Soils at the temperate forest edge: An investigation of soil characteristics and carbon dynamics

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HIGHLIGHTS

- Soil carbon (%) and enzyme activity are lower at the forest edge than interior.
- Soil pH, [Ca] and [Mg] are higher at the forest edge than interior.
- Soil [Na] is higher at the forest edge than interior for roadside edges only.
- Soils are sandier at the edge than interior and have increased freeze-thaw cycling.

GRAPHICAL ABSTRACT
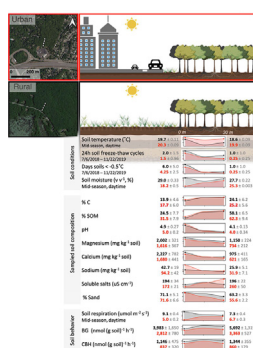
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ABSTRACT

Global proliferation of forest edges through anthropogenic land-use change and forest fragmentation is well documented, and while forest fragmentation has clear consequences for soil carbon (C) cycling, underlying drivers of belowground activity at the forest edge remain poorly understood. Increasing soil C losses *via* respiration have been observed at rural forest edges, but this process was suppressed at urban forest edges. We offer a comprehensive, coupled investigation of abiotic soil conditions and biotic soil activity from forest edge to interior at eight sites along an urbanization gradient to elucidate how environmental stressors are linked to soil C cycling at the forest edge. Despite significant diverging trends in edge soil C losses between urban and rural sites, we did not find comparable differences in soil % C or microbial enzyme activity, suggesting an unexpected decoupling of soil C fluxes and pools at forest edges. We demonstrate that across site types, soils at forest edges were less acidic than the forest interior ($p < 0.0001$), and soil pH was positively correlated with soil calcium, magnesium and sodium content (adj $R^2 = 0.37$), which were also elevated at the edge. Compared to forest interior, forest edge soils exhibited a 17.8 % increase in sand content and elevated freeze-thaw frequency with probable downstream effects on root turnover and decomposition. Using these and other novel forest edge data, we demonstrate that significant variation in edge soil respiration (adj $R^2 = 0.46$; $p = 0.0002$) and C content (adj $R^2 = 0.86$; $p < 0.0001$) can be explained using soil parameters often mediated by human activity (*e.g.*, soil pH, trace metal and cation concentrations, soil temperature), and we emphasize the complex influence of multiple, simultaneous global change drivers at forest edges. Forest edge soils reflect legacies of anthropogenic land-use and modern human management, and this must be accounted for to understand soil activity and C cycling across fragmented landscapes.

1. Introduction

Forest fragmentation is globally ubiquitous with >70 % of the world's forest area located within 1 km of a forest edge (Haddad et al., 2015) and >17.5 % of temperate forest area within 30 m of a forest edge (Morreale et al., 2021). Forest fragmentation diminishes intact forest area and exposes trees and soils to novel 'forest edge' conditions. Forest edges resulting from human land-use experience perturbed microclimates distinct from the forest interior, with critical implications for ecosystem function and carbon (C) cycling both above- and belowground. Unlike the forest interior, forest edges are laterally exposed, leading to elevated growing season temperatures and moisture stress (Garvey et al., 2022; Harper et al., 2005; Matlack, 1993).

More C is stored in soils worldwide than in the atmosphere and vegetation combined (Jackson et al., 2017; Scharlemann et al., 2014), but despite this and other key roles of soil in biogeochemical cycling and plant nutrition, the vast majority of research into forest edge dynamics has been focused aboveground on biodiversity and microclimates (Franklin et al., 2021). Soil respiration (*i.e.*, CO_2 efflux from soil microbes and roots) is recognized as one of the largest fluxes in the global C cycle (Schlesinger and Andrews, 2000) and is often characterized as increasing exponentially with temperature (Lloyd and Taylor, 1994). At rural forest edges, warmer soil temperatures lead to increased rates of soil C loss (Garvey et al., 2022; Smith et al., 2019). Conversely in urban areas, soil respiration rates have been observed to be suppressed at the forest edge relative to the forest interior despite increases in temperature (Garvey et al., 2022). Increases in respiration rates at the forest edge of rural forests could be indicative of declining soil C stores in these forest edges. However, decreases in edge soil CO_2 efflux could result in greater C storage in urban forests, which would be in agreement with previous studies suggesting urban forests have the potential to be a stronger net C sink per unit forest area than their rural counterparts (Hardiman et al., 2017; Reinmann et al., 2020).

Observed differences in soil CO_2 effluxes between urban and rural forest edges may be explained by adjacent land-use, as conditions at the forest edge intensify in developed areas where edges experience multiple, simultaneous global change drivers exacerbated by human activity that can influence soil acidity and microbial decomposition dynamics. Human land-use, particularly urbanization, can amplify heat and moisture stress (Oke et al., 2017), as well as exacerbate increased atmospheric deposition and fertilizer inputs at the edge (Rao et al., 2014; Weathers et al., 2001). Human activity, both historical and ongoing, can even affect soil texture (Herrmann et al., 2020), cation inputs (Kupka et al., 2021), and heavy metal pollution (Peryea and Creger, 1994). However, few studies address how forest fragmentation intersects with urbanization, and this knowledge gap is acute in temperate forests where urban development remains the key driver of edge creation and persistence (Foster et al., 2010; Hall et al., 2002). Urbanization describes a layered and complex network of environmental stimuli that operate on multiple scales (Blair, 2001), and 'urban' can refer to parameters such as human population density, the degree of surrounding impervious surface area (ISA; *e.g.*, pavement), or proximity to busy roads—all of which can contribute to the distinct conditions driving soil activity near the forest edge in developed areas (Caron et al., 2023; Garvey et al., 2022; Raciti et al., 2012).

There is a need to study forest edges *in situ* in a warming and increasingly urbanized world, as simultaneous global change drivers (*e.g.*, rising temperatures, urbanization, fragmentation) can have non-additive effects on the direction and magnitude of resulting changes in soil properties and processes (Rillig et al., 2019). Distinct environmental conditions at the forest edge could both stimulate and suppress soil microbial activity depending on stimuli intensity and co-occurrence (Garvey et al., 2022; Caron et al., 2023). Soil composition, acidity, microbial enzyme activity and freeze-thaw cycling may all vary from the forest edge to interior with significant consequences for soil C dynamics. Soil pH is a key factor in organic matter decomposition, both directly through its effects on the soil microbial community and extracellular enzyme activity (EEA), as well as indirectly through its effects on aboveground plant species and litter production.

Extracellular enzymes are secreted into the soil matrix by bacteria and fungi to generate the majority of soil organic matter (SOM) decomposition in northern temperate forest soils (Schneider et al., 2012) and can serve as an indicator of soil decomposition rates and nutrient demand by microorganisms (Sinsabaugh et al., 2008). Winter soil freeze-thaw cycles can also affect decomposition by damaging fine roots and promoting root turnover (Cleavitt et al., 2008; Sanders-DeMott et al., 2018; Song et al., 2017). Current understanding of forest edges lacks a comprehensive characterization of these interrelated soil properties that are fundamental to C cycling, introducing large uncertainty to estimates of biogenic C emissions and storage.

