

# Diverging patterns at the forest edge: Soil respiration dynamics of fragmented forests in urban and rural areas

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## Abstract

As urbanization and forest fragmentation increase around the globe, it is critical to understand how rates of respiration and carbon losses from soil carbon pools are affected by these processes. This study characterizes soils in fragmented forests along an urban to rural gradient, evaluating the sensitivity of soil respiration to changes in soil temperature and moisture near the forest edge. While previous studies found elevated rates of soil respiration at temperate forest edges in rural areas compared to the forest interior, we find that soil respiration is suppressed at the forest edge in urban areas. At urban sites, respiration rates are 25% lower at the forest edge relative to the interior, likely due to high temperature and aridity conditions near urban edges. While rural soils continue to respire with increasing temperatures, urban soil respiration rates asymptote as temperatures climb and soils dry. Soil temperature- and moisture-sensitivity modeling shows that respiration rates in urban soils are less sensitive to rising temperatures than those in rural soils. Scaling these results to Massachusetts (MA), which encompasses 0.25 Mha of the urban forest, we find that failure to account for decreases in soil respiration rates near urban forest edges leads to an overestimate of growing-season soil carbon fluxes of >350,000 Mg C. This difference is almost 2.5 times that for rural soils in the analogous comparison (underestimate of <143,000 Mg C), even though rural forest area is more than four times greater than urban forest area in MA. While a changing climate may stimulate carbon losses from rural forest edge soils, urban forests may experience enhanced soil carbon sequestration near the forest edge. These findings highlight the need to capture the effects of forest fragmentation and land use context when making projections about soil behavior and carbon cycling in a warming and increasingly urbanized world.

## KEY WORDS

carbon, CO<sub>2</sub>, forest edge, forest fragmentation, rural, soil respiration, soil temperature, urban

## 1 | INTRODUCTION

Soils store more than three times the amount of carbon (C) contained in the atmosphere (Lal, 2008), but considerable uncertainty remains around soil carbon dynamics in a changing world (Bradford et al.,

2016). Our understanding of carbon cycling in forest soils comes largely from studies of intact forests (Melillo et al., 2017), but these forests do not represent the majority of global forest land cover. The world's forests are heavily fragmented, and more than 70% are within 1 km of a forest edge (Haddad et al., 2015). It is therefore

critical to investigate how soil carbon storage will change in the face of climbing global temperatures and pervasive land-use change, such as forest fragmentation and urbanization (Bradford et al., 2016; Carey et al., 2016; Smith et al., 2018, 2019).

Many recent studies about deforestation focus on the forest area that is lost, often ignoring the secondary and long-lasting impacts of land cover change on the forested ecosystems that remain. Deforestation creates forest edges exposed to conditions distinct from the forest interior (Smith et al., 2018). Forest edges tend to be both hotter and drier than the forest interior due to increased wind and light exposure (Harper et al., 2005; Matlack, 1993), and they often experience enhanced rates of atmospheric nitrogen (N) inputs (Remy et al., 2016; Weathers et al., 2001). The distance of edge influence into the forest interior can vary across processes and biomes, with soil abiotic conditions (e.g., temperature, moisture) and biotic processes often altered within at least the first 20 m from the forest edge (Meeussen et al., 2020; Smith et al., 2019).

Mounting evidence suggests that the unique microenvironment at the forest edge alters carbon cycling relative to the interior forest (Chaplin-Kramer et al., 2015; Meeussen et al., 2020; Reinmann et al., 2020; Remy et al., 2016; Smith et al., 2019). At temperate forest edges, trees tend to have greater aboveground biomass and rates of growth than trees in the forest interior, potentially enhancing carbon sequestration in aboveground biomass (McDonald & Urban, 2004; Meeussen et al., 2020; Morreale et al., 2021). However, terrestrial forests store nearly half of their carbon in the top meter of soil (Pan et al., 2011) and recent studies report increased soil carbon dioxide ( $\text{CO}_2$ ) fluxes, or soil respiration, from rural forest edges that are attributed to elevated soil temperatures near the edge compared to the forest interior (Reinmann et al., 2020; Smith et al., 2019). Increasing global temperatures are expected to lead to further soil carbon losses via soil respiration, providing powerful positive feedback on planetary warming (Bond-Lamberty & Thomson, 2010). However, current models and predictions for future carbon losses from the soil do not account for unique soil respiration fluxes at the forest edge (Luo et al., 2016). Soil carbon losses associated with increased temperatures are likely to be magnified under future climate change (Bond-Lamberty & Thomson, 2010), and failure to account for differential losses near the forest edge could lead to serious errors in estimates of biogenic carbon emissions (Smith et al., 2019).

The few studies of forest fragmentation effects on soils have focused on rural forest edges, away from intensive ongoing human activities that can further exacerbate elevated temperatures, dryness, and levels of nitrogen throughfall near the edge (Reinmann et al., 2020; Remy et al., 2016; Smith et al., 2019; Weathers et al., 2001). However, urban expansion is a pivotal driver of land-use change (Seto et al., 2012), and small, fragmented forest patches dominate urban areas (Trlica et al., 2020). In the northeastern quarter of the US, more than 23% of forest area is within 30 m of a forest edge created by anthropogenic deforestation and changes in land use (Smith et al., 2018), and by 2050, four northeastern states are projected to be more than one half urban land (Nowak & Walton, 2005). Urban soils are subject to biogeochemical perturbations distinct

from their fragmented rural forest counterparts and experience a variety of disturbances, including intensive, and extensive management with implications for local carbon budgets (Decina et al., 2016; Hundertmark et al., 2021; Vasenev et al., 2018). Intensively managed, non-forested urban soils demonstrate substantial increases in respiration compared to soils in nearby "natural" systems due in part to increased applications of compost and mulch (Crum et al., 2016; Decina et al., 2016; Vasenev et al., 2018). However, soil respiration patterns at urban forest edges have yet to be characterized.

Soil respiration has traditionally been modeled as an exponential function positively correlated with temperature (Lloyd & Taylor, 1994). While studies of soil respiration responses to warming in rural forest interiors demonstrate that soil carbon losses increase with initial warming (Melillo et al., 2002, 2011), the magnitude of this effect varies over time (Bradford et al., 2016; Melillo et al., 2017), suggesting a more nuanced relationship between respiration and chronic soil warming than previously thought (Jenkinson et al., 1991; Post et al., 1982). Further, increased soil temperatures can also lead to heat and moisture stress, suppressing decomposition and soil respiration (Carey et al., 2016; Crockatt & Bebber, 2015; Khomik et al., 2009). These varied responses are critical to understanding soil respiration behavior near forest edges in developed areas, where soil warming at the edge associated with increased incident radiation (Reinmann & Hutyra, 2017; Reinmann et al., 2020) can be further exacerbated by the urban heat island effect (Oke et al., 2017).

Other conditions near the forest edge, such as increases in soil nitrogen availability, are also likely to intensify with proximity to urbanization and affect soils (Contosta et al., 2011; Frey et al., 2013). Greater tree canopy exposure near the forest edge can lead to heightened throughfall nitrogen inputs (Weathers et al., 2001), and this is likely to increase with human activity and anthropogenic nitrogen emissions. Excess soil nitrogen loading can impede organic matter decomposition and decrease microbial respiration rates (Ramirez et al., 2012; Treseder, 2008). Forest edges are also exposed to heightened air pollutant concentrations (Weathers et al., 2001), and forests adjacent to roads may experience increased salt inputs from de-icing applications in winter (Bryson & Barker, 2002).

In many respects, forest edges offer an observational counterpart to global change manipulation experiments, providing an opportunity to study the effects of multiple global change drivers simultaneously, including warming, urbanization, and changes in water and nitrogen availability. The influences of forest edges are typically omitted from climate and ecosystem models (Reinmann et al., 2020), and the response of soil respiration, in particular, represents a substantial missing piece of our understanding of the landscape and regional-scale carbon cycling.

We quantified the effects of forest fragmentation and urbanization on soil  $\text{CO}_2$  fluxes along an urbanization gradient. We hypothesized that soil respiration rates are greater in urban and rural forest edges relative to the forest interior, but the magnitude of the increase is substantially greater in urban areas due to heightened temperatures near the edge, despite other adverse conditions.

## 2 | MATERIALS AND METHODS

### 2.1 | Site descriptions and urbanization history

This study was conducted along an urbanization gradient from urban Boston to rural central Massachusetts (MA). Due to historical settlement patterns, development in MA radiated out from east to west, and the earliest settlements developed into present-day urban centers across the state (Hall et al., 2002). The state has a long history of deforestation driven by agriculture and urban expansion but also experienced forest expansion after agriculture shifted westward in the 1850s (Foster, 2010; Hall et al., 2002). These land-use changes have resulted in patches of heavily fragmented and urbanized forests in MA (Reinmann et al., 2020). Urbanization is a dominant driver of continuing land cover change and forest loss in this area (Foster, 2010; Hall et al., 2002).

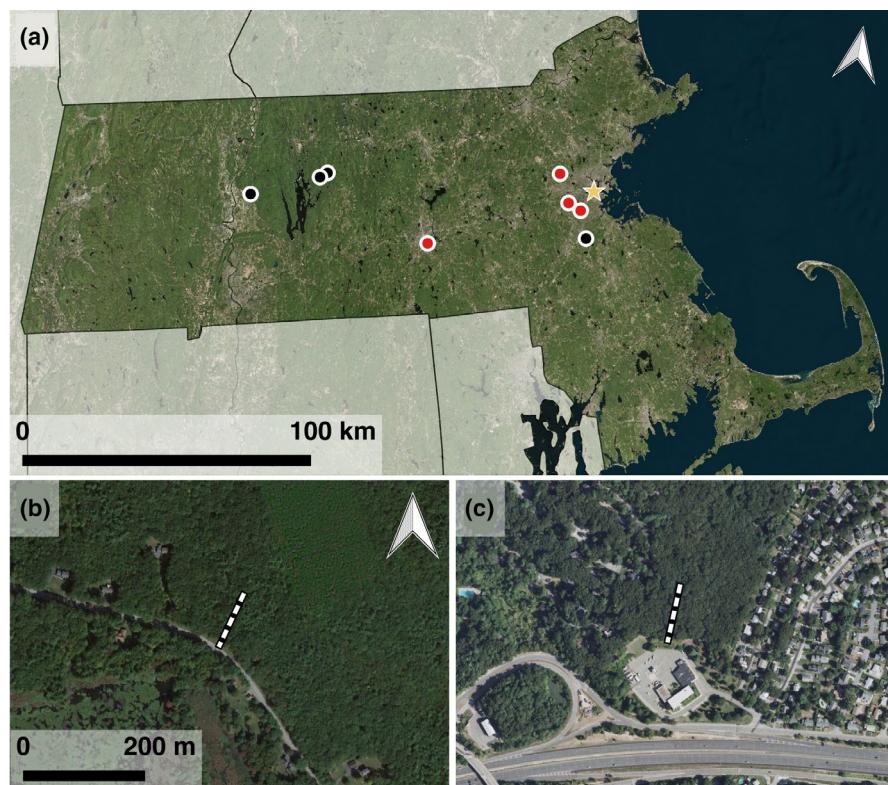
From May to June 2018, we established eight field sites at forest edges along the urban to rural gradient in MA (Figure 1a; Figure S1). All sites are temperate, mixed-deciduous forests typical of southern New England (Duveneck et al., 2015), and site selection was designed to reduce variation due to forest type. All sites are primarily dominated by oaks (e.g., *Quercus rubra*, *Q. velutina*) and maples (e.g., *Acer rubrum*, *A. saccharum*). Typical of MA soils, all sites are located on Leptic Podzols, soils developed on thick glacial drift deposits that tend to be acidic and have mesic soil temperature regimes (Digital Soil Map of the World, 2021; National Cooperative Soil Survey et al., 1975).

