

Links between biomass and tree demography in a northern hardwood forest: a decade of stability and change in Hubbard Brook Valley, New Hampshire

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Abstract: We resurveyed a network of sampling plots ($n = 371$) 10 years after its establishment in Hubbard Brook Experimental Forest (New Hampshire, USA) to quantify recent trends in tree biomass and demography. We found no significant change in live-tree biomass during the decade. Total biomass was $246 \text{ Mg}\cdot\text{ha}^{-1}$ (95%CI = 235–258) in 1995–1996 and $245 \text{ Mg}\cdot\text{ha}^{-1}$ (95%CI = 234–256) in 2005–2006. Annual mortality during the period for trees ≥ 10 cm diameter at breast height (1.37 m) averaged $9.7 \text{ trees}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (95% CI of annual mortality rate = $1.36\%–1.84\%\cdot\text{year}^{-1}$). Tree recruitment into the census pool was $8.4 \text{ trees}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (95% CI = 5.8–10.6). Although overall forest biomass remained constant, there were marked shifts in the relative dominance of the canopy species. For example, the live biomass of *Betula alleghaniensis* Britton declined by 7%, whereas the live biomass of *Picea rubens* Sarg. increased by 6% and that of *Acer saccharum* Marshall increased by 4%. There was no instance of recruitment significantly exceeding mortality for the major species. Relative growth rates ranged from $1.03\%\cdot\text{year}^{-1}$ for *Betula papyrifera* Marshall to $1.99\%\cdot\text{year}^{-1}$ for *Abies balsamea* (L.) Mill. Our results confirmed earlier reports that the forest at Hubbard Brook is no longer aggrading. Current live-tree biomass is lower than expected. Although effects of novel disturbances documented on a regional level have not led to directional changes in tree demography at Hubbard Brook, we suggest that these novel stressors are depressing the biomass potential of the forest.

Résumé : Nous avons remesuré un réseau de placettes échantillons ($n = 371$) 10 ans après son établissement à la forêt expérimentale d'Hubbard Brook (New Hampshire, É.-U.) pour quantifier les tendances récentes de la démographie et de la biomasse des arbres. Nous n'avons observé aucun changement significatif dans la biomasse des arbres au cours de la décennie. La biomasse totale atteignait $246 \text{ Mg}\cdot\text{ha}^{-1}$ (IC de 95 % = 235–258) en 1995–1996 et $245 \text{ Mg}\cdot\text{ha}^{-1}$ (IC de 95 % = 234–256) en 2005–2006. Pendant cette période, la mortalité annuelle des arbres ≥ 10 cm de diamètre à hauteur de poitrine (1,37 m) a été en moyenne de $9,7 \text{ arbres}\cdot\text{ha}^{-1}\cdot\text{an}^{-1}$ (IC de 95 % du taux annuel de mortalité = $1,36–1,84 \%\cdot\text{an}^{-1}$). Le recrutement d'arbres dans le bassin d'inventaire atteignait $8,4 \text{ arbres}\cdot\text{ha}^{-1}\cdot\text{an}^{-1}$ (IC de 95 % = 5,8–10,6). Bien que la biomasse forestière globale soit demeurée constante, il y a eu des changements marqués dans la dominance relative des espèces formant le couvert. Par exemple, la biomasse vivante de *Betula alleghaniensis* Britton a diminué de 7 % tandis que celle de *Picea rubens* Sarg. a augmenté de 6 % et celle d'*Acer saccharum* Marshall de 4 %. Aucun épisode de recrutement n'a excédé la mortalité des principales essences. Le taux de croissance relatif variait de $1,03 \%\cdot\text{an}^{-1}$ pour *Betula papyrifera* Marshall à $1,99 \%\cdot\text{an}^{-1}$ pour *Abies balsamea* (L.) Mill. Nos résultats confirment les rapports antérieurs qui mentionnent que la forêt d'Hubbard Brook n'est plus en train de s'améliorer. La biomasse courante des arbres vivants est plus faible que prévu. Même si les effets de nouvelles perturbations documentées à l'échelle régionale n'ont pas entraîné de changements directionnels dans la démographie des arbres à Hubbard Brook, nous croyons que ces nouveaux stress réduisent la biomasse potentielle de la forêt.

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Introduction

Recent reports that live-tree biomass has stopped accumulating at the Hubbard Brook Experimental Forest in the

White Mountains of New Hampshire, despite expectations of continued growth (Fahey et al. 2005; Siccama et al. 2007), raise concern about the future of the northern forest ecosystem — the expanse of forestland in the northeastern United

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States (US) and southeastern Canada (Likens and Franklin 2009). The suspected causes range from climate change to invasive pests to atmospheric pollution (Likens and Franklin 2009). In this regard, the northern forest is not unique. Such stressors are influencing the contemporary ecology of many forests (e.g., Driscoll et al. 2001; Eschtruth and Battles 2008; Allen et al. 2010).

Although long-term trends in biomass accumulation provide a useful synoptic perspective on ecosystem function, they do not capture the details of species-specific changes in tree mortality, recruitment, or growth (Harcombe 1987). These demographic parameters provide insight into population dynamics and can help detect the impact of novel stressors. For example, Beckage et al. (2008) linked a warming climate to observed declines in boreal forest species in the Green Mountains of Vermont. One consequence of the invasive insect responsible for beech bark diseases (*Cryptococcus fagisuga* Lind.) is a marked increase in recruitment by the host species, American beech (*Fagus grandifolia* Ehrh.) (Jones and Raynal 1987). Decreased growth of red spruce (*Picea rubens* Sarg.) and sugar maple (*Acer saccharum* Marsh.) trees in the northeastern US has been attributed to atmospheric pollution (Driscoll et al. 2001). However, demographic responses to stressors do not occur in a vacuum. Observed change must be considered within an appropriate ecological context.

For the northern forest, disturbance history and past land use fundamentally shape the current structure and function (Foster 2002). Although these forests are older and wilder than any time in the last two centuries (Irland 1999), they are still recovering from a legacy of clearing for agriculture or harvesting for timber (Cogbill et al. 2002). As part of the recovery, change is expected in terms of both forest biomass and tree demography.