To understand forest soil C cycling across complex landscapes, we need to develop a holistic view of the edge soil ecosystem and elucidate how different soil environmental stressors vary and interact at forest edges. Here, we offer new data and insights from an observational study conducted at forest edges along an urbanization gradient in New England to characterize belowground responses to forest fragmentation across different types of land-use. We measured soil percent (%) C, microbial enzyme activity, pH, texture, trace metal concentrations, and freeze-thaw frequency. We used this novel, multifaceted characterization of soils to elucidate soil C dynamics and their drivers from forest edge to interior across an urbanization gradient, and we asked the following questions: i) do soil % C, C effluxes *via* soil respiration, and potential soil enzyme activity vary across edge-to-interior and urbanization gradients, and if so, how? ii) do forest edges adjacent to roads or other development reflect human land-use in soil composition, trace element concentrations and/or pH, and if so, how? iii) how does lateral exposure at the forest edge affect soil temperature dynamics, particularly in winter? Finally, we evaluated the combined effects of the biotic and abiotic attributes on soil C using both uni- and multivariate analyses to advance understanding of forest edge soils and C cycling. We hypothesized that variation in soil C fluxes and pools from forest edge to interior may ultimately be explained using soil properties often mediated by human land-use.

2. Methods

2.1. Study area & site design

This study is part of the Urban New England (UNE) project (Garvey et al., 2022; Caron et al., 2023), containing eight forest sites along an urban to rural gradient across the heavily fragmented forests of Massachusetts (MA). Across the state, 27.5 % of forest area is within 20 m of a non-forest edge, and in a developed area such as the city of Boston, that portion jumps to 79.5 % (Reinmann et al., 2020). For the purposes of this analysis, we used metrics of ISA, population density, distance to an urban center (Boston Common in Boston, MA), and Census Designated Place classification to classify the urbanization intensity surrounding each forest edge site. Our study sites range from urban Boston to rural central MA, and we classified four UNE forest edge sites as urban and four as rural (Garvey et al., 2022). We also noted that three field sites (two urban and one rural) are immediately adjacent to paved roads, while the remaining five abut more porous landcovers such as fields and clearings. Levels of inorganic nitrogen (N), sodium (Na), chloride, and sulfate deposition are typically greater in the Boston area than in central MA where the rural Harvard Forest field sites are located (National Trends Network, 2020; Conrad-Rooney et al., *in review*). Forests at all sites are primarily dominated by oaks (*e.g.*, *Quercus rubra*, *Q. veluntina*) and maples (*e.g.*, *Acer rubrum*, *A. saccharum*), and soils are inceptisols, typical of MA (Natural Resources Conservation Service, 2019). At rural sites, observed mean daytime air temperatures were 22.5 ± 0.39 °C (95 % confidence interval) in the summer (June, July, August 2018 and 2019) and −1.5 ± 0.31 °C in the winter (December 2018; January, February 2019), with 123 cm of precipitation on average evenly distributed throughout the year (National Climatic Data Center, n.d.). At urban sites, observed mean daytime air temperatures were 24.2 ± 0.15 °C in summer and 1.1 ± 0.25 °C in winter, with approximately 111 cm precipitation evenly distributed throughout the year (National Climatic Data Center, n.d.).

Field sites were established in summer 2018, and we installed a transect orthogonal to the forest edge (defined by the tree stem line) extending 90 m into the forest interior at each site. Unless otherwise noted, two adjacent soil measurements were taken at 0, 15, 30, 60, and 90 m from the forest edge at all sites (Fig. 1). Replicates from the same distance from forest edge at a given site were averaged before being incorporated into larger summary statistics and analysis. For more detailed UNE site descriptions see Garvey et al. (2022) and Caron et al. (2023).

2.2. Soil respiration

We extended the soil respiration measurements reported in Garvey et al. (2022; data ranging July – October 2018 and April – November 2019) to include soil respiration measurements from the growing season of 2021. Following Garvey et al. (2022), PVC soil respiration collars (Fig. 1) were used for monthly measurements from April 22 to October 21, 2021 using a LI-COR LI8100A soil respiration chamber system (± 1.5 % stated accuracy for CO_2 reading; (*LI-8100A Specifications*, 2021)) between 08:00 and 17:00 local time. Soil temperature and volumetric water content (VWC) were measured concurrently using Hanna Instruments Thermistor Thermometer (± 0.4 °C for one year excluding probe error; *Waterproof Thermistor Thermometer: HI93510N*, 2021) and Field Scout TDR 150 (± 3 %; *TDR 150 Soil Moisture Meter with Case*, 2021), respectively, or using LiCOR auxiliary probes (± 1.5 °C, 0–50 °C for Omega Soil Temperature Probe (6000-09TC); *6400-09 Soil CO2 Flux Chamber Instruction Manual*, 2003). For further details regarding soil respiration methods, see Garvey et al. (2022).

2.3. Soil sampling

Soils samples were co-located within approximately 0.5 m of soil respiration collars (Fig. 1) and collected during the 2018 and 2019 growing seasons ($n = 40$ per sampling event). At each distance from the forest edge, the full depth of the organic horizon was sampled using 10×10 cm soil samples (ranging 2.5–7 cm depth). These samples were used to assay potential extracellular enzyme activity (EEA) and collected once in the early growing season (May 21–23, 2019), twice in the mid-season (August 15–23, 2018 and July 15–17, 2019), and once in the late season (Sept 17–20, 2019). August 2018 EEA samples were additionally subsampled for soil C, N and trace element analysis, and July 2019 EEA samples were subsampled for soil pH measurements. Also during the July 2019 sampling event, 10 cm depth soil cores (2.4 cm radius) were taken co-located with soil respiration collars, and organic and mineral soil horizons were separated and measured for depth in the field. Mineral horizon soil was then used for soil texture

analysis. After sampling, all soils were kept on ice, transported back to the laboratory at Boston University on the day of sampling, and processed within 24–48 h of collection. Samples were passed through a 2 mm sieve. Fresh soil samples were used to measure soil pH, while samples for EEA were frozen at -80 °C and subsamples for additional elemental and/or texture analysis were dried at 65 °C.

2.3.1. Soil extracellular enzyme assays

Potential EEA in 2018 (one growing season sampling) and 2019 (three growing season samplings) was assayed for the following enzymes: cellobiohydrolase (CBH; an exocellulase), β-glucosidase (BG; hydrolyzes cellobiose into glucose), β-xylosidase (BX; degrades xylose in hemicellulose), β-glucuronidase (BGLU; degrades glucuronic acid in hemicellulose), α-glucosidase (AG; degrades starch), β-N-acetyl-glucosaminidase (NAG; degrades chitin), and acid phosphatase (AP; mineralizes phosphorus). These enzymes were assayed using standard fluorometric (4-methylumbelliferone-linked substrates) assays at a pH of 4.8 (German et al., 2011; Talbot et al., 2015). Lignin-degrading enzymes polyphenol oxidase (PPO), and peroxidase (PER) were assayed using oxidative methods (L-DOPA substrate) at a pH 4.8 (German et al., 2011; Talbot et al., 2015). Leucine aminopeptidase (LAP; degrades polypeptides) EEA was measured using fluorometric (7-amino-4-methylcoumarin substrates) assays at a higher pH of 6.8 to ensure sufficient fluorescence.

