

Edge effects enhance carbon uptake and its vulnerability to climate change in temperate broadleaf forests

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Forest fragmentation is a ubiquitous, ongoing global phenomenon with profound impacts on the growing conditions of the world's remaining forest. The temperate broadleaf forest makes a large contribution to the global terrestrial carbon sink but is also the most heavily fragmented forest biome in the world. We use field measurements and geospatial analyses to characterize carbon dynamics in temperate broadleaf forest fragments. We show that forest growth and biomass increase by $89 \pm 17\%$ and $64 \pm 12\%$, respectively, from the forest interior to edge, but ecosystem edge enhancements are not currently captured by models or approaches to quantifying regional C balance. To the extent that the findings from our research represent the forest of southern New England in the United States, we provide a preliminary estimate that edge growth enhancement could increase estimates of the region's carbon uptake and storage by $13 \pm 3\%$ and $10 \pm 1\%$, respectively. However, we also find that forest growth near the edge declines three times faster than that in the interior in response to heat stress during the growing season. Using climate projections, we show that future heat stress could reduce the forest edge growth enhancement by one-third by the end of the century. These findings contrast studies of edge effects in the world's other major forest biomes and indicate that the strength of the temperate broadleaf forest carbon sink and its capacity to mitigate anthropogenic carbon emissions may be stronger, but also more sensitive to climate change than previous estimates suggest.

climate change | forest fragmentation | land cover change | terrestrial carbon cycle | tree growth

Despite advances in measurement and remote sensing methods for carbon (C) accounting, considerable uncertainty remains in estimates of the global forest C sink and the C implications of deforestation (1–4). Expansion of agricultural and developed land has reduced global forest cover by one-third (5) and led to emissions of up to 146 Pg C to the atmosphere since 1850 (3). These changes in land cover and land use have also resulted in widespread landscape fragmentation, with 20% of the world's remaining forest within 100 m of a forest's edge (6). Compared with the forest interior, forest edges often experience altered growing conditions because of novel microenvironment conditions that typically include higher temperatures, vapor pressure deficit, wind, and availability of resources, such as light and nutrients (7–10). Consequently, the effects of deforestation on the terrestrial C cycle extend into adjacent forest fragments (10–12), with a growing body of research from tropical rainforests (10), temperate rainforests (11), and boreal forests (12) showing widespread increases in tree mortality and reductions in biomass near the forest's edge. Edges were recently associated with a 10% reduction in tropical forest C density (13), which highlights the importance of considering landscape fragmentation when quantifying regional C balance (14). Furthermore, the potential for forest edge effects to exacerbate forest response to climate extremes (15) confounds conventional understanding of feedbacks between the terrestrial C cycle and climate. Although C cycle–climate feedback

models, which play a crucial role in projecting future climate, are becoming increasingly sophisticated and consider the direct effects of deforestation on the terrestrial C cycle, lack of sufficient empirical data precludes parameterization necessary to capture edge effects.

In light of the globally important implications of extensive and ongoing forest fragmentation for ecosystem processes, quantitative characterization of the effects of fragmentation on forest growth and its response to climate is essential for constraining forest C balance and climate projections. The temperate broadleaf forest has a C sink equivalent to ~60% of the global net forest sink (1) and is the most heavily fragmented (6) forest biome in the world. However, although it is also one of the most heavily studied ecosystems, the effects of fragmentation on temperate broadleaf forest growth and C storage and its sensitivity to climate remain poorly understood.

