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Decadal change of forest biomass carbon stocks and tree demography in the Delaware River Basin

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ABSTRACT

Quantifying forest biomass carbon (C) stock change is important for understanding forest dynamics and their feedbacks with climate change. Forests in the northeastern U.S. have been a net carbon sink in recent decades, but C accumulation in some northern hardwood forests has been halted due to the impact of emerging stresses such as invasive pests, land use change and climate change. The Delaware River Basin (DRB), sited in the southern edge of the northern hardwood forest, features diverse forest types and land-use histories. In 2001–2003, the DRB Monitoring and Research Initiative established 61 forest plots in three research sites, using Forest Service inventory protocols and enhanced measurements. These plots were revisited and re-measured in 2012–2014. By comparing forest biomass C stocks in the two measurements, our results suggest that the biomass C stock of the DRB forest increased, and was thus a carbon sink over the past decade. The net biomass C stock change in the Neversink area in the north of the DRB was 1.94 Mg C ha^{-1} yr^{-1}, smaller than the biomass C change in the French Creek area (2.52 Mg C ha^{-1} yr^{-1}, southern DRB), and Delaware Water Gap Area (2.68 Mg C ha^{-1} yr^{-1}, central DRB). An increase of dead biomass C accounted for 20% of the total biomass C change. The change of biomass C stocks did not correlate with any climatic or topographic factors, but decreased with increasing stand age, and with tree mortality rate. Mortality rates were highest in the smallest size class. In most of the major tree species, stem density decreased, but the loss of biomass from mortality was offset by recruitment and growth. The demographic changes differ dramatically among species. The living biomass of chestnut oak, white oak and black oak decreased because of the large mortality rate, while white pine, American beech and sweet birch increased in both biomass and stem density. Our results suggest that forests in the DRB could continue to be a carbon sink in the coming decades, because they are likely at a middle successional stage. The linkage between demography of individual trees species and biomass C change underscores the effects of species-specific disturbances such as non-native insects and pathogens on forest dynamics, and highlights the need for forest managers to anticipate these effects in their management plans.

1. Introduction

As global forest C stocks have increased consistently in the past several decades, their potential to sequester additional atmospheric carbon dioxide (CO_2) is considered a mitigation strategy to reduce global warming (Luyssaert et al., 2007; Pan et al., 2011; Ciais et al., 2013). Quantifying forest biomass C stock change and identifying the factors causing changes are important to understand forest dynamics and its feedback with climate change, and to successfully implement forest carbon management strategies (Hyvonen et al., 2007; Bonan, 2008). However large uncertainty still exists as forest biomass is highly heterogeneous (both spatially and temporally), and its dynamics are determined by different factors at different scales (Birdsey et al., 2006; Pan et al., 2013).

It is widely accepted that seasonal weather and climate regulate short-term fluctuations of carbon uptake, while disturbance history and management control C stock change on decadal time scales (Barford et al., 2001; Williams et al., 2012). Climatic, topographic and geologic factors determine forest dynamics across a broader range of environmental conditions, while stand age and gap dynamics control biomass accumulation at smaller spatial scales (Brandeis et al., 2009; Yi et al., 2010). Living tree biomass

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is one of the largest and most active C pools in forest ecosystems (Woodbury et al., 2007), and its dynamics are driven by the balance among three forest demographic changes: growth, recruitment and mortality (including harvesting). Each of these demographic changes can vary with age and species (Vanderwel et al., 2013a; Rozendaal and Chazdon, 2015). Long-term, periodic biometric measurements provide a unique opportunity to not only investigate forest biomass C dynamics at the regional scale, but also link biomass C stock with demographic change (Curtis et al., 2002; Xu et al., 2014).

Based on inventory data, forests in the northeastern U.S. are an overall net sink for atmospheric carbon in recent decades (Turner et al., 1995; Lu et al., 2013). However, C accumulation in some northern hardwood forests has been halted due to the impact of emerging stresses such as invasive pests, land use change and climate change (Brooks, 2003; Siccama et al., 2007; Duarte et al., 2013). Small scale disturbances such as invasive pests, disease and selective harvesting may affect species differently, and increase C turnover at regional scales (Makana et al., 2011). The Delaware River Basin (DRB), situated in the southern edge of the northern hardwood forest, features diverse forest types and land-use histories. Most of the forests in the DRB are secondary forests recovering from agricultural land use, with stand ages around 80–100 years. Succession in the DRB during the recovery process may affect forest biomass C change (Xu et al., 2012). These forests are sensitive to the controlling factors defining forest dynamics; thus, quantifying the biomass C stock in DRB forests acts as the basis for regional C cycle assessment and is essential for effective forest C management.

During 2001 to 2003 a set of forested plots were established in the DRB, and their total biomass C stock (including above- and belowground biomass, but not including fine roots; see below) was measured in a multi-agency program known as the Collaborative Environmental Monitoring and Research Initiative (CEMRI). Here we report the results of re-measuring these plots using the same measurement protocols in 2012–2013. By comparing forest biomass C in the two measurements, and carefully documenting demographic changes, the major goals of this study are: (1) to quantify biomass C stock change in the DRB forest during the recent decade, (2) to investigate the controlling factors of forest biomass C stock change at the regional scale, and (3) to examine the impact of tree demographic change on biomass C change by comparing biomass C change in different size groups and tree species.

2. Methods

2.1. Research area

The Delaware River is one of the major rivers in the mid-Atlantic region of the United States, draining an area of about 33,000 km^2 in Pennsylvania, New Jersey, New York, Delaware, and Maryland. The Delaware River Basin is characterized by a humid continental climate, with mean annual temperature of 9–12 °C and mean annual precipitation of 1143 mm (Kauffman et al., 2008). The DRB is located in the eco-zone of deciduous forests and is ecologically diverse, comprised of five physiographic provinces and multiple species assemblages that represent most of the major eastern U.S. forest types (Murdoch et al., 2008).

Three areas in the DRB were selected as intensive monitoring and research sites for process-level studies in forested landscapes: the Neversink River Basin (NS) in the northern, mostly forested region of the Appalachian Plateau province; the Delaware Water Gap Area (DEWA) with three small watersheds (Adams Creek, Dingman's Falls and Little Bushkill) lying in the central Appalachian Plateau Province; and the French Creek Watershed (FC) in the midbasin Piedmont province (Fig. 1).

