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Key Points:
- Soil respiration increases with proximity to temperature forest edges
- Edge soil respiration enhancements are driven by large positive gradients in soil temperature
- Forest edge carbon dynamics are generally omitted from ecosystem models and carbon accounting frameworks

Supporting Information:
- Supporting Information S1

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Evidence for Edge Enhancements of Soil Respiration in Temperate Forests

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Abstract Forest fragmentation impacts carbon uptake and storage; however, the magnitude and direction of fragmentation impacts on soil respiration remain poorly characterized. We quantify soil respiration rates along edge-to-interior transects in two temperate broadleaf forests in the eastern United States that vary in climate, species composition, and soil type. We observe average soil respiration rates 15–26% higher at the forest edge compared to the interior, corresponding to large gradients in soil temperature. We find no significant difference in the sensitivity of soil respiration to temperature between the forest edge and interior. Fragmentation and resultant shifts in microenvironment alter forest productivity and soil respiration near forest edges. Ecosystem models do not currently represent edge dynamics, but given the prevalence of landscape fragmentation and its effect on carbon cycling along forest edges, this omission likely introduces an important source of uncertainty in our understanding of terrestrial carbon dynamics with a changing landscape and climate.

Plain Language Summary Forests continuously release carbon dioxide into the atmosphere via the decomposition of soil organic matter and biological activities of belowground organisms in a process known as soil respiration. When intact forests are broken up (either naturally or by humans), the remaining fragments experience distinct environmental conditions near the edges. Previous work shows that temperate forests can capture and store more atmospheric carbon per unit area near forest edges; however, it is unknown how the presence of forest edges impacts the rate of carbon loss via soil respiration. Here we measure soil respiration rates along forest edges, where the local soil temperatures tend to be warmer than the forest interior. We find that near the edges, soil respiration rates are higher than the forest interior. We attribute the increased soil respiration rate to warmer forest edge soil temperatures. Our results suggest that estimates of soil respiration in the temperate forest region may be underestimating biological emissions of carbon dioxide. Altogether, our research identifies an important phenomenon previously unaccounted for in our understanding of the carbon cycle with important implications for estimating forest carbon exchanges in fragmented landscapes, particularly as the climate continues to warm.

1. Introduction

Fragmented landscapes occupy a rapidly increasing portion of global land area, yet the impact of fragmentation on forest carbon fluxes has only recently begun to receive attention. More than 70% of the world's remaining forest area is located within 1 km of a forest edge (Haddad et al., 2015) and in the northeastern United States, nearly 25% of forest area is within 30 m of an edge (Smith et al., 2018). Forest fragmentation produces microenvironmental gradients near forest edges, commonly referred to as edge effects, that include increased exposure to solar radiation (Davies-Colley et al., 2000; Matlack, 1993), warmer temperatures (Chen et al., 1993), and drier conditions (Gehlhausen et al., 2000). Within the temperate forest region, the most fragmented forest biome in the world (Haddad et al., 2015), edge effects enhance the carbon accumulation rate and stocks in aboveground biomass with aboveground forest productivity and biomass reported to increase 89% and 64%, respectively, within 20 m of forest edges (Reinmann & Hutyra, 2017). However, the impact of edge effects on soil respiration rates is poorly understood.

Soils store the majority of the world's terrestrial organic carbon, and soil carbon fluxes act as a major control on atmospheric CO_2 concentrations (Jobbágy & Jackson, 2000). Soil respiration represents the aggregate

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CO_2 flux from belowground autotrophic (plant roots) and heterotrophic (soil microorganisms and macroorganisms) processes and constitutes the second largest land-atmosphere carbon exchange behind gross primary productivity (Raich & Schlesinger, 1992). Soil respiration rates are primarily controlled by soil temperature (Lloyd & Taylor, 1994) but are also regulated by soil moisture content (Davidson et al., 1998), ecosystem productivity (Högberg et al., 2001), and substrate quality/quantity (Wan & Luo, 2003). Forest edge effects likely impact belowground carbon dynamics via gradients in local soil conditions that include warmer temperatures (Chen et al., 1993), drier soils (Pohlman et al., 2009), and increases in carbon and nitrogen availability (Remy et al., 2016).

This study quantifies the impact of edge effects on soil respiration rates in temperate forest fragments by testing the hypothesis that increases in soil temperature with proximity to forest edges stimulate soil respiration rates. We measure soil respiration fluxes coincident with soil temperature and moisture over multiple years along edge-to-interior transects in Massachusetts and Maryland, USA. We compare the sensitivity of soil respiration to soil temperature between the forest edge and interior and model soil respiration rates over the course of a year.