Background

For the northern hardwood forest, much of our understanding of the appropriate ecological context has come from observations and experiments at Hubbard Brook Experimental Forest (HBEF). The model of ecosystem development posed by Bormann and Likens (1979) describes both the pattern of biomass accumulation following catastrophic disturbance and the directed changes in tree composition. The model proposes that subsequent to an initial dip immediately following the disturbance (reorganization phase), tree biomass accumulates to a maximum (aggradation phase), after which there is a loss in biomass (transition phase). In the final period, total biomass across a forested landscape fluctuates around a mean (shifting mosaic steady-state phase).

Changes in forest composition accompany this pattern of biomass accumulation. In general terms, species with differing life history strategies express their dominance sequentially as resource availability changes with forest development following large-scale disturbance. In specific terms, a dense shrub canopy dominated by raspberries (*Rubus* spp.) emerges soon after (2–3 years) the disturbance. However, the raspberries are quickly (6–8 years) supplanted by pin cherry (*Prunus pensylvanica* L. f.), an extreme pioneer tree species (Marks 1974). After 25–35 years, the pin cherry canopy declines (largely due to nutrient limitations)

and subsequently releases mid-successional species such as red maple (*Acer rubrum* L.) and paper birch (*Betula papyrifera* Marsh. var. *papyrifera*) (Leak 1991; Fahey et al. 1998; Allison et al. 2003). With time, yellow birch (*Betula alleghaniensis* Britton) becomes an increasingly important component of the aggrading forest (Leak 1991). Eventually (80–120 years after the initiating disturbance), these species are supplanted (transition phase) by the slower growing, more understory tolerant, and longer lived species sugar maple and American beech (Nicholson et al. 1979). Vegetational stability (shifting mosaic steady-state phase) is maintained via gap phase replacement by a mix of yellow birch, beech, and sugar maple (Schwarz et al. 2001). At the higher elevations in Hubbard Brook Valley, beech and maple are replaced by red spruce and balsam fir (*Abies balsamea* (L.) Mill.) (Bormann et al. 1970). At issue for HBEF is the fact that biomass has stopped accumulating earlier in the successional sequence and at a lower level than expected (Fahey et al. 2005; Siccama et al. 2007).

The goal of this study was to evaluate the impact of potential novel stressors on the northern forest while accounting for the dynamism inherent in second-growth forests. We quantified recent trends in forest biomass and tree demography at HBEF. Our analysis focused on landscape-level patterns and processes. Our approach relied on a network of permanent plots spanning the entire Hubbard Brook Valley. Specifically, we addressed the following questions.

1. Is the pattern of biomass stabilization observed at finer scales representative of the larger landscape?
2. Do successional changes in tree composition explain observed patterns in live-tree biomass and demography?
3. How do the regional tree declines (e.g., beech, sugar maple, red spruce) impact trends in biomass and demography?

Methods

Site description

The Hubbard Brook Experimental Forest is a 3160 ha reserve located in the White Mountains of central New Hampshire, USA (43°56'N, 71°45'W). The climate is continental, characterized by short, warm summers and long, cold winters. On average, HBEF receives 1395 mm (standard deviation (SD) = 189 mm) of precipitation per year, part of which is captured in snow pack persisting from December until April (Bailey et al. 2003). Mean annual temperature is 5.5 °C (SD = 0.61 °C); daily temperatures average from –8.5 °C in January to 18.8 °C in July (Bailey et al. 2003). Elevations range from 222 m at the eastern entrance to Hubbard Brook Valley to 1015 m at the highest point on the western border (Mt. Kineo; Fig. 1). The most common forest type in the valley is the northern hardwood forest. The canopy is dominated by three deciduous tree species: beech, sugar maple, and yellow birch. Above 750 m in elevation (upper one-third of the valley), the forest canopy includes significant components of two coniferous tree species — red spruce and balsam fir — along with the deciduous tree paper birch. The forest is considered representative in vegetation and climate of the northern hardwood forest complex, which extends from the north-central US into southeastern Canada (USDA Forest Service 1996).

Fig. 1. Map of Hubbard Brook Valley (Schwarz et al. 2003) with multiscale forest dynamics and tree population plot network (i.e., bird area, watershed 6, valley-wide plots). HBEF, Hubbard Brook Experimental Forest.

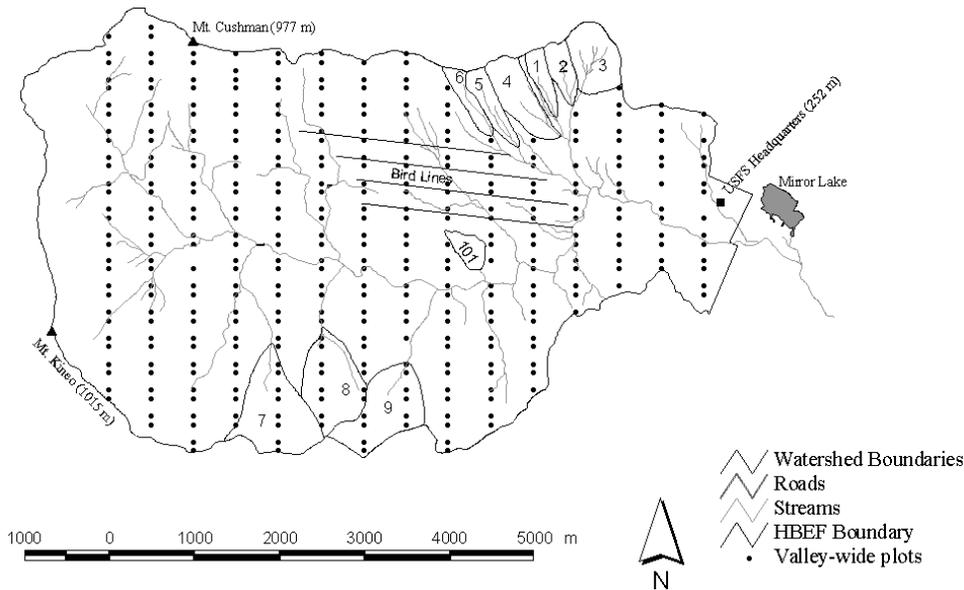


Table 1. Database summary

Years sampled	No. of plots	Area sampled (ha)	Initial live stem count	Final live stem count
1995–1996, 2005–2006	348	17.27	10 423	10 076
1997–2006	23	1.15	680	649

Most of the research at HBEF has been conducted in six experimental watersheds on a south-facing slope located in the northeastern corner of the valley (Fig. 1). Watershed 6 (W6, 13.23 ha in size and between 549 and 792 m in elevation) serves as a reference watershed and has been periodically measured since 1965. The study area in Siccama et al. (2007) refers to the 2.5 km² area located immediately west of the research watersheds. It is co-located with bird demography research (hence the identification as “Bird Lines” in the bird area in Fig. 1) and encompasses a forest community dominated by northern hardwood species (i.e., nearly equal importance of beech, sugar maple, and yellow birch).