During 2001–2003, 68 inventory plots were randomly located in the three sites. Within each plot, all trees with diameter at breast height (DBH) greater than 5 inches (12.7 cm) were measured and marked, and the specific locations of the plots were mapped. In 2012–2013, 61 forested plots of the 68 original plots were revisited and biomass parameters were re-measured using the same protocols. Seven plots were not revisited due to accessibility issues such as permission from the landowner. Between the two measurements some plots had been disturbed by human activities, such as clear-cut or land use change. Anthropogenic disturbance was recorded in the field and while disturbed plots were included in the determination of biomass estimates, they were not included in the demographic analyses. The number of usable plots for demographic analyses was therefore reduced from the original 68 to 55 plots.

2.2. Field measurements and biomass C calculations

The plot design and sampling method follow the forest inventory protocols in the two measurements, including additional variables that were specified for the intensive study sites (Fig. 2; U.S. Department of Agriculture, 2014). Each plot has four round subplots, in total covering an area of 672.44 m^2. Live and dead trees, stumps and residue materials were measured in each subplot. DBH, total and bole height, tree species, and status change (e.g., live versus dead) of each tree were recorded. A laser rangefinder was used to measure the tree and bole heights. Each subplot has one microplot (area: 13.49 m^2) and three transects (length: 7.92 m). Live and dead sapling (1 in. < DBH < 5 in.), seedling (DBH < 1 in.), shrub and herb coverage were measured in the microplots. Coarse woody debris and fine woody debris were measured along the transects.

Within each plot, two trees close to the subplots that represent the dominant species and growing condition of the forest stand were selected as site trees. The age of the site trees was measured by counting rings in a tree core. The stand ages of plots were determined as the mean age of the two site trees.

Field measurement data from the original 2001 to 2003 inventory were acquired from a U.S. Forest Service (USFS) database generated by the CEMRI project (http://www.fs.fed.us/ne/global/research/drb/summary.html). Data from the two inventories were compiled into a single database for biomass C calculations. Cole et al. (2013) provides a detailed description of the database, which contains CEMRI project data on tree biomass.

Biomass of live trees, dead trees, saplings, seedlings, shrubs, coarse woody debris, fine woody debris, and stumps were each calculated and summed for each of the two survey periods. Fine root biomass was the only biomass pool not estimated in either survey in this study. As a result, we assumed that fine root biomass did not change between the two sampling periods. The species-specific allometric equations from Jenkins et al. (2004) were used to calculate above-ground tree biomass (Suppl. Table 1) as described in Cole et al. (2013). The proportion of coarse roots biomass to above-ground biomass was estimated based on DBH for each species as described in Jenkins et al. (2004) and Cole et al. (2013). The total biomass of each tree was the sum of above-ground biomass and coarse roots. Dead tree biomass was multiplied by a reduction factor according to their decade classes and species groups (Waddell, 2002) to subtract the biomass loss from decomposition. Biomass of coarse woody debris and fine woody debris were calculated using standard equations (Woodall and Williams, 2005). Stump biomass was calculated as coarse root biomass multiplied by the reduction factor according to the decade classes. A conversion factor of 0.5 was used to convert biomass to C stock. The biomass C change of