2. Materials and Methods

2.1. Site Descriptions

2.1.1. Harvard Forest

The Harvard Forest (HF) is a temperate, mixed deciduous forest located in Petersham, Massachusetts. The forest is largely made up of 85 to 120 years old, second-growth stands that followed widespread harvesting and agricultural clearing in the 1800s (Foster & Aber, 2004). In May 2016, six 600-m^2 plots were installed along forest edges at the HF, measuring 20 m along the forest edge and extending 30 m into the forest perpendicular to the forest edge (Figures 1a and 1c). The plots were established in well-drained, *Quercus sp./Acer sp.*-dominated stands. Soils were developed on glacial till deposits and are predominantly mapped as Woodbridge series coarse loam soils with little clay content (Natural Resources Conservation Service, 2018). Mean summer (June, July, and August) air temperatures are 19.5 °C and mean winter (December, January, and February) air temperatures are −3.2 °C (Boose, 2018).

The plots were installed at multiple edge aspects and adjacent land cover types (three meadows, two pastures, and one road). Within each plot, a pair of polyvinyl chloride soil respiration collars 20 cm in diameter × 7 cm tall and located 10 m apart was inserted approximately 2 cm into the soil at four distances from the edge (0, 10, 20, and 30 m; Figure S1 in the supporting information). Each plot had $n = 8$ collars for a total of $n = 48$ collars. Following installation, collars were left in the soil for at least 2 weeks to equilibrate. Soil temperature and moisture at 10-cm depth were logged hourly using soil temperature (onset HOBO Pendant Datalogger) and soil moisture (onset Soil Moisture Smart Sensor) sensors located every 10 m along the center plot transect (i.e., 0, 10, 20, and 30 m from the forest edge).

During the growing seasons (May to October) of 2017 and 2018, measurements of soil respiration were made monthly in 2017 and weekly in 2018 using a LiCor LI-8100A soil respiration system with survey chamber (LiCor Biosciences). Respiration was measured between 8:00 and 16:00 local standard time; sampling order was varied to avoid sampling at the same time of day. Beginning in 2018, soil temperature and soil moisture probe measurements at 10-cm depth were recorded at the collar concurrent with the flux measurement (Hanna Instruments Thermistor Thermometer and Field Scout TDR 100, respectively). In addition to the logged soil temperature and moisture, 487 of the 977 observations of soil respiration at the HF included colocated point measurements of soil temperature and 362 included colocated point measurements of soil temperature and soil moisture.

2.1.1.1. Additional HF Data

We complement our HF edge plot measurements of soil respiration with interior forest measurements made from 1995 to 2010 within the footprint of the Environmental Measurement Station's (EMS) eddy flux tower (42.537755°N, −72.171478°W; Davidson & Savage, 2017). The forest interior respiration data were collected at six sites along a northwest and southwest transect from the EMS tower. Sites ranged from poorly drained swamp to well-drained uplands but for the purposes of this comparison; we only use data collected at well-drained sites in mixed-deciduous forest. Measurements of soil respiration were taken weekly to biweekly with concurrent measurements of soil temperature at 10-cm depth and soil moisture at 15-cm depth. We