For EEA assays, a 1 g subsample of soil was homogenized with 50 mL of 50 mM sodium acetate buffer (pH 4.8) or a 200 mg subsample was homogenized with 10 mL of 0.2 mM phosphate buffer (pH 6.8). All assays were conducted at 10 °C. We report resource-specific enzyme activity at forest edges (i.e., activity per g SOM), leveraging previous characterization of SOM at UNE sites using loss on ignition data (Caron et al., 2023), in addition to enzyme activities normalized to g soil. EEA per g soil reflects overall microbial community activity, while resource-specific EEA describes microbial efficiency, allowing us to investigate decomposition dynamics related to soil quality.

2.3.2. Other soil properties

A 5 g subsample of fresh, sieved organic horizon soil sampled in July 2019 was used to measure soil pH in a 1:2 soil/water mixture (see Caron et al. (2023) for more details). A 7 mg subsample of sieved, organic horizon soil from August 2018 was dried, ground and analyzed for % C and N content using an elemental analyzer (NC 2500 Elemental Analyzer, CE Elantech, Lakewood, NJ, USA). A dried, ground 1 g subsample of sieved, organic horizon soil (Aug 2018) was also analyzed by the Cornell Nutrient Analysis Lab for concentrations of Na, calcium (Ca), magnesium (Mg), lead (Pb), and arsenic (As) using EPA method 3050 for soil sample digestion
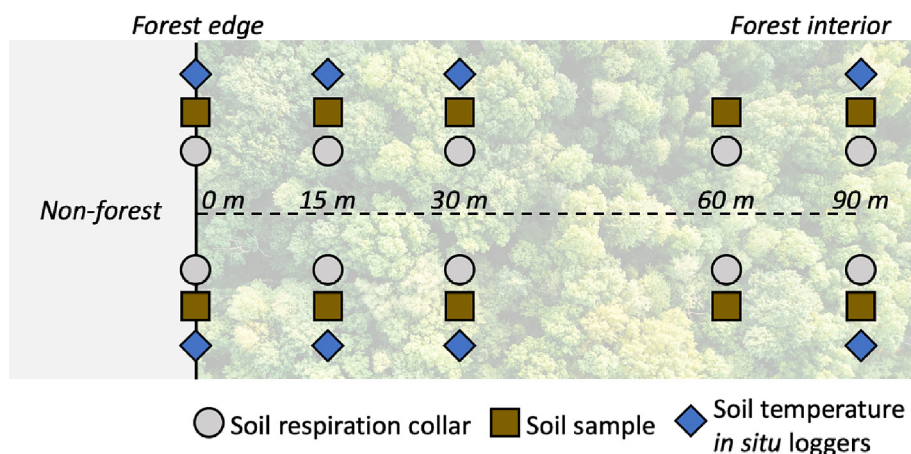

Fig. 1. UNE forest edge field site design. Soil respiration collars (grey circles) were installed in pairs at 0, 15, 30, 60 and 90 m from the edge approximately 5 m from the transect center (distance from center not to scale), and hand probe measurements of soil temperature and soil moisture were taken concurrently with all soil respiration measurements. Soil samples (brown squares) were co-located with soil respiration collars. Soil temperature *in situ* loggers (blue diamonds) collected data half-hourly at seven out of eight sites.

on a hot block with nitric acid and 6010B for ICP-OES for total elemental concentrations in mg kg^{-1} soil.

Sieved mineral horizon soils from soil cores collected in July 2019 were dried and ground using mortar and pestle, and a 40 g subsample was used to determine soil texture as % sand, silt and clay, respectively, using the hydrometer method over a period of 6 h (Soil Survey Staff, 2014).

2.4. In situ soil monitoring

Sensors at seven UNE field sites (four urban, three rural; $n = 28$) logged soil temperatures (5 cm depth; Fig. 1) half-hourly from July 6, 2018 to November 22, 2019 using Onset HOBO Pendant Data Loggers (± 0.53 °C, 0–50 °C; *HOBO Pendant Temperature/Light Data Logger 8K, 2021*). Soils were considered frozen if the 24 h mean soil temperatures were less than -0.5 °C. Freeze-thaw transitions were defined as shifts where soils were frozen one day, and then not frozen the following day (24 h soil temperature mean greater than -0.5 °C). Other conditions such as soil moisture (10 cm depth) and air temperature (~ 1.5 m above the ground) were also logged at these distances at seven research sites using Onset Soil Moisture Smart Sensors (± 3 % in most soil conditions; (*10HS Soil Moisture Smart Sensor: S-SMD-M005, 2021*)) and Onset HOBO Temperature/Relative Humidity Data Loggers (± 0.2 °C, 0–70 °C; (*HOBO U23 Pro v2 Temperature/Relative Humidity Data Logger, 2021*)), respectively.

2.5. Statistical analysis & model selection

All data quality assurance and statistical analyses were performed in R version 4.2.2 (R Core Team, 2022). Unless otherwise noted, reported values for soil % C, EEA, pH, trace metal concentrations, % sand and all other variables are means with standard error. We compare individual soil parameters both at the edge and interior and between site types (*e.g.*, urban or rural, roadside or non-roadside). We report significance as $p < 0.05$ resulting from F tests on one-way ANOVAs for two-group comparisons and Tukey HSD for multiple group comparisons. Except where otherwise noted, differences among urbanization classes were not statistically significant. As a robustness check on our statistical framework and sampling design, we additionally tested for potential site-level confounding factors using a linear mixed effects modeling approach (Lenth, 2016; Pinheiro et al., 2019) that includes site as a random effect on the intercept (*sensu* Garvey et al., 2022). We found that inclusion of site as a random effect did not meaningfully affect our results (Table S1), and therefore we do not use mixed effects models for our reported analyses. To compare soils at the forest edge to soils in the forest interior, we refer to values from 0 m as 'edge' and the mean of values from 30 to 90 m as 'interior', in accordance with previous forest edge literature regarding the depth of edge influence (Caron et al., 2023; Garvey et al., 2022; Meeussen et al., 2020; Reinmann and Hutyra, 2017).

Principle component analysis (*prcomp* function; Venables and Ripley, 2002) was applied to mean potential EEA per g soil across sampling events to reduce the 10 enzyme variables to two factors, principle components 1 and 2 (hereafter soil enzyme PC1 and soil enzyme PC2, respectively), following previous studies of soil EEA from across the continental U.S. (Talbot et al., 2013, 2014) and the globe (Sinsabaugh et al., 2008). This was repeated for resource-specific enzyme activity per g SOM (resource-specific enzyme PC1 and resource-specific enzyme PC2, respectively). A linear regression model (*lm* function) was used to investigate the relationship between soil pH and concentrations of Mg, Ca and Na.

