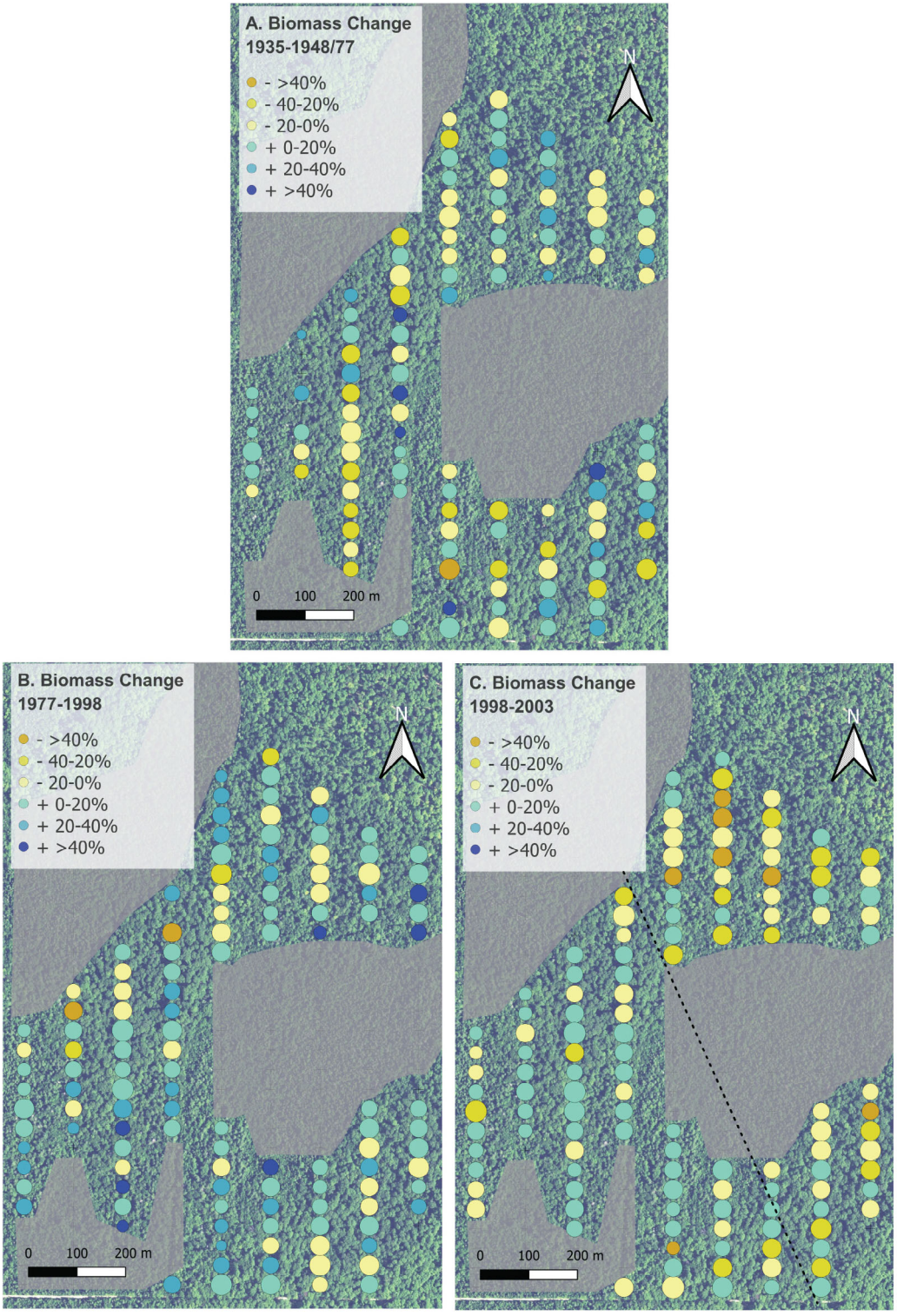

Fig. 6. Spatial distribution of biomass density change for selected time intervals. Size of symbol in each map is

(Fig. 6. *Continued*)

proportional to biomass density at the beginning of the indicated interval; color corresponds to proportional change in biomass from large losses (yellows) to gains (blues). Losses due to the 2002 windstorm (C) and the inferred post-1935 inferred disturbance (A) are concentrated in different parts of the RNA, and significantly asymmetrically distributed across a diagonal line (C). Changes over the 1977–1998 interval (B) are less spatially concentrated and are predominantly gains in biomass; other intervals (not shown) are similar to the 1977–1998 interval (B).