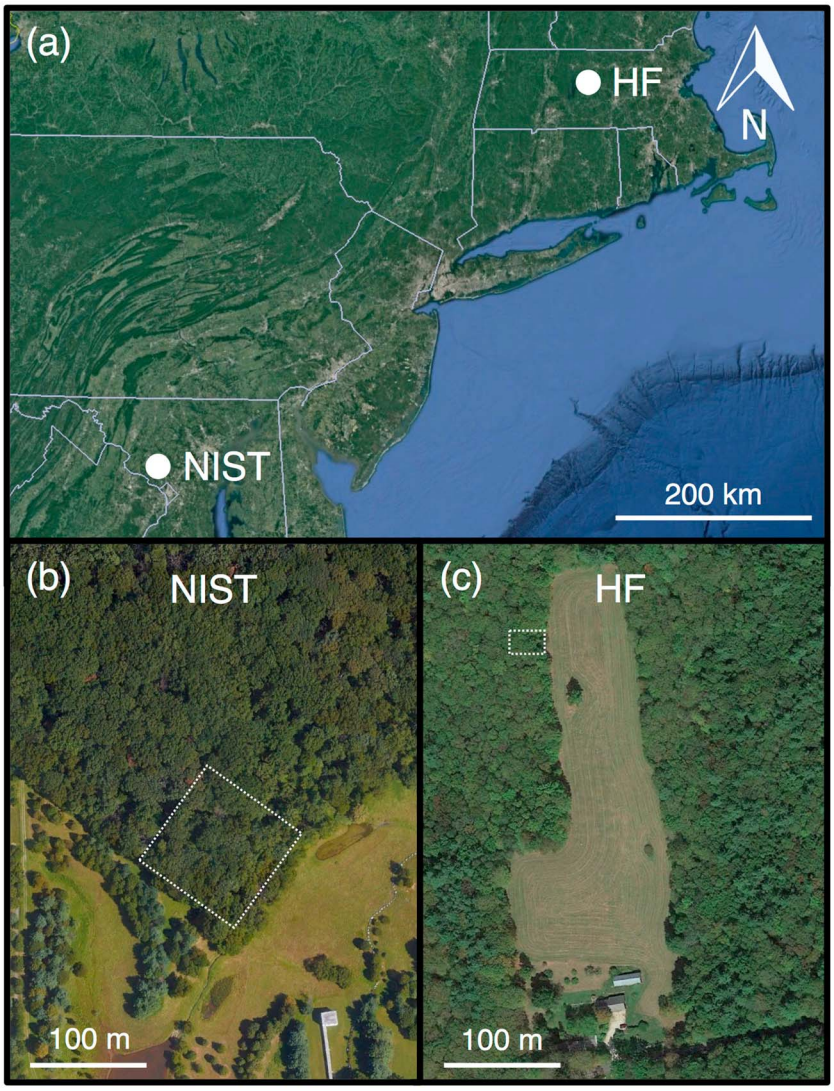

Figure 1. (a) Location of research plots at the Harvard Forest (HF) in Massachusetts, USA, and National Institute of Standards and Technology (NIST) in Maryland, USA. (b) Aerial view of 1-ha plot at NIST site. (c) Aerial view of one of six 600-m^2 HF plots. Imagery: ©2017 Google.

use hourly logged values of soil temperature and moisture at the EMS tower to compare our observations of hourly soil temperature at the edge and to predict hourly respiration rates over the course of a year.

2.1.2. National Institute of Standards and Technology

In May 2017, a 100-m × 100-m plot was installed along the edge of a 26-ha forest fragment on the campus of the National Institute of Standards and Technology (NIST) in Gaithersburg, Maryland (Figure 1). This plot was established as a Forested Optical Reference for the Evaluation of Sensor Technology, with soil respiration providing a key ground validation for remote sensing technologies. The plot is in a moderately well-drained, *Liriodendron tulipifera/Quercus sp.*-dominated stand with a 3-m-wide stream flowing through the plot approximately 25 m from the forest edge. Soils are mapped as a Glenelg series silt loam with a high clay content and low levels of soil organic matter (Natural Resources Conservation Service, 2018). Mean summer (June, July, and August) air temperatures are 23.5 °C and mean winter (December, January, and February) air temperatures are 1 °C (National Climatic Data Center, 2018).

The plot has a southeastern aspect and is adjacent to an unmanaged grassland (Figure 1b). Thirty-three pairs of 15.5-cm-diameter × 7-cm-tall polyvinyl chloride soil collars were placed in duplicate at five distances (0, 12.5, 25, 50, and 75 m; Figure S1) from the forest edge for a total sample size of n = 66 collars. Soil