Single linear regression models were also used to characterize the potential relationships between mean mid-season (June 1 – Sept 15 2018, 2019, 2021) soil respiration rate and organic horizon % C with other soil measurements (*e.g.*, temperature, moisture, pH), and a full list of variables can be found in Table S2. (Note that soil freeze-thaw was not included in the regression analysis, because data are not available at all sites. Soil temperature and moisture refer to measurements taken concurrently with soil respiration during the mid-growing season.) Multiple linear regression models for soil respiration rate and soil % C were constructed using the same suite of predictor variables and were subsequently evaluated using stepwise Akaike's information criterion (AIC) model selection (*stepAIC* function from package *MASS* using direction 'both' for stepwise search; (Saifuddin et al., 2021; Talbot et al., 2014; Venables and Ripley, 2002)). Resource-specific enzyme PC1 and resource-specific enzyme PC2 were excluded from multiple-predictor models due to co-linearity with soil enzyme PC1, soil enzyme PC2 and % SOM, as well as their lower explanatory power (Table S2). Each model of respiration and % C was fit using a total of 40 data points, with 5 values for each soil parameter provided per site (0, 15, 30, 60, 90 m). To account for small sample sizes, we additionally calculated second-order AIC (AICc; *AICc* function (Burnham and Anderson, 2002; Hurvich and Tsai, 1989)). For respiration and % C respectively, AICc, adjusted R^2 and p value were used to compare the full models containing all parameters with the most parsimonious models resulting from stepwise selection. To further evaluate how well our resulting characterization of soil C dynamics captured trends observed across urbanization and edge-to-interior gradients, we extended our model inter-comparison to include models of respiration and soil C predicted by urbanization class (*i.e.*, urban or rural) and distance from edge (DFE), as well as models predicted by temperature and moisture only. Because soil % C is far less variable than soil respiration rate over the growing season, we did not directly compare metrics of model fit between the two.
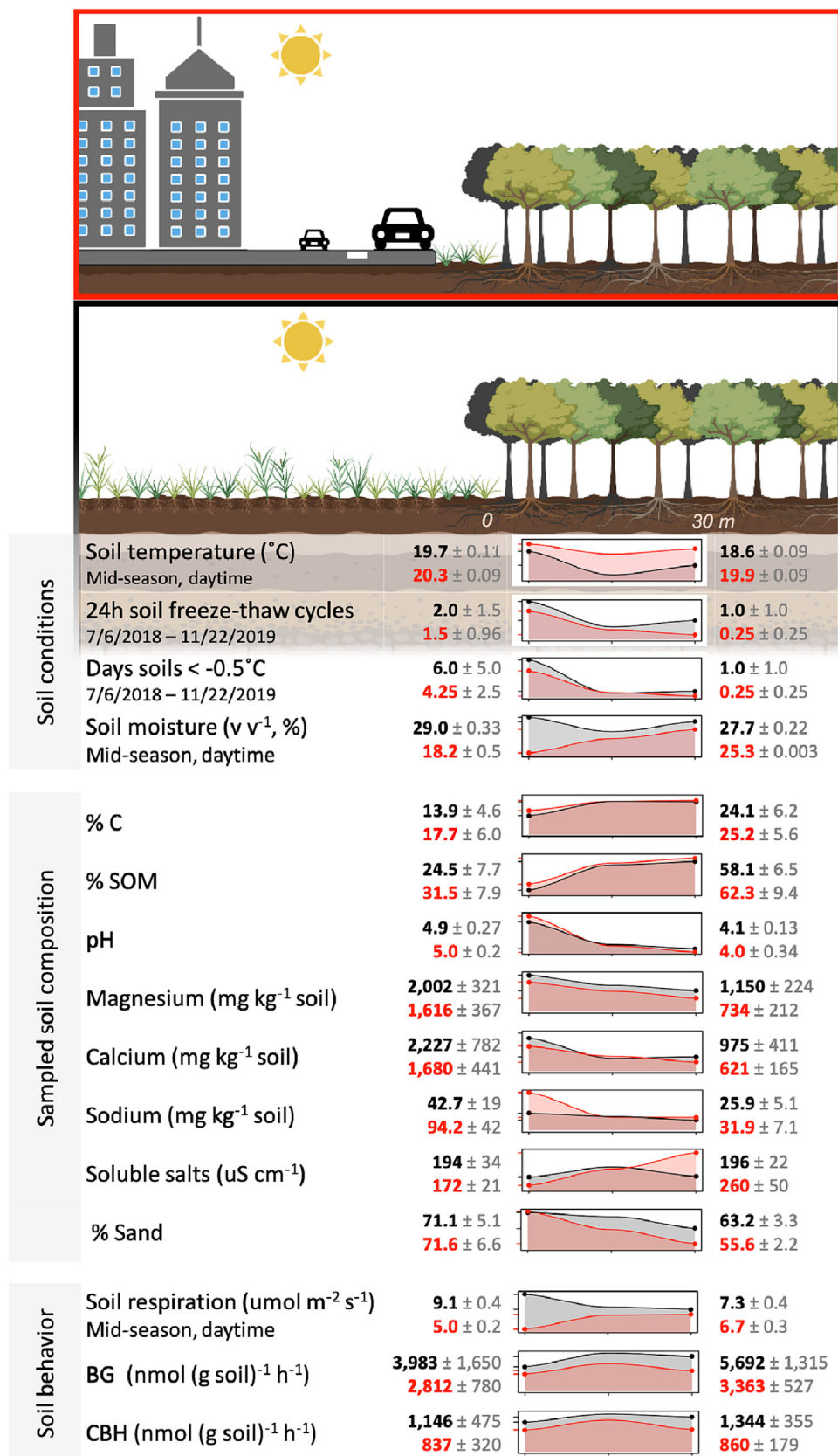
3. Results & discussion

We leveraged a multi-factorial field study to compare soil % C with soil respiration rates along the edge-to-interior gradient and found an unexpected decoupling between soil C fluxes and the soil C pool at the forest edge. We characterized additional soil conditions from edge to interior to find that significant variation in soil C fluxes and pools was explained by soil parameters typically influenced by human land-use (*e.g.*, soil pH, trace metal and cation concentrations, mean soil temperature), in addition to soil enzyme activity and % SOM. Our results demonstrate the complex, interacting consequences of forest fragmentation and urbanization on belowground processes and function.

3.1. Relationships between soil C, respiration and potential enzyme activity across edge-to-interior and urbanization gradients

We found that organic horizon soil % C at the forest edge was lower compared to the forest interior (0 m: 15.8 $\pm$ 3.6 %, 30–90 m: 25.1 $\pm$ 2.0 %; $p = 0.029$) (Fig. 3a). Despite these edge-to-interior trends, we found no significant correlation between soil % C and mean soil respiration flux (Figs. 2, 3, Table S2). In contrast to rates of soil respiration, we found that % C trends did not depend on urbanization class ($p > 0.2$). Lower mean soil % C at forest edges relative to the interior is driven particularly by soils at Hammond Woods, Sutherland Woods, Blue Hills, and Harvard

Fig. 2. Summary of reported data from the UNE project for soils at rural (black) and urban (red) forest edges. Curves reflect mean values for soil parameters at 0, 15, 30 m fit with loess smoothing for urban and rural edges respectively. Mean values and standard error at 0 m and 30 m are provided for urban and rural soils in red and black text. Edge illustrations created using Biorender.com.
Soil conditions refer to soil temperature and moisture data logged half-hourly at 5 cm depth along the forest edge transect *in situ* from July 6, 2018 to November 22, 2019. Mid-season refers to June 1 – September 15, and daytime refers to 08:00–17:00. *Sampled soil composition* refer to measurements collected using soil samples or subsamples along the forest edge transect that were then processed in the laboratory. *Soil behavior* refers to measurements of soil activity, where soil respiration was collected *in situ* using an infrared gas analyzer and soil chamber, and soil enzyme activity (BG, CBH) was assayed in the laboratory on field-collected organic horizon soil samples. Enzyme data reflect the mean across sampling events.