ranging from 294 Mg/ha in 1948 to 361 Mg/ha in 1998, while values for individual plots varied several-fold in extreme cases. High spatial variation in biomass density at the Dukes RNA (Figs. 1, 6), may be both historically and environmentally influenced. Higher biomass density in sugar maple-dominated portions of the stand may be related to inherently higher soil fertility (Woods 2000). A well-developed ortstein hardpan associated with "mixed" patches may reduce rooting depth, resulting in higher wind disturbance rates (Woods 2004, 2007). However, variation in biomass trajectories among plots within compositionally defined patches is large as well, and likely influenced by disturbance history and long-lasting legacy effects of disturbance.

Similarity between average biomass values for 1935 and 2018–2019 may be less an indication of equilibrial dynamics than an artifact of those particular dates. Biomass dynamics at the Dukes RNA involve both large decade-scale fluctuations and high spatial variation at the plot scale. Interpretations of shorter temporal windows within the 1935–2019 study period would likely reach different conclusions about biomass trends. Longer study periods might introduce variation beyond that observed in the last 84 yr, given that northwestern Great Lakes forests are known to experience more severe disturbances at century scales (Canham and Loucks 1984, Frelich and Lorimer 1991, Zhang et al. 1999, Schulte and Mladenoff 2005). Magnuson (1990) cautions against drawing conclusions about long-term system behavior from short-term data (framing this warning as the "invisible present" problem), and interpretation of biomass dynamics in old-growth forests is vulnerable to this risk; conclusions may be an artifact of study period. Despite this, the 84-yr record from the Dukes RNA is one of the longest available for old-growth temperate forests, matched for length and scale only for Poland's Białowieża Forest (Brzeziecki et al. 2020).

Intermediate disturbance and living biomass dynamics

Two intermediate disturbances about 60 yr apart interrupted longer-term increasing trends in biomass density and set bounds on biomass fluctuations over the 84 yr of record. Plots most affected by the 2002 windstorm and post-1935 inferred disturbances were spatially clustered at scales of 100s of m, and largely non-overlapping (Fig. 6). Plot-scale biomass declines in other periods, particularly in the half-century from 1945 to 1998, were relatively few and spatially scattered. Following the 2002 windstorm, about 40% of plots showed at least slight initial further decreases in the first subsequent sampling interval (2003–2008), but over 80% showed increasing biomass density by the 2013–2018 interval. Sampling resolution does not permit a similarly close look at patterns following the post-1935 inferred disturbance.

Dynamics following the 2002 blowdown suggest that initiation of post-disturbance biomass recovery may be lagged by a decade or more. While growth response of small, suppressed stems occurs rapidly (K.D. Woods, *unpublished data*), stems smaller than the threshold for inclusion in this study contribute a very small proportion of stand biomass, even in the most disturbed plots. Full recovery of biomass density in plots affected by the post-1935 disturbance required upwards of a half-century, with pre-disturbance biomass density in more intensively disturbed plots attained only after 50–60 yr (Fig. 3). Plots most affected by the 2002 windstorm showed variable dynamics in the subsequent decade, some losing further biomass over the subsequent decade due to delayed mortality of storm-damaged trees (unpublished field notes). By 2013–2018, plots damaged in 2002 windstorm

showed generally increasing biomass density, but the most disturbed plots reached only about 60% of pre-storm values. These observations suggest that a regime of intermediate disturbances recurring at intervals of several decades can be consistent with indefinite biomass fluctuations within the range of values observed here.

Patchy, intermediate-intensity blowdowns, as observed here may be as important in shaping forest dynamics over the long-term as rarer catastrophic disturbances (Stueve et al. 2011). The two disturbances occurring during the Dukes RNA study, while less severe than some classed as "intermediate" by Stueve et al. (2011), nonetheless have had large and long-lasting effects on stand-scale biomass dynamics as well as community structure and composition (Woods 2007, Firm et al. 2009). Regional analyses of historical and tree-ring records for the Upper Peninsula of Michigan suggest an approximate stand-scale return time for wind disturbance comparable to the 2002 windstorm of around 70 yr (Frelich and Lorimer 1991), in relatively close accord with observations for the Dukes RNA.