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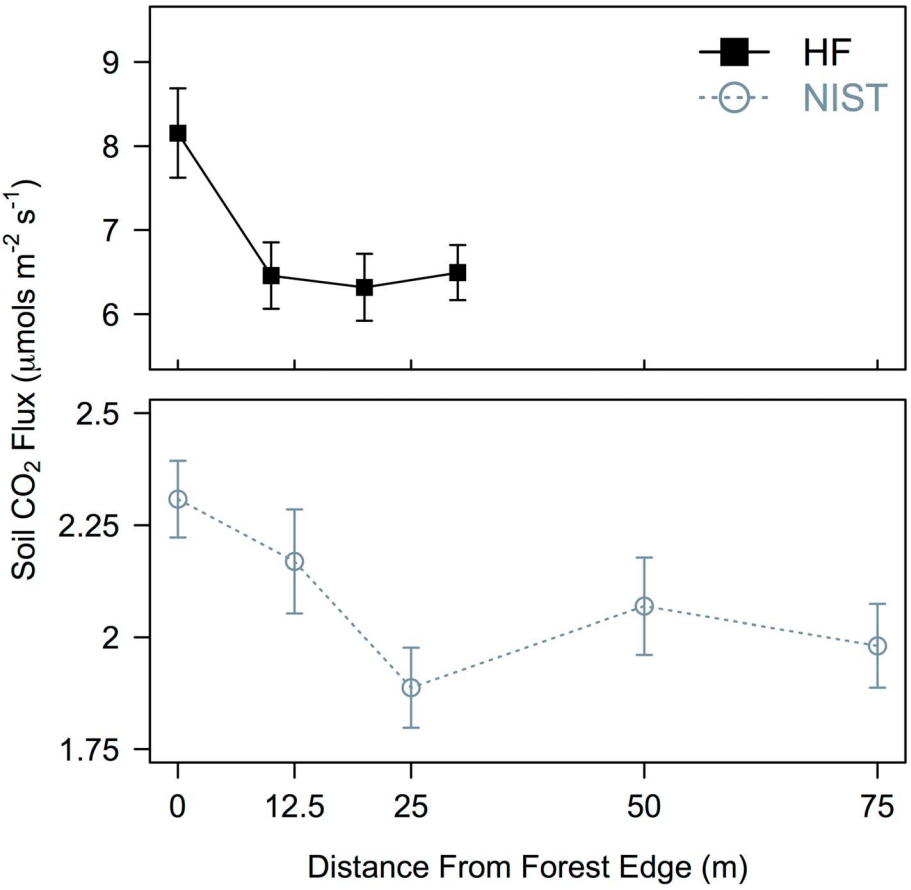

Figure 2. Mean growing season (May to October) soil respiration rates (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) as a function of distance from the forest edge (m) at the National Institute of Standards and Technology (NIST) and Harvard Forest (HF). Error bars are 95% confidence intervals. See Figure S3 for histograms of observations in each site.

temperature and moisture at 10-cm depth were logged hourly using 22 soil temperature sensors (onset HOBO Pendant Datalogger) located at 11 locations throughout the plot and 20 soil moisture sensors (onset Soil Moisture Smart Sensor) located at 5 locations (Figure S1).

During the growing seasons (May to October) of 2017 and 2018, soil respiration measurements were made weekly to biweekly using a soil respiration backpack system with a CO_2 gas analyzer (LiCor LI-840A) following the vented design described by Savage and Davidson (2001). Measurements were generally taken over the course of two consecutive days between 8:00 and 16:00 local standard time and the order collars were sampled in was varied. When possible, soil temperature and soil moisture probe measurements at 10-cm depth were recorded at the collar simultaneous with the flux measurement (Hanna Instruments Thermistor Thermometer and Field Scout TDR 100, respectively). Of the 1,713 observations of soil respiration at the NIST, 1,416 include colocated point measurements of soil temperature and 533 include colocated point measurements of soil temperature and soil moisture.

2.2. Temperature Response and Modeling

We quantify the response of soil respiration to soil temperature using a nonlinear regression model in the form:

$$Rs = \beta_0 * \exp^{(\beta_1 * Ts)}, \quad (1)$$

where Rs is the soil respiration rate (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) and Ts is the soil temperature at 10-cm depth (°C). The Q_{10}, or the factor by which soil respiration increases with a 10 °C change in soil temperature (Davidson & Janssens, 2006), is calculated as