This study quantifies the edge effect on forest growth and C storage in temperate broadleaf forests using data collected from forest fragments in Massachusetts, United States. We focus on forests dominated by oak species (*Quercus* spp.), because they are the most common forest types (Fig. S1), and oaks are the most common tree genus in North America's more than 130 Mha temperate broadleaf forest (16, 17). Across a series of plots 20-m wide and extending 30 m from the forest's edge to its interior, we quantified the basal area (BA; i.e., cross-sectional area of wood),

Significance

A large proportion of the world's forest is highly fragmented, but our understanding of forest carbon dynamics and their response to climate largely comes from unfragmented forests, which presents an important mismatch between landscapes that we study and those that we aim to characterize. We find that temperate broadleaf forest growth and biomass in southern New England increase substantially from forest interior to edge. However, forest growth reductions with climate stress increase with proximity to the edge, pointing to important interactions between forest fragmentation and climate change. We show that, by not accounting for edge effects, current approaches to quantifying regional and global carbon balance may underestimate carbon sequestration and not accurately represent forest growth response to future climate change.

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tree growth rates, and soil properties. We use soil and coarse woody debris (CWD) data, BA, and basal area increment (BAI; i.e., annual wood increment) in a linear mixed effects model framework to quantify relative changes in C storage and growth from the forest's interior to edge. Tree core analysis indicates that forest age in the plots used for this study ranges from 61 to 84 y, which is similar to 60% of forests in southern New England (Fig. S1). All forest edges were created more than 30 y ago, and we used historical climate records to isolate climate drivers of interannual variability in tree and forest growth.

Results and Discussion

Forest Growth and C Storage. We find that forest edge effects substantially enhance aboveground forest growth and C storage. The forest BAI (hereafter “forest growth”) and BA increase by $89 \pm 17\%$ ($P < 0.001$) and $64 \pm 12\%$ ($P < 0.001$), respectively, from the forest's interior (20- to 30-m segment) to edge (0- to 10-m segment) (Fig. 1). Oaks make up $74.8 \pm 7.1\%$ of the BA in our plots (Fig. 1) and a plurality (35%) of the forest biomass in southern New England (18). Oak relative BA varied across plots, but we find no significant effect of species composition on the magnitude of forest growth response to edge effects ($P > 0.40$) (Table S1). Furthermore, there is no discernable effect of solar

aspect on the pattern or magnitude of the forest growth and C storage response to edge effects ($P = 1$). Increased light availability near forest edges is likely an important mechanism driving the observed increase in forest growth, analogous to increases in tree growth after precommercial thinning treatments used by silviculturists and foresters. Oak radial growth has been shown to nearly double after even low levels of thinning (19). Similarly, research across 91 sites in Massachusetts indicates that radial growth rates of individual oak trees nearly double after the clearing of adjacent land for development (20). Although overall forest growth consistently increases with proximity to the edge, we find that the growth response of individual trees varies with patterns in tree stem density. In forests where stem density increases with proximity to the edge, the growth rate of individual trees generally remains constant, whereas in forest stands where stem density does not vary across the plot, the growth rate of individual trees generally increases (Fig. S2); each mechanism results in higher overall forest growth. Although previous work in temperate forest fragments has focused on either growth of individual trees (21) or tree stem density (22), our findings suggest that neither metric alone provide a good proxy for growth at the forest scale.

In contrast to the aboveground processes, analyses of eight soil samples from each plot suggest that total C and N content and root biomass in the top 10 cm of the soil do not vary with proximity to the forest's edge ($P > 0.05$). Similarly, from a series of seven 20-m-long transects in each plot, we observe no patterns in CWD between the forest's interior and edge ($P = 0.13$), suggesting that, in contrast to other forest types (10–12), fragmentation might not increase rates of tree turnover in temperate broadleaf forests.

Edge Effects on Climate Sensitivity of Forest Growth. Although forest growth is consistently higher near the forest's edge than in the interior, the magnitude of this edge enhancement varied with annual climate. We find that interannual variability in forest growth more than doubles with proximity to the forest's edge from a range of $0.28 \pm 0.04 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ in the forest's interior to a range of $0.58 \pm 0.12 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ in the 0- to 10-m forest segment (Fig. 2 and Fig. S3). Heat stress, defined here as the number of days in June and July above 27°C (the July average high temperature in Boston, MA), alone explained 30% (0–10 m from forest edge) to 36% (10–20 and 20–30 m from forest edge) of the interannual variability in forest growth between 1990 and 2014 ($P < 0.01$) (Fig. 2). These findings are in agreement with earlier studies that show the adverse effects of high temperatures during early summer on growth of oak trees in the eastern United States (23) and forest net primary productivity (NPP) in New England (24). In our study, results from linear regression models indicate that declines in forest BAI in response to heat stress increase from 0.004 to $0.011 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ for each additional day above 27°C between the forest's interior and edge, respectively (Fig. 2).