Interlocking feedback: disturbance legacies and forest structure and composition

Correlations among biomass density, disturbance history, and changes in stand structure are suggestive of regulatory feedback. Two trends are particularly notable. First, in intervals between disturbances, particularly in plots not affected by recent disturbances, canopy trees of the largest size classes increasingly dominate biomass pools. Stems >65 cm dbh never constituted more than 9% of stems >14.5 cm dbh by number, but their contribution to total biomass increased from about 25% to 40% from 1948 to 1998. Stems >75 cm dbh, <4% of all trees, tripled in proportional biomass contribution, from about 5% to 15%. Specific estimates for biomass contributions of large trees are subject to unknown biases in allometric equations (see *Methods*), but the trends noted change very little with equations applied. A 90-cm dbh *Acer saccharum* is estimated to contribute about 7 Mg biomass, over 20% of average plot total biomass; even if this value is a 25% overestimate, the contribution of a single large tree to plot biomass remains disproportionately large (and under-estimates may be equally likely). Even with potential biases, high plot biomass is strongly correlated with the presence of large trees, which is, in turn a function of time since significant disturbance. Globally, in compilations by Lutz et al. (2012, 2018), the largest 1% of stems often account for >50% of total forest biomass, but eastern North American sites in Lutz et al. (2018) average only about 25%. However, most of these sites are previously managed stands. Values for the Dukes RNA, and for the nearby (old-growth) Huron Mts. (Woods 2014), using the same size threshold, are also substantially lower than the global average. The Huron Mts. study also shows increasing proportional contributions of large stems to total biomass, but no other studies assess trends in large-tree biomass proportions over decadal time-scales for eastern North American old-growth forests.

Second, in both observed disturbance events, plots with higher biomass density experienced the greatest biomass loss. Since the largest trees likely have elevated vulnerability to windthrow mortality, due to both age-related wood decay and larger canopy exposure to wind (Woods 2000, 2004, Papaik et al. 2005), this might be expected. The vulnerability to windthrow of areas with higher biomass and larger canopy trees may also be enhanced by more complex canopy structure (Fahey et al. 2015), creating more exposure to wind stress. If structural changes associated with increasing biomass density are associated with increased vulnerability to biomass loss due to windthrow, vulnerability to disturbance and biomass loss should be, in part, a function of time since disturbance. Relatively recently disturbed patches are likely to be more resistant to biomass loss in a given disturbance event. At the Dukes RNA, plots most affected by the post-1935 inferred disturbance reached pre-disturbance biomass densities after 50–60 yr but were little affected by the 2002 windstorm, suggesting resistance to windthrow, perhaps due to persistent structural legacies of the earlier disturbance. Conversely patches long free of significant disturbance are likely more vulnerable to significant living biomass loss in windstorms. Both primary and long-lasting secondary effects of intermediate and major disturbances are likely to be important drivers in any general model of biomass dynamics in old-growth forests. Intrinsic developmental feedbacks appear to reinforce a

disturbance-driven "patch mosaic" over multiple cycles of intermediate disturbance.

Substrate differences and related compositional differences across the stand may affect how these feedbacks play out. Areas with most damage due to the 2002 storm were in hardwood-dominated portions of the stand and, in part, areas with a shallow hardpan where limited rooting depth may increase vulnerability to uprooting (Peterson 2000, Mitchell 2013). While hemlock-dominated areas sustained little damage in 2002, the inferred earlier disturbance did affect areas currently with high hemlock dominance. Differences in species and substrate properties likely affected risk of wind disturbance, but we are unable to quantify such effects here.

Thus, while the tree-scale, small-gap shifting mosaic model of Bormann and Likens (1979) does not adequately explain the biomass dynamics observed, a more complex, multi-scale shifting mosaic model may be an appropriate conceptual model. Such a dynamic might result in relatively stable biomass over larger spatial extents and longer time intervals. However, the time-scales involved may overlap with those at which environmental change typically drives community changes. In any case, our data set does not allow assessment of dynamics at these spatial and temporal scales.

Regional and global context

Biomass densities at the Dukes RNA were substantially higher than regional averages and global estimates for temperate forests, when managed and post-management forests are included. Thurner et al. (2014) used remote sensing data to estimate an average of 5.8 kg C/m^2 in temperate deciduous and mixed forest (including estimated below-ground biomass, not addressed here). This is equivalent to about 116 Mg biomass/ha, similar to estimates for eastern North American forests (Brown et al. 1999), but about half the aboveground-only biomass densities observed here. While that study averaged over a wide range of forest ages and conditions, the comparison suggests that old-growth temperate forests have much higher biomass densities than is typical of modern temperate forests as a whole.