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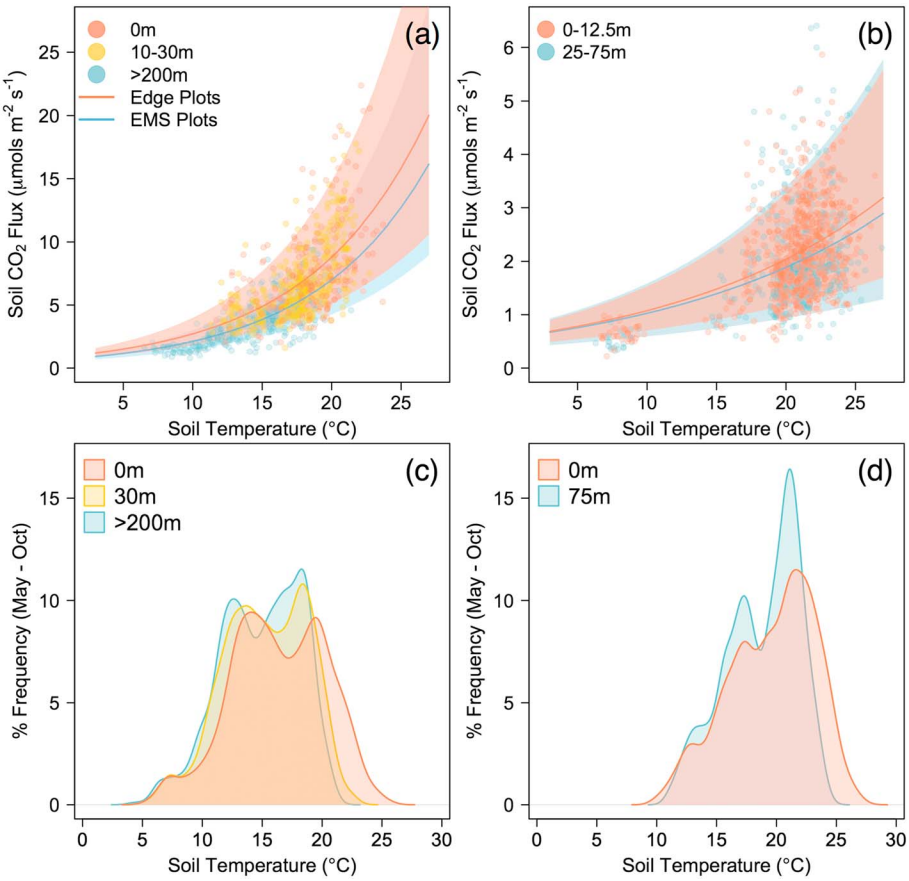

Figure 3. (top) Relationship between soil respiration rates (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) and soil temperature (°C) at 10-cm depth at various distances from the edge at the Harvard Forest (a) and National Institute of Standards and Technology (b). Model fits are nonlinear regression models and shaded error regions represent 95% confidence intervals of the fitted parameters β_0 and β_1 in equation (1). (bottom) Frequency distribution of hourly logged soil temperature (°C) during the growing seasons (May to October) of 2017/2018 at the Harvard Forest (c) and National Institute of Standards and Technology (d). EMS = Environmental Measurement Station.

$$Q_{10} = \exp^{(10 * \beta_1)} \tag{2}$$

We use a generalized additive model and hourly measurements of local soil conditions to predict soil respiration rates in each site at various distances from the edge between August 2017 and July 2018. The structure of the model is

$$\ln(Rs) = \beta + s(Ts) + s(VWC) + \varepsilon, \tag{3}$$

where β is the intercept of the model, $s(Ts)$ is a smooth spline function of soil temperature (°C), s (VWC) is a smooth spline function of volumetric water content (%), and ε is the Gaussian distributed error of the model (see Table S1 and Figure S2 for detailed model diagnostics and parameter outputs). Previous work shows that annual soil respiration fluxes can be estimated based on year-round measurements of soil temperature/moisture (Davidson et al., 1998; Giasson et al., 2013; Rey et al., 2002).

We estimate hourly soil respiration rates at the HF using the average continuously logged soil temperature and moisture at 0 and 30 m from the forest edge across the six edge plots and continuously logged soil temperature and moisture at the HF EMS tower (>200 m from the nearest edge). NIST hourly estimates use continuously logged soil temperature and moisture data collected at 0 and 75 m from the southeastern facing edge of the plot. Hourly flux estimates are summed to compute annual carbon fluxes in units of megagrams of carbon per hectare per year. Unless otherwise noted, we refer to the forest edge as the start of the forest