Observed mean daytime (08:00–17:00) air temperatures in rural sites were  $22.5 \pm 0.39^\circ\text{C}$  (95% confidence interval) in the summer (June, July, August 2018, and 2019) and  $-1.5 \pm 0.31^\circ\text{C}$  in the winter

(December 2018; January, February 2019), and they receive approximately 123 cm precipitation evenly distributed throughout the year (National Centers for Environmental Information, 2021). Mean observed daytime air temperatures in urban sites were  $24.2 \pm 0.15^\circ\text{C}$  and  $1.1 \pm 0.25^\circ\text{C}$  in the summer and winter, respectively (Figure S2), and they receive approximately 111 cm precipitation evenly distributed throughout the year (National Centers for Environmental Information, 2021). The prevailing wind direction across MA is largely westerly (data from Logan Airport, station #14739; Worcester, station #94746, Natural Resources Conservation Service & National Water and Climate Center, 2010).

We characterized the degree of urbanization intensity surrounding each forest site using impervious surface area (ISA; MassGIS Data: Impervious Surface 2005, 2007), population density (US Census Bureau, 2010), and distance to Boston Common in downtown Boston (*sensu* Raciti et al., 2012), as well as whether the field site fell within the boundaries of a census-designated place (CDP) (US Census Bureau, 2021). Impervious surfaces refer to surfaces such as concrete, pavement, and other structures that prevent water from infiltrating into the soil. *Sensu* Raciti et al. (2012), percent ISA was estimated for a  $990 \times 990$  m area centered around the 0 m point for each site transect (MassGIS Data: Impervious Surface, 2005, 2007). CDPs are defined by the US Census Bureau and are the statistical equivalent of incorporated places, such as cities and towns, referring to locally recognized, closely settled areas (US Census Bureau, 2018). Four sites were classified as rural and four as urban (Table 1; Figure S1).

On average, the Boston area received  $3.88 \text{ kg N ha}^{-1}\text{year}^{-1}$  of inorganic nitrogen deposition from 2016 to 2019 (data from U.S.



**FIGURE 1** (a) Location of eight field sites along an urbanization gradient in Massachusetts. Black points indicate rural research sites, red points indicate urban research sites, and the yellow star is Boston Common in downtown Boston. (b) Aerial view of one of our forest edge sites at Harvard Forest in Petersham, MA, one of four rural research sites. (c) Aerial view of our forest edge site in Lexington, MA, one of four urban research sites. Black and white dotted lines indicate the 90 m site transect from forest edge to interior [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

TABLE 1 Study site characteristics

Site	City or Town (MA)	Distance to Boston Common (km)	% Impervious surface area	Population density by zip code (people/km <sup>2</sup> )	Edge aspect	Adjacent land cover	Within Census Designated Place	Urbanization category
Arnold Arboretum	Boston	8.01	26.17	4,099.4	NW	Paved road	Yes	Urban
Hammond Woods	Newton	9.63	13.59	1,473.1	E	Paved road	Yes	Urban
Sutherland Woods	Lexington	13.20	27.46	679.8	SW	Cleared slope, parking lot	Yes	Urban
Broad Meadow	Worcester	60.41	25.99	2,079.2	SW	Powerline easement	Yes	Urban
Harvard Forest (04)	Petersham	95.16	0.64	12.2	E	Open field	No	Rural
Harvard Forest (05)	Leverett	119.12	10.74	31.4	W	Clearing, private residence	No	Rural
Harvard Forest (06)	Petersham	92.63	4.04	12.2	SW	Paved road	No	Rural
Blue Hills Observatory	Milton	16.34	6.43	801.4	NE	Ski slope	No	Rural

National Atmospheric Deposition Program (NADP) sites MA22 and MA98, as well as high levels of sodium ( $8.52 \text{ kg Na}^+ \text{ ha}^{-1} \text{ year}^{-1}$ ), chloride ( $18.60 \text{ kg Cl}^- \text{ ha}^{-1} \text{ year}^{-1}$ ), and sulfate ( $5.58 \text{ kg SO}_4^{2-} \text{ ha}^{-1} \text{ year}^{-1}$ ) deposition (National Trends Network, 2020). In contrast, an NADP site in central MA (MA08; ~15 km from Petersham research sites) received  $2.53 \text{ kg N ha}^{-1} \text{ year}^{-1}$  over the same period. Sodium, chloride, and sulfate were also prevalent in a deposition in central MA from 2016 to 2019, but similar to nitrogen, levels were much lower at  $1.43 \text{ kg Na}^+ \text{ ha}^{-1} \text{ year}^{-1}$ ,  $2.60 \text{ kg Cl}^- \text{ ha}^{-1} \text{ year}^{-1}$ , and  $3.13 \text{ kg SO}_4^{2-} \text{ ha}^{-1} \text{ year}^{-1}$  (National Trends Network, 2020). Note that NADP monitoring sites tend to be located away from urban areas and point sources of pollution, so these values may underestimate deposition in more developed areas.

At each of the eight sites, we established a single transect orthogonal to the forest edge (defined by the tree stem-line) and extended 90 m into the forest interior (Figure 1b,c; Figure S1). To characterize the effects of a single forest edge and avoid confounding by multiple edges, we purposefully chose forested sites with a minimum of 100 m of uninterrupted forest on the three non-edge sides of the transect. Sites were installed with a variety of edge aspects and adjacent to varying land cover types (Table 1; Figure S1). Breaks in forest cover that extended at least 25 m from the tree stem-line and were visible in high-resolution Google Earth images were considered forest edges. Google Earth high-resolution images also indicated that all forest edges in this study have been fragmented for at least 25 years prior to our measurements; however, further land-use history data was not available. Three out of four forest edge sites designated as “urban” border busy roads and/or pavement with heavily traveled sidewalks. One rural forest edge research site also borders a road but experiences much less foot and car traffic and its surrounding forest is far more intact than its urban counterparts (Figure S1). While surrounding open areas bordering edges in this study appear to be regularly maintained (e.g., mowed, cleared), only forest edges without obvious signs of forest management were used in this study.

## 2.2 | Field data collection

Along each transect, we installed a pair of PVC soil respiration collars at 0, 15, 30, 60, and 90 m from the forest edge ( $n = 10$  collars per transect; 80 collars total). Respiration collars were 20.2 cm in diameter, mounted in the soil approximately 4 cm deep and extending aboveground roughly 4 cm. Respiration collars were left to equilibrate for at least two weeks before data collection began. Soil respiration measurements were taken July 30–October 29, 2018 and April 25–November 8, 2019 using a LI-COR LI-8100A soil respiration chamber system ( $\pm 1.5\%$  accuracy for  $\text{CO}_2$  reading; LI-8100A Specifications, 2021) every two weeks between 08:00 and 17:00 local time. During the early-spring and fall of 2019 (April, October, and November), respiration measurements were taken every three weeks. The time of measurement was randomized across sites and distances from the edge, and measurements were

not taken during precipitation events. Our sampling interval is limited to the snow-free period of April–November because the vast majority of soil respiration occurs during the snow-free portion of the year (Giasson et al., 2013), and there are profound logistical difficulties and artifacts associated with taking soil respiration measurements through the snow during winter months. Unless otherwise noted, the growing season refers to the entire period of respiration data collection (i.e., April 25 through November 8). We refer to June 1–September 15 as the mid-growing season, and the remainders of the data collection window are referred to as shoulder seasons.

Soil temperature and volumetric soil water content (VWC) were measured concurrently with soil respiration using hand-probes at 10 cm and 7.6 cm depth, respectively. Soil temperature probes measure temperature at depth, while VWC probe measurements integrate moisture over the depth range. Depending on instrument availability, these co-located measurements were taken with a Hanna Instruments Thermistor Thermometer ( $\pm 0.4^\circ\text{C}$  for one year excluding probe error; Waterproof Thermistor Thermometer: HI93510N, 2021) and Field Scout TDR 150 ( $\pm 3\%$ ; TDR 150 Soil Moisture Meter with Case, 2021), respectively, or using LiCOR auxiliary probes ( $\pm 1.5^\circ\text{C}$ , 0–50°C for Omega Soil Temperature Probe (6000-09TC); 6400-09 Soil CO<sub>2</sub> Flux Chamber Instruction Manual, 2003). Hand-probe measurements provide a critical snapshot of abiotic conditions at the time of respiration measurements but provide only a partial picture of overall site conditions. Because they are taken with respiration measurements, hand-probe measurements are taken only during the daytime and not during periods of precipitation. Soil temperature and VWC were also continuously-logged at 10 cm depth every 30 min using Onset HOBO Pendant Data Loggers ( $\pm 0.53^\circ\text{C}$ , 0–50°C; HOBO Pendant Temperature/Light Data Logger 8K, 2021) and Onset Soil Moisture Smart Sensors ( $\pm 3\%$  in most soil conditions; 10HS Soil Moisture Smart Sensor: S-SMD-M005, 2021), respectively, in seven of the eight transects at 0, 15, 30, and 90 m

from the edge. Air temperature at ~1.5 m above the ground was also logged at these distances at seven research sites using Onset HOBO Temperature/Relative Humidity Data Loggers ( $\pm 0.2^\circ\text{C}$ , 0–70°C; HOBO U23 Pro v2 Temperature/Relative Humidity Data Logger, 2021).

### 2.3 | Soil temperature and moisture response modeling

The relationships between soil respiration and both soil temperature and moisture were characterized using multiple response models. Probe point measurements of temperature and moisture were used in this modeling to most closely represent the concurrent and proximate soil conditions at each respiration measurement location. Following Bond-Lamberty et al. (2011), ordinary least squares (OLS) and non-linear fitting algorithms were used depending on the model: exponential Q<sub>10</sub> (van't Hoff, 1898), logistic (Richards, 1959), Lloyd & Taylor (Lloyd & Taylor, 1994) and gamma (Khomik et al., 2009) (Table S1). The gamma model is a relatively flexible empirical model and is described in Equation (1):

$$R_s = (T_{40})^{\beta_0} e^{\beta_1 + (\beta_2 T_{40})} \quad (1)$$

where  $R_s$  is the soil respiration rate in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , and  $T_{40}$  is soil temperature at 10 cm depth ( $^\circ\text{C}$ ) shifted by 40°C (i.e.,  $T_{40}$  = measured temperature +40°C; *sensu* Khomik et al., 2009).  $\beta_0$ – $\beta_2$  are fitted parameters (Table 2; Table S1).

We further used gamma models to integrate the relationship between soil respiration and temperature as mediated by volumetric soil moisture:

$$R_s = (T_{40})^{\beta_0} e^{\beta_1 + (\beta_2 T_{40}) + (\beta_3 \text{VWC})} \quad (2)$$

TABLE 2 Gamma model fitted parameters

Model	Urbanization category	$\beta_0$	$\beta_1$	$\beta_2$	$\beta_3$	$\beta_4$	$\beta_5$	$n$	Adj $R^2$
Gamma ( $T_{40}$ )	Urban	18.90	-59.00	-0.28	-	-	-	411	0.41
	Rural	21.65	-67.88	-0.32	-	-	-	394	0.46
Gamma ( $T_{40}$ + VWC)	Urban	22.16	-70.14	-0.34	2.03	-	-	409	0.48
	Rural	17.77	-56.81	-0.24	1.28	-	-	394	0.50
Gamma ( $T_{40}$ * VWC)	Urban	13.68	-42.21	-0.21	-12.29	0.26	-	409	0.54
	Rural	8.31	-26.15	-0.10	-11.34	0.23	-	394	0.53
Gamma ( $T_{40}$ * VWC + NearEdge <sub>0m15m</sub> )	Urban	14.09	-43.62	-0.21	-11.81	0.25	0.16	409	0.56
	Rural	8.15	-25.66	-0.103	-11.29	0.23	-0.043	394	0.53
Gamma ( $T_{40}$ * VWC + DFE)	Urban	14.35	-44.453	-0.22	-11.43	0.24	0.0026	409	0.56
	Rural	8.33	-26.21	-0.11	-11.34	0.29	0.000044	394	0.53

Note:  $R_s$  is the soil respiration rate in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .  $T_{40}$  is soil temperature at 10 cm depth in degrees Celsius ( $^\circ\text{C}$ ) shifted by 40°C. VWC is volumetric soil moisture (v/v) at 7.6 cm depth. NearEdge<sub>0m15m</sub> is a binary categorical term describing soils 0–15 m from the forest edge or 30–90 m into the forest interior, while DFE represents each discrete distance from forest edge to the interior (m).  $\beta_0$ – $\beta_5$  are fitted model parameters.  $n$  refers to the sample size used to parameterize each model. Adj  $R^2$  is the  $R$ -squared value adjusted for the number of terms in the model.

$$R_s = (T_{40})^{\beta_0} e^{\beta_1 + (\beta_2 T_{40}) + (\beta_3 VWC) + \beta_4 (T_{40} \times VWC)} \quad (3)$$

where VWC is volumetric soil water content (v/v) at 7.6 cm depth, and  $\beta_0 - \beta_4$  are fitted model parameters (Table 2; Table S1). In Equation (2), soil temperature and moisture are additive, whereas in Equation (3) we include an interaction term. Models were fit to all respiration data, regardless of urbanization category (urban or rural), and also fit to urban and rural data separately.