Projections of old-growth biomass densities from studies of successional northern hardwood forests (Whittaker et al. 1974, Crow 1978) tend to be higher than typical values observed here. These projections have typically assumed quasi-equilibrial status driven primarily by 'gap-phase' dynamics in old-growth stands. Models not incorporating effects of rarer intermediate or more severe disturbances within the long-term dynamics of old-growth forests are likely to yield overestimates.

Direct comparisons among old-growth forests are limited by available data. However, average biomass densities of 300–350 Mg/ha in upland mesic forests at the Dukes RNA (Table 1) are comparable to several earlier estimates for old-growth forests in the northwestern Great Lakes region (Mroz et al. 1985, Morrison 1990, Rutkowski and Stottlemyer 1993). Forests throughout this region are compositionally similar and subject to similar wind disturbance regimes (Schulte and Mladenoff 2005), supporting inference of similar interactions between disturbance legacies, disturbance probability, and biomass accumulation. However, substantially higher biomass densities of 400–450 Mg/ha were observed at the nearby Huron Mts. (Woods 2014). Such variation may be due to local variation in disturbance regimes, but may also be a result of biases in site selection and temporal sampling. For example, intentional selection of plots "representative" of old-growth stereotypes, or shorter sampling intervals that fail to capture rarer, more severe disturbances could both result in overestimates of biomass density. In the current study, the regular grid of ca. 125 sample plots minimizes selection bias and captures local variation in biomass density, and multiple sampling periods over >80 yr should reduce bias that might arise in shorter-term studies.

Biomass estimates for old-growth temperate forests east of the northwestern Great Lakes region are few, but comparatively low values have been reported for some stands in New England (Hoover et al. 2012). This may be consistent with our assessment that legacies of more severe disturbances are important in shaping biomass dynamics. Hurricanes are known to cause more extensive, and more frequent severe disturbance in New England than is typical for wind disturbance in the Great Lakes region (Foster and Boose 1992, Boose et al. 2001, Busby et al. 2009). Even given similar composition, this difference might be predicted to result in lower

biomass values. In general, regional differences in type, frequency, and intensity of disturbance should drive differences in long-term biomass densities in old-growth forests. Types of disturbance other than windthrow may also account for regional differences. For example, ice storms in eastern Canada and the northeastern United States (Duguay et al. 2001, Hooper et al. 2001, Lafon 2004), with distinctive patterns of damage (Melancon and Lechowicz 1987, Proulx and Greene 2001), likely have long-term effects on biomass dynamics in old-growth stands that are not yet documented.

More globally, some other regions of cool-temperate deciduous forest in Europe and east Asia are dominated by species closely related to those dominant at the Dukes RNA. Some old-growth forests in Europe are known to experience similar regimes of occasional patchy, intermediate-severity wind disturbances (Nagel et al. 2007, 2017, 2021), and a similar feedback between disturbance history and vulnerability seems likely (Schurman et al. 2018). The large, decade-scale fluctuations in biomass density observed at the Dukes RNA may be typical of late-successional forest throughout much of the temperate region globally, and some studies suggest long-term approximate carbon neutrality (Nord-Larsen et al. 2019). Higher biomass densities observed in some cases (Busing 1993, Molina-Valero et al. 2021) may, in large part, be a consequence of lower long-term frequency of intermediate and severe disturbance.

Implications for environmental change

Results from the Dukes RNA may have significant indirect implications regarding effects on forest biomass of climate and other environmental changes. Projections of regional climates under greenhouse-induced warming include increased frequency and severity of extreme weather events (Dale et al. 2001, Reichstein et al. 2013) as well as more complex changes in drivers of ecosystem dynamics (McDowell et al. 2020). We show that infrequent, major wind disturbances play a major role in shaping biomass pools over decades to centuries. Increased frequencies of such events, even without considering effects on physiological function or species distributions, could ultimately lead to lower landscape-averaged living biomass density in old-growth temperate forest, producing at least a transient carbon-source status. Stand responses to increased disturbance frequencies could, at the same time, be complicated by the feedback described above between tree size distributions and vulnerability to blowdown, since younger stands are likely to be more resistant to wind disturbance. Changing disturbance regimes, and consequent changes in mosaic dynamics, at timescales of decades to centuries further limit potential for equilibrium of biomass pools even at landscape scales.