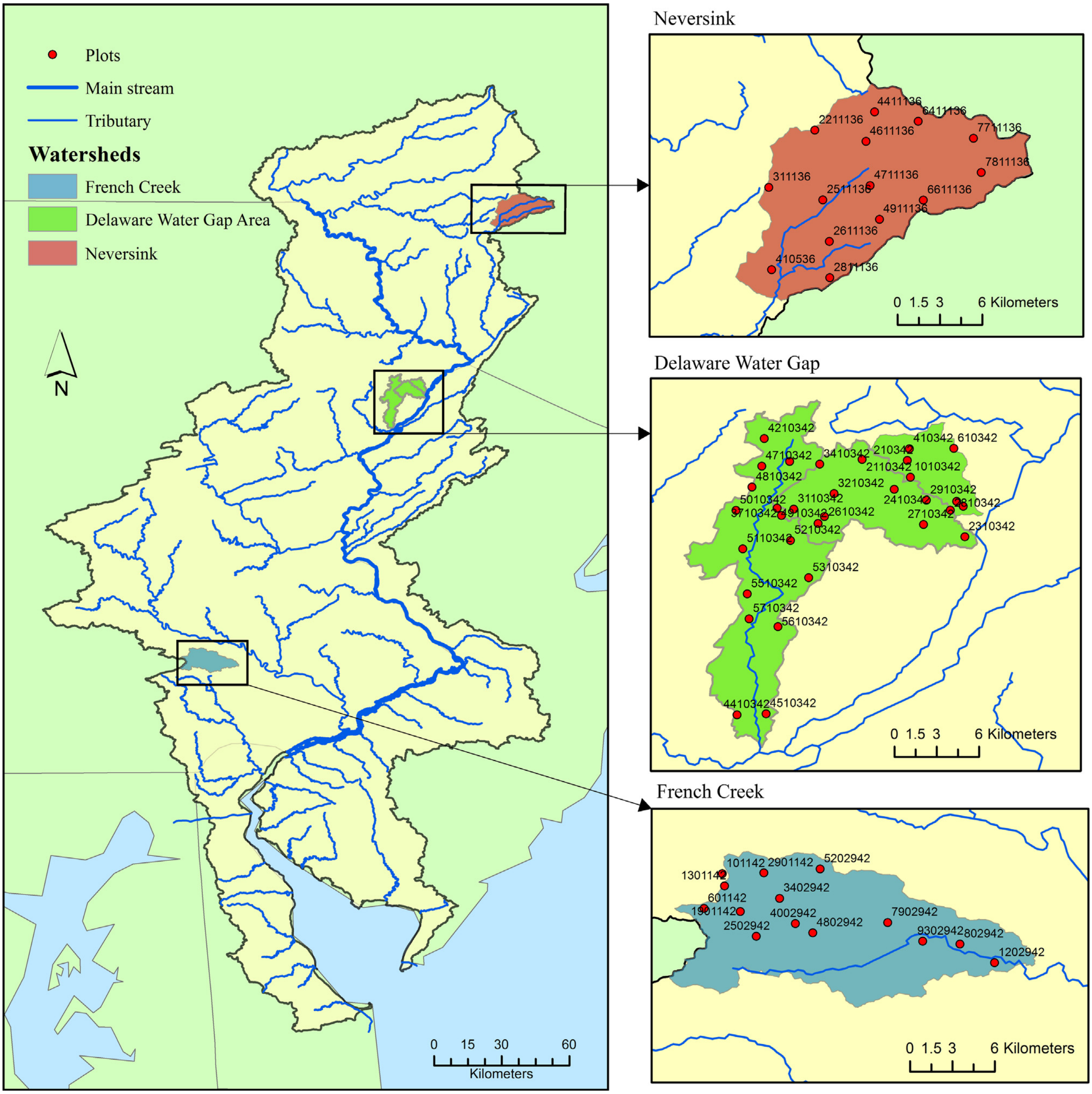

Fig. 1. The hydrological boundary of the Delaware River Basin and the main stream and tributaries of the Delaware River. The three research areas of the current study are shown in different shading color. The red dots represent the locations of forest biomass plots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

each component was calculated as the difference of biomass C in the two measurements divided by the number of years between the two measurements in each of the plot.

2.3. Data analysis

Mean topographic and climatic factors for each site (Table 1) were spatially averaged from spatial data layers based on the coordinated of each plots. The elevation data was derived from Global Land Cover Characterization datasets with a spatial resolution of 1 km (https://lta.cr.usgs.gov/GLCC), and temperature and precipitation data were derived from the PRISM Gridded Climate data as 30-year means from 1981 to 2010 with a spatial resolution of 800 m (http://www.prism.oregonstate.edu/normals/, Thornton et al., 2014). Wet deposition data were inorganic nitrogen deposition at a spatial resolution of 1 km and averaged from 1983 to 2007 (Grimm, 2008). Plot-scale climate and N deposition data were the non-spatially averaged data mentioned above, while the elevation data were values directly measured in the field. Measured topographic data was found to be essentially the same as database values.

Biomass C stocks in each component and their changes between the two measurements were averaged by site and in all plots combined. In addition, all live trees were classified into size classes by their DBH using 5 cm intervals from 10 to 40 cm (size classes 1–6). Trees with DHB 40–50 cm were classified as size class 7 and trees DBH > 50 cm were classified to size class 8. The biomass C stocks of living tree were summed by each tree size class. Mortality rates

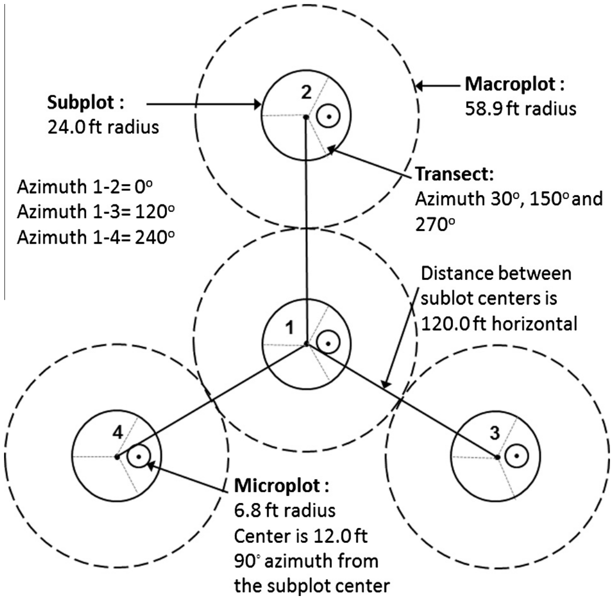

Fig. 2. Plot design used for forest measurement (Revised from U.S. Department of Agriculture, Forest Service. (2002)). Trees within each subplot were measured. Sapling and seedlings were measured in microplots. Coarse and fine woody debris were measured on transects.

(% yr^{-1}) of each plot and each size class were calculated by solving the equation:

$$(1-M)^n = 1 - \frac{N_{dead}}{N_{live1}}$$

where M is the mortality rates, N_{dead} is the number of trees that died between the two measurements, N_{live1} is the number of live trees in the first measurement, and n is the number of years between the two measurements. The mortality rates and proportions of biomass C from each tree size class in the two measurements were compared to examine the structure change in each site.

Tree species richness (S), Shannon's diversity index (H), and evenness (E_H) were calculated for each plot using the live tree data in the second measurement to represent the species diversity at plot level. Species importance values were determined for each site and species following Forrester et al., 2003 (Suppl. Table 2):

$$\text{Importance values} = (\text{relative live density} + \text{relative live basal area}) \div 2$$

The 15 most important species in each site were selected and their biomass C and density change was examined. Biomass C loss from mortality was calculated as the biomass C of trees that were live in the first measurement and died before the second measurement. Biomass C gain from recruitment was calculated as the biomass of new ingrowth trees in the second measurement. Biomass C gain from growth was calculated as the biomass increase for trees living in both of the two measurements.

Differences among the three sites in total biomass C and biomass C change were compared using one-way ANOVA. Type II (major axis) regression analysis was used to test correlations between biomass C stock changes and biotic (stand age, tree mortality rate, Shannon's biodiversity index) and abiotic (slope, elevation, temperature, precipitation, and wet nitrogen deposition) factors in all plots combined to detect regional patterns.

A non-metric multidimensional scaling (NMS) analysis was conducted using PC-ord (Version 6.08, MjM Software, Gleneden Beach, Oregon, U.S.A.) on the basis of live tree data to differentiate the species composition in the three sites. Species that were present in only one plot were removed from the database, after which one plot in FC had only 4 trees remaining and was thus also removed from the database. As a result, data for 60 plots and 28 species (Suppl. Table 3) were used in the NMS analysis. NMS ordination was run using $k = 3$ dimensions, as this led to significantly lower stress than the two-dimensional model and was not substantially improved by using four dimensions. One-way ANOVA on plot scores of the first two NMS axes was used to test for differences in species composition among the three sites. Statistically significant differences between each pair of sites were compared using the Wilcoxon method.