The edge effect on climate sensitivity of forest growth suggests the potential for interactions between land cover change and climate change. To estimate a first approximation of potential changes in the forest edge growth enhancement under climate change, we used downscaled climate projections from Phase 5 of the Coupled Model Intercomparison Project (CMIP5) (Table S2) (25). These climate projections indicate that southern New England is likely to experience an average of 48.2–56.6 d above 27°C during June and July between 2080 and 2099 under the Intergovernmental Panel on Climate Change Representative Concentration Pathway 4.5 (RCP4.5; low emissions) and RCP8.5 (high emissions) scenarios, respectively. These projections suggest that forest exposure to heat stress could nearly double (1990–2014 mean is 29 d) by the end of the 21st century, reducing forest growth by 33–42% from the forest's interior to edge under the RCP 8.5 scenario (Fig. 2).

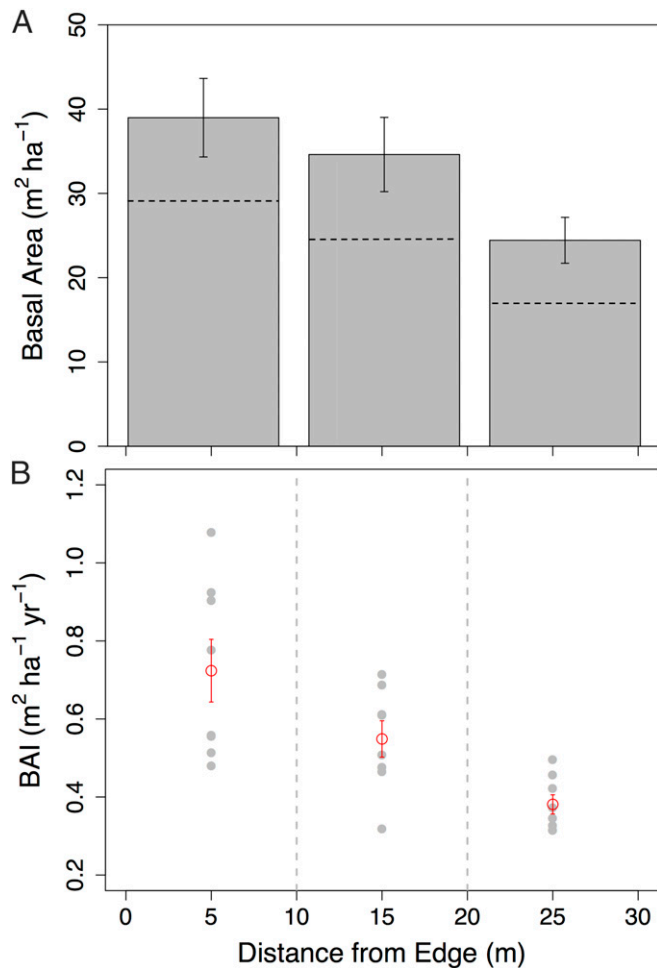


Fig. 1. Response of forest biomass and growth to forest edge effects. (A) Total BA (gray bars) and contribution from oak trees (dashed lines) with distance from the forest's edge averaged across plots (slope = -7.275 ; $P < 0.001$). (B) Forest BAI (2005–2014 mean) with distance from the forest's edge (slope = -0.1713 ; $P < 0.001$) for each plot (gray circles; $n = 8$ for each forest segment) and means of all plots (red circles). Error bars represent SEM.