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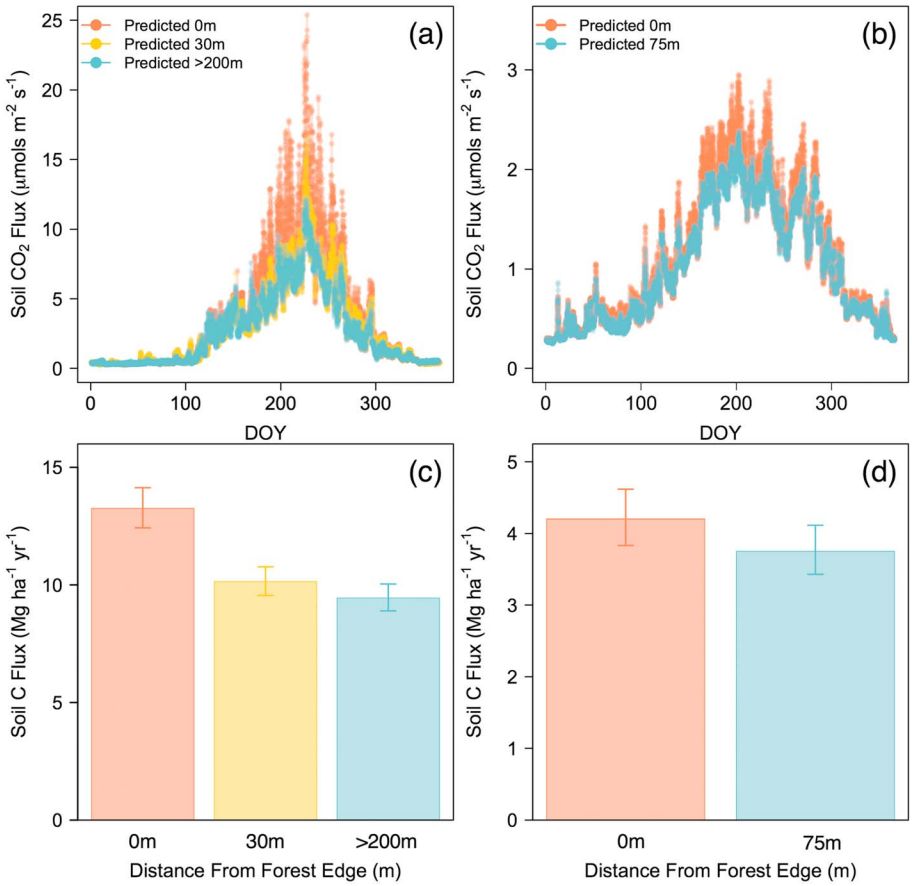

Figure 4. (top) Modeled hourly soil respiration rates (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) at various distances from the forest edge at the Harvard Forest (a) and National Institute of Standards and Technology (b). (bottom) Modeled annual soil carbon flux ($Mg \cdot ha^{-1} \cdot year^{-1}$) at various distances from the forest edge at the Harvard Forest (c) and National Institute of Standards and Technology (d). Error bars are 95% confidence intervals.

edge transects (i.e., 0 m from the forest edge) and the forest interior as the furthest point along the transects (30 m from the forest edge at the HF and 75 m from the forest edge at the NIST site). All reported errors are 95% confidence intervals and all statistical analyses and modeling were conducted using R Statistical Software 3.5 (R Core Team, 2018).

3. Results

3.1. Forest Edge Gradients

We observe strong positive gradients in soil respiration with proximity to forest edges. Mean growing season respiration rates were 26% higher at the forest edge (8.2 ± 0.5 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) than 30 m into the forest interior (6.5 ± 0.3 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$; $p < 0.01$) at the HF. At the NIST, overall soil respiration rates were nearly 70% lower than at the HF, but mean growing season respiration rates showed a similar trend with proximity to the edge, with respiration rates 15% higher at the forest edge (2.3 ± 0.1 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) than 75 m into the forest interior (2.0 ± 0.1 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$; $p < 0.01$; Figure 2). While we observe elevated soil respiration rates only at the forest edge at the HF, we observe significant soil respiration enhancements up to at least 12.5 m into the forest at the NIST (Figure 2).

3.2. Temperature Response

There was no significant difference in the Q_{10} response between the forest edge and interior at either the HF ($p = 0.59$) or NIST ($p = 0.66$). At the HF, we observed a Q_{10} of 3.2 ± 0.4 within 30 m of an edge and 3.3 ± 0.4 at the EMS tower (Figure 3a). At the NIST, we observed a lower mean Q_{10} value than HF, that is, soil

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respiration rates were less sensitive to soil temperatures, with values of 1.9 ± 0.2 within 12.5 m of an edge and 1.8 ± 0.2 beyond 12.5 m from the edge (Figure 3b).

At both sites, we observed a greater frequency of high soil temperatures during the growing season at the forest edge than in the forest interior (Figures 3c and 3d). At the HF, mean growing season soil temperatures at the forest edge (16.4 ± 0.1 °C) were 9% higher than 30 m into the forest interior (15.0 ± 0.1 °C; $p < 0.01$) and 12% higher than at the EMS tower (14.6 ± 0.1 °C; $p < 0.01$; Figure 3c). At the NIST, mean growing season soil temperatures at the forest edge (19.6 ± 0.1 °C) were 5% higher than 75 m into the forest interior (18.7 ± 0.1 °C; $p < 0.01$; Figure 3d). All of our observations of soil respiration were made during the day, but nighttime forest interior soil temperatures were often higher than nighttime forest edge soil temperatures (Figure S4).