After selecting the gamma model described in Equation (3) for both rural and urban sites based on residual sum of squares (RSS), Akaike Information Criterion (AIC; Akaike, 1998), and adjusted  $R^2$  (Table 2; Table S1), we evaluated differences in soil behavior near the forest edge compared to those in the forest interior by adding a categorical term to Equation (3). The categorical term indicates if measurements were taken 0–15 m from the forest edge to determine if temperature-moisture sensitivity near the forest edge was significantly different from the forest interior for rural and urban soils, respectively:

$$R_s = (T_{40})^{\beta_0} e^{\beta_1 + (\beta_2 T_{40}) + (\beta_3 VWC) + \beta_4 (T_{40} \times VWC) + \beta_5 \text{NearEdge}_{0m15m}} \quad (4)$$

where  $\text{NearEdge}_{0m15m}$  is a binary categorical term describing measurements taken either 0–15 m from the forest edge or 30–90 m into the forest interior, and  $\beta_0 - \beta_5$  are fitted model parameters (Table 2; Table S1). We aggregated to a 0–15 m interval following the distance from edge (DFE) influence findings from other temperate forests (Harper et al., 2005; Reinmann et al., 2020; Smith et al., 2019). Analysis of variance (ANOVA; Girden, 1992) was used to determine if temperature-moisture sensitivity for respiration was significantly different for soils 0–15 m from the edge relative to soils 30–90 m into the forest interior within each of the two urbanization classes (rural or urban). We also evaluated DFE for each discrete distance (Table 2; Table S1), but we did not see a meaningful improvement in model performance and continued our analysis with the term  $\text{NearEdge}_{0m15m}$  for parsimony.

In this analysis, we do not attempt to partition autotrophic and heterotrophic respiration and assume that they change proportionally in response to stimuli near the forest edge. Previous work from Reinmann and Hutyra (2017) found that root biomass does not change significantly with distance from the edge; in this analysis, we assume that the ratio of heterotrophic to autotrophic respiration is also unchanged.

## 2.4 | Estimating and scaling soil $\text{CO}_2$ efflux

Median hourly soil temperature and volumetric water content from continuously-logging sensors were used to create composite soil time series for “typical” urban and rural soils closer to the forest edge ( $\leq 20$  m) and further into the forest interior ( $> 20$  m). This 20 m threshold was used to scale our results using the available binary edge/interior forest classification done by Reinmann et al. (2020)

and to allow for a direct comparison of above- and belowground edge effects across studies. Where possible, gaps in continuously-logged VWC data at rural sites were filled using archival data from nearby forest edge sites (Smith, 2019; 2687 VWC values filled out of 67,271 total observations; nearby forest edge sites located on Harvard Forest property approximately 3 km from Petersham research sites). The remaining data gaps in VWC data from dataloggers were filled by linearly interpolating between adjacent hourly time points (2809 observations).

We used the mean area under the curve to calculate average soil temperatures and VWC values for average urban and rural soils 0–20 m and 20–90 m from the forest edge. We then used these temperature-moisture time series to predict hourly soil respiration fluxes across the growing season for urban and rural soils, respectively. When estimating fluxes, Equation (3) was used to model soil respiration rates only if an ANOVA indicated that inclusion of a  $\text{NearEdge}_{0m15m}$  term did not significantly affect the model performance, as was the case for rural soils. If an ANOVA indicated that inclusion of  $\text{NearEdge}_{0m15m}$  was statistically significant, as for urban soils, Equation (4) was used to model soil respiration rates. Respiration estimates were then scaled to the state of MA using CDPs to identify urban areas. Using ArcGIS Pro, we estimated the fraction of forest within 20 m of a non-forest edge within CDPs, as well as for all other lands outside of CDP boundaries (sensu Reinmann et al., 2020; US Census Bureau, 2021). We then scaled soil respiration estimates for all forested areas in MA, regardless of forest type, treating CDPs as urban and all other land areas in MA as rural. While not explicitly accounted for in our analyses, the forest edge aspect is likely to affect soil processes like respiration near the edge through its effects on soil temperature and soil moisture (Matlack, 1993). Because our sites cover a range of edge orientations, we are likely indirectly capturing the effects of aspects on soil temperature, moisture, and, therefore, soil respiration across our results.

## 2.5 | Statistical analysis

All data quality assurance and statistical analyses were performed in R version 3.6.2 (R Core Team, 2019). We used standard OLS regression as implemented in R core packages using the *lm* function (Chambers, 1992) and non-linear least squares regression with the *nls* function (Bates & Chambers, 1992) and *nls.lm* function from the package *minpack.lm* (Elzhov et al., 2016) to fit models of soil respiration temperature-moisture sensitivity. We used linear mixed-effects models (*lme* function from package *nlme*; Pinheiro et al., 2019 and *lsmeans* function from package *lsmeans* with a post hoc Tukey's range test; Lenth, 2016) to calculate average soil respiration, temperature, and moisture values at varying distances from the forest edge. Distance from the forest edge (continuous data) and urbanization category (urban or rural) were treated as fixed effects, and the site was included as a random effect (intercept) to account for repeated measurements. Note that unless otherwise specified, all values reported are means with standard error, summary statistics

reflect the full growing season dataset, and we report significance as  $p < .05$ .

### 3 | RESULTS

#### 3.1 | Soil respiration at the edge

Rates of soil respiration showed diverging patterns near forest edges between urban and rural sites, particularly during the mid-growing season (Figure 2a). We observed that soil respiration rates are generally elevated at 0 m from the forest edge (hereafter referred to as the “forest edge”) in rural areas compared to respiration rates further into the forest interior, while respiration rates were suppressed at the urban forest edge relative to the urban interior forest (Figure 2a; Figure S3a). Over the full period of data collection, the mean forest edge soil respiration rate at rural sites was  $6.92 \pm 0.43 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , and rural respiration rates declined up to 30 m into the forest interior. In contrast, rates of soil respiration in urban sites were 25% lower at the forest edge ( $4.06 \pm 0.42 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) compared to  $5.45 \pm 0.33 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on average from 15–90 m into the urban forest interior ( $p = .0003$ ). Soil respiration fluxes 15–90 m into the interior were not significantly different from one another in urban and rural forests, respectively ( $p > .35$ ).

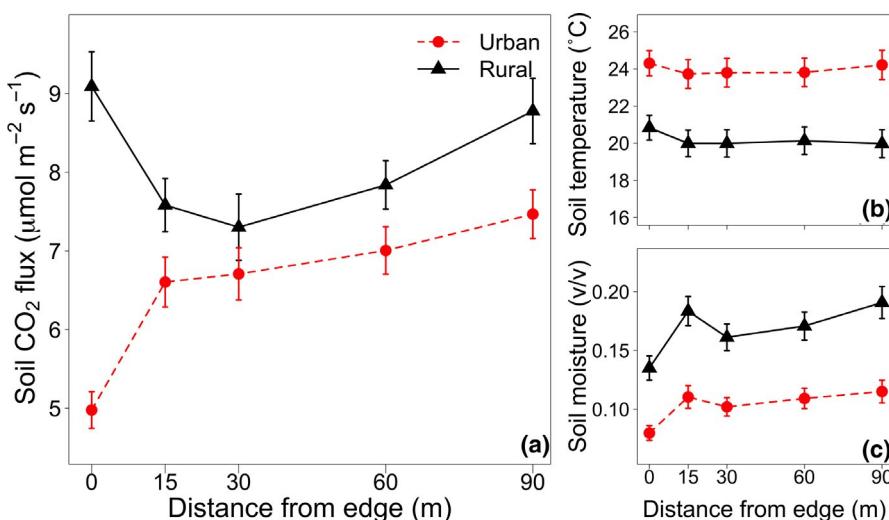
At the time of soil respiration measurements over the season, mean soil temperatures in urban sites were  $2.78 \pm 1.4^\circ\text{C}$  warmer than in rural forest sites ( $p = .097$ ). Urban and rural soils alike were significantly drier at the forest edge relative to 15–90 m into the forest interior (hand probe; urban,  $p = .0047$ ; rural,  $p = .0074$ ). Data from point measurements also suggest that VWC at rural sites tended to be higher than at urban sites ( $p = .0402$ ). Frequency distribution plots from continuously-logging sensors additionally show that soils in urban forest sites experienced warm temperatures and severe dryness more frequently than soils in rural forest sites, particularly during the mid-growing season (Figure 3a,b; Figure S6). During the mid-growing season, dataloggers indicated that soil temperatures between urban and rural sites were more significantly

different during the daytime than nighttime (urban vs. rural: daytime,  $p = .016$ ; nighttime,  $p = .12$ ), and a similar trend was true for VWC (daytime  $p = .41$ ; nighttime  $p = .17$ ).

#### 3.2 | Soil conditions and respiration through the season

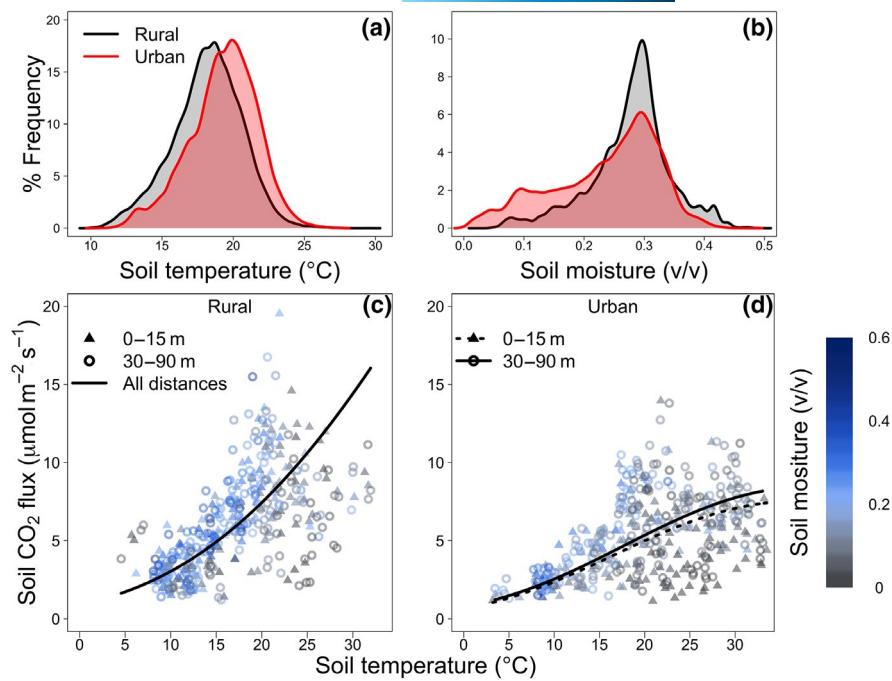
The divergence in soil respiration rates at the forest edge between rural and urban sites occurred during the mid-summer months when soil temperature and moisture content were most different between urban and rural soils (Figure 4; Table 3; Figure S5). In the early growing season (April, May 2019), we observed no significant difference between mean urban and rural respiration rates ( $p = .08$ ) or daytime (08:00–17:00) datalogger measurements of soil temperature ( $p = .15$ ) and moisture ( $p = .97$ ). Environmental conditions began to diverge in June 2019, at the start of the mid-growing season, with urban soils becoming hotter than their rural counterparts throughout the transect ( $p = .02$ ; datalogger). For rural and urban soils during this time, conditions 0–15 m from the forest edge began to deviate from those further into the interior. Temperatures near the forest edge became hotter than those in the forest interior ( $p < .0001$ ; datalogger) and additionally became significantly drier at the edge than the interior in June ( $p < .0001$ ; datalogger).