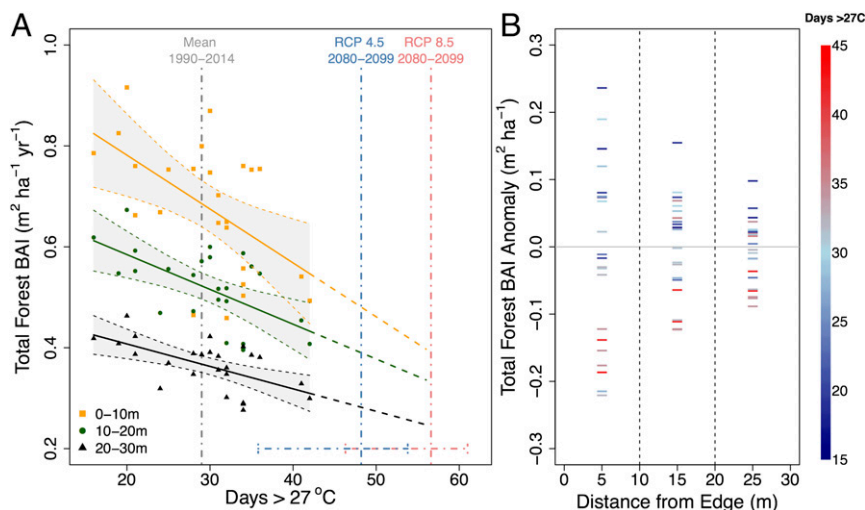


Fig. 2. Forest growth response to growing season heat stress. (A) Relationship between total forest BAI for 1990–2014 and heat stress (number of days in June and July with air temperature above 27 °C). Data are partitioned into segments of 0–10 (slope = -0.011 ; $P = 0.009$; $r^2 = 0.30$), 10–20 (slope = -0.007 ; $P = 0.002$; $r^2 = 0.36$), and 20–30 m (slope = -0.004 ; $P = 0.001$; $r^2 = 0.36$) from the forest’s edge and represent means across the plots measured in this study. Gray shaded areas indicate the 95% confidence intervals. Vertical lines indicate the mean numbers of days above 27 °C for 1990–2014, 2080–2099 CMIP5 RCP4.5, and 2080–2099 CMIP5 RCP8.5. The horizontal blue and red dotted bars represent the range in the mean number of days >27 °C across the CMIP5 ensemble model runs. (B) Forest BAI anomaly and heat stress for each 10-m forest segment; mean forest BAI between 1990 and 2014 was used as the reference period. In each panel, $n = 25$ for each forest segment.

Regional Implications of Forest Edge Effects. We used the 2011 National Land Cover Database (NLCD) land cover maps (26) to scale up our data to southern New England (Massachusetts, Connecticut, and Rhode Island) as a first approximation of the landscape-scale implications of the forest edge effect on growth and C storage in the temperate broadleaf forest. This region of the northeastern United States includes forestland (64%) interspersed with large population centers and developed (27%) and agricultural (7%) land. Across the 2.2 million ha forest in southern New England, US Forest Inventory and Analysis (FIA) data indicate that forest NPP and aboveground C storage are $4.8 \pm 0.18 \text{ Tg C y}^{-1}$ and $179 \pm 2.9 \text{ Tg C}$, respectively (18). However, although the FIA data (Table S3) are commonly used to quantify forest growth and C storage at regional to national scales [e.g., the work by Woodbury et al. (27)], FIA sampling was not designed to capture the effects of edges and fragmentation

on forest growth and biomass. Across southern New England, 9.6% and 17.8% of the forest are within 10 and 20 m of the forest’s edge, respectively (Fig. 3 and Table S3). To the extent that the plots that we studied represent forest edge growth enhancement throughout southern New England, the forest edge effect could increase aboveground growth and C storage of the 2.2 million ha forest that remains in southern New England by $13 \pm 3\%$ (0.6 Tg C y^{-1}) and $10 \pm 1\%$ (17 Tg C), respectively. Although additional research is necessary to develop robust regional estimates, these findings show the potential of the edge growth enhancement in the temperate broadleaf forest to play an important role in offsetting declines in the C sink associated with deforestation and urban development. However, our results should not be interpreted as support of fragmentation as a management strategy. Even accounting for a forest edge growth enhancement, the current regional forest C sink of southern New England is 31%