3.3. Annual Fluxes

We find considerable increases in annual soil carbon fluxes at the forest edge. Using a generalized additive model relating soil respiration rates to soil temperature and moisture (model results in Table S1 and Figure S2), we estimate the annual soil carbon flux at the forest edge at the HF (13.3 ± 0.8 Mg C·ha^{-1}·year^{-1}) to be 32% higher than the annual soil carbon flux 30 m from the edge (10.1 ± 0.6 Mg C·ha^{-1}·year^{-1}; $p < 0.01$) and 41% higher than the annual soil carbon flux at the EMS tower (9.4 ± 0.5 Mg C·ha^{-1}·year^{-1}; $p < 0.01$; Figures 4a and 4c). Our modeled estimates agree well with annual ecosystem respiration estimates from the HF EMS eddy flux tower if we assume soil respiration accounts for approximately 70% of ecosystem respiration (Bolstad et al., 2004; Yuste et al., 2005) as the mean annual ecosystem respiration rate over the 10 most recent years of available data (2006 to 2015) is 13.7 Mg C·ha^{-1}·year^{-1} (Munger & Wofsy, 2018). At the NIST, we estimate the annual soil carbon flux at the forest edge (4.3 ± 0.4 Mg C·ha^{-1}·year^{-1}) to be 13% higher than the annual soil carbon flux 75 m from the edge (3.8 ± 0.3 Mg C·ha^{-1}·year^{-1}; $p < 0.01$; Figures 4b and 4d).

4. Discussion and Conclusion

4.1. Temperate Forest Edge Carbon Balance

Forests are a globally important carbon sink, offsetting nearly one third of anthropogenic carbon emissions (Le Quéré et al., 2018). The strength of the forest carbon sink varies spatially and temporally and depends on climatic trends, disturbances, and the resultant balance between forest growth, mortality, and respiration dynamics. In response to a changing climate, soil warming experiments provide strong empirical support for the hypothesis that increases in global temperatures will stimulate the rate of soil carbon losses, driving a positive carbon-climate feedback that could accelerate rates of global warming (Crowther et al., 2016). Furthermore, fragmentation represents a key landscape disturbance and the observations of soil respiration and temperature gradients with proximity to forest edges described in this study add to a growing body of literature pointing to the high capacity of forest fragmentation to alter forest carbon cycling (Bowering et al., 2006; Briber et al., 2015; Brinck et al., 2017; Reinmann & Hutyra 2017).

Positive soil respiration gradients near temperate forest edges offset a fraction of observed enhancements in aboveground production and biomass. However, while not a direct comparison, our estimates of annual forest edge soil respiration increases of 32% and 13% at the HF and NIST, respectively, are likely not large enough to offset the 89% aboveground net carbon uptake enhancement observed in nearby temperate forest fragments (Reinmann & Hutyra, 2017). Soil respiration is the largest of several contributors to ecosystem respiration (Bolstad et al., 2004), and it is likely that increases in biomass and forest growth coupled with warmer air temperatures near temperate forest edges will also positively correlate with increases in aboveground autotrophic respiration (Reinmann & Templer, 2016) offsetting even more of the edge growth enhancement. Nonetheless, due to enhancements in both respiration and growth, carbon cycling rates currently appear to accelerate near temperate forest edges.

The forest edge is warmer than the forest interior on average, but we find the forest edge tends to lose heat faster than the forest interior at night. Warmer nighttime forest interior soils likely offset a portion of the daytime edge respiration enhancement when considering the net forest edge soil respiration enhancement over the course of the year. We observe warmer soil temperatures in the forest interior during 20% and 55% of growing season nights at the HF and NIST, respectively.

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Forest fragmentation increases the proportion of forest edge across the landscape, heightening the vulnerability of the remaining forest to climate change and extreme conditions. The forest edge is warmer and drier than the forest interior (Davies-Colley et al., 2000) and growth at the forest edge has been reported to decline three times faster in response to heat stress than the forest interior (Reinmann & Hutyra, 2017). As such, future climate projections of warmer temperatures and increases in the frequency and severity of droughts (IPCC (Intergovernmental Panel on Climate Change), 2014) are forecasted to diminish the forest edge growth enhancement (Reinmann & Hutyra, 2017). In contrast, we observe strong exponential increases in soil respiration with warmer temperatures (Figure 3) and as increasing trends are already being observed in global soil carbon fluxes (Bond-Lamberty & Thompson, 2010), our results suggest that respiration rates will likely increase at an accelerated rate near the forest edge than the forest interior. Although temperature is the primary control on soil respiration, drought conditions can decrease respiration rates (Davidson et al., 1998) and could potentially mitigate a portion of temperature associated increases in soil respiration.