Soil conditions	Soil temperature (°C) Mid-season, daytime	**19.7** ± 0.11 **20.3** ± 0.09		**18.6** ± 0.09 **19.9** ± 0.09	
	24h soil freeze-thaw cycles 7/6/2018 − 11/22/2019	**2.0** ± 1.5 **1.5** ± 0.96		**1.0** ± 1.0 **0.25** ± 0.25	
	Days soils < -0.5°C 7/6/2018 − 11/22/2019	**6.0** ± 5.0 **4.25** ± 2.5		**1.0** ± 1.0 **0.25** ± 0.25	
	Soil moisture (v v⁻¹, %) Mid-season, daytime	**29.0** ± 0.33 **18.2** ± 0.5		**27.7** ± 0.22 **25.3** ± 0.003	
Sampled soil composition	% C	**13.9** ± 4.6 **17.7** ± 6.0		**24.1** ± 6.2 **25.2** ± 5.6	
	% SOM	**24.5** ± 7.7 **31.5** ± 7.9		**58.1** ± 6.5 **62.3** ± 9.4	
	pH	**4.9** ± 0.27 **5.0** ± 0.2		**4.1** ± 0.13 **4.0** ± 0.34	
	Magnesium (mg kg⁻¹ soil)	**2,002** ± 321 **1,616** ± 367		**1,150** ± 224 **734** ± 212	
	Calcium (mg kg⁻¹ soil)	**2,227** ± 782 **1,680** ± 441		**975** ± 411 **621** ± 165	
	Sodium (mg kg⁻¹ soil)	**42.7** ± 19 **94.2** ± 42		**25.9** ± 5.1 **31.9** ± 7.1	
	Soluble salts (uS cm⁻¹)	**194** ± 34 **172** ± 21		**196** ± 22 **260** ± 50	
	% Sand	**71.1** ± 5.1 **71.6** ± 6.6		**63.2** ± 3.3 **55.6** ± 2.2	
Soil behavior	Soil respiration (umol m⁻² s⁻¹) Mid-season, daytime	**9.1** ± 0.4 **5.0** ± 0.2		**7.3** ± 0.4 **6.7** ± 0.3	
	BG (nmol (g soil)⁻¹ h⁻¹)	**3,983** ± 1,650 **2,812** ± 780		**5,692** ± 1,315 **3,363** ± 527	
	CBH (nmol (g soil)⁻¹ h⁻¹)	**1,146** ± 475 **837** ± 320		**1,344** ± 355 **860** ± 179	

Forest 06 sites (Fig. S1), which all experience ongoing direct human influence due to their proximity to roads, a ski slope and other development, rather than adjacency to fields or less active management as at other sites.

Using extracellular enzyme assays and principle component analyses, we found that soil enzyme PC1 (a metric of overall soil enzyme activity across sampling events) explained 66.98 % of the variation in EEA and captured a decline in overall enzyme activity from interior to edge (Fig. S2). All assayed enzyme rates per g soil tended to be lower at the forest edge compared to the forest interior regardless of urbanization class ($p < 0.1$), except CBH, a cellulose-degrading enzyme whose activity was not significantly different between edge and interior ($p = 0.49$; Fig. S2, Table S3). Soil enzyme PC1 was significantly positively related to both soil % C and soil respiration, and it explained 75 % of variation in % soil C, though only 20 % of variation in soil respiration rates (Fig. 3, Table S2). We note that while soil enzyme PC2 was not a meaningful predictor of soil respiration rate or % C (Table S2), it parsed enzymes by target-type and separated oxidases PPO and PER, as well as nitrogen-targeting LAP, from the other hydrolytic enzymes (Fig. S2), similar to previous studies of these enzymes in temperate forest soil (Talbot et al., 2013, 2014). Despite diverging trends in rates of soil respiration in forest edges between urban and rural sites, differences between urban and rural EEA were insignificant for all enzymes except BG, a cellulase that had greater activity at rural sites compared to urban ($p = 0.02$) and LAP, a protein-targeting enzyme that had slightly lower activity in rural sites ($p = 0.032$).

Unlike enzyme rates per g soil, potential EEA normalized per g SOM across all sampling events was significantly higher at the forest edge compared to mean activity in the forest interior for cellulases CBH and BG, as well as AG, BGLU, BX and PPO ($p < 0.014$). Furthermore, resource-specific activities for CBH and BG were significantly greater at rural edges compared to urban edges ($p < 0.011$; Fig. S2 inset). Resource-specific

enzyme PC1 correlated with these edge-to-interior trends but explained limited variance in soil % C and was not a significant predictor of mean soil respiration flux (Fig. S2, Table S2). Observed trends in BG and CBH resource-specific EEA are anticorrelated with % SOM, which was significantly lower at the forest edge relative to interior ($p = 0.031$, Fig. 2; Caron et al. (2023)). At urban sites, the decline in edge % SOM was paralleled by a decline in soil respiration rates, yet edge respiration rates at rural sites were elevated despite declines in % SOM.

Reported differences in % SOM and resulting trends in resource-specific EEA from edge to interior may be underpinned by differences in substrate inputs such as plant litter at urban and rural edges, though litter was not assessed at UNE sites. Some studies have found that litter depth decreases with proximity to edge (Matlack, 1993), but this finding is not universal (Marchand and Houle, 2006; Schedlbauer and Miller, 2022). Further, while some studies found decelerated litter mass loss with urbanization attributed to heavy metal exposure (Cotrufo et al., 1995; Pavao-Zuckerman and Coleman, 2005), others found that urbanization leads to decreases in litter structural carbohydrate content and accelerated litter decomposition rates (Dorendorf et al., 2015).

In addition to substrate inputs, the complex connections between % SOM, potential EEA and soil C cycling can be mediated by *in situ* temperature and moisture availability. For comparability across sites and within forest edge-to-interior transects, all EEA assays were conducted in the lab at a constant temperature (10 °C); yet average soil temperatures can vary from forest edge to interior. Soils at our UNE sites can be up to 1.8 and 0.71 °C warmer at the forest edge than the interior during the mid-growing season daytime for rural and urban soils, respectively (Garvey et al., 2022). Mean annual temperature can significantly affect resource-specific activity of CBH and NAG (Sinsabaugh et al., 2008). To address edge temperature dynamics not captured in our laboratory design, we
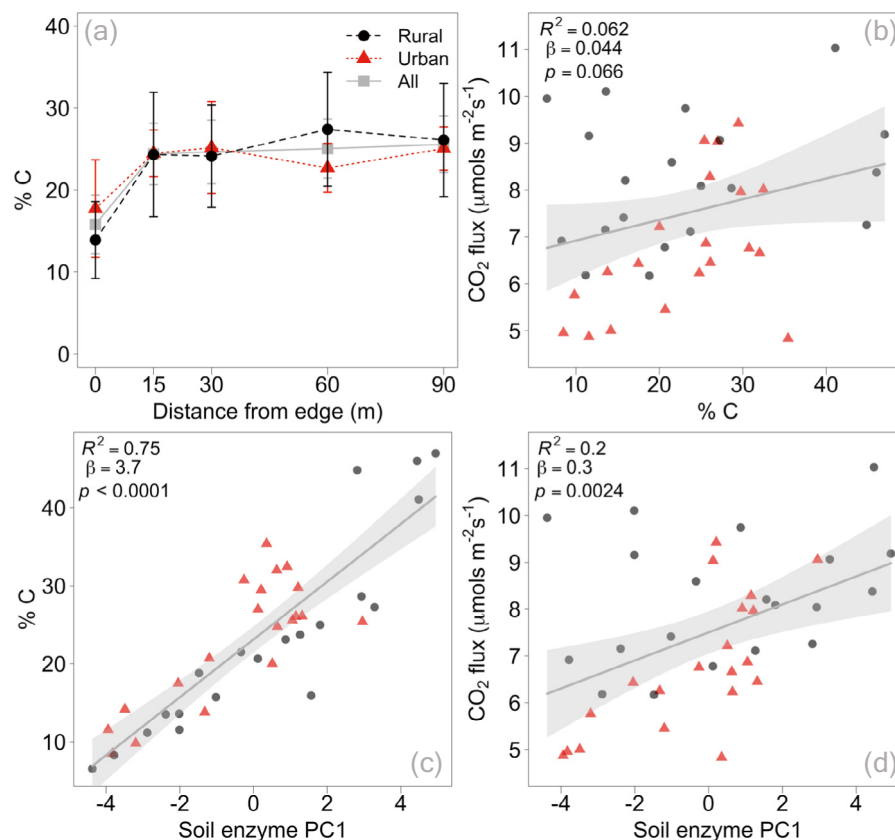