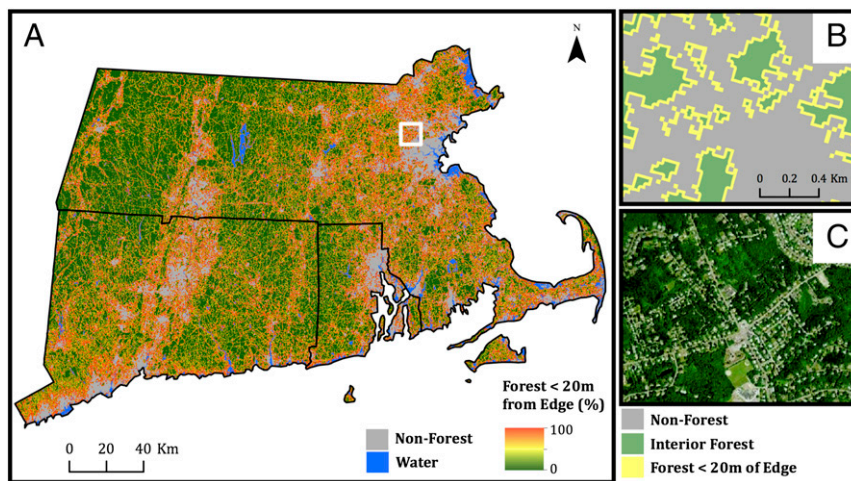


Fig. 3. (A) Spatial patterns in the proportion of forest within 20 m of an edge across southern New England (states outlined in black) at 100-m resolution. B and C show mapped forest fragmentation and satellite imagery (Google Earth), respectively, of the area surrounding one of our research locations in eastern Massachusetts (within the white outlined box in A).

lower than it would have been in the absence of the 1.4-Mha net decline in forest area since the precolonial era (28). Forest fragmentation also has many other well-documented adverse impacts on biodiversity and ecosystem services (6).

Forest age, forest type, and land cover adjacencies were not considered when scaling our plot-level data to the forests of southern New England, but these characteristics may play important roles in determining the magnitude of the forest edge growth enhancement and its response to climate. The forest fragments studied here, like the forests of southern New England and more broadly, the temperate broadleaf forest of the eastern United States, are relatively young (i.e., <100 y old) (Fig. S1). Although age-related decline in forest growth is a widely observed phenomenon, the underlying mechanisms and timing of growth decline are complicated (29), and it is unclear how the forest edge growth enhancement observed here will evolve with stand age. Growth rates of at least some broadleaf forests in southern New England have been increasing in recent decades, despite forest ages of 75–110 y (30). Furthermore, Briber et al. (20) show that individual oak trees across a wide range in size and age exhibit a strong growth enhancement after the creation of a forest edge. However, as the forests of southern New England and the eastern United States age and become more structurally complicated but also, more fragmented, understanding relationships between forest age, species composition, and edge growth enhancement will be necessary for accurate modeling of forest C balance. BA data that we collected from an additional series of plots across oak, mixed broadleaf, and mixed broadleaf/conifer forests in central and eastern Massachusetts suggest that the forest edge enhancement that we describe above for our intensively surveyed plots transcends numerous forest types (Fig. S4). However, future work should build on our findings and characterize edge effects on growth and climate sensitivity in additional forest types and regions within the temperate broadleaf forest. Additionally, the land use and land cover adjacent to a forest edge can be important drivers of forest edge microenvironment conditions by influencing variables, such as temperature (e.g., road vs. vegetated surfaces) and resource availability (e.g., irrigated and fertilized lawn or cropland vs. meadow or unamended lawn), and we suggest that the associated effects on forest growth be further explored.