In July and August of 2018 and 2019, soil respiration rates at the forest edge of urban sites deviated significantly from those at 0 m from the edge of rural sites ( $p < .001$ ). Urban soil respiration rates 0–15 m from the edge were also significantly different from rates 30–90 m into the urban forest interior at this time ( $p = .0011$ ; Figure 4; Table 3; Figure S5). Continuously-logging sensors indicate that urban soils overall remained warmer during the daytime than rural soils through July and August ( $p = .017$ ), but for both rural and urban soils alike, conditions 0–15 m from the forest edge continued to be both hotter ( $p < .0001$ ) and drier ( $p < .0001$ ) than the respective forest interior (Figure S4). Rural soils experienced peak daytime soil temperatures in August with a mean of  $19.4 \pm 0.24^\circ\text{C}$ , and in the same month, they reached their peak soil respiration flux with an average rate of  $9.62 \pm 0.39 \mu\text{mol}$

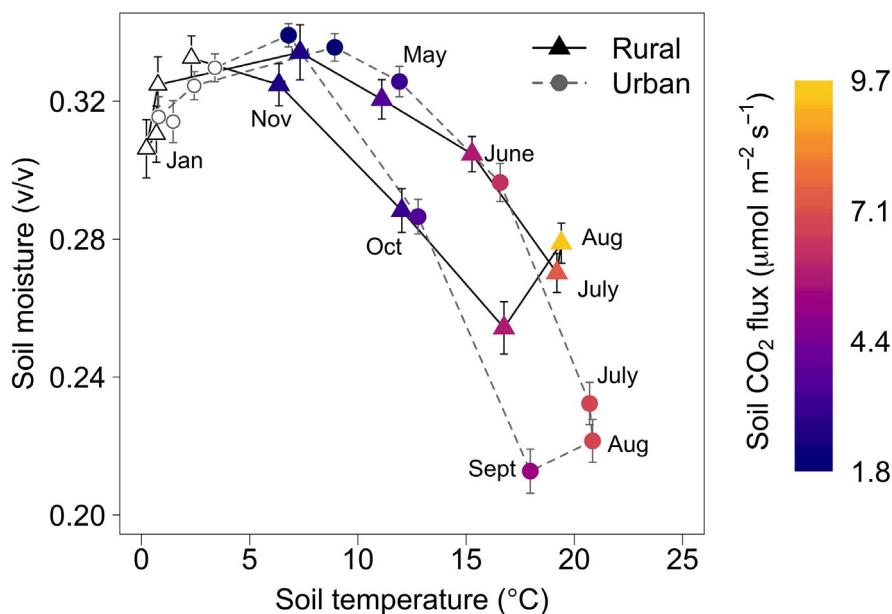


**FIGURE 2** Mean soil respiration rates ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) as a function of distance from the edge (a) for urban and rural sites during the mid-growing season (June 1–September 15). Mean mid-season soil temperature (b;  $^\circ\text{C}$ ) and volumetric soil moisture (c; v/v) point measurements were taken at the time of respiration measurement. Measured respiration, temperature, and moisture are data shown; bars around each point are standard error around the mean [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**FIGURE 3** Frequency distribution of mean hourly logged soil temperature (a; °C) and moisture (b; v/v) for the 2018 and 2019 growing season (measured data; 24 h). Soil respiration temperature sensitivity as affected by soil moisture, illustrated using a gamma model for rural (c; Equation 3) and urban (d; Equation 4, model fits 0–15 m vs 30–90 m;  $p < .0001$ ) soils. Gamma models are plotted against soil temperature, holding soil moisture constant at the mean value for rural soils, urban soils 0–15 m, and urban soils 30–90 m, respectively. Soil temperature and moisture values for (c), (d) and gamma modeling come from point measurements taken concurrently with measurements of soil respiration. Points on panels (c) and (d) reflect measured data from point measurements [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 4** Monthly hysteresis curve of mean daytime soil temperature (°C) and moisture (v/v) at urban and rural sites (logged half-hourly; 08:00–17:00). Point color indicates monthly mean soil  $\text{CO}_2$  efflux in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (urban vs rural: mid-growing season,  $p = .026$ ; August only,  $p = .0026$ ; shoulder seasons,  $p = .81$ ). Open points are months where respiration measurements were not taken. Full, measured dataset, and all distances from the edge are shown. Error bars around each point are 95% confidence intervals around the mean [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



$\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Figure 4). Urban soils also experienced peak temperatures and fluxes during August, but while the mean daytime temperature was  $20.8 \pm 0.21^\circ\text{C}$ , mean urban soil respiration was only  $6.99 \pm 0.48 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Figure 4). Both urban and rural soils were driest on average during September, containing  $21.0 \pm 1.6$  and  $25.3 \pm 1.9\%$  VWC, respectively (datalogger). By September 2018 and 2019, urban and rural soil temperature, moisture, and respiration rates began to converge again (temperature:  $p = .0102$ ; VWC:  $p = .13$ ; respiration:  $p = .36$ ). Continuously-logged daytime soil temperature and moisture values were not significantly different between urban and rural sites throughout the remainder of the year (temperature:  $p = .086$ ; VWC:  $p = .99$ ).

It is worth noting that at 90 m from the forest edge in rural sites, soil respiration fluxes during the period of data collection were not

significantly different from those at any other distance along the transect, including rates at 0 m from the forest edge ( $p > .3$ ; Table 3). There was a small but significant increase in daytime VWC at 90 m relative to 0–60 m from the forest edge for rural sites ( $+3.2 \pm 0.1\%$ ,  $p < .0001$ ; datalogger), with a commensurate decrease in soil temperature ( $-1.1 \pm 0.06^\circ\text{C}$ ,  $p < .0001$ ; datalogger).

### 3.3 | Respiration temperature- and moisture-response modeling

Based on goodness of fit and significance metrics, we selected the gamma model from Equation (3) to represent the temperature

TABLE 3 Soil respiration, temperature, and moisture results

Urbanization category	Distance from edge (m)	Mid-growing season (June 1–September 15)			Shoulder seasons (April 25–May 31, September 16–November 8)		
		Soil respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Soil temperature (°C)	Soil moisture (v/v or %)	Soil respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Soil temperature (°C)	Soil moisture (v/v or %)
Rural	0	9.1 ± 0.49	18.9 ± 0.28	28.5 ± 2.2	4.2 ± 0.33	12.2 ± 0.18	32.3 ± 1.5
	15	7.6 ± 0.49	17.3 ± 0.28	24.8 ± 2.2	3.1 ± 0.33	11.7 ± 0.18	26.4 ± 1.5
	30	7.3 ± 0.49	18.0 ± 0.28	27.8 ± 2.2	3.1 ± 0.33	11.8 ± 0.18	31.8 ± 1.5
	60	7.8 ± 0.49	–	–	3.7 ± 0.33	–	–
	90	8.8 ± 0.49	16.7 ± 0.28	30.3 ± 2.2	3.9 ± 0.33	11.6 ± 0.18	32.1 ± 1.5
Urban	0	5.0 ± 0.48	19.5 ± 0.24	18.1 ± 1.9	2.9 ± 0.33	12.9 ± 0.16	26.5 ± 1.3
	15	6.6 ± 0.48	18.7 ± 0.24	21.6 ± 1.9	3.5 ± 0.33	12.6 ± 0.16	29.9 ± 1.3
	30	6.7 ± 0.48	18.8 ± 0.24	25.2 ± 1.9	3.5 ± 0.33	12.5 ± 0.16	30.4 ± 1.3
	60	7.0 ± 0.48	–	–	3.6 ± 0.33	–	–
	90	7.4 ± 0.48	18.6 ± 0.24	26.9 ± 1.9	3.7 ± 0.33	12.5 ± 0.16	29.7 ± 1.3

Note: Soil respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), temperature (°C), and volumetric soil moisture (v/v) values were presented as means with standard error. Soil temperature and moisture values reflect continuously-logged measurements taken every 30 min (measured data, 24 h). Shoulder season windows are trimmed to reflect the range of field data collection.

sensitivity of soil respiration as affected by VWC for rural forest edge soils. While an ANOVA indicated that model fits for rural soils were not significantly different when the  $\text{NearEdge}_{0\text{m}15\text{m}}$  was included ( $p = .27$ ), the inclusion of the edge/interior categorical term for urban soils significantly affected model fit ( $p < .0001$ ). Therefore, Equation (4) was used to model and scale urban forest soil respiration fluxes, while Equation (3) was used for rural soils (Table 2; Table S1).

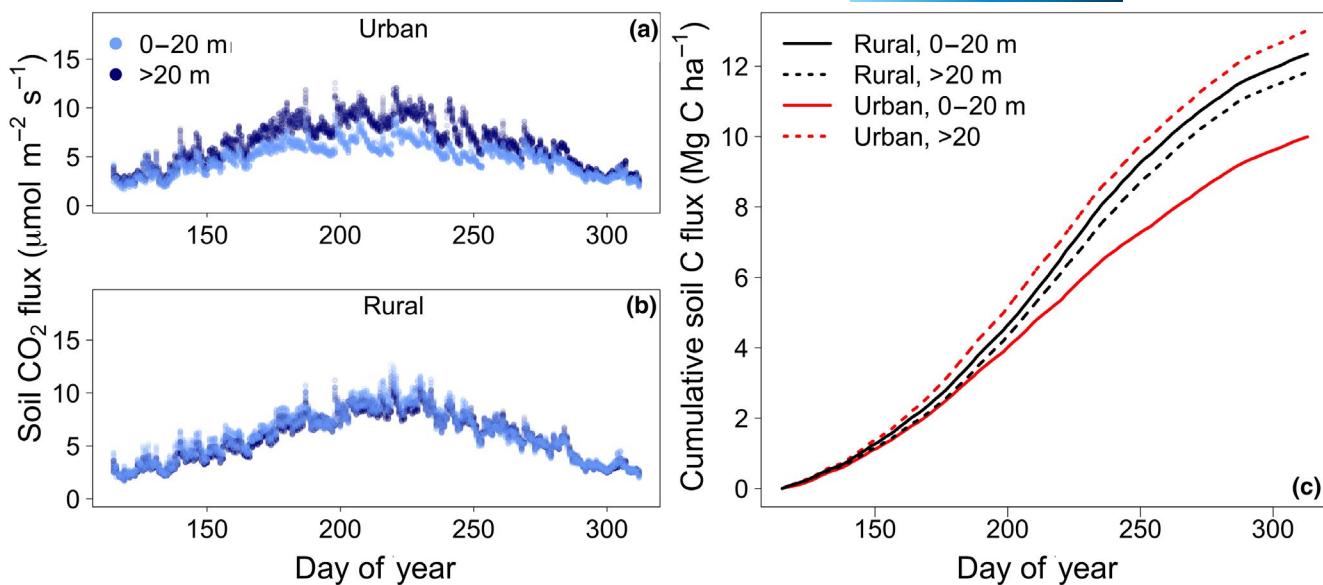
We find that respiration rates in rural soils were more sensitive to changes in temperature than in urban soils (Figure 3; Figure S6;  $p < .0001$ ). In the case of rural soils, the gamma model took the shape of an exponential function with rural soil respiration rates continuing to increase with rising temperatures (Figure 3c). In urban sites, the gamma model took a more asymptotic form with more frequent dryness and elevated temperatures as compared to rural soils (Figure S5). We observed that rates of respiration in urban sites at all distances began to an asymptote as soils approached extreme temperatures above ~25°C (Figure S7b), but this was most pronounced for soils 0–15 m from the forest edge (Figure 3). Model estimates indicate that urban soil respiration rates were significantly lower 0–15 m from the forest edge relative to 30–90 m from the forest edge, independent from VWC and temperature ( $p < .0001$ ; Table 2; Figure 3c,d), suggesting differences in the sensitivities of urban edge and interior soil behavior. Note that the shape of the relationship between urban soil respiration and soil temperature and moisture is not contingent on the inclusion of the  $\text{NearEdge}_{0\text{m}15\text{m}}$  term. When a unified model for urban soils at all distances from the edge was used, we still saw a separation in the respective responses of urban and rural soils (Figure S7).