Fig. 3. Mean organic horizon soil % C (a) as a function of distance from the forest edge for all UNE field sites (grey), urban sites only (red), and rural sites only (black). Error bars represent standard error. Panels (b) – (d) show regressions between mean soil respiration flux and organic horizon soil % C (b), soil % C and soil enzyme PC1 (c) and soil respiration and soil enzyme PC1 (d); urban data points are shown in red and rural in black, and the grey line reflects the line of best fit for all data with 95 % confidence interval. Adjusted R^2, β (slope), and p-values are provided for each linear regression.

additionally assayed BG, AP, NAG, PPO and PER at a range of temperatures from 16 to 25 °C for a small subset of samples (Fig. S4). We found that changes in temperature generally did not affect the direction of trends in EEA from forest edge to interior, though it did affect the magnitude of change (activity tended to increase with incubation temperature, but this difference was not significant across enzymes; $p > 0.1$). This limited analysis suggests that we were able to capture EEA dynamics in the laboratory temperature-controlled environment, and though variance in field soil temperatures from forest edge to interior likely plays a key role in *in situ* enzymatic activity, we do not expect that accounting for these temperature differences would allow EEA to better explain trends in respiration at the forest edge.

Synthesizing observed trends in soil respiration flux, EEA, % C and % SOM, we find that EEA per g soil tracks primary growth resources (*i.e.*, % C and SOM) from edge to interior at UNE sites, but overall soil community metabolism (*i.e.*, CO_2 efflux) generally does not. Resource-specific enzyme activity (Fig. S2 inset) suggests that in rural systems, C substrates at the forest edge may experience heavier decay activity because soil microbes are starved for resources. While SOM at the forest edge was comparably low in urban and rural systems, urban edge microbial activity may be further hampered by additional stressors associated with human activity and development. These combined results may suggest a slowing of soil C cycling at the urban temperate forest edge.

3.2. Soil composition: forest edge to interior trends and legacies of human management

3.2.1. Decreases in soil acidity at the edge

Soil pH was significantly elevated at the forest edge relative to the forest interior across forest edge sites (Fig. 4a; Caron et al., 2023) but was not significantly different for urban and rural sites ($p > 0.5$) despite opposing trends in edge soil respiration. Across all eight sites, we found that mean soil pH was 4.96 ± 0.16 at 0 m from the forest edge and fell to 4.05 ± 0.1 in the forest interior ($p < 0.0001$). Controls on soil C accumulation differ with pH (Malik et al., 2018), suggesting that soil C pools and accumulation pathways at the forest edge may reflect trends in soil pH. In lime-addition experiments, increases in soil pH are associated with increases in soil C accumulation, corresponding with decreases in basal respiration (Melvin et al., 2013; Sridhar et al., 2022; Taylor et al., 2021). However, a meta-analysis of acid addition experiments in soils found decreasing soil pH was also associated with decreases in soil respiration, root biomass, and microbial biomass C (Meng et al., 2019), making it difficult to predict how the changes in soil pH near the forest edge we report ultimately influence soil C cycling.

Critically, soil acidity is a significant control on activity of soil extracellular enzymes (German et al., 2011), adding additional nuance to the interpretation of EEA observations at our forest edge sites. Similar to soil temperature, all EEA assays were conducted at a consistent pH for comparability across transects (pH 6.8 for LAP, pH 4.8 for all others). Wang et al. (2012) found that the pH optimum for cellulolytic enzymes like CBH and BG was 5.3 ± 0.9 (for ligninases, 4.2 ± 0.9), and deviation from the pH optimum significantly reduces potential activity per g soil. Soil pH was significantly higher at the forest edge compared to the interior, suggesting that differences in *in situ* EEA between edge and interior may be even more variable than those found in controlled lab experiments. To better understand decomposition dynamics in fragmented forests, future assays of EEA should include an explicit accounting of the substantial differences in soil pH, as well as temperature, from forest edge to interior. Disentangling the individual effects of soil acidity, temperature, and EEA may be further explored through additional measurements of the soil microbial community and its function at forest edges (*e.g.*, microbial community composition and genomic sequencing).
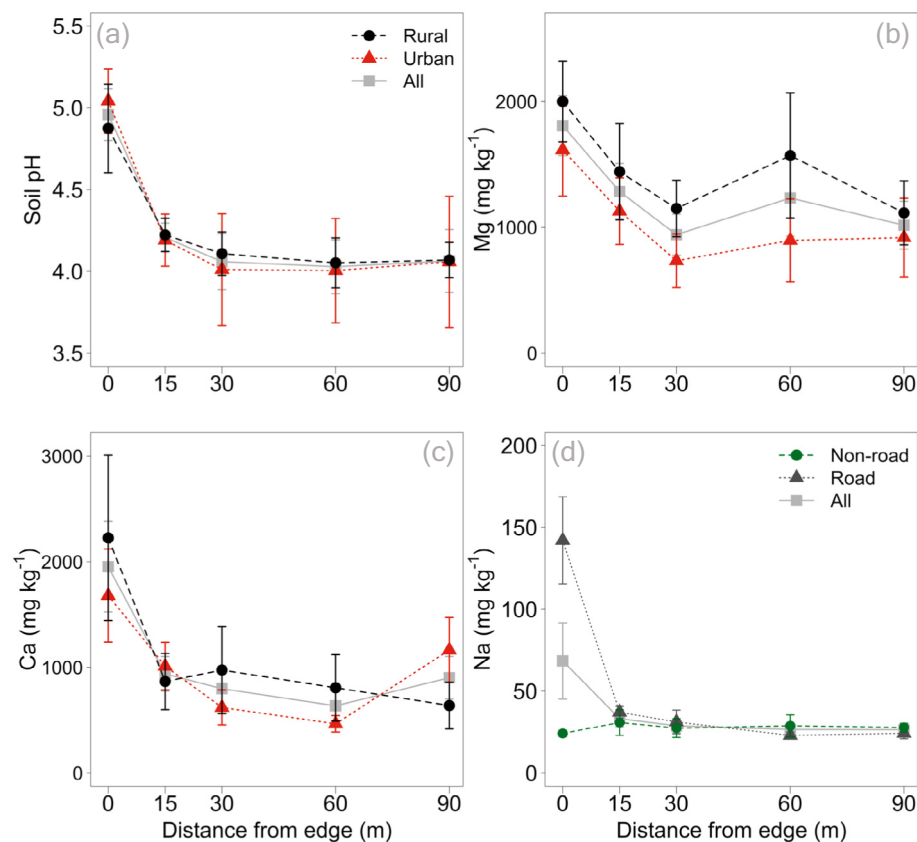