3. Results

3.1. Forest biomass C stock change and its components

In the 61 plots that were revisited in 2012–2013, the mean biomass C stock in the second measurement was 161.2 Mg C ha^{-1}. The net biomass C stock change between the two measurements was 2.01 Mg C ha^{-1} yr^{-1}. Among the 61 plots, six plots had visible disturbances in the past decade. The biomass C loss in the disturbed plots was up to 9.72 Mg C ha^{-1} yr^{-1} (Fig. 3). In the remaining 55 undisturbed plots, the total biomass C stocks were 146.7 Mg C ha^{-1} in FC, 114.7 Mg C ha^{-1} in DEWA, and 159.3 Mg C ha^{-1} in NS in the first measurement during 2001–2003 (Table 2). In the second measurement during 2012–2014 of the same 55 undisturbed plots, the total biomass C stocks were 172.1 Mg C ha^{-1} in FC, 142.2 Mg C ha^{-1} in DEWA, and 185.1 Mg C ha^{-1} in NS. The forests in the most northern site (NS), with higher elevation, and greater precipitation and nitrogen deposition, had larger biomass C pool than the other sites. The net biomass C stock change between the two measurements was 2.52 Mg C ha^{-1} yr^{-1} in FC, 2.68 Mg C ha^{-1} yr^{-1} in DEWA, and 1.94 Mg C ha^{-1} yr^{-1} in NS. The mean biomass C stock change in all the undisturbed plots was 2.45 Mg C ha^{-1} yr^{-1}. The undisturbed forests in the DRB were therefore a net carbon sink over the recent decade (i.e., the mean of each site was above the zero line in Fig. 3). The total biomass C change did not differ among the three sites ($p = 0.76$).

Among all biomass components, live trees were the largest C pool and C sink over the past decade (Table 2). On average, live tree biomass contributed 76.9% of the total biomass C change. Dead biomass was also an important contributor to total biomass C change (20.1%). Dead trees and CWD were the two largest C pools in dead biomass. Variation in biomass C change among plots was large, especially in the dead biomass components (Table 2).

Table 1
Environmental conditions in the three research sites in the Delaware River Basin. All data were extracted from geographic information layers, and mean values for each site are shown. The elevation data was derived from Global Land Cover Characterization datasets (https://lta.cr.usgs.gov/GLCC). Annual temperature and precipitation are 30-year means from 1981 to 2010 (Thornton et al., 2014). Wet deposition is inorganic nitrogen deposition from 1983 to 2007 (Grimm, 2008).

	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Wet deposition (kg N ha^{-1})	Average stand age
French Creek (FC)	166	11.16	1171	6.55	85
Delaware Water Gap (DEWA)	360	8.53	1219	6.33	107
Neversink (NS)	773	5.75	1503	6.44	91

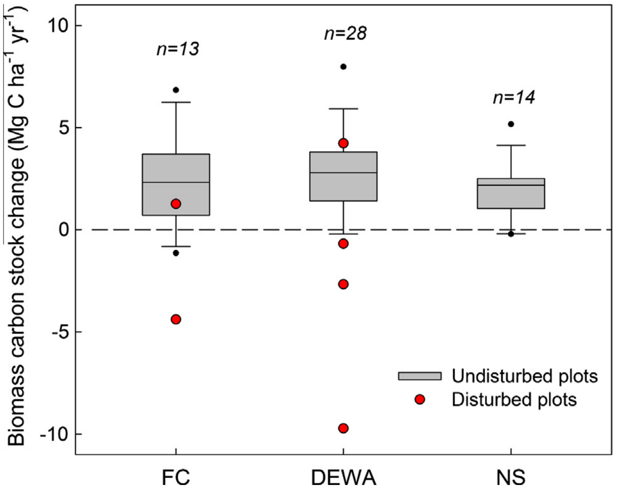

Fig. 3. Biomass C stock changes in the three research sites and for all plots combined. Red dots represent the six disturbed plots. Boxes above the zero line represent increasing biomass C stock. Lines in the boxes show the median and the 25% and 75% quantiles, while bars outside the boxes show the 5% and 95% quantiles. Outliers are shown as black dots. FC: French Creek, DEWA: Delaware Water Gap, NS: Neversink. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Total biomass C stocks in the two measurements (unit: Mg C ha^{-1}) and biomass C stock change in different components (unit: g C m^{-2} yr^{-1}) in each site and in all plots combined. Standard deviations among plots are given in the parentheses. *p* values show the statistical significance of differences among sites in a one-way ANOVA. (* represents statistical significance at $p < 0.05$, and ** represents statistical significance at $p < 0.01$).

	FC ($n = 13$)	DEWA ($n = 28$)	NS ($n = 14$)	Total ($n = 55$)	*p* value
Total Biomass C (Mg C ha^{-1})					
2001–2003	146.7 (50)	114.7 (39)	159.3 (37)	133.6 (45)	0.004**
2012–2014	172.1 (56)	142.3 (51)	185.1 (45)	160.2 (53)	0.017*
Biomass C change (g C m^{-2} yr^{-1})					
Live tree	216.0 (255)	204.8 (262)	131.1 (117)	188.7 (231)	0.56
Dead tree	57.3 (104)	20.2 (50)	−12.8 (113)	30.8 (106)	0.18
Sapling	−6.0 (21)	−6.2 (28)	18.4 (40)	0.2 (31)	0.036*
Seedling	1.2 (6)	10.2 (13)	2.1 (4)	6.0 (11)	0.010*
CWD	5.8 (45)	18.0 (63)	36.0 (37)	19.7 (54)	0.34
FWD	−15.5 (29)	5.5 (29)	1.2 (14)	−0.5 (27)	0.06
Stump	−8.2 (33)	−5.0 (37)		−6.0 (36)	0.80
Live biomass	212.1 (262)	210.7 (258)	151.2 (108)	195.9 (228)	0.84
Dead biomass	40.2 (131)	57.0 (122)	42.6 (104)	49.3 (118)	0.49
Total	252.3 (224)	267.7 (247)	193.9 (142)	245.2 (218)	0.76

3.2. Controlling factors in biomass C change

For all undisturbed plots combined, the change in biomass C stock between the two measurements was poorly correlated with climatic and topographic factors, although the three sites have very different environmental conditions (Table 3, Fig. 4). Stronger correlations were detected between biomass C change and biotic factors (Table 3, Fig. 4). The change in biomass C decreased significantly with tree mortality rate between the two measurements ($r = 0.417$, $p < 0.01$). Biomass C change was negatively correlated with stand age ($r = -0.232$, $p = 0.09$). No significant correlation was detected between biomass C change and tree species diversity.