We estimated hourly soil respiration fluxes using the temperature-moisture response curves for rural (Equation 3) and urban (Equation

4) soils and composite time series for soil temperature and moisture 0–20 m and 20–90 m from the forest edge (Figure 5a,b). Over the course of the growing season, soils in a typical urban forest 0 to 20 m from the edge may respire up to 2.35 Mg C  $\text{ha}^{-1} \text{yr}^{-1}$  less than soils in a typical rural forest edge over the same area (Figure 5c). We then scaled these modeled respiration fluxes to the state of MA, considering forest area within CDP as urban and all other forest areas in MA as rural. In rural forests of MA, we observed that of the 1.18 Mha of non-CDP forest area, 23.4% is within 20 m of a non-forest edge (Reinmann et al., 2020). In the state's urban forests, however, 45.8% of the 0.25 Mha of CDP forest area is within 20 m of a non-forest edge (Figure 6; Reinmann et al., 2020). When growing season respiration fluxes for rural soils 0–20 m from the forest edge were modeled independently from those >20 m into the forest interior, we found that the total respiration flux during the growing season was not meaningfully different and increased only 1.0% (142,223.8 Mg C  $\text{yr}^{-1}$ ) relative to when all forested area is treated as the interior. When the same analysis was done in CDPs and urban respiration rates 0–20 m from the forest edge were modeled separately from those >20 m into the interior, the growing season soil respiration flux was 352,511.8 Mg C  $\text{yr}^{-1}$  (10.6%) lower than when all forested area is treated as the interior.

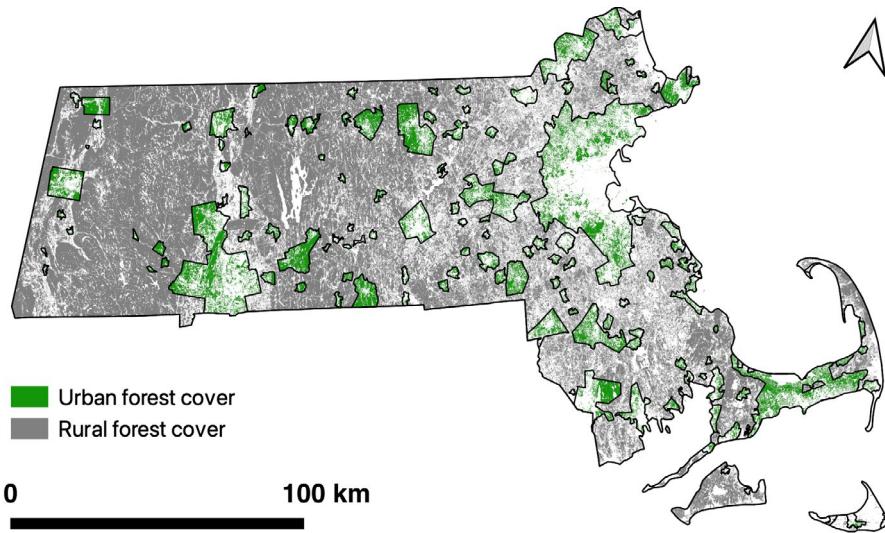
## 4 | DISCUSSION

With urbanization and forest fragmentation increasing around the globe, it is imperative to determine how rates of soil respiration and resulting losses from critical soil carbon pools vary near forest edges. While previous studies have found elevated rates of soil respiration at forest edges compared to interiors in temperate forests (Smith et al., 2019), we surprisingly observed that soil respiration rates were suppressed at the forest edge specifically in urban areas, likely due



**FIGURE 5** Modeled hourly respiration rates ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) for soils 0–20 m from the forest edge and soils >20 m into the forest interior for a typical urban (a) and rural (b) fragmented forest over the growing season. (c) The cumulative sum of modeled soil carbon fluxes ( $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ ) for soils 0–20 m from the edge and soils >20 m into the forest interior for a typical urban and rural forest. Growing season model estimates from April 25 to November 8 are shown, to reflect our field data collection window [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**FIGURE 6** Forest cover in Massachusetts in urban areas (Census Designated Places; forests shown in green) and rural areas (non-CDP; forests shown in grey) (MassGIS Data: Land Use 2005, 2009; US Census Bureau, 2021) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



to the high temperature and low moisture conditions experienced by soil communities at these locations. In combination with higher aboveground productivity at the temperate forest edge (Morreale et al., 2021; Reinmann & Hutyra, 2017), potential reductions in urban soil CO<sub>2</sub> losses have critical implications for ecosystem carbon sequestration in developed areas. While previous results suggested that rural edge soil temperatures may lead to unaccounted for carbon losses (Smith et al., 2019), our results suggest urban edges may enhance soil carbon storage through reduced respiration losses.

When we considered the amount of forest within 20 m of a non-forest edge in urban and rural areas across MA, we found that failure to account for differences in urban soil respiration fluxes near the edge led to an overestimate of soil growing season respiration fluxes of more

than 350,000 Mg C yr<sup>-1</sup> for just 0.25 Mha of the urban forest. This suggests that ignoring the effects of forest edges in urban sites may lead to inaccurate estimates of the amount of carbon stored in and lost from urban forest soils. These findings highlight the need to consider urban and rural landscapes independently when quantifying landscape and regional carbon balances in a changing world (Reinmann et al., 2020).

#### 4.1 | Temperature and moisture sensitivity in urban and rural forests

A meta-analysis by Carey et al. (2016) showed that soil respiration rates worldwide increased with temperature up to 25°C and then

began to decline, suggesting that increasing temperatures around the globe could lead to regionally variable responses in soil respiration. Our results emphasize that soil carbon responses to global change vary not only due to climate, but also with land-use and urbanization context.

While soil moisture and temperature are tightly linked and are considered the primary controls on soil respiration, studies of respiration sensitivity often focus exclusively on temperature. Soil moisture can improve model fit when there is low variation in soil temperature, as is the case in the tropics (Davidson et al., 2000; Vargas & Allen, 2008) or in temperate soils when soil moisture becomes limiting (Savage & Davidson, 2001). The soils in our study displayed a wide range of both soil temperatures and moisture content, where soil conditions varied substantially from forest edge to interior; and urban soils near the forest edge, in particular, experienced severe soil dryness. Our final model selection indicates interactions between soil temperature and VWC differ between urban and rural forests and suggests that relationships between soil temperature and respiration commonly used to characterize global forest cover do not capture soil respiration dynamics in urban forests, particularly those near the forest edge (Figure 3).

Similar to soil warming experiments that have found increases in soil temperatures lead to increased rates of soil respiration (Frey et al., 2013; Melillo et al., 2017), we observed increases in soil respiration near rural forest edges from 0–30 m that can be attributed to warmer edge soil temperatures. In agreement with previous studies, we found that modeled rural forest soil respiration sensitivity to temperature and moisture at the edge was not meaningfully different from that of the interior (Smith et al., 2019). However, our observed decreases in soil respiration near urban forest edges suggest the presence of moisture and/or temperature thresholds in this response. The divergence between urban and rural respiration rates was driven by large changes in mid-season conditions (particularly July and August) when soils were warm and dry enough to cross these thresholds regularly. Unlike the exponential increase in respiration with the temperature that we observed in rural soils, soil temperature and respiration began to decouple in urban soils as temperatures climbed and soils dried (Figure S7). Further, rates of respiration at urban forest edges were even less sensitive to changes in temperature than in the urban forest interior (Figure 3), suggesting that forest soils near the urban forest edge are distinctly different in some way from soils in the forest interior. These findings are in contrast with previous studies that have observed increased temperature sensitivity in aboveground net primary productivity near the urban forest edge compared to both urban forest interiors and rural forests (Reinmann & Hutyra, 2017; Reinmann et al., 2020).

We attributed the slight increase in rural soil respiration at 90 m from the edge largely to changes we observed in forest canopy structure and land-use at rural sites between 60 and 90 m into the forest interior, such as trails, seasonal streams, and canopy gaps, that likely affect soil respiration rates. The small but significant increase in rural VWC we observed at 90 m from the forest edge suggests that site differences in the rural forest interior may allow soils to

remain wetter during periods of water stress, thereby buffering potential declines in soil respiration. Because our modeling results suggest that rural forest soil respiration sensitivity to temperature and moisture at the edge is not meaningfully different from that of the interior, observed rural respiration fluxes can be attributed to site-specific conditions at the time of measurement.

Coupled with results from prior studies (Reinmann et al., 2020; Smith et al., 2019), the patterns in soil CO<sub>2</sub> effluxes we observed suggest that while relative differences in rural soil respiration 0–30 m from the edge were driven by the distinct temperature and moisture conditions at the forest edge, there could be additional factors affecting soil respiration at the edge in urban areas. These findings exemplify the disconnect between rural forested landscapes traditionally used for ecological exploration and rapidly expanding fragmented, urban landscapes. Classically defined relationships between soil respiration and temperature alone do not capture key nuances in soil respiration dynamics for fragmented forests in urban areas.

## 4.2 | Dynamic responses near the forest edge

While traditional soil respiration-temperature response models predict increases in carbon losses with warming, decreases in soil respiration rates at urban forest edges despite warm temperatures may be driven by local, short-term responses to heat and water stress that are particularly intense at the urban forest edge. Heat stress can lead to decreased rates of respiration and limited microbial enzyme activity (Davidson et al., 2006; Khomik et al., 2009). Soil dryness tends to co-occur with extreme temperatures near urban edges in mid- to late-summer (Figure 4; Figure S6), and severe dryness can cause water and substrate limitation leading to decreases in respiration (Allison & Treseder, 2008; Henry, 2013; Savage & Davidson, 2001). These severe stressors could contribute to the suppression of soil respiration near the urban forest edge. For example, coarse woody debris decomposition can be impeded at the forest edge due to moisture limitation, and this may contribute to the patterns we observe (Crockatt & Bebber, 2015).

However, the forest edges characterized in this study are more than 25 years old, and there may also be long-term mechanisms at work. The soil microbial communities in this study have experienced a long legacy of extreme edge conditions (Figure 2c, d; Figure S6). Resulting changes in microbial biomass and/or microbial carbon use efficiency at developed forest edges due to prolonged exposure to severe temperatures, dryness, or other extreme conditions could play a pivotal role in soil behavior. Prolonged elevated temperatures from soil warming experiments at Harvard Forest and elsewhere have been shown to lead to depletion of labile substrates in soil (Frey et al., 2013), reductions in microbial biomass (Frey et al., 2008), reductions in microbial carbon use efficiency (Allison et al., 2010; Steinweg et al., 2008), and thermal adaptation of microbial respiration (Bradford et al., 2008). The previous land-use history of each forest site is likely also to play a role in soil behavior, including potentially affecting soil carbon stores (Ziter & Turner, 2018); however

further land-use history data for our field sites were not available at this time.