Conclusions

Here, we provide a comprehensive analysis of edge effects on temperate broadleaf forest growth and C storage as well as an analysis of the importance of edge effects as a mediator of forest growth response to climate. Our findings in conjunction with earlier research (20–22) show that the paradigm describing forest edge biomass dynamics in tropical rainforests (10), temperate rainforests (11), and boreal forests (12) may not be applicable to the temperate broadleaf forest. Forest ecosystems that have exhibited edge-related declines in biomass typically have either large, tall stature trees (up to 50–60 m) or shallow roots, and these factors are commonly associated with increased wind-induced tree mortality (10–12, 31). By contrast, the modest height stature (generally <25 m), deciduous nature, and relatively deep roots of trees in the temperate broadleaf forest likely bolster its resilience to increased wind exposure near the forest's edge and allow the remaining forest to capitalize on greater resource availability (e.g., light) (8). We posit that global patterns in the response of forest growth and biomass to edge effects are generally driven by a combination of increased vulnerability to disturbance (i.e., wind, drought, and fire) and an increase in light availability. Recently, an edge-related 10% decline in biomass was reported for the world's tropical forest (13), which assuming proportional declines in C uptake, would reduce the tropical forest C sink by 0.27 Pg C y⁻¹ (1). By contrast, applying our estimated 13% edge enhancement on forest growth in southern New England to the world's temperate forest suggests that temperate forest edge effects could potentially

offset 37% [0.10 Pg C y⁻¹ (1)] of edge-related declines in the tropical forest C sink and ~10% of global emissions from land use and land cover change (32).

Despite advances in accounting methods, there is still considerable uncertainty in estimates of the global terrestrial C sink (3, 4). Monitoring efforts, such as national forest inventory programs (e.g., US FIA) and FluxNet, have often been used to quantify C storage and rates of sequestration of US forests at regional to global scales (1, 33–35); however, these approaches were not designed to capture the effects of edges and fragmentation on forest growth and biomass and do not capture this important determinant of forest C balance and its sensitivity to climate. Consequently, current accounting methods may not capture forest C balance and its sensitivity to climate. Empirical field data (including this study) highlight the profound edge-related changes in above-ground C cycling that occur in remnant forests after fragmentation across a broad range of forest biomes. Given the continued forest fragmentation, edge effects will play an important role in constraining estimates of the terrestrial C sink and its feedback with climate.

Materials and Methods

Site Description. Field data for this study were collected from temperate broadleaf forest fragments in eastern Massachusetts, United States in the towns of Belmont (42.24° N, 71.11° W, 10 m above sea level) and Lynn (42.29° N, 70.59° W, 30 m above sea level). Eastern Massachusetts has a heterogeneous fragmented landscape consisting of forest (48% of the land area) interspersed with mostly developed (30% of land area) and agricultural land covers (10%). The climate is humid continental with warm summers and cold, snowy winters. Boston has mean maximum monthly temperatures of 2.1 °C in January and 27.4 °C in July and receives ~1,100 mm precipitation evenly distributed throughout the year (36).

The landscape of eastern Massachusetts, similar to much of the eastern United States, was nearly entirely forest before European colonization (~1600), but rapid agricultural expansion reduced forest cover to less than 30% of land area by the middle of the 19th century (28, 37). Agricultural abandonment in the late 19th and 20th centuries facilitated natural regeneration of the forest, which is the source of much of the region's current forest cover. The fragmented nature of the modern landscape is the product of forest fragments regenerating adjacent to maintained cropland and pastures, high road density, and urban expansion into regenerating forests. Oak species (*Quercus* spp.) are one of the most common tree genera in the region's forests, and forest canopy height is typically 15–25 m.