Hubbard Brook Valley was selectively logged in the late 1800s and then again between 1906 and 1920. By 1920, 40% of the valley was “cutover” (C.V. Cogbill, personal communication). The next series of major disturbances occurred in the 1930s, with small-scale logging, the 1938 hurricane that caused blowdown, and subsequent salvage logging. The most intense blowdowns were all in the northeastern corner of the valley, on fairly steep south- or southeast-facing slopes and ridges (Peart et al. 1992). In 1955, the USDA Forest Service set aside the entire valley for watershed management studies. A more recent disturbance occurred in 1998 when an ice storm caused considerable structural damage to the forest. Most of the damage was restricted to an elevation band between 600 and 800 m (Rhoads et al. 2002), and by 2001, leaf area had recovered in affected areas (Weeks et al. 2009). Nevertheless, the ice storm added to the already complex landscape-level variations in disturbance history. As a result, the age structure of the forest in Hubbard Brook Valley can best be described as multiaged (mainly 60–120 years old),

with most of the present-day trees established after the 1906 and 1920 cuts along with a few holdovers that predate these disturbances. Overall, coarse-scale disturbances occur relatively rarely, and so the natural disturbance regime in the northeastern US is dominated by fine-scale disturbances such as mortality of individual trees or small groups (Bormann and Likens 1979).

Data collection

In 1995–1997, a network of 371 circular forest vegetation plots was established across the entire Hubbard Brook Valley (minus the experimental watersheds) to track individual tree growth and population demography (Schwarz et al. 2001). We resurveyed these same plots a decade later. Specifically, plots established in 1995 ($n = 200$) were surveyed in the summer of 2005, whereas those established in 1996 ($n = 148$) and 1997 ($n = 23$) were surveyed in the summer of 2006. Thus, the time interval between surveys was typically 10 years, but for 23 of the plots, the interval was 9 years (Table 1). This difference is accounted for in our analyses.

The north–south distances between plots alternate between 100 m and 200 m, whereas the west–east distance is 500 m (Fig. 1). In the original survey, the size of the plot area varied so that each plot would contain 50 to 60 canopy-sized trees. As a result, some of the plots at higher elevations in more dense forests encompassed a smaller area. Of the 371 plots, 364 are 0.05 ha in area (12.62 m radius), and the rest are 0.0314 ha in area (10 m radius). We refer to this network as the “Valley-wide” plots (Fig. 1).

In the original survey, all live trees ≥ 10 cm diameter at breast height (1.37 m) (dbh) were permanently tagged and

measured to the nearest 0.1 cm dbh and identified to species. The understory tree composition of each plot was measured in a 2 m wide transect that spanned the north–south diameter of the plot. Tree saplings ≥ 2 cm dbh and < 10 cm dbh were measured to the nearest 0.1 cm dbh and identified to species. A detailed description of methods of the original survey can be found in Schwarz et al. (2003). For the resurvey, live trees that had grown into the 10 cm dbh class and had not been previously tagged were permanently tagged and added to the database as “recruits”. For all tagged trees, we recorded dbh to the nearest 0.1 cm, identified the species, and assessed vigor status and canopy class.

During the resurvey, care was taken to maintain consistency and avoid remeasurement biases. In simple terms, the core tasks of the resurvey were to account definitively for all live trees in the initial survey, to detect all new trees that grew into the ≥ 10 cm dbh class, and to record precisely species and measure dbh. For some forests, diameter measurements and species identifications can be an issue (Condit 1998), but at Hubbard Brook, they are not. Using procedures applied in this study (Supplementary data: Tree census protocols),¹ repeated measures of dbh routinely yield precision rates of $\pm 2.7\%$ (relative root mean square error; Gonzalez et al. 2010). In terms of species identification, seven common species dominate in Hubbard Brook Valley and tree richness totaled only 19 species. All are well documented with distinguishing stem, bark, and leaf characteristics. The error rate of species identification (almost entirely due to blunders) was 1.2% (110 of 9490 surviving trees were misidentified and corrected in the resurvey).

Data analysis

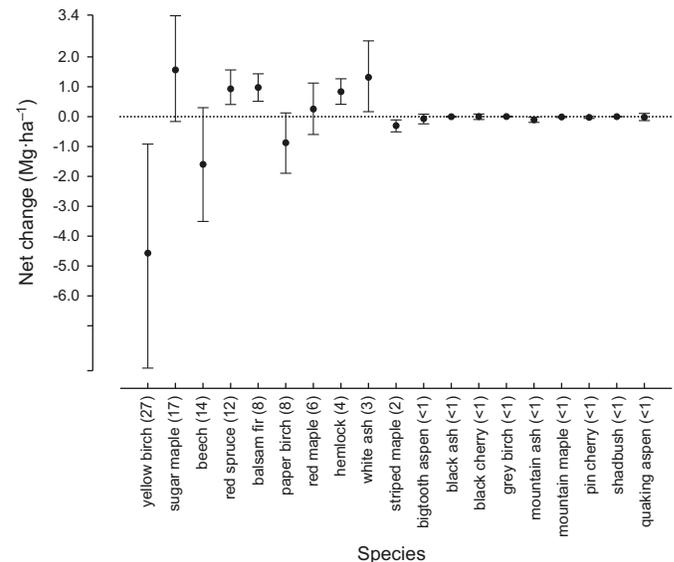
To detect changes in the Hubbard Brook forest over the study period, we first estimated live-tree biomass in the two census periods. We calculated mortality, recruitment, and growth of survivors to capture the demographic details that contributed to changes in biomass. All analyses of change accounted for the unequal sample periods (23 plots were measured after 9 years, and 348 were measured after 10 years).

Although the biomass estimates were calculated for all 19 species present in the Hubbard Brook Valley, our main analysis focuses on the seven most important species — yellow birch, sugar maple, beech, red spruce, balsam fir, paper birch, and red maple (Fig. 2). Importance values represent the sum (normalized from 0 to 100) of each species' relative basal area and relative density.