#### 4.3 | Potential interactions with other global changes

Not all forest edges are created equal. The conditions experienced at an anthropogenic forest edge near human development or surrounded by pavement are very different from those experienced at a forest edge in a rural area that opens to a grassy field and without urban heat island impacts. Forest edges surrounded by increasing urbanization are likely to be influenced by interactions between multiple different global change drivers, and it is critical to note that biotic and abiotic changes induced by forest edges can operate on varying length scales from less than 1 m to up to 100 m into the forest interior (Meeussen et al., 2020; Reinmann & Hutyra, 2017; Smith et al., 2019).

Prior studies have observed elevated atmospheric nitrogen inputs at the forest edge (Remy et al., 2016; Weather et al., 2001), and in European temperate forests, nitrogen has been pointed to as a key mechanism behind forest edge responses (Meeussen et al., 2020). If nitrogen throughfall is sufficiently high, it can decrease microbial biomass, inhibit the production of organic matter-degrading enzymes and suppress soil respiration (Treseder, 2008), ultimately leading to soil carbon accumulation (Frey et al., 2014). However, while atmospheric nitrogen inputs are up to two times greater in urban compared to rural areas in MA (Decina et al., 2018; National Trends Network, 2020; Rao et al., 2014), nitrogen throughfall rates in our study region are still comparatively low relative to throughfall rates in European studies of forest fragmentation (Rao et al., 2014; Remy et al., 2016) and may not be sufficiently high to affect soil respiration behavior.

Forest edges near human development, especially roadways, experience elevated concentrations of  $\text{CO}_2$  and are unprotected from lateral inputs, such as salt and sand from road snow removal (Bryson & Barker, 2002; Gately et al., 2013), as well as heavy metals and polycyclic aromatic hydrocarbons (PAHs) from fossil fuel combustion (Apeagyei et al., 2011; Zehetner et al., 2009). Elevated atmospheric  $\text{CO}_2$  leads to increased plant fine root production and exudation, increasing microbial biomass, and soil respiration (Paterson et al., 1997; Zak et al., 2000). Road salt application is common practice in many cold winter locations, and salt spray can penetrate up to 10 m into the forest (Bryson & Barker, 2002; Lundmark & Jansson, 2008). This spray accumulates in soils along roadside edges over time, inhibiting soil respiration through decreases in microbial biomass and soil organic matter content (Bryson & Barker, 2002; Rath & Rousk, 2015). Heavy metals and PAHs can also lead to significant decreases in soil respiration as they accumulate in soils, affecting microbial biomass, and decreasing community diversity (Chodak et al., 2013; Deary et al., 2018).

To our knowledge, the effect of the size of the open patch bordering the forest edge has yet to be investigated; but forest break

size likely plays an important role in the conditions and level of disturbance that forest soils near the edge experience. The size of the open area bordering a forest edge may affect solar radiation exposure, wind, and atmospheric deposition patterns, as well as the degree and type of human activity near the edge. The complex drivers at the forest edge are intrinsically linked to human activity and affect not only how much carbon is lost from soils, but also how it is lost and by whom in the soil community. Understanding the relative contributions of these contrasting stimuli at the forest edge over both the short- and long-term is critical to modeling how soils behave at the forest edge in different conditions.

#### 4.4 | Implications on a heterogeneous landscape

The soil respiration responses we observed at the forest edge are pronounced, but their impact on ecosystem carbon cycling varies across the growing season and with the relative proportion of fragmented forests in urban and rural areas. In Massachusetts, 27.5% of all forests are within 20 m of a non-forest edge, but the prevalence of fragmentation across the landscape is not uniform. Urban forests within CDPs are far more heavily fragmented than non-CDP forest areas (Figure 6), and forests near urban areas and agriculture are more likely to be fragmented than those in less developed areas (Reinmann et al., 2020; Smith et al., 2018). Accounting for differential urban soil conditions and behavior 0–20 m from the forest edge and >20 m into the forest interior within CDPs led to a growing season soil respiration decrease of more than  $352,511 \text{ Mg C yr}^{-1}$  (10.6%) relative to when all urban forested area was modeled as the interior. This was almost 2.5 times the difference in flux estimates for rural soils in the analogous comparison ( $+142,223.8 \text{ Mg C yr}^{-1}$ ), even though forest area within CDPs is less than one quarter that of all other forest areas in MA (Figure 6). Over the entire 0.25 Mha of the urban forest, soil respiration decreased more than  $1.38 \text{ Mg C ha}^{-1} \text{yr}^{-1}$ , meaning that the effect per hectare of the forest was almost 12 times greater in urban CDPs than in rural, non-CDP forest areas. Thus, our results demonstrate that failure to include differential soil fluxes at the forest edge will have substantial implications for local and large-scale carbon accounting, particularly in more developed areas. Urban expansion continues to drive deforestation in the northeastern US (Foster, 2010; Hall et al., 2002). By 2050, more than 118,000 km<sup>2</sup> of US forestland is projected to be subsumed by urbanization, a land area roughly the size of the state of Pennsylvania (Nowak & Walton, 2005).

These results highlight the role of urban forest soils, particularly urban forest edge soils, as potential carbon sinks. Coupled with increased aboveground productivity at the temperate forest edge and the highly fragmented nature of urban forests, these findings may agree with previous studies suggesting that urban forests have the potential to be a stronger carbon sink per unit forest area than rural forests (Hardiman et al., 2017; Reinmann et al., 2020). However, it is plausible that the lower soil respiration fluxes we observed near the urban forest edge could be indicative of reduced edge soil carbon

sequestration (Bae & Ryu, 2021; Schlesinger, 1995). A recent meta-analysis showed that soils in urban green spaces can contain significantly less carbon than soils in undisturbed forests (Chien & Krumins, 2021); however investigation of trends in soil carbon stocks near the forest edge remains limited (Bae & Ryu, 2021). This research is not an argument for the fragmentation of forests in cities as a carbon sequestration strategy; carbon lost in the creation of forest edges will outweigh any potential additional carbon storage by soils or accelerated growth at the edge (Reinmann & Hutyra, 2017; Reinmann et al., 2020). Further, whether the observed differences in biogenic carbon fluxes at the forest edge result in a forest edge carbon source or sink is highly dependent on management, and we do not manage our urban forests for above- or below-ground carbon sequestration.

Forests edges adjacent to residential and commercial properties are commonly used as dumping grounds for trash and organic yard waste, which could significantly affect soil carbon fluxes. Recent work demonstrates that management decisions in non-forested urban soils can lead to large increases in soil respiration compared to nearby forest interiors (Decina et al., 2016), and similar management decisions, such as irrigation and mulch application, can be applied to forests adjacent to residential lands. While not the focus of this study, this work highlights the importance of individual land management decisions in broader carbon cycling and emphasizes the fragility of the developed forest edge carbon balance. It is possible that certain land-use adjacencies and management practices could offset or even cancel out the decrease in soil carbon efflux we observe at urban edges.

## 4.5 | Conclusions

This study supports the growing perspective that studying global change drivers independently can lead to incomplete conclusions (Wolkovich et al., 2012). Forest edges can be a confluence of multiple facets of global change, including warming temperatures, urbanization, nitrogen loading, and more. Explicitly studying these distinct anthro-ecological systems allows us to elucidate the interactions between global change drivers that would otherwise only be possible through expansive and costly manipulation experiments. Studies of forest fragmentation effects in rural areas alone previously suggested positive effects of fragmentation on soil respiration. However, when the effects of urbanization were considered, we observed changes in both the magnitude and direction of soil respiration responses.

This study characterized soils on the forested side of the forest edge boundary, but the results were shaped by activity beyond the forest in adjacent land areas and underscore the inherent complexity of forest edges. Understanding the altered state of fragmented forest soils is imperative for accurately quantifying biogenic carbon fluxes because the relationship between respiration and soil temperature at the forest edge is unlikely to remain constant with future climate change. Forest fragmentation and human activity alter the biogeochemical state of forest soils, and further environmental and

land cover change will affect how soils and their carbon fluxes respond in a warming and increasingly urbanized world.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Harvard Forest Data Archive HF423 (v.1) and Environmental Data Initiative at <https://doi.org/10.6073/pasta/9df1903343144e49e5a9407f01d5ac3b>.

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## REFERENCES

Akaike, H. (1998). Information Theory and an Extension of the Maximum Likelihood Principle. In *Selected papers of Hirotugu Akaike* (pp. 199–213). Springer. [https://doi.org/10.1007/978-1-4612-1694-0\\_15](https://doi.org/10.1007/978-1-4612-1694-0_15)

Allison, S. D., & Treseder, K. K. (2008). Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Global Change Biology*, 14(12), 2898–2909. <https://doi.org/10.1111/j.1365-2486.2008.01716.x>

Allison, S. D., Wallenstein, M. D., & Bradford, M. A. (2010). Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience*, 3(5), 336–340. <https://doi.org/10.1038/ngeo846>

Apeagyei, E., Bank, M. S., & Spengler, J. D. (2011). Distribution of heavy metals in road dust along an urban-rural gradient in Massachusetts. *Atmospheric Environment*, 45(13), 2310–2323. <https://doi.org/10.1016/j.atmosenv.2010.11.015>

Bae, J., & Ryu, Y. (2021). The magnitude and causes of edge effects on soil organic carbon stocks within and across urban to rural forest patches. *Landscape and Urban Planning*, 215, 104223. <https://doi.org/10.1016/j.landurbplan.2021.104223>

Bates, D. M., & Chambers, J. M. (1992). Nonlinear Models. In J. M. Chambers, & T. J. Hastie (Eds.), *Statistical Models in S*. Wadsworth & Brooks/Cole.

Bond-Lamberty, B., Bronson, D., Bladyka, E., & Gower, S. T. (2011). A comparison of trenched plot techniques for partitioning soil respiration. *Soil Biology and Biochemistry*, 43(10), 2108–2114. <https://doi.org/10.1016/j.soilbio.2011.06.011>

Bond-Lamberty, B., & Thomson, A. (2010). Temperature-associated increases in the global soil respiration record. *Nature*, 464(7288), 579–582. <https://doi.org/10.1038/nature08930>

Bradford, M. A., Davies, C. A., Frey, S. D., Maddox, T. R., Melillo, J. M., Mohan, J. E., Reynolds, J. F., Treseder, K. K., & Wallenstein, M. D. (2008). Thermal adaptation of soil microbial respiration to elevated temperature. *Ecology Letters*, 11(12), 1316–1327. <https://doi.org/10.1111/j.1461-0248.2008.01251.x>

Bradford, M. A., Wieder, W. R., Bonan, G. B., Fierer, N., Raymond, P. A., & Crowther, T. W. (2016). Managing uncertainty in soil carbon feedbacks to climate change. *Nature Climate Change*, 6(8), 751–758. <https://doi.org/10.1038/nclimate3071>

Bryson, G. M., & Barker, A. V. (2002). Sodium accumulation in soils and plants along Massachusetts roadsides. *Communications in Soil Science and Plant Analysis*, 33(1–2), 67–78. <https://doi.org/10.1081/CSS-120002378>

Carey, J. C., Tang, J., Templer, P. H., Kroeger, K. D., Crowther, T. W., Burton, A. J., Dukes, J. S., Emmett, B., Frey, S. D., Heskel, M. A., Jiang, L., Machmuller, M. B., Mohan, J., Panetta, A. M., Reich, P. B., Reinsch, S., Wang, X., Allison, S. D., Banninger, C., ... Tietema, A. (2016). Temperature response of soil respiration largely unaltered with experimental warming. *Proceedings of the National Academy of Sciences of the United States of America*, 113(48), 13797–13802. <https://doi.org/10.1073/pnas.1605365113>

Chambers, J. M. (1992). Linear Models. In J. M. Chambers, T. Hastie, & D. Pregibon (Eds.), *Statistical Models in S* (1st ed.). Chapman & Hall/CRC.

Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N. M., Gerber, J. S., West, P. C., Mandle, L., Engstrom, P., Baccini, A., Sim, S., Mueller, C., & King, H. (2015). Degradation in carbon stocks near tropical forest edges. *Nature Communications*, 6, 10158. <https://doi.org/10.1038/ncomms10158>

Chien, S.-C., & Krumins, J. A. (2021). Natural versus urban global soil organic carbon stocks: A meta-analysis. *Science of The Total Environment*, 807, 150999. <https://doi.org/10.1016/j.scitenv.2021.150999>

Chodak, M., Gołebiewski, M., Morawska-Płoskonka, J., Kuduk, K., & Niklińska, M. (2013). Diversity of microorganisms from forest soils differently polluted with heavy metals. *Applied Soil Ecology*, 64, 7–14. <https://doi.org/10.1016/J.APSoIL.2012.11.004>

Contosta, A. R., Frey, S. D., & Cooper, A. B. (2011). Seasonal dynamics of soil respiration and N mineralization in chronically warmed and fertilized soils. *Ecosphere*, 2(3), art36. <https://doi.org/10.1890/ES10-00133.1>

Crockatt, M. E., & Bebbert, D. P. (2015). Edge effects on moisture reduce wood decomposition rate in a temperate forest. *Global Change Biology*, 21(2), 698–707. <https://doi.org/10.1111/gcb.12676>

Crum, S. M., Liang, L. L., & Jenerette, G. D. (2016). Landscape position influences soil respiration variability and sensitivity to physiological drivers in mixed-use lands of Southern California, USA. *Journal of Geophysical Research: Biogeosciences*, 121(10), 2530–2543. <https://doi.org/10.1002/2016JG003469>

Davidson, E. A., Janssens, I. A., & Luo, Y. (2006). On the variability of respiration in terrestrial ecosystems: Moving beyond Q 10. *Global Change Biology*, 12(2), 154–164. <https://doi.org/10.1111/j.1365-2486.2005.01065.x>

Davidson, E. A., Verchot, L. V., Henrique Cattânia, J., Ackerman, I. L., & Carvalho, J. E. M. (2000). Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry*, 48, 53–69. <https://doi.org/10.1023/A:1006204113917>

Deary, M. E., Ekumankama, C. C., & Cummings, S. P. (2018). Effect of lead, cadmium, and mercury co-contaminants on biodegradation in PAH-polluted soils. *Land Degradation & Development*, 29(6), 1583–1594. <https://doi.org/10.1002/LDR.2958>

Decina, S. M., Hutyra, L. R., Gately, C. K., Getson, J. M., Reinmann, A. B., Short Gianotti, A. G., & Templer, P. H. (2016). Soil respiration contributes substantially to urban carbon fluxes in the greater Boston area. *Environmental Pollution*, 212, 433–439. <https://doi.org/10.1016/j.envpol.2016.01.012>

Decina, S. M., Templer, P. H., & Hutyra, L. R. (2018). Atmospheric inputs of nitrogen, carbon, and phosphorus across an urban area: Unaccounted fluxes and canopy influences. *Earth's Future*, 6(2), 134–148. <https://doi.org/10.1002/2017EF000653>

Digital Soil Map of the World. (2021). Food and Agriculture Organization of the United Nations. <https://data.apps.fao.org/map/catalog/srv/eng/catalog.search#/metadata/446ed430-8383-11db-b9b2-000d939bc5d8>

Duvaneck, M. J., Thompson, J. R., & Wilson, B. T. (2015). An imputed forest composition map for New England screened by species range boundaries. *Forest Ecology and Management*, 347, 107–115. <https://doi.org/10.1016/j.foreco.2015.03.016>

Elzhov, T. V., Mullen, K. M., Spiess, A.-N., & Maintainer, B. B. (2016). minpack.lm: R interface to the levenberg-marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds. *R Package Version*, 1(2-1), 1–14.

Foster, D. R., Aber, J., Cogbill, C., Hart, C., Colburn, E., D'Amato, A., Donahue, B., Driscoll, C., Ellison, A., Fahey, T., Hall, B., Hunter, M., Irland, L., Keeton, W., Kittredge, D., Lambert, K., Levitt, J., Lilieholm, R., Orwig, D., & Thompson, J. (2010). Wildlands and woodlands, farmlands and communities: Broadening the vision for New England. In *Wildlands and Woodlands: A Vision for the New England Landscape*. Harvard Forest; Harvard University Press. <http://www.wildlandsandwoodlands.org>

Frey, S. D., Drijber, R., Smith, H., & Melillo, J. (2008). Microbial biomass, functional capacity, and community structure after 12 years of soil warming. *Soil Biology and Biochemistry*, 40(11), 2904–2907. <https://doi.org/10.1016/j.soilbio.2008.07.020>

Frey, S. D., Lee, J., Melillo, J. M., & Six, J. (2013). The temperature response of soil microbial efficiency and its feedback to climate. *Nature Climate Change*, 3(4), 395–398. <https://doi.org/10.1038/nclimate1796>

Frey, S. D., Ollinger, S., Nadelhoffer, K., Bowden, R., Brzostek, E., Burton, A., Caldwell, B. A., Crow, S., Goodale, C. L., Grandy, A. S., Finzi, A., Kramer, M. G., Lajtha, K., LeMoine, J., Martin, M., McDowell, W. H., Minocha, R., Sadowsky, J. J., Templer, P. H., & Wickings, K. (2014). Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. *Biogeochemistry*, 121(2), 305–316. <https://doi.org/10.1007/s10533-014-0004-0>

Gately, C. K., Hutyra, L. R., Wing, I. S., & Brondfield, M. N. (2013). A Bottom up Approach to on-Road CO<sub>2</sub> Emissions Estimates: Improved Spatial Accuracy and Applications for Regional Planning. *Environmental Science and Technology*, 47, <https://doi.org/10.1021/es304238v>

Giasson, M.-A., Ellison, A. M., Bowden, R. D., Crill, P. M., Davidson, E. A., Drake, J. E., Frey, S. D., Hadley, J. L., Lavine, M., Melillo, J. M., Munger, J. W., Nadelhoffer, K. J., Nicoll, L., Ollinger, S. V., Savage, K. E., Steudler, P. A., Tang, J., Varner, R. K., Wofsy, S. C., ... Finzi, A. C. (2013). Soil respiration in a northeastern US temperate forest: a 22-year synthesis. *Ecosphere*, 4(11), art140. <https://doi.org/10.1890/ES13.00183.1>

Girden, E. (1992). ANOVA: Repeated Measures. SAGE Publications, Inc. <https://doi.org/10.4135/9781412983419>

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townsend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2), 1–9. <https://doi.org/10.1126/sciadv.1500052>

Hall, B., Motzkin, G., Foster, D. R., Syfert, M., & Burk, J. (2002). Three hundred years of forest and land-use change in Massachusetts, USA. *Journal of Biogeography*, 29(10–11), 1319–1335. <https://doi.org/10.1046/j.1365-2699.2002.00790.x>

Hardiman, B. S., Wang, J. A., Hutyra, L. R., Gately, C. K., Getson, J. M., & Friedl, M. A. (2017). Accounting for urban biogenic fluxes in regional carbon budgets. *Science of the Total Environment*, 592, 366–372. <https://doi.org/10.1016/j.scitotenv.2017.03.028>

Harper, K. A., MacDonald, S. E., Burton, P. J., Chen, J., Brososke, K. D., Saunders, S. C., Euskirchen, E. S., Roberts, D., Jaiteh, M. S., & Esseen, P.-A. (2005). Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, 19(3), 768–782. <https://doi.org/10.1111/j.1523-1739.2005.00045.x>

Henry, H. A. L. (2013). Reprint of "Soil extracellular enzyme dynamics in a changing climate". *Soil Biology and Biochemistry*, 56, 53–59. <https://doi.org/10.1016/j.soilbio.2012.10.022>

HOBO U23 Pro v2 Temperature/Relative Humidity Data Logger (2021). Onset. <https://www.onsetcomp.com/products/data-loggers/u23-001a/>

Hundertmark, W. J., Lee, M., Smith, I. A., Bang, A. H. Y., Chen, V., Gately, C. K., Templer, P. H., & Hutyra, L. R. (2021). Influence of landscape management practices on urban greenhouse gas budgets. *Carbon Balance and Management*, 16(1), <https://doi.org/10.1186/s13021-020-00160-5>

Jenkinson, D. S., Adams, D. E., & Wild, A. (1991). Model estimates of CO<sub>2</sub> emissions from soil in response to global warming. *Nature*, 351(6324), 304–306. <https://doi.org/10.1038/351304a0>

Khomik, M., Arain, M. A., Liaw, K.-L., & McCaughey, J. H. (2009). Debut of a flexible model for simulating soil respiration–soil temperature relationship: Gamma model. *Journal of Geophysical Research*, 114(G3), G03004. <https://doi.org/10.1029/2008JG000851>

Lal, R. (2008). Carbon sequestration. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1492), 815–830. <https://doi.org/10.1098/rstb.2007.2185>

Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, 69(1), 1–33. <https://doi.org/https://doi.org/10.18637/jss.v069.i01>

LI-8100A Specifications (2021). LI-COR Environmental. [https://www.licor.com/env/products/soil\\_flux/specifications.html](https://www.licor.com/env/products/soil_flux/specifications.html)

Lloyd, J., & Taylor, J. A. (1994). On the temperature dependence of soil respiration. *Functional Ecology*, 8(3), 315. <https://doi.org/10.2307/2389824>

Lundmark, A., & Jansson, P. E. (2008). Estimating the fate of de-icing salt in a roadside environment by combining modelling and field observations. *Water, Air, and Soil Pollution*, 195(1–4), 215–232. <https://doi.org/10.1007/s11270-008-9741-9>

Luo, Y., Ahlström, A., Allison, S. D., Batjes, N. H., Brovkin, V., Carvalhais, N., Chappell, A., Ciais, P., Davidson, E. A., Finzi, A., Georgiou, K., Guenet, B., Hararuk, O., Harden, J. W., He, Y., Hopkins, F., Jiang, L., Koven, C., Jackson, R. B., ... Zhou, T. (2016). Toward more realistic projections of soil carbon dynamics by Earth system models. *Global Biogeochemical Cycles*, 30(1), 40–56. <https://doi.org/10.1002/2015GB005239>

MassGIS Data: Impervious Surface 2005 (2007, February). Mass.Gov. <https://www.mass.gov/info-details/massgis-data-impervious-surface-2005>

MassGIS Data: Land Use 2005 (2009, June). Mass.Gov. <https://www.mass.gov/info-details/massgis-data-land-use-2005>

Matlack, G. R. (1993). Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation*, 66(3), 185–194. [https://doi.org/10.1016/0006-3207\(93\)90004-K](https://doi.org/10.1016/0006-3207(93)90004-K)

McDonald, R. I., & Urban, D. L. (2004). Forest edges and tree growth rates in the North Carolina Piedmont. *Ecology*, 85(8), 2258–2266. <https://doi.org/10.1890/03-0313>

Meeussen, C., Govaert, S., Vanneste, T., Haesen, S., Van Meerbeek, K., Bollmann, K., Brunet, J., Calders, K., Cousins, S. A. O., Diekmann, M., Graae, B. J., Iacopetti, G., Lenoir, J., Orczewska, A., Ponette, Q., Plue, J., Selvi, F., Spicher, F., Sørensen, M. V., ... De Frenne, P. (2020). Drivers of carbon stocks in forest edges across Europe. *Science of the Total Environment*, 759, 143497. <https://doi.org/10.1016/j.scitotenv.2020.143497>

Melillo, J. M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., Burrows, E., Bowles, F., Smith, R., Scott, L., Vario, C., Hill, T., Burton, A., Zhou, Y. M., & Tang, J. (2011). Soil warming, carbon–nitrogen interactions, and forest carbon budgets. *Proceedings of the National Academy of Sciences of the United States of America*, 108(23), 9508–9512. <https://doi.org/10.1073/pnas.1018189108>