3.3. Forest demographic changes

Large trees (>35 cm DBH) made greater contributions to the living biomass, especially in FC where the largest size class (>45 cm DBH) accounted for 37.8% of the total live tree biomass. Live tree biomass increased between the two measurements in all size classes, but the change in biomass was greater in large size classes than in small size classes (Fig. 5a–c). Mortality rates were also greater in smaller size class (10–20 cm DBH, Fig. 6d) compared to trees in the middle size class (20–35 cm DBH). High variability was observed in large size class mortality rates because there were few large trees (>35 cm DBH, Fig. 5d).

Table 3
Type II (major axis) correlations between biomass C change and environmental factors. (* represents statistical significance at $p < 0.05$, and ** represents statistical significance at $p < 0.01$).

Variable	Slope	Intercept	R^2	*p*
Slope (degree)	4.13	216	0.010	0.47
Elevation (m)	−0.18	320	0.037	0.16
Precipitation	−6.09	963	0.033	0.18
Temperature	18.48	92	0.030	0.21
Total biomass (2001–2003)	0.004	189	0.089	0.25
Mortality rate	−56.52	335	0.173	<0.01**
Stand age	−2.13	454	0.054	0.09*
Shannon's diversity index	−92.91	368	0.032	0.19

Tree species composition of forests in NS was significantly different from FC and DEWA, but forests in FC and DEWA had more similar species composition. In results of NMS, all of the NS plots were in the lower-left quadrant, with only 4 plots from FC and DEWA (Fig. 6). The NS plots had significantly smaller scores on both of the axes comparing with FC and DEWA (axis 1: NS vs FC $p < 0.01$, NS vs. DEWA $p < 0.01$, axis 2: NS vs FC $p < 0.01$, NS vs. DEWA $p < 0.01$). However the difference between FC and DEWA was not significant on both of the axes (axis 1: $p = 0.73$, axis 2: $p = 0.59$). Forests in NS were dominated by maple–beech–birch forest, while in FC and DEWA consisted of tree species typical of a southern deciduous type of oak-hickory forest. The DEWA site, located between the other two sites from north to south, was a transition zone for tree species (Table S1).

Over the past decade, in spite of reduced stem density, the biomass C stock increased in the 15 most important species in the DRB forest (Fig. 7). Growth of existing trees accounted for most of the biomass C increase, while recruitment contributed little to total biomass C change. Conversely, mortality played an important role in counterbalancing growth and recruitment. Because of the high mortality rate, the living biomass of chestnut oak, white oak and black oak declined in FC and DEWA. White pine, red oak and sweet birch increased in both biomass and stem density in the oak-hickory forests in DEWA. In the maple–beech–birch forests in NS, the stem density of American beech, and biomass C stock of yellow birch and hemlock increased dramatically.

4. Discussion

4.1. The large biomass C sink in the DRB forests

The average biomass C stock in the DRB forest was smaller than previously reported for old growth forests in the region (Gunn et al., 2014; McGarvey et al., 2015), but comparable with the average biomass C stocks in deciduous forests of the northeast U.S. estimated by forest inventory data (Nunery and Keeton, 2010). The change of biomass C stocks over the past decade in the DRB forest was greater than other long-term biomass measurement in northern hardwood forests, such as the Adirondack Mountains (Bedison et al., 2007) and the Hubbard Brook Valley (van Doorn et al., 2011). The change in biomass C stock was also greater than the national average of biomass C stock change during 2000–2007 (Pan et al., 2011).