Biomass estimates

Stem volume was computed using species-specific allometric equations calculated for trees harvested within Hubbard Brook Valley (Whittaker et al. 1974). See Supplementary data¹ for details (Biomass estimate) and a complete table of coefficients (Supplementary Table S1). For the most important species in the valley, separate equations were derived for trees sampled across the elevation gradient. For the less common tree species that were not specifically sampled, we assigned equations for morphologically similar species. These allometric equations have been validated with direct harvest-based measurements of aboveground tree biomass at Hubbard

Fig. 2. Valley-wide changes in aboveground biomass ($\text{Mg}\cdot\text{ha}^{-1}$). Error bars represent 95% confidence intervals of the mean. Numbers in parentheses represent 1995–1996 importance values. See Table 3 for species names.



Brook (Siccama et al. 1994; Arthur et al. 2001; Fahey et al. 2005). On average, there was less than a 3% difference between harvest-based and allometric-based biomass estimates (Fahey et al. 2005).

Demography

Analysis of forest demography was based on calculations of annual mortality, recruitment, and growth rates. Annual mortality ($\%\cdot\text{year}^{-1}$) was computed as follows (Condit et al. 2006):

$$[1] \quad \text{Annual mortality rate} = \frac{\ln(N_0) - \ln(N_t)}{t}$$

where N_0 is the number of live individuals at the beginning of the census, N_t is the number of live individuals at the end of the census interval, and t is the length of the census interval. To facilitate comparisons with recruitment, we converted these annual rates to density-based rates (annual mortality \times initial density = $\text{trees}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$).

Recruitment rates (k , $\text{individuals}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) were initially calculated from direct observations of recruits in the plots since the last inventory. However, this measurement does not account for any recruits that grow into the minimum size (10 cm dbh) during the interval but do not survive to be counted during the resurvey. To account for those individuals that are newly recruited but die before they can be recorded at the next survey, we used demography data from the bird area in HBEF (which was sampled at two-year intervals; Siccama et al. 2007) to estimate the 10-year “loss rate” in recruitment. Specifically, if the bird lines had been sampled in 10-year intervals rather than two-year intervals, 4.6% of the recruits would have been missed (mean = $0.81 \text{ trees}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$; standard error (SE) = $0.25 \text{ trees}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$). This loss rate was included in our final estimates of recruitment. A limitation of this approach is that the bird area does not

¹Supplementary data are available with the article through the journal Web site (nrcresearchpress.com/cjfr).

Table 2. Density and biomass summary based on live trees ≥ 10 cm dbh. Standard errors (SEs) are based on plot-scale variation.

	1995–1996	2005–2006	10-year change	SE of 10-year change
Density (trees·ha ⁻¹)	607.71	587.40	-20.31	4.75
Basal area (m ² ·ha ⁻¹)	29.32	29.36	0.04	0.22
Aboveground biomass (Mg·ha ⁻¹)	203.85	202.36	-1.53	2.01
Belowground biomass (Mg·ha ⁻¹)	42.60	42.54	-0.06	0.35
Total biomass (Mg·ha ⁻¹)	246.45	244.90	-1.59	2.36

represent the higher elevation subalpine conifer forest. The subalpine zone is characterized by high turnover and smaller stems, so we can assume that the loss rate is underestimated for the areas that fall into the subalpine zone.

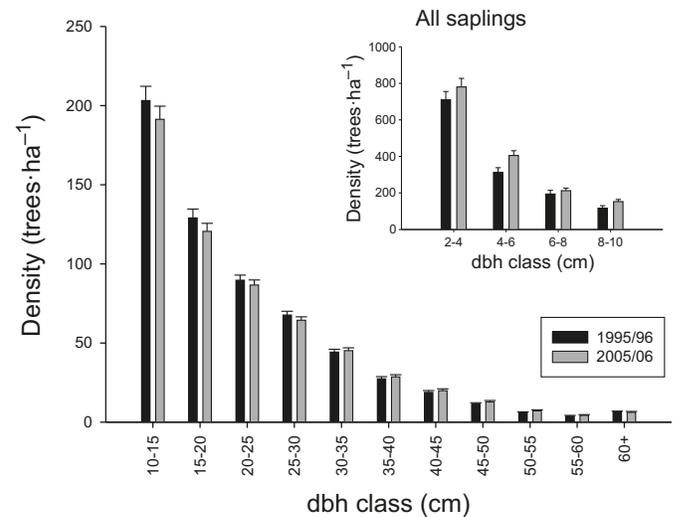
Relative growth rate was calculated as in Condit et al. (2006), where k represents the individual trees, j represents censuses, and t is the time interval between j and $j + 1$:

$$[2] \quad G_k = \frac{\ln(\text{dbh}_{k,j+1}) - \ln(\text{dbh}_{k,j})}{t}$$

Growth measurements can be problematic as measurements between surveys may be taken at slightly different heights on the bole or structural changes can leave part of the bole missing or damaged, resulting in negative or exceptionally large changes in dbh. Of the 9486 trees with diameters in both 1995–1996 and 2005–2006, 11 trees were omitted due to tree structural problems (e.g., split bole) that made it impossible to accurately measure changes in dbh. We also excluded statistical outliers for each species by using the first quartile (q_1), the third quartile (q_3), and a multiple of the interquartile range (iqr) to define outliers. The iqr approach is a nonparametric analytical method that identifies outliers via an unbiased statistical determination of data distribution (Sokal and Rohlf 1981). The data were first ranked from lowest numerical value to highest, and the median and quartiles of the data set were determined. Observations that lay outside of $q_1 - (1.5 \times iqr)$ and $q_3 + (1.5 \times iqr)$ were excluded from the growth analysis. This process omitted, at the most, 3.2% of trees of a single species from the growth analysis (beech: 39 out of 1222). Among the abundant species (importance value > 3), the smallest percentage of excluded outliers was 1.7% of the original data set (paper birch). Negative growth changes were recalculated by adding the species-specific minimum growth change (if it was negative) to the 2005–2006 dbh.