4.2. Implications for Carbon Accounting

Much of our current understanding of forest carbon fluxes comes from the study of intact forest systems, particularly relying on eddy covariance measurements. The fundamental aerodynamic assumptions of eddy covariance methodologies require homogeneity within the fetch of the eddy flux tower (Lee et al., 2006), introducing a strong selection bias against fragmented landscapes and the distinct carbon dynamics found within them. Despite pervasive global fragmentation and substantial impacts of fragmentation on forest carbon dynamics, carbon cycle models and accounting initiatives currently lack the necessary empirical data to parameterize and model forest edge dynamics at large scales. Edge dynamics are generally omitted from estimates of forest carbon pools and fluxes. Our estimates of increased soil carbon fluxes of 3.2–3.9 Mg C·ha^{-1}·year^{-1} at the HF edges are larger than the average net ecosystem production within the footprint of the EMS eddy flux tower (2.9 Mg C·ha^{-1}·year^{-1}; Munger & Wofsy, 2018). Soil respiration enhancements of such magnitude could be enough to shift the balance of some forests from a carbon sink to a carbon source near edges.

Partitioning the forest edge respiration response between autotrophic and heterotrophic processes is unclear. At the HF, autotrophic respiration only accounts for about 20% of total soil respiration (Melillo et al., 2002) and to our knowledge, the only study quantifying root biomass near forest edges found no significant trends in root biomass with proximity to the edge (Reinmann & Hutyra, 2017). Constant root biomass coupled with observed positive relationships between photosynthesis and soil respiration (Tang et al., 2005) suggest that enhanced forest productivity could increase the contributions of autotrophic processes near the forest edge. Further, parsing the respective roles of roots versus soil microbes in the forest edge soil respiration enhancement will have important implications for our understanding of the interactions of edge effects with climate change and the extent to which forest edge respiration is coupled with productivity.

The drivers and intensity of forest fragmentation could also influence the forest edge respiration response. While we observe large enhancements of soil respiration in rural (HF) and suburban (NIST) forest fragments, the response in urban forest fragments may differ due to enhanced atmospheric nitrogen inputs (Decina et al., 2017; Rao et al., 2013). Atmospheric nitrogen deposition can be more than 40% higher at the forest edge than the forest interior (Weathers et al., 2001). Increased soil nitrogen availability has been shown to decrease both heterotrophic and autotrophic soil respiration rates (Janssens et al., 2010; Sun et al., 2014). Consequently, the respiration dynamics along forest edges and net forest carbon balance in industrial regions may differ from those of rural forests.

Forest edge effects on carbon dynamics also vary by biome (Smith et al., 2018). To our knowledge, this is the first study quantifying the impact of edge effects on soil respiration rates, and there exists considerable uncertainty and probable spatial variability in respiration responses across forest types (Giasson et al., 2013). In our study alone, we observe large differences in Q_{10} factors between the cooler HF site and warmer NIST site, corresponding to a larger respiration enhancement at the HF. Previous studies show that Q_{10} factors are generally higher in cooler regions (Chen & Tian, 2005) indicating that the magnitude of the edge respiration response may vary with latitude. Similarly, the enhancements in forest edge productivity and biomass observed in the temperate region contradict trends in forest edge carbon storage in boreal (Jönsson et al., 2007) and tropical forests (Laurance et al., 1997).

Our findings indicate that forest fragmentation and edge effects introduce large changes in the soil microenvironment that produce significant changes in overall soil respiration rates. This study reinforces the concept of a distinct forest edge environment as forest fragmentation simultaneously stimulates forest productivity and respiration in temperate forests, with important implications for carbon balance accounting. While typically not considered, the indirect effects of land cover change and deforestation on carbon cycling (e.g., edge effects) are likely introducing an unaccounted source of uncertainty in our estimates of the global carbon budget. Ubiquitous global fragmentation suggests that consideration of edge effects and their interactions with climate change is critical to accurately characterize the world's forests.

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