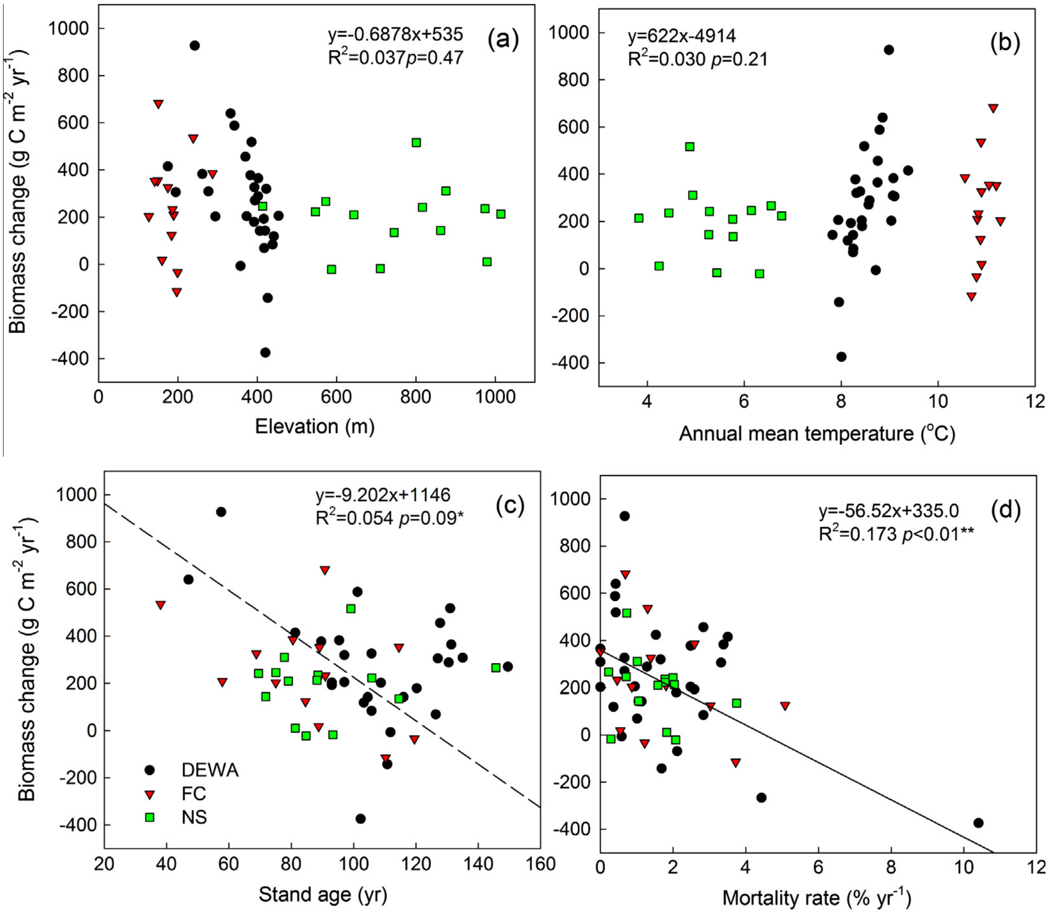

Fig. 4. Relationship between biomass C stock change and environmental (a and b) and biotic (c and d) factors among all the undisturbed plots. Plots in the three sites are shown in different colors and shapes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Forest biomass C stocks differed significantly among the three sites (Table 2). Larger potential biomass C stocks in the maple–beech–birch forest and fewer disturbances at high elevation may be responsible for the larger biomass C stock in the NS (Turner et al., 1995). For the two sites dominated by oak-hickory forest (i.e., FC and DEWA), FC had a larger biomass C stock but smaller biomass C change, suggesting that the plots in FC were in a later successional stage compared to the plots in DEWA. The greater contribution of biomass C from the largest size classes and the high mortality rate in smaller size classes in the FC (Fig. 5a and d) also indicated forest maturity. Although the average stand age in FC was younger than in DEWA (Table 1), possibly because a warmer climate and greater atmospheric N deposition in FC compared to DEWA and NS (Table 1) has allowed the forest in FC to accumulate more biomass C in a shorter period of time, and the growth rate of biomass C might have started to decline earlier (Odum, 1960; Anderson-Teixeira et al., 2013). In contrast, biomass C stocks increased at a greater rate in DEWA because the forests may be in a relatively earlier successional stage and have greater potential to sequester more biomass C in the future.

Dead biomass was a substantial C pool in the DRB forests, but its change was also highly variable. The coefficients of variance ranged from 214% to 325% in the three sites (Table 2). Changes in dead biomass were negatively correlated with live biomass changes at the plot level (Suppl. Fig. 1), suggesting that biomass C lost from live biomass is transferred to, and can be preserved in, dead biomass for at least a decade. Dead biomass can thus function as a buffering C pool, reducing the C turnover rate at the ecosystem scale (Woods, 2014). McGarvey et al. (2015) demonstrated that the contribution of dead biomass to the total biomass C stock is larger in old-growth forest compared to the surrounding younger forest in the mid-Atlantic region, which includes the DRB. As a result, we might expect dead biomass C pools to increase in the future as the DRB forest ages.

4.2. Environmental versus biotic factors in determining biomass C change

The observed lack of correlation with climatic and topographic factors for biomass C change is likely because the plot variation in forest biomass is much larger than the spatial variation in environmental factors (as illustrated by scattering in a wide range vertically, but clustering in a small range horizontally in Fig. 4a and b). The environmental factors were not adequate to explain the variation in biomass C change within each site, while biological factors such as tree mortality rate and stand age appeared to be more important in determining variation in biomass C stock changes. Our results suggest that forest biomass C change at the regional scale was mostly driven by internal community-level processes such as competition and natural succession, more so than external environmental factors. This is consistent with previous studies that concluded that the direct effect of climatic variables on long-term forest dynamics may be small compare to successional processes and disturbances (Kardol et al., 2010; Nowacki and Abrams, 2015; Zhang et al., 2015).

To explain the lack of correlation between environmental factors and biomass C change, two points need to be mentioned. First, this result does not mean that forest biomass C is unaffected by cli-

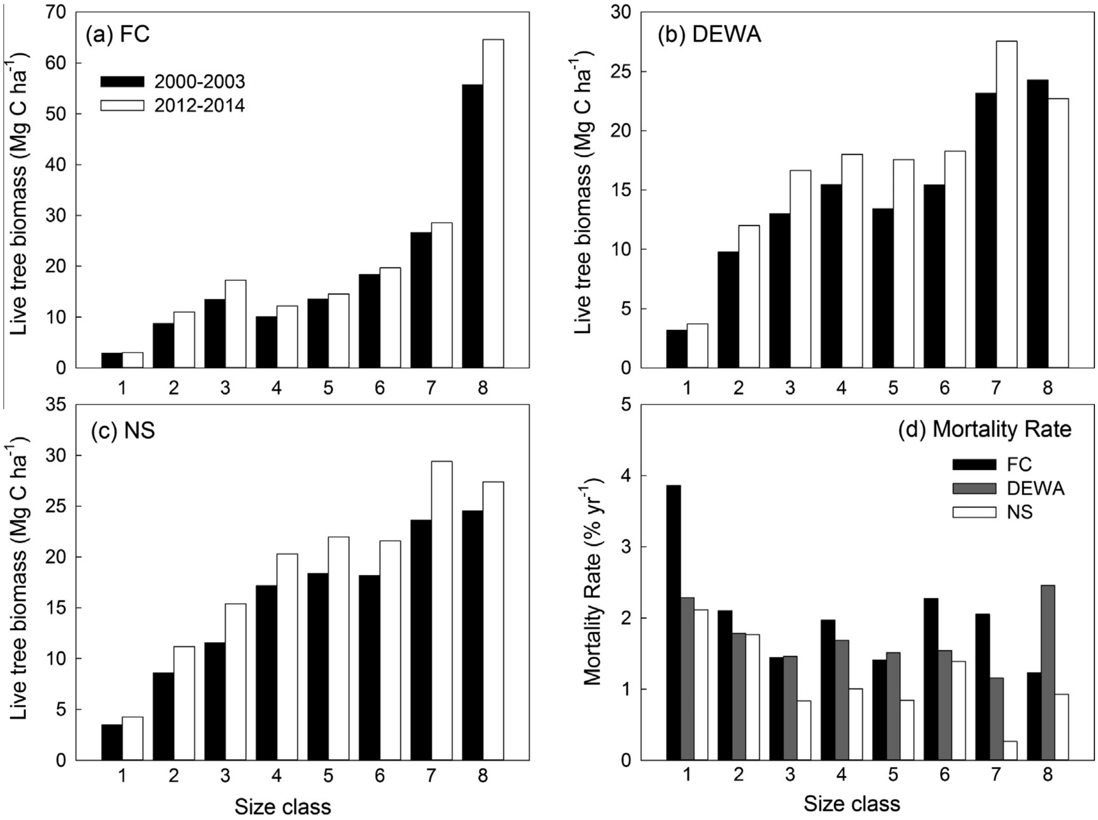

Fig. 5. Live tree biomass C and mortality rates in different tree size classes. Live tree biomass C in the two measurements in (a) French Creek, (b) Delaware Water Gap, and (c) Neversink. Mortality rates (d) of the three research sites between the two measurements. The three sites are shown in different shades.