Uncertainty analysis

To detect statistically relevant changes in forest biomass and tree demography, we analyzed the uncertainty associated with key metrics. Non-overlap of 95% confidence intervals (or their Bayesian equivalent, credibility intervals) was used as the standard of significant change. We used Monte Carlo sampling to account for error propagation in biomass estimates (sensu Fahey et al. 2005) and hierarchical Bayesian analysis (sensu Condit et al. 2006) to account for error propagation in tree demographic parameters. See Supplementary data (Uncertainty analysis)¹ for details. For summaries of basic forest metrics (e.g., density and basal area) and subsets of analysis (e.g., biomass by elevation), we reported means and standard errors to describe the central tendency and variation in these metrics. We refrained from estimating standard con-

Fig. 3. Histogram of tree density of all species by diameter size class (dbh, diameter at breast height). Error bars represent 1 standard error based on plot-scale variation.

fidence intervals to avoid comparison with our more comprehensive analyses.

Results

Live-tree biomass in Hubbard Brook Valley did not change during the decade. Total biomass was 246 Mg·ha⁻¹ (95%CI = 235–258) in 1995–1996 and 245 Mg·ha⁻¹ (95%CI = 234–256) in 2005–2006. Basal area tracked biomass, remaining essentially constant at 29 m²·ha⁻¹. Although there was a net decrease in tree (≥ 10 cm dbh) density of 3% from 608 to 587 trees·ha⁻¹ (Table 2), this decline was not statistically significant (paired t test, $p = 0.28$). Nor were there dramatic changes in the size class distribution. For both inventories, the distributions by dbh class were similar (Fig. 3).

In contrast to the constancy in overall forest biomass, there were species-level shifts across the valley (Fig. 2). Of 19 tree species, two declined significantly in aboveground biomass, whereas four increased. The biggest net change occurred in the most important species — yellow birch. Because of large losses from mortality and negligible gains from recruitment (Table 3), yellow birch suffered a 7% decline in biomass over 10 years, -4.57 Mg·ha⁻¹ (95% CI = -8.42 to -0.92). However, yellow birch remained the single most important species in the valley (2005–2006 importance value = 27). Increases in live-tree biomass for the three conifer species in the valley — balsam fir, red spruce, and eastern hemlock (*Tsuga canadensis* L. Carr.) — helped to offset these losses (Fig. 2).

Table 3. Aboveground biomass contribution (in Mg·ha⁻¹) of mortality, recruitment, and growth to net change in biomass.

Species	Loss from mortality	Gain from recruitment	Gain from growth of survivors
Yellow birch, <i>Betula alleghaniensis</i> Britton	10.17	0.13	5.7
Sugar maple, <i>Acer saccharum</i> Marsh.	3.29	0.22	4.64
Beech, <i>Fagus grandifolia</i> Ehrh.	6.47	0.87	3.97
Red spruce, <i>Picea rubens</i> Sarg.	1.39	0.42	1.92
Balsam fir, <i>Abies balsamea</i> (L.) Mill.	1.52	0.70	1.79
Paper birch, <i>Betula papyrifera</i> Marsh var. <i>papyrifera</i>	2.42	0.10	1.44
Red maple, <i>Acer rubrum</i> L.	1.57	0.03	1.81
Eastern hemlock, <i>Tsuga canadensis</i> (L.) Carr.	0.12	0.05	0.91
White ash, <i>Fraxinus americana</i> L.	0.38	0	1.72
Striped maple, <i>Acer pensylvanicum</i> L.	0.71	0.25	0.15
Mountain ash, <i>Sorbus americana</i> Marsh.	0.16	0.02	0.04
Black cherry, <i>Prunus serotina</i> Ehrh.	0.04	0	0.03
Quaking aspen, <i>Populus tremuloides</i> Michx.	0.06	0	0.03
Bigtooth aspen, <i>Populus grandidentata</i> Michx.	0.1	0	0.03
Mountain maple, <i>Acer spicatum</i> Lam.	0.02	0.01	0
Pin cherry, <i>Prunus pensylvanica</i> L. f.	0.03	0	0
Shadbush, <i>Amelanchier</i> spp.	0	0	0
Black ash, <i>Fraxinus nigra</i> Marsh.	0	0	0
Grey birch, <i>Betula populifolia</i> Marsh.	0	0	0
Total	28.46	2.78	24.19

In terms of demography, three of the seven major tree species significantly declined during the decade (Fig. 4A). Again the largest change was in yellow birch: mortality exceeded recruitment by 1.4 trees·ha⁻¹·year⁻¹ (Table 4). The observed declines in paper birch and red maple populations (Fig. 4A) were less severe. There was no instance of recruitment significantly exceeding mortality for the major species. Of the minor species, only white ash (*Fraxinus Americana* L.) experienced a significant change of -0.06 trees·ha⁻¹·year⁻¹ due to lack of recruitment (Table 4).

More than half of the tree species had no recruitment into the 10 cm dbh size class (Table 4). Mortality rates ranged widely from 0.2%·year⁻¹ for the shade-tolerant hemlock to 21.5%·year⁻¹ for the shade-intolerant early-successional pin cherry. Hemlock had a significantly lower mortality rate than the other two shade-tolerant species (beech and sugar maple; Niinemets and Valladares 2006). The understory maple species (Lei and Lechowicz 1990) — mountain maple (*Acer spicatum* Lam.) and striped maple (*Acer pensylvanicum* L.) — had a much higher mortality rate compared with other species. Only balsam fir, beech, and red spruce had a higher than 1 tree·ha⁻¹·year⁻¹ recruitment rate.

Of the seven major tree species (Fig. 4A), balsam fir — the fastest growing common species — grew at nearly twice the rate (1.99%·year⁻¹) of the slowest growing common species — paper birch (1.03%·year⁻¹). Populations experiencing numerical declines (e.g., yellow birch, paper birch, red maple) also had low relative growth rates (Fig. 4; Table 4). Balsam fir, red spruce, and beech grew significantly faster than all other species in the valley (Table 4).