Fig. 4. Mean organic horizon soil pH (a), Mg (b; mg kg^{-1} soil), Ca (c; mg kg^{-1}), and Na (d; mg kg^{-1}) content as a function of distance from the forest edge. Mean values for all UNE field sites are in light grey. Panels (a) – (c) additionally show mean values for urban sites only (red), and rural sites only (black); and panel (d) shows mean values for roadside (dark grey) and non-road edges (green). Error bars represent standard error.

3.2.2. Drivers of soil pH at the forest edge

While other studies have found increases in soil pH at the forest edge (Honnay et al., 2002; Remy et al., 2017), a consistent explanation for the observed pH changes from forest edge to interior is lacking. Some studies suggest that increases in pH may be attributable to grassy encroachment at the forest edge (Malmivaara-Lämsä et al., 2008), but we observed increases in soil pH even at forest edges that do not have grass or shrub belts. Soil pH is also sensitive to other soil inputs such as atmospheric deposition of cations and N, tree stemflow, and fertilizers, all of which have been shown to be elevated at the forest edge (Shiklomanov and Levia, 2014; Weathers et al., 2001; Wuyts et al., 2013).

We posit that the increases we observed in soil pH at forest edges are underpinned by increased rates of cation deposition at the forest edge as reported in other studies (Kupka et al., 2021; Wuyts et al., 2013). We observed increases in soil Ca, Mg and Na concentrations at forest edges compared to the interior, thus supporting the potential link between soil pH and cation inputs (Fig. 4). Across all UNE forest edge sites, we found that total mean soil Mg content was 1809 ± 237 mg Mg kg^{-1} at the forest edge, compared to 1065 ± 128 mg Mg kg^{-1} in the forest interior (p = 0.0077). While Mg concentrations were slightly higher along rural transects than urban, this difference was not statistically significant (p = 0.066). We additionally found that soil Ca content was 1953.6 ± 428 mg Ca kg^{-1} at the forest edge compared to 778.9 ± 109 mg Ca kg^{-1} in the interior (p = 0.00061), and urban and rural sites were not significantly different from one another (p > 0.6).

Changes in surface roughness as non-forested land transitions to forest can lead to increases in atmospheric inputs, including Ca and Mg influxes, near the edge (Devlaeminck et al., 2005; Remy et al., 2016; Weathers et al., 2001); and relative amounts of atmospheric inputs likely vary with the intensity of surrounding human development and emissions, as well as with the size of the open patch bordering the forest edge. A study of

edge tree stemflow chemistry found higher pH and greater acid neutralization capacity compared to that of interior trees (Shiklomanov and Levia, 2014). Changes in stemflow neutralization capacity and elevated rates of atmospheric deposition near the forest edge likely contribute to increases in edge soil Ca and Mg concentrations at our study sites and have consequential effects on soil pH values. Differences in soil Ca and Mg values across urban and rural sites may also be due to differences in edge leaf area previously observed in our study region (Reinmann et al., 2020). Edge soil Ca concentrations may be further affected by historical adjacent land-use of limestone for development or agriculture (Sridhar et al., 2022), though we are not aware of previous limestone use at the UNE field sites. Finally, changes in soil pH from forest edge to interior may also be affected by trends in acidic deposition or other N inputs (Weathers et al., 2001; Wuyts et al., 2013), but these inputs would be expected to decrease soil pH and therefore would not explain the observed decreases in soil acidity at the forest edge (Påhlsson and Bergkvist, 1995). While we could not precisely attribute the increases in Ca and Mg to more specific drivers, it is critical for future studies to investigate potential sources.

UNE roadside edges have significantly elevated concentrations of Na near the forest edge (0 m: 142.1 ± 26.6 mg Na kg^{-1}, 30–90 m: 26.2 ± 2.7 mg kg^{-1}, p < 0.0001) (Fig. 4d). This suggests that forest edge soils immediately abutting roads in our study area have an additional, unique cation source: Na from road salt. Road edge Na concentrations were also significantly different from edge values at the five non-road edge sites (0 m: 24.3 ± 1.9 mg/kg; p < 0.0001). In addition to Mg and Ca, elevated Na concentrations also play a role in determining edge soil acidity, and a simple linear model of soil pH as predicted by (soil [Mg] + [Ca] + [Na]) performed well (adj R^2 = 0.37, p < 0.0001). Rock salt, or sodium chloride (NaCl), is one of the most common de-icing materials used in MA (VHB, 2022), and previous investigations of roadside forest edge soils connected
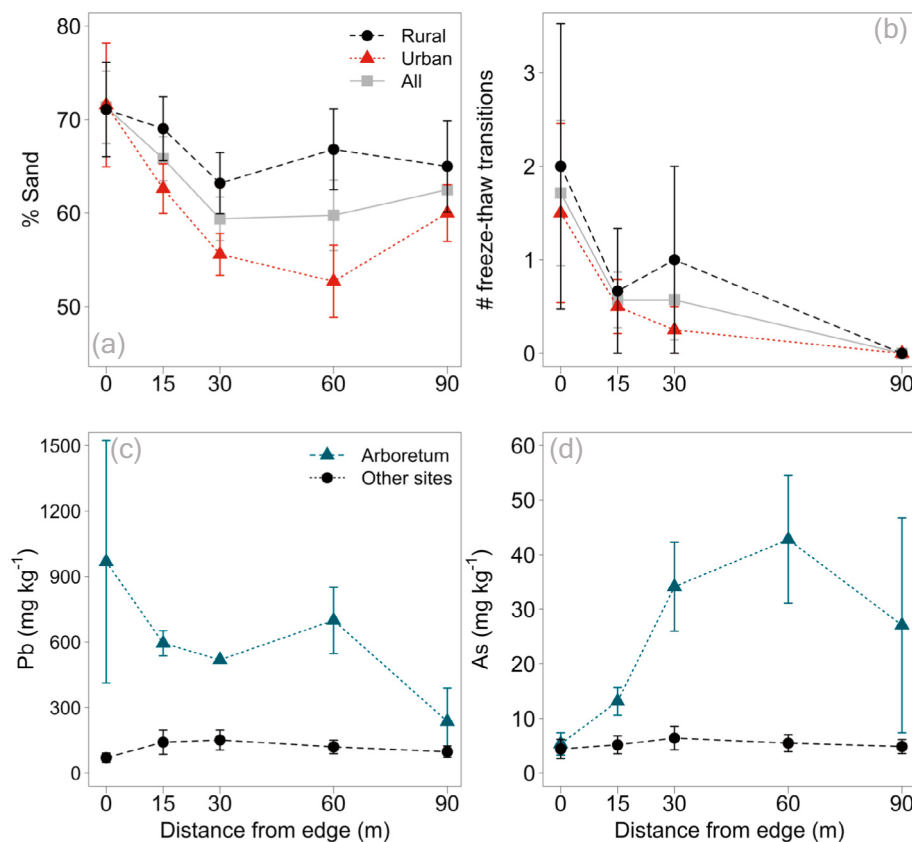