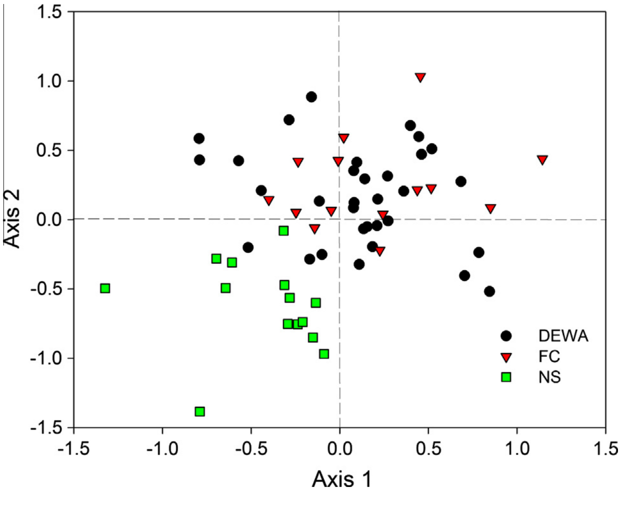

Fig. 6. Results from the NMS for live trees in the second measurement (2012–2014). Points represent individual plots sampled and sites are represented by different colors. See Suppl. Table 3 for the loading score of species.

mate change in the DRB. Caspersen et al. (2000) previously concluded that forest biomass C change results from a combination of natural growth and enhancement by climate change, whose effects cannot be easily separated. Second, environmental factors may determine demographic change and disturbance regime, and therefore may have indirect impacts on biomass C change (Vanderwel et al., 2013b; Baez et al., 2015). However, these effects are not strong enough to be detected at such small spatial scales compared to the more dominant influence of plot dynamics. Long term observations at more sites are needed to address the interactions between factors.

The observed negative correlation between stand age and biomass C change (Fig. 4c) is consistent with the forest succession model, which predicts a decline in forest growth with increasing stand age (Williams et al., 2012). Our observed correlation was not particularly strong because the range of stand ages in our DRB plots was relatively narrow, and the correlation was mostly driven by the three plots with the youngest stand ages. The observation that younger forests accumulated more biomass C than older forest over the past decade still indicated that most of the forests in the DRB had reached or passed the stage of maximum growth rate. While still accumulating C and thus acting as a sink, the rate at which C may be sequestered in the future may decrease as the age distribution shifts toward older stands in the DRB forest.

Although live biomass C loss from mortality could be preserved in the ecosystem as dead biomass for several decades, tree mortality rates still had a significant impact on biomass C change (Fig. 4d). A larger proportion of the spatial variation in biomass C change can be explained by tree mortality rate, rather than the average tree growth rate (Table 3), indicating the importance of tree mortality in determining forest dynamics (Purves et al., 2008; Xu et al., 2012). It has been reported that tree mortality rates vary with climate, forest density, species and succession stage (Bell, 1997; Brown and Schroeder, 1999; Lutz and Halpern, 2006; Bond-Lamberty et al., 2014).

4.3. Demographic changes in different size classes and species

Large trees played an important role in determining forest biomass C stock in the DRB forest. The largest 10% of trees accounted for 47% of the live tree biomass in FC, 41% in DEWA and 38% in NS.