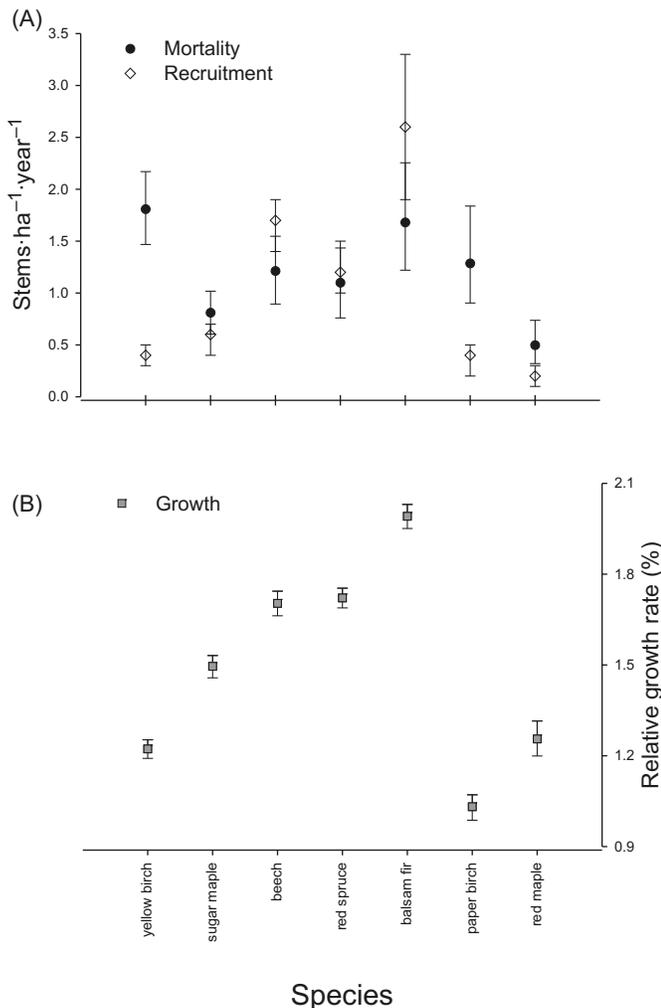
Discussion

Our results confirmed the earlier reports that biomass accumulation has ceased at Hubbard Brook Experimental Forest. For the reference watershed (W6; Fig. 1), Fahey et al.

(2005) reported that live-tree biomass (trees ≥ 10 cm dbh) had peaked in 1982 and subsequently (1982–1997) fluctuated around a mean of 225 Mg·ha⁻¹. Siccama et al. (2007) reported a similar pattern in biomass accumulation nearby (Fig. 1, bird lines). During a comparable interval, live-tree biomass in the bird lines increased by only 3% from 251 Mg·ha⁻¹ in 1981 to 259 Mg·ha⁻¹ in 2001. Despite that these two study areas sampled only the mid-elevation forests on the south-facing slope, the pattern held for the valley-wide sample. We found no change in live-tree biomass between 1995–1996 and 2005–2006 (Table 2). Forests throughout Hubbard Brook Valley are no longer aggrading, contradicting the predictions of the forest development model of Bormann and Likens (1979).

Siccama et al. (2007) attributed the decline in biomass accumulation to a decrease in tree growth. The aboveground biomass increment in the bird lines averaged 2.8 Mg·ha⁻¹·year⁻¹, a rate comparable with the 2.4 Mg·ha⁻¹·year⁻¹ calculated for the valley-wide plots (Table 3). Both rates are considerably less than the 6.1 Mg·ha⁻¹·year⁻¹ observed in the early 1960s at Hubbard Brook (Whittaker et al. 1974) and the 4.85 Mg·ha⁻¹·year⁻¹ average rate of accumulation between 1965 and 1977 (Likens and Bormann 1995). Fahey et al. (2005) also noted the unusual mortality of sugar maple trees in the upper reaches of W6. Between 1987 and 2002, 40% of the stems died, yielding an annual mortality of 2.7%·year⁻¹ (Juice et al. 2006). Based on these findings and the regional pattern of periodic declines in sugar maple (Horsley et al. 2002; Long et al. 2009), Siccama et al. (2007) predicted more widespread increases in sugar maple mortality. However, across the valley, the annual mortality of sugar maple (1.01%·year⁻¹; Table 4) was well within the expected rates for mature northern hardwood forests (Fahey 1998). More striking was the incipient decline in yellow birch. In the bird lines, yellow birch accounted for 29% of the loss in biomass due to mortality between 1991 and

Fig. 4. Valley-wide tree mortality, recruitment, and growth of the seven major species in Hubbard Brook Valley. Error bars represent 95% credibility interval of the mean. See Table 3 for species names.



2001. In the valley-wide plots, yellow birch contributed 36% of the biomass losses via mortality (Table 3), yellow birch mortality exceeded recruitment (Fig. 4), and its growth rate was among the slowest observed (eight out of 15 species; Table 4). In addition, the contribution of yellow birch to the sapling (2–10 cm dbh) pool remains minimal (3% of the total sapling pool in 2005–2006; 40/1550 trees·ha⁻¹; Solomonoff 2007). By every measure, yellow birch abundance in the valley dropped sharply between 1995–1996 and 2005–2006.

One explanation of yellow birch decline may involve the land-use history of Hubbard Brook Valley. Many of the largest (and presumably oldest) trees in the valley are yellow birch. This skew in the size distribution has been attributed to the relatively low value of yellow birch to the turn-of-the-century loggers (C.V. Cogbill, personal communication). The density of large yellow birch trees (dbh > 60 cm) in 1995–1996 was about 5 trees·ha⁻¹, twice as many large trees than sugar maple and three times more than beech (Solomonoff 2007). In general, large trees did die at a higher rate (2.10%·year⁻¹ vs. 1.58%·year⁻¹), and 39% of the yellow birch

biomass loss from mortality (Table 3) was due to the death of large trees. However, the skewed size distribution does not entirely account for the loss of yellow birch. As noted above, recruitment was not keeping pace with mortality, and the growth of surviving trees was low (Table 4).