The effects of other environmental changes are difficult to predict and complicated by complex interactions of direct and indirect effects of temperature and moisture availability on rates of photosynthesis, respiration, and decay (Hyvönen et al. 2007). Large anthropogenic increases in nitrogen deposition and direct CO_2 fertilization effects may drive temporary increases in productivity of North American temperate forests (Aber and Magill 2004, Pregitzer et al. 2008, Bobbink et al. 2010), but these increases may be less pronounced in old-growth forests (McDowell et al. 2020). These more direct effects may be outweighed by the long-term consequences of changed disturbance regimes.

Conclusions

What are general implications of our findings for the role of old-growth forests in the carbon cycle, and the potential effects of environmental change? The unique, long-term data set from old-growth forests at the Dukes RNA shows generally increasing biomass density over sampling intervals accounting for over 2/3 of the 84-yr study period, but significant, disturbance-driven decreases, occurring primarily in two short intervals, approximately balance those longer-term increases. Thus, while short-term observations would have a high probability of encountering increasing biomass density (suggesting carbon sink status), longer-term data shows no directional trend in biomass pools for the full 84-yr study interval. Effects of one documented disturbance (2002 windstorm) and one undocumented, inferred disturbance (1935–1948) suggest linkages between vulnerability to intermediate wind disturbance and stand structure as shaped by disturbance history and intrinsic successional

trends. Legacy effects of intermediate disturbances appear to drive feedbacks reinforcing a "shifting mosaic" within-stand model of biomass density dynamics and structural development.

Our interpretations, however, are subject to two important caveats. First, our data set remains limited in both spatial and temporal scale compared to the intrinsic functional scales of old-growth forest communities. The interactions just described may not apply, for example, in more intense, larger-scale wind disturbances, but the rarity of such events, combined with the rarity of old-growth forest stands, so far prevents address of this possibility. Second, our analyses address only living, aboveground biomass pools. Persistent legacies of intermediate (or larger) disturbances are likely to further influence biomass and carbon dynamics by producing very large, pulsed inputs to the coarse woody debris pool, which may buffer observed variations in carbon pools in living biomass, depending on decay rates of dead wood. The effects of disturbance on below-ground carbon pools are poorly understood, but may cause short-term reduction in soil carbon (Scharenbroch and Bockheim 2008).

Even though this study suggests no long-term trend in aboveground biomass density, long-term average values over 300 Mg/ha indicate that old-growth temperate forests can, on an areal basis, constitute a very large biomass carbon reservoir compared to previously managed stands. Soil organic carbon and coarse woody debris would likely enhance this difference (Tyrrell and Crow 1994, Woods 2014). Thus, regional management targeting increased area of forests in old-growth status could result in a substantial carbon sink. Enhanced "old-growth" properties over large areas of previously managed forests could establish a significant carbon sink that might persist for a century or more (Gunn et al. 2014). However, if windthrow events become either more frequent or more intense under future climates, regional biomass densities may tend to decrease.

Ecosystem dynamics in late-successional forests play out at multi-decade or century timescales, and biomass pool trajectories (carbon sink-source status) of old-growth forests can only be understood and predicted with knowledge of disturbance histories and probabilities. Not only is stand biomass shaped by rare disturbance events, the likelihood and consequences of such events may be dependent on stand history. Conclusions drawn from short-term studies that miss rare events with significant legacy effects can lead to misinterpretation of system dynamics (Magnuson 1990); short-term dynamics at the Dukes RNA would likely lead to an interpretation of the stand as a carbon sink.

Assumptions of stand-scale equilibrial status in old-growth forests, maintained by gap-phase "shifting mosaic" dynamics, are likely misleading, although our results could be consistent with shifting mosaic dynamics applied at larger landscape scales and over longer time periods. Long-term datasets and perspectives are irreplaceably important in understanding these systems and phenomena. Such data sets are extremely few, especially for old-growth forests, and establishment of new long-term studies has a very long "latency" period before quantitative, long-term insights can be gained; salvaging, curating, and maintaining existing long-term studies and data sets for old-growth forests should be given critical priority.

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Data Availability

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.16383312.v1

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3871/full