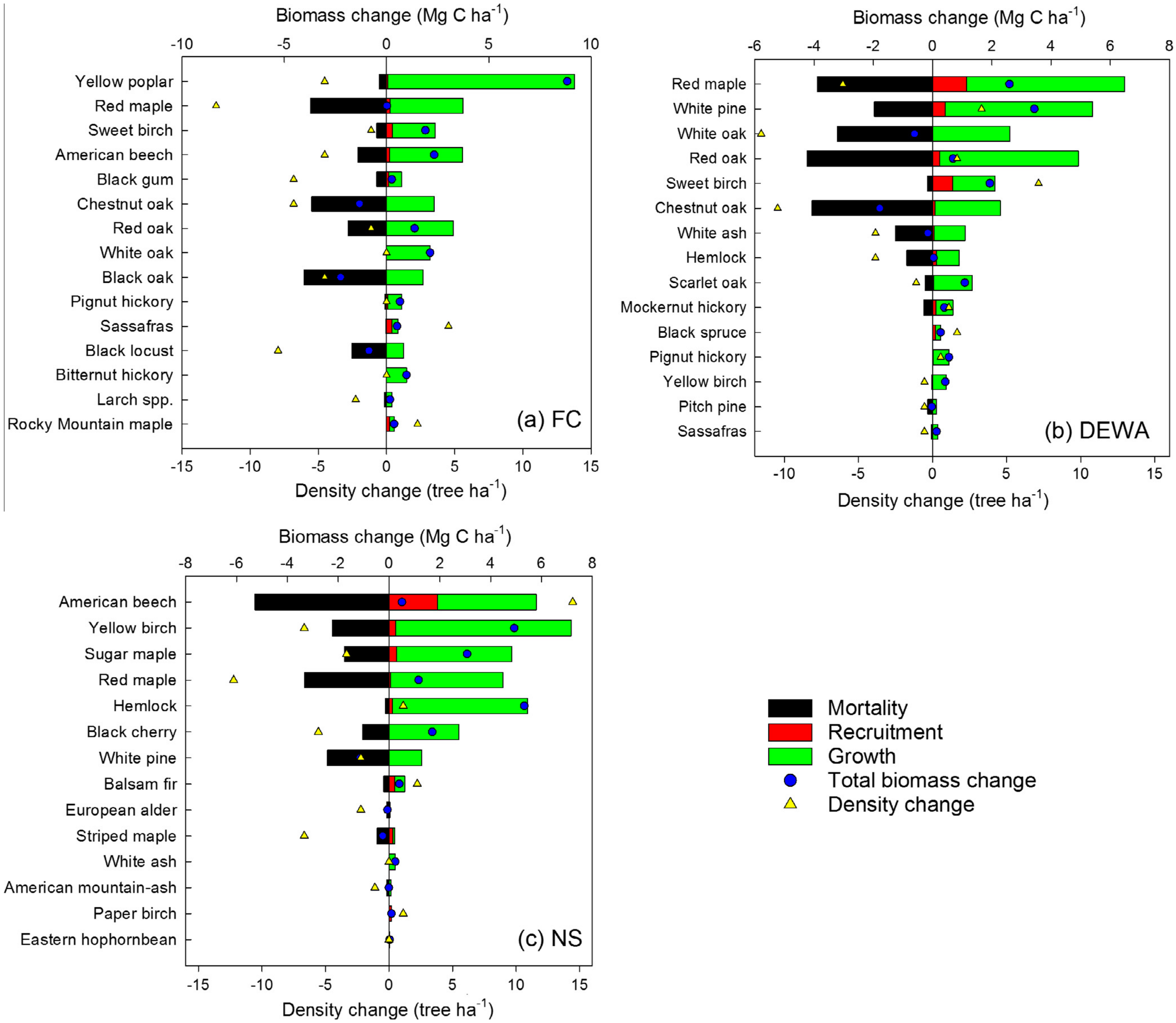

Fig. 7. Stem density and biomass C change in the fifteen most important species in the tree sites in the DRB forests: (a) French Creek, (b) Delaware Water Gap, and (c) Neversink. The lengths of the bars represent the biomass C gain from recruitment and growth and biomass C loss from mortality. Data points on the left side of the zero line represent decrease in stem density or biomass C stocks, and on the right side of the zero line represent increase in stem density or biomass C stocks. See Suppl. Table 1 for species Latin names.

Between the two measurements, more biomass C was accumulated in the larger size classes than smaller size classes (Suppl. Table 4), which is consistent with other studies (Fedrigo et al., 2014). Biomass C increases in large trees can be attributed to increased number of large trees as a result of shifting forest age structure (as small trees grow into large ones), and to faster growth rates of large trees because they have better access to more resources such as light and water than do small trees (Stephenson et al., 2014). The fact that large trees in the DRB forests are still growing rapidly indicated a large potential for biomass C increase in the future. In this study, most of the trees in the largest size class (50–70 cm DBH) are comparable to only the middle size class in the old-growth forest of the Mid-Atlantic (McGarvey et al., 2015). This comparison further suggests that the forests in the DRB are likely in a stage of middle succession, and could continue to be a carbon sink in the future, although C sequestration rate may decline.

The highest mortality rates were observed in the smallest tree size class (especially in FC, where the forest biomass largely consisted of the largest size class, Fig. 5a and d), which can be explained by severe competition in the understory layer. Once individual tree height reaches the canopy height, growth is not limited by light and the mortality rate decreases (Bell, 1997; Miura et al., 2001). Our observations contrast with the pattern of mortality rate increasing with stem size as reported in an old-growth forest (Runkle, 2013). It is observed that as forests age, the peak of mortality biomass C loss shifts from young, small trees to large, dominant trees (Bond-Lamberty et al., 2014; Woods, 2014; Rozendaal and Chazdon, 2015). However, increased mortality rate in large trees was only present in DEWA, which has the largest sample size (number of trees = 953), and not in FC and NS, which both have a smaller number of trees in the largest size class.

Stem density decreased in most of the major species, probably due to the self-thinning process caused by resource competition during forest development (Coomes and Allen, 2007). Although tree density decreased, live tree biomass C stock in the DRB forest still increased because the loss of biomass C from mortality was offset by recruitment and growth in most of the dominant species. However, the balance between growth, recruitment and mortality varies dramatically among species. Our results reflect the importance of species-specific disturbances such as non-native insects and diseases, which may threaten a single species or genus of trees (Lovett et al., 2002; Flower et al., 2013). These disturbances are gradually changing the species composition in the DRB forest and may have profound impacts on biomass C stock change by altering the demographic change in different tree species (Hicke et al., 2012; Fahey et al., 2013).

For example, in the oak-hickory forests in FC and DEWA, oak species (e.g. chestnut oak and black oak in FC, white oak and chestnut oak in DEWA) are declining in both stem density and biomass C stock. The possible reasons for oak decline include regional selective harvesting and defoliation induced by gypsy moth outbreaks, or infestation of sudden oak death (Murdoch et al., 2008).

In the maple–beech–birch forests in NS, the most dominant species, American beech, was affected by infestations of beech bark disease (Griffin et al., 2003; Lovett et al., 2013), causing the largest biomass C loss from mortality (mostly from the largest size class) and the largest biomass C gain from recruitment among all the species and sites. These results implied that the forests in the NS are in the aftermath phase of the disease, in which the disease may stimulate regeneration and change the forest structure (Houston, 1994; Forrester et al., 2003).

4.4. Implications for regional C cycle and forest management

In this study, periodic long-term field measurements of tree and forest biomass allowed the quantification of total biomass C stock change and how the demographics of individual tree species contributed to the total biomass change of the forest. Our results showed that forest biomass in the DRB was a relatively large carbon sink over the past decade compared with other sites in the Northeast U.S. and the national average. It is likely that the DRB forest will continue to be a carbon sink in the coming decades, because the forest is in its middle rather than a late successional steady state (Odum, 1969). These results can serve as a reference level according to international standards for evaluating the potential of forest management and forest health protection to increase biomass C sequestration in the DRB forest in the future (FAO, 2015).

We found that biomass C stock changes were driven by tree demographic change, which varied with tree size and species. This highlights the potential importance of species-specific disturbances such as insects and pathogens which have become major determinants of individual tree species demographic changes, and how the changing frequency and severity of these disturbances might impact forest biomass C sequestration. Our results can provide important information for understanding forest recovery processes in major forest types of the northeastern U.S., and for improving ecological modeling and forest management at the regional scale. Forest management strategies need to pay close attention to the species that show declines in density and biomass over time, or are likely to show such declines in the near future, especially late successional species susceptible to biotic disturbances, to ensure sustainable forest development and a continuing biomass carbon sink.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.04.045.

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