Vegetation dynamics

In some respects, the observed decline in yellow birch follows the expectation for secondary succession in New Hampshire. As Allison et al. (2003) noted, yellow birch plays a major role in the recovery following clear-cutting (Bormann and Likens 1979). Although the disturbance history at Hubbard Brook cannot simply be defined as clear-cutting, most of the present-day forest is comprised of trees established after logging operations in the early 1900s. Yellow birch is an early arrival and the dominant species during the transition from aggrading phase to steady state (Leak 1991). In 1995, the yellow birch age structure in Hubbard Brook consisted of some older individuals that predated the turn-of-the-century logging along with cohorts of 75-year-olds (dating from 1920s diameter-limit cutting) and 57-year-olds (salvage harvest from 1938 hurricane). Given this age structure, a decline in the importance of yellow birch is not unexpected. The yellow birch population is growing old. Of a random selection of tree cores (*n* = 24) from the largest yellow birch trees (dbh class = 31.8–99.5 cm) sampled in an ongoing demographic study in HBEF plots, 41% were at least 80 years old, whereas 16% were at least 100 years old (N.S. van Doorn, unpublished data). In addition, recruitment and relative growth were significantly less for yellow birch than for its two northern hardwood associates, sugar maple and beech (Table 4). This trend toward a reduced importance of yellow birch as the forest matures matches results from other northern hardwood stands in the region (Bedison et al. 2007). However, yellow birch remains the dominant species in the nearby old-growth northern hardwood forest (580–1000 m elevation) at the Bowl Research Natural Area (Schwarz et al. 2001) and the second dominant (after sugar maple) in three old-growth northern hardwood forests (466–945 m elevation) in Adirondack Park, New York (Leopold et al. 1988).

Other expected shifts in tree composition are well underway. The intolerant pioneer species including pin cherry and two species of aspen have virtually disappeared from the valley (due to extremely high mortality rates and zero recruitment; Table 4). Similar to yellow birch, the mid-tolerant species paper birch and red maple are expected to reach maximum importance in the transition phase of forest recovery and then decline (Bormann and Likens 1979). In terms of demography, both of these species have entered the declining stage of their importance in Hubbard Brook Valley as mortality outpaces recruitment (Fig. 4). The extent to which the severe region-wide ice storm in 1998 (Irland 1999) contributed to observed high mortality and slow growth of paper birch is unknown. Shortle et al. (2003) suggested that the storm may have been an instigating event that precipitated high mortality in slow-growing and (or) diseased paper birch trees. However, an initial assessment of the ice storm on trees at Hubbard Brook (Rhoads et al. 2002) found only an intermediate level of damage to paper birch trees. Finally, it appears that Hubbard Brook is an exception to the region-wide expansion of red maple (*sensu* Abrams 1998).

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Table 4. Mortality, recruitment, and relative growth rates by species for all trees ≥ 10 cm dbh. Reported values are the means. Errors in brackets represent 95% credibility intervals.

Species	Area-based mortality rate (%·year ⁻¹)	Mortality rate (trees·ha ⁻¹ ·year ⁻¹)	Recruitment rate (trees·ha ⁻¹ ·year ⁻¹)	Relative growth (%)
Yellow birch	1.52 [1.34–1.69]	1.81 [1.47–2.17]	0.4 [0.3–0.5]	1.22 [1.19–1.25]
Sugar maple	1.01 [0.86–1.13]	0.81 [0.60–1.02]	0.6 [0.4–0.8]	1.50 [1.46–1.53]
Beech	1.57 [1.32–1.79]	1.21 [0.89–1.55]	1.7 [1.4–1.9]	1.70 [1.66–1.74]
Red spruce	1.13 [0.95–1.25]	1.10 [0.76–1.43]	1.2 [1.0–1.5]	1.72 [1.69–1.75]
Balsam fir	2.11 [1.89–2.38]	1.68 [1.22–2.25]	2.6 [1.9–3.3]	1.99 [1.95–2.03]
Paper birch	1.86 [1.65–2.20]	1.28 [0.90–1.84]	0.4 [0.2–0.5]	1.03 [0.99–1.07]
Red maple	1.54 [1.26–1.88]	0.50 [0.32–0.74]	0.2 [0.1–0.3]	1.26 [1.20–1.32]
Eastern hemlock	0.17 [0.12–0.41]	0.04 [0.02–0.14]	0.3 [0.1–0.5]	1.31 [1.25–1.37]
White ash	0.61 [0.38–1.06]	0.06 [0.02–0.15]	0	0.65 [0.54–0.75]
Striped maple	9.21 [7.71–10.81]	1.17 [0.75–1.69]	0.6 [0.4–0.8]	1.28 [1.14–1.41]
Mountain ash	9.98 [7.42–13.46]	0.33 [0.12–0.66]	0.2 [0–0.3]	1.15 [0.86–1.46]
Black cherry	2.31 [0.54–5.42]	0.02 [0.00–0.11]	0	0.54 [0.10–0.92]
Quaking aspen	2.17 [0.41–7.98]	0.01 [0.00–0.07]	0	0.76 [0.27–1.24]
Bigtooth aspen	2.31 [0.54–5.42]	0.01 [0.00–0.03]	0	0.79 [0.24–1.35]
Mountain maple	12.90 [5.06–28.73]	0.06 [0.01–0.24]	0.2 [0–0.3]	0.87 [0.14–1.59]
Pin cherry	21.47 [6.15–59.82]	0.07 [0.00–0.39]	0	—
Shadbush	2.03 [0.29–6.71]	0.01 [0.00–0.04]	0	0.61 [0.03–1.14]
Black ash	4.30 [0.48–16.71]	0.00 [0.00–0.04]	0	—
Grey birch	2.31 [0.54–5.42]	0.00 [0.00–0.01]	0	—
Total	1.59 [1.36–1.84]	9.65 [7.88–11.67]	8.4 [5.8–10.6]	1.1 [0.9–1.4]

Regional tree declines

During the last several decades, researchers have documented the impact of several novel disturbances on the structure and function of the northern forests. First, reduced site quality has led to increases in mortality and decreases in growth for some species. For example, acidic deposition combined with cold winter conditions has caused declines in red spruce (Battles et al. 1992; DeHayes 1992). In addition, Ca²⁺ and Mg²⁺ leaching, also primarily due to acidic deposition, has resulted in increased mortality and decreased growth for sugar maple (Long et al. 1997, 2009; Fahey 1998; Likens et al. 1998; Horsley et al. 2000). As noted above, sugar maple has exhibited increased mortality (2.7%·year⁻¹) at high elevation in the reference watershed (W6) at HBEF; nearly half of the stems >10 cm dbh died between 1985 and 2000 (Fahey et al. 2005). Notably, the sites in W6 where sugar maple has declined probably are marginal with particularly thin, acidic soils in comparison with overall conditions in HBEF (Juice et al. 2006). This reinforces the regional observation of sugar maple decline (Long et al. 1997, 2009; Horsley et al. 2000). Introduced pests may also play a role. Beech bark disease (a complex of the exotic beech scale, *Cryptococcus fagisuga* Lindinger, and fungi *Nectria* spp.) causes growth reduction and increased mortality, particularly of larger beech trees (Forrester et al. 2003; Runkle 2007). A retrospective analysis of the spread of beech bark disease places its arrival at Hubbard Brook Valley in the 1950s (Morin et al. 2007), and its effects on beech trees were noted at Hubbard Brook in 1977 (Cleavitt et al. 2008). The importance of these novel stressors lies in the fact that they affect three of the dominant late-successional species: red spruce, sugar maple, and beech. Thus declines in these species have the potential to impact productivity at the later stages of forest development.