During the summer of 2015, we established eight plots, each 20-m wide along the forest's edge and extended 30 m into the forest's interior. Previous work in similar forests of the eastern United States showed that edge effects on forest microenvironment largely dissipate within 20 m of the edge (8), and we assume that the 20- to 30-m segment of each plot in our study is representative of the forest's interior. The forest edge of each plot was at least 30 y old; had a southern ($n = 3$), northern ($n = 3$), or eastern ($n = 2$) orientation; and was adjacent to either a meadow or residential development with single-family homes and yards consisting of lawns, landscaping, and ornamental trees (Table S4). Oak and pine are the most common and second most common genera in these plots, respectively (Table S1).

Soil Analyses. We collected two soil samples to a depth of 10 cm in each of four locations (0, 10, 20, and 30 m from the forest's edge) in each plot ($n = 8$ samples per plot) along a transect perpendicular to the center of the forest edge using a 5-cm-diameter bulk density soil corer. Roots and rocks were separated from the soil using a 2-mm sieve. The dry soil mass of each soil sample was estimated from the percentage change in soil mass of a 10-g subsample after it was dried to a constant weight at 65 °C. Dry root biomass was also quantified by drying to a constant weight at 65 °C. Rock volume, which was determined using a water displacement method, was subtracted from the volume of the soil core to calculate soil bulk density. Sieved soil samples were homogenized by plot and sampling location ($n = 2$ per sampling location in each plot), and C and N contents were determined using a CE Elantech NC2500 CN Analyzer (CE Elantech).

Forest Mensuration. Within each plot, the diameter at breast height (DBH) and species were recorded for every living tree larger than 5 cm DBH, and the location of each tree was mapped using a coordinate system. The BA of each tree was calculated following

$$BA = \pi \times \left(\frac{DBH}{2}\right)^2. \quad [1]$$

Forest BA of each forest segment (see below) was calculated for each plot by summing the BA values of the trees measured within each forest segment.

We collected two 5-mm tree cores (90° apart from one another) from each oak tree larger than 10 cm DBH in each plot. In addition, for one-half of the plot area, we collected cores from every tree larger than 10 cm DBH, regardless of genus. Tree cores were extracted from each tree 1.4 m above the ground. In total, 408 cores were collected ($n = 2$ cores per tree \times 204 trees). Dried and mounted cores were sanded to a flat surface using successively finer sandpaper grits from 120 to 800.

Tree and Forest Growth. Tree cores were scanned using a high-resolution color scanner (Epson Perfection V700 Photo), and ring increments were measured to 0.001 mm using WinDENDRO 2012 (Regent Instruments, Inc.) image analysis software. Cross-dating was done visually with the statistical assistance of COFECHA (38).

To control for tree size effects on ring widths, raw tree ring measurements were converted to BAI following

$$BAI = (R_n^2 \pi) - (R_{n-1}^2 \pi), \quad [2]$$

where R_n is the radius of the tree at the end of year n , and R_{n-1} is the radius of the tree at the end of the previous year. The radius at the end of the most recent full year of growth (2014) for each tree was determined at the time of tree core sampling. For each tree, mean BAI was calculated from two cores collected from that tree; if both cores were not usable, only one core was used. Forest BAI of each forest segment (see below) was calculated for each plot by summing the BAI values of the trees cored within each plot.

Trees were binned into forest segments of 0–10, 10–20, and 20–30 m from the forest's edge to facilitate quantification of edge effects on stem density, BA, and BAI. Forest BA and BAI of each forest segment were calculated by summing BA and BAI across all trees within each segment.

We used the line-intercept method to quantify patterns in CWD between the forest's edge and interior [e.g., the work by Keller et al. (39)]. Seven 20-m transects running parallel to the forest's edge at 5-m intervals from 0 to 30 m from the forest's edge were established in each plot using measuring tapes. All CWD larger than 2 cm in diameter that intersected each transect was measured using calipers. The cross-sectional area of CWD was calculated from diameter measurements and summed for each transect.