Melillo, J. M., Frey, S. D., DeAngelis, K. M., Werner, W. J., Bernard, M. J., Bowles, F. P., Pold, G., Knorr, M. A., & Grandy, A. S. (2017). Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science*, 358(6359), 101–105. <https://doi.org/10.1126/science.aan2874>

Melillo, J. M., Steudler, P. A., Aber, J. D., Newkirk, K., Lux, H., Bowles, F. P., Catricala, C., Magill, A., Ahrens, T., & Morrisseau, S. (2002). Soil warming and carbon-cycle feedbacks to the climate system. *Science*, 298(5601), 2173–2176. <https://doi.org/10.1126/science.1074153>

Morreale, L. L., Thompson, J. R., Tang, X., Reinmann, A. B., & Hutyra, L. R. (2021). Elevated growth and biomass along temperate forest edges. *Nature Communications*, 12(1), 7181. <https://doi.org/10.1038/s41467-021-27373-7>

National Centers for Environmental Information (2021). U.S. Climate Normals Quick Access. NOAA. <https://www.nci.noaa.gov/access/us-climate-normals/#dataset=normals-annualseasonal&timeframe=30&location=MA&station=USW00014739>

National Trends Network (2020). National Atmospheric Deposition Program. <http://nadp.slh.wisc.edu/NTN/>

Natural Resources Conservation Service, & National Water and Climate Center (2010, February 19). USDA: Wind rose resources. <https://www.nrcs.usda.gov/wps/portal/wcc/home/climateSupport/windRoseResources/>

Nowak, D. J., & Walton, J. T. (2005). Projected urban growth (2000–2050) and its estimated impact on the US forest resource. *Journal of Forestry*, 103(8), 383. <https://doi.org/10.1093/jof/103.8.383>

Oke, T. R., Mills, G., Christen, A., & Voogt, J. A. (2017). *Urban Climates*. Cambridge University Press. <https://doi.org/10.1017/978139016476>

Pan, Y., Chen, J. M., Birdsey, R., McCullough, K., He, L., & Deng, F. (2011). Age structure and disturbance legacy of North American forests. *Biogeosciences*, 8(3), 715–732. <https://doi.org/10.5194/bg-8-715-2011>

Paterson, E., Hall, J. M., Rattray, E. A. S., Griffiths, B. S., Ritz, K., & Killham, K. (1997). Effect of elevated CO<sub>2</sub> on rhizosphere carbon flow and soil microbial processes. *Global Change Biology*, <https://doi.org/10.1046/j.1365-2486.1997.t01-1-00088.x>

HOBO Pendant Temperature/Light Data Logger 8K (2021). Onset. <https://www.onsetcomp.com/products/data-loggers/ua-002-08/>

Pinheiro, J., Bates, D., DebRoy, S. S., & Sarkar, D. (2019). nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-140. <https://cran.r-project.org/package=nlme>

Post, W. M., Emanuel, W. R., Zinke, P. J., & Stangenberger, A. G. (1982). Soil carbon pools and world life zones. *Nature*, 298(5870), 156–159. <https://doi.org/10.1038/298156a0>

R Core Team. (2019). R: A language and environment for statistical computing. In R Foundation for Statistical Computing.

Raciti, S. M., Hutyra, L. R., Rao, P., & Finzi, A. C. (2012). Inconsistent definitions of "urban" result in different conclusions about the size of urban carbon and nitrogen stocks. *Ecological Applications*, 22(3), 1015–1035. <https://doi.org/10.1890/11-1250.1>

Ramirez, K. S., Craine, J. M., & Fierer, N. (2012). Consistent effects of nitrogen amendments on soil microbial communities and processes across biomes. *Global Change Biology*, 18(6), 1918–1927. <https://doi.org/10.1111/j.1365-2486.2012.02639.x>

Rao, P., Hutyra, L. R., Raciti, S. M., & Templer, P. H. (2014). Atmospheric nitrogen inputs and losses along an urbanization gradient from Boston to Harvard Forest. MA. *Biogeochemistry*, 229–245, <https://doi.org/10.1007/s10533-013-9861-1>

Rath, K. M., & Rousk, J. (2015). Salt effects on the soil microbial decomposer community and their role in organic carbon cycling: A review. *Soil Biology and Biochemistry*, 81, 108–123. <https://doi.org/10.1016/j.soilbio.2014.11.001>

Reinmann, A. B., & Hutyra, L. R. (2017). Edge effects enhance carbon uptake and its vulnerability to climate change in temperate broadleaf forests. *Proceedings of the National Academy of Sciences*, 114(1), 107–112. <https://doi.org/10.1073/pnas.1612369114>

Reinmann, A. B., Smith, I. A., Thompson, J. R., & Hutyra, L. R. (2020). Urbanization and fragmentation mediate temperate forest carbon cycle response to climate. *Environmental Research Letters*, 15(11), 114036. <https://doi.org/10.1088/1748-9326/abff16>

Remy, E., Wuyts, K., Boeckx, P., Ginzburg, S., Gundersen, P., Demey, A., Van Den Bulcke, J., Van Acker, J., & Verheyen, K. (2016). Strong gradients in nitrogen and carbon stocks at temperate forest edges. *Forest Ecology and Management*, 376, 45–58. <https://doi.org/10.1016/j.foreco.2016.05.040>

Richards, F. J. (1959). A flexible growth function for empirical use. *Journal of Experimental Botany*, 10(2), 290–301. <https://doi.org/10.1093/jxb/10.2.290>

Savage, K. E., & Davidson, E. A. (2001). Interannual variation of soil respiration in two New England forests. *Global Biogeochemical Cycles*, 15(2), 337–350. <https://doi.org/10.1029/1999GB001248>

Schlesinger, W. H. (1995). Soil Respiration and Changes in Soil Carbon Stocks. In G. M. Woodwell, & F. T. Mackenzie (Eds.), *Biotic Feedbacks in the Global Climatic System: Will the Warming Feed the Warming?* (1st ed., pp. 159–168). Oxford University Press.

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences of the United States of America*, 109(40), 16083–16088. <https://doi.org/10.1073/pnas.1211658109>

Smith, I. A. (2019). Evidence for edge enhancements of soil respiration in temperate forests - Harvard Dataverse. In Harvard Dataverse. <https://doi.org/10.7910/DVN/ZLRKK2>

Smith, I. A., Hutyra, L. R., Reinmann, A. B., Marrs, J. K., & Thompson, J. R. (2018). Piecing together the fragments: elucidating edge effects on forest carbon dynamics. *Frontiers in Ecology and the Environment*, 16(4), 213–221. <https://doi.org/10.1002/fee.1793>

Smith, I. A., Hutyra, L. R., Reinmann, A. B., Thompson, J. R., & Allen, D. W. (2019). Evidence for Edge Enhancements of Soil Respiration in Temperate Forests. *Geophysical Research Letters*, 46(8), 4278–4287. <https://doi.org/10.1029/2019GL082459>

6400-09 Soil CO<sub>2</sub> Flux Chamber Instruction Manual (2003). [www.licor.com](http://www.licor.com)

S10HS Soil Moisture Smart Sensor: S-SMD-M005 (2021). Onset. <https://www.onsetcomp.com/products/sensors/s-smd-m005/>

Steinweg, J. M., Plante, A. F., Conant, R. T., Paul, E. A., & Tanaka, D. L. (2008). Patterns of substrate utilization during long-term incubations at different temperatures. *Soil Biology and Biochemistry*, 40(11), 2722–2728. <https://doi.org/10.1016/j.soilbio.2008.07.002>

TDR 150 Soil Moisture Meter with Case. (2021). Spectrum Technologies. <https://www.specmeters.com/soil-and-water/TDR-150-soil-moisture-meter-with-case/>

Thermistor, Waterproof, & Thermometer: HI93510N. (2021). Hanna Instruments. <https://www.hannainst.com/hi93510n-waterproof-thermistor-thermometer.html>

Treseder, K. K. (2008). Nitrogen additions and microbial biomass: A meta-analysis of ecosystem studies. *Ecology Letters*, 11(10), 1111–1120. <https://doi.org/10.1111/j.1461-0248.2008.01230.x>

Trlica, A., Hutyra, L. R., Morreale, L. L., Smith, I. A., & Reinmann, A. B. (2020). Current and future biomass carbon uptake in Boston's urban forest. *Science of the Total Environment*, 709, 136196. <https://doi.org/10.1016/j.scitotenv.2019.136196>

National Cooperative Soil Survey, National Soil Survey Committee of Canada, & Agriculture Organization of the United Nations. (1975). FAO-UNESCO Soil map of the world (Vol. 2). United Nations Educational.

US Census Bureau. (2010). Total population, 2010 Census. <https://data.census.gov/cedsci/table?q=population&g=8600000US01054,01604,02021,02131,02421,02459&y=2010&tid=DECENNIALSF12010.P1>

US Census Bureau. (2018). Census Designated Places (CDPs) for the 2020 Census-Final Criteria. In *Federal Register*. <https://www.federalregister.gov/documents/2018/11/13/2018-24571/census-designated-places-cdps-for-the-2020-census-final-criteria>

US Census Bureau. (2021, January 15). TIGER/Line Shapefile, 2017, state, Massachusetts, Current Place State-based. Data.Gov. <https://catalog.data.gov/dataset/tiger-line-shapefile-2017-state-massachusetts-current-place-state-based>

van't Hoff, J. H. (1898). *Lectures on Theoretical and Physical Chemistry*. Edward Arnold.

Vargas, R., & Allen, M. F. (2008). Diel patterns of soil respiration in a tropical forest after Hurricane Wilma. *Journal of Geophysical Research*, 113(G3), G03021. <https://doi.org/10.1029/2007JG000620>

Vasenev, V. I., Castaldi, S., Vizirskaya, M. M., Ananyeva, N. D., Shchepetova, A. S., Mazirov, I. M., Ivashchenko, K. V., Valentini, R., & Vasenev, I. I. (2018). Urban soil respiration and its autotrophic and heterotrophic components compared to adjacent forest and cropland within the Moscow Megapolis. In V. I. Vasenev, E. Dovletyarova, Z. Cheng, & R. Valentini (Eds.), *Megacities 2050: Environmental consequences of urbanization* (pp. 18–35). Springer. [https://doi.org/10.1007/978-3-319-70557-6\\_4](https://doi.org/10.1007/978-3-319-70557-6_4)

Weathers, K. C., Cadenasso, M. L., & Pickett, S. T. A. (2001). Forest edges as nutrient and pollutant concentrators: Potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conservation Biology*, 15(6), 1506–1514. <https://doi.org/10.1046/j.1523-1739.2001.01090.x>

Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., Pau, S., Regetz, J., Davies, T. J., Kraft, N. J. B., Ault, T. R., Bolmgren, K., Mazer, S. J., McCabe, G. J., McGill, B. J., Parmesan, C., Salamin, N., Schwartz, M. D., & Cleland, E. E. (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature*, 485(7399), 494–497. <https://doi.org/10.1038/nature11014>

Zak, D. R., Pregitzer, K. S., King, J. S., & Holmes, W. E. (2000). Elevated atmospheric CO<sub>2</sub>, fine roots and the response of soil microorganisms: A review and hypothesis. *New Phytologist*, 147(1), 201–222. <https://doi.org/10.1046/j.1469-8137.2000.00687.x>

Zehetner, F., Rosenfellner, U., Mentler, A., & Gerzabek, M. H. (2009). Distribution of road salt residues, heavy metals and polycyclic aromatic hydrocarbons across a highway-forest interface. *Water, Air, and Soil Pollution*, 198(1–4), 125–132. <https://doi.org/10.1007/S11270-008-9831-8/FIGURES/5>

Ziter, C., & Turner, M. G. (2018). Current and historical land use influence soil-based ecosystem services in an urban landscape. *Ecological Applications*, 28(3), 643–654. <https://doi.org/10.1002/EAP.1689>

## SUPPORTING INFORMATION

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