There is no evidence that any of these species are currently experiencing widespread decline in Hubbard Brook Valley.

Indeed, robust growth of surviving red spruce (Fig. 4) coupled with balanced mortality and recruitment (Fig. 4) led to a net increase in aboveground biomass (Fig. 2). Also, none of the observed rates of growth, survival, and mortality (Fig. 4) suggests imminent losses of either sugar maple or beech. However, at the current stage of forest development in Hubbard Brook, it seems that sugar maple and beech should be doing more than holding their own in terms of biomass accumulation over the past decade. The fact that sugar maple trees (juveniles and adults) responded positively to modest Ca additions (Juice et al. 2006) on W1 (paired with reference W6) suggests that sugar maple productivity may be constrained by soil calcium status on these especially acidic soils. Also, there was a marked difference in mortality by size class in beech, with the larger trees (>30 cm dbh) dying at a rate of 3.2%·year⁻¹, more than twice as fast as smaller trees (≤ 30 cm dbh, 1.2%·year⁻¹). This concentration of mortality in the larger size classes is symptomatic of beech bark disease effects on the population (e.g., Forrester et al. 2003). Thus, although sugar maple and beech were not declining, air pollution and exotic pests may be reducing their potential for growth during forest recovery.

In contrast to beech and sugar maple, the three common conifer species in Hubbard Brook Valley — red spruce, balsam fir, and hemlock — all showed significant increase in aboveground biomass (Fig. 2). For spruce and fir, these accumulations in biomass were largely due to the rapid growth of survivors (Table 3; Table 4). In terms of relative growth, balsam fir was the fastest growing species in the valley (Fig. 4). For hemlock, the increase was due to a combination of moderate growth with minimal mortality (Table 4). This positive response of the conifers during the decade was unexpected given the turnover in spruce and fir trees observed at a similar elevation in a similar forest in the mountains of Vermont (Beckage et al. 2008). Also, although Beckage et al. (2008)

noted the other drivers of change in the northern forest (e.g., beech bark disease and acid deposition), climate warming was also implicated in the decline of the boreal forest species. Model projections of potential climate change impacts on trees in the northeastern US also predicted losses in red spruce, balsam fir, and hemlock (Iverson et al. 2008). If climate warming does start to shift the hardwood species uphill as Beckage et al. (2008) observed in Vermont, then declines in the extant canopy trees is a necessary precursor. As yet, we see no evidence in the HBEF of an incipient range shift.

The observed constancy of live-tree biomass in Hubbard Brook Valley during the last decade is a result of losses from mortality balancing gains from growth and recruitment. However, the cause of the discrepancy between predicted and measured biomass levels remains to be established. No general model of forest dynamics can be expected to project site-specific site details. The trajectory of Hubbard Brook Valley is just one well-studied example from a much larger and more varied regional forest. Moreover the land-use history of Hubbard Brook is more complex than the theoretical trajectory considered in Bormann and Likens (1979), namely that of an even-aged forest recovering from a catastrophic disturbance (e.g., hurricane, clear-cut harvest). As noted above, the history of Hubbard Brook Valley includes a mixture of selective logging and multiple disturbances. However, in general terms, the Hubbard Brook Valley does fit the criteria of the northern forest in terms of its climate, ecology, and geology. Thus it is striking how poorly the empirical results matched the conceptual pattern. One explanation is that the initial model (Bormann and Likens 1979) overestimated the magnitude of biomass accumulation. Estimates of above-ground live-tree biomass from old-growth northern hardwood forests in New Hampshire (208 Mg·ha⁻¹; Martin and Bailey 1999) and New York (195.7 Mg·ha⁻¹; Forrester et al. 2003) suggest that current live-tree biomass in Hubbard Brook Valley may be closer to the steady-state end point than expected. Yet forest growth and yield simulations for forests at Hubbard Brook also project increasing biomass. Starting with the forest inventory for W6 in 1965, Fahey et al. (2009) used the Forest Vegetation Simulator (Dixon 2003) to project above-ground live-tree accumulation from 1965 to 2002. Similar to the conceptual model, observed rates of biomass accumulation fell short of the site-specific, statistical projections. Thus the recent pattern of biomass accumulation at Hubbard Brook matches neither theoretical nor statistical expectations. Because neither model accounted for the novel stressors that have recently emerged in the region, we suggest that, in aggregate, these new phenomena are depressing the biomass potential of the forest at Hubbard Brook.

Based on 10 years of observed data, it is likely that in the near future, the mid-tolerant species will be less abundant in the valley. Paper birch, red maple, and yellow birch are not recruiting well. In these three species, the recruitment bases (10–15 cm) amount to fewer trees than the next larger size class, suggesting that recruitment will continue to be a problem. Late-successional species (beech and sugar maple in the northern hardwood zone; red spruce and balsam fir in higher elevations) will likely remain dominant, but unless they continue growing without losses in mortality, there is little possibility that overall biomass will begin to aggrade.

In conclusion, although effects of novel disturbances docu-

mented on a regional level have not led to directional changes in HBEF tree demography, it is possible that tree growth rates are lower than they would have been in absence of the stressors. Perhaps it is time to reevaluate the existing conceptual model by incorporating the effects of chronic stress. Tree mortality, growth, and recruitment over a representative landscape comprise the vital signs of the forest ecosystem and must be monitored over the long term to better explain the increasingly complicated effects of multiple stressors in the northeastern US (Likens and Franklin 2009). A relatively new method that could provide insight into the demographic patterns observed at Hubbard Brook is the neighborhood approach (Canham et al. 2006). This approach emphasizes the importance of species-specific, local-scale interactions in determining the success of individual trees and could potentially be used to identify the future trajectory of tree communities.

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