Climate Data. We used historical climate records to isolate climate drivers of interannual variability in tree and forest growth between 1990 and 2014. Climate records were obtained for Boston, Massachusetts from the National Climate Data Center. Climate variables include minimum, mean, and maximum air temperature and precipitation at daily, monthly, and seasonal timescales and Palmer Drought Severity Index at monthly and seasonal timescales. One plot had many trees within 10 m of the forest's edge that were too young to have a time series that extended back to 1990, and therefore, for this plot, we only used data back to 2004.

We used statistically downscaled coupled Atmosphere–Ocean General Circulation Models climate projections from the CMIP5 (25) to estimate a first approximation of potential changes in spatial patterns of forest growth with proximity to the edge under the Intergovernmental Panel on Climate Change RCP 4.5 and RCP 8.5 scenarios (40). Model ensemble simulations (Table S2) were retrieved for the period 2080–2099 for 242 1/8°-grid cells encompassing southern New England (from 41.4375° N to 42.6875° N and from 73.4375° W to 70.8125° W).

We used our plot-level results to quantify the C implications of forest fragmentation at the landscape and regional scales of southern New England (Massachusetts, Connecticut, and Rhode Island), because the climate and species composition of the forest fragments used in this study are representative of much of the forest in this region (Fig. S1 and Table S5). Using ArcGIS with the 2011 NLCD 30-m resolution land cover layer (26), we created buffers to quantify the forest area within 10 and 20 m of the forest's edge. The NLCD uses the Anderson Land Cover Classification System to define four forest categories, which we consolidated into one.

Forest C density (megagrams C hectare⁻¹) and aboveground net primary productivity (ANPP) were obtained for southern New England using the Carbon OnLine Estimator (COLE) Tool [COLE v. 3.0; accessed October of 2016; www.ncasi2.org/GCOLE3/gcole.shtml] (18), which is a web suite of applications that uses FIA plot-level data to generate a range of user-defined forestry statistics and C estimates (33, 41). We use the variables “Carbon–Aboveground Live Tree” and “Biomass–Sound Annual Growth” for C density and ANPP, respectively. The COLE output includes means, sample size, and SE. We assume that these C densities are representative of the forest interior (defined here as >20 m from the forest's edge). To quantify C density within segments of 0–10 and 10–20 m from the forest's edge, we apply our field data characterizing the relative (i.e., percentage) change in BA from the forest's edge to interior. We use the same approach for quantifying forest growth (i.e., BAI) within segments of 0–10 and 10–20 m from the forest's edge.

BA Only Plots. In addition to the data collected from the “core plots” described above, during the summer of 2016, we quantified relative changes in BA between 0 and 40 m from the forest edge in 13 plots across eastern and central Massachusetts. Transects consisting of four 10-m fixed radius semi-circular plots extending 0–40 m from the forest edge were used to efficiently quantify patterns in BA. This approach requires substantially less time than a full census and coring of trees in a plot but provides good estimates of relative changes in BA between the forest edge and interior that are highly correlated with the complete survey approach described above for our core plots ($r^2 = 0.91$; $P = 0.003$). These plots include a range of forest types and edge characteristics (Table S4) and are intended to compliment data from the core plots and broaden the scope of this study.

Statistical Analyses. All statistical analyses were conducted in R, version 3.0.2 (R Core Team). Forest edge effects on soil C, N, and bulk density; CWD; BA; and BAI were quantified using linear mixed effects models [lme function (42)] with forest segment (i.e., 0- to 10-, 10- to 20-, and 20- to 30-m segments from the forest's edge) or transect distance from edge in the case of CWD as the fixed effect and plot as the random effect. The 10-y mean BAI (2005–2014) of each forest segment was used to compare forest growth rates across forest segments. Although this approach does not account for changes in forest growth associated with mortality during this period, it is appropriate for quantifying relative changes in forest growth, because we do not find evidence of differences in CWD and by inference, mortality rates across forest segments (Results and Discussion). Climate drivers of interannual variability in the mean forest growth for each forest segment across all plots were quantified using multiple linear regression analyses. Unless otherwise indicated, all values reported are means and SE. An rms approach was used to propagate uncertainty of COLE and field data for each variable scaled to the landscape level.

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