Fig. 5. Mean mineral horizon sand percentage (a; %), number of 24 h freeze-thaw cycles from July 6, 2018 to November 22, 2019 (b), and mean organic horizon soil Pb (c; mg kg^{-1} soil) and As (d; mg kg^{-1}) content as a function of distance from the forest edge. Panels (a) – (b) show for all UNE field sites (grey), urban sites only (red), and rural sites only (black). Panels (c) – (d) show the arboretum site (cyan) compared to the 7 other UNE sites (black). Error bars represent standard error.

increases in edge soil pH to increases in Na concentrations resulting from road salt (Bryson and Barker, 2002; Kupka et al., 2021). We note that while Na levels at roadside edges indicate a cumulative effect of road salt application, we did not see a corresponding increase in soil electrical conductivity at the edge, a measure of soil soluble salt content (Fig. 2; Caron et al. (2023)). However, soil conductivity measurements were made in mid-summer and may have been diluted by runoff expected at forest edges adjacent to pavement. Soils with high levels of soluble salts typically show decreases in soil respiration and soil microbial biomass (Rath and Rousk, 2015).

3.2.3. Local behavior, local impacts: soil texture, lead & arsenic

Human activities can significantly modify the forest edge by altering soil texture (Herrmann et al., 2020), as well as through heavy metal inputs *via* local pollution and pesticide use. We found that mineral horizon soil sand content tended to be elevated at the forest edge relative to the interior across UNE sites (0 m: 71.3 ± 3.9 %, 30–90 m: 60.5 ± 1.7 %; $p = 0.0064$). This edge-to-interior trend was particularly pronounced for urban forests (Fig. 5a), and elevated edge sand content may be driven by sand import or other adjacent development, winter road treatments, and disturbance activity. Sandy soils are highly porous and tend to be associated with low fertility (Yost and Hartemink, 2019), and sandier soils at the forest edge could influence edge-to-interior trends in aboveground plant growth. Soil % sand may help explain declines in edge soil C storage, particularly for forest edges in urban areas that are also highly susceptible to heat stress (Reinmann and Hutyra, 2017), and we find that though % sand is not a significant predictor of soil respiration rate, it is significantly negatively correlated with soil % C (Table 1).

We also predicted that declines in soil respiration at urban forest edges would be related to heavy metal pollution in urban areas due to the stress

Table 1

Soil respiration rate (a) and organic horizon soil % C (b) regression modeling ($n = 40$). Single linear regressions of soil respiration rate and soil % C with other soil measurements (*e.g.*, temperature, moisture, pH) were conducted, and significant models ($p < 0.05$) are shown. Bold type denotes best model fit resulting from stepwise AIC approach. *DFE* refers to distance from the forest edge (m) as a continuous variable, and *urbanization class* indicates urban or rural. See Table S2 for full list of variables, fitted model parameters, and complete regression results.

Model predictors	Model p value	Adjusted R^2	AICc
a) Respiration			
pH	0.01	0.13	149.07
% SOM	0.04	0.079	151.23
[Pb]	0.05	0.076	151.35
Soil enzyme PC1	0.002	0.20	145.76
Temperature + VWC + pH + [Ca] + [Na] + [Mg] + [Pb]	**0.0002**	**0.46**	**139.64**
Urbanization class	0.002	0.20	145.8
DFE	0.1	0.04	152.84
DFE + urbanization class	0.002	0.24	144.74
DFE * urbanization class	0.001	0.30	143.27
Temperature + VWC	0.2	0.037	154.43
Temperature * VWC	0.3	0.018	156.74
b) Soil % C			
Temperature	0.04	0.09	302.66
pH	0.0001	0.30	291.55
% SOM	<0.0001	0.69	259.16
% Sand	0.01	0.14	300.09
[Mg]	<0.0001	0.47	280.61
Soluble salt content	<0.0001	0.42	284.15
Soil enzyme PC1	<0.0001	0.75	250.71
Temperature + soil enzyme PC1 + [Na] + soluble salt content	**<0.0001**	**0.86**	**231.59**
Urbanization class	0.96	−0.026	307.05
DFE	0.1	0.034	304.61
DFE + urbanization class	0.3	0.0085	307.08
DFE * urbanization class	0.5	−0.0095	309.33
Temperature + VWC	0.12	0.061	304.92
Temperature * VWC	0.21	0.0429	307.20

metals pose for soil microbes (Pan and Yu, 2011) and aboveground plant communities (Kushwaha et al., 2018). We specifically anticipated elevated soil Pb concentrations at roadside forest edges due to historical leaded gasoline combustion by vehicles. However, our results show that soil Pb concentration explained little variance in soil respiration flux and % soil C despite the differences we found across sites (Tables 1, S2), and only one UNE field site (an arboretum) had significant edge-to-interior trends in soil Pb (Fig. 5). At the arboretum, mean soil Pb concentration was 603.3 ± 119 mg kg^{-1}, which was more than five times greater than the mean soil Pb concentration of the other seven UNE sites (116.2 ± 16.7 mg Pb kg^{-1}; $p = 0.0018$) and considerably elevated compared to mean background levels in MA (72.2 ± 20.6 mg kg^{-1}, US EPA, 2016). Soil Pb concentrations at the arboretum site were variable from edge to interior, and the value at 90 m was significantly lower than values closer to the edge (90 m *vs* 60 m, $p = 0.071$; 90 m *vs* 0 m, $p = 0.00056$). At the other seven field sites, soil Pb concentration did not vary significantly different from edge to interior ($p > 0.5$).

We posit that the elevated Pb concentrations at the arboretum are attributable to past application of lead arsenate (PbHAsO₄) in the proximate area. Lead arsenate was a popular pesticide used in tree fruit orchards up until the late 1950s, leaving behind heavily contaminated soils (Peryea and Creger, 1994; Yokel and Delistraty, 2003). The arboretum land was formerly home to orchards and gardening (Wilson, 2006), and the land surrounding the UNE study area was likely affected by state-mandated spraying for spongy moth that occurred in the early 20th century (Mcmanus and Csóka, 2007; D. Schissler, personal communication, August 19, 2022; *Special Report of the State Board of Agriculture on the Work of Extermination of the Ocneria Dispar Or Gypsy Moth. Acts of 1891, Chapter 210*, 1892). This is further supported by our soil As data. Similar to Pb, the arboretum was the only site with elevated soil As concentrations, with a mean value of 24.5 ± 6.8 mg As kg^{-1}, and concentrations varied significantly from edge to interior (0 m *vs*. 30–90 m: $p < 0.0001$) (Fig. 5). The opposing trends in Pb and As from edge to interior may be due to Pb immobilization and subsequent As leaching at the forest edge (Kalbasi et al., 1995). The mean As concentration for all other sites was significantly lower at 5.27 ± 0.72 mg As kg^{-1} ($p < 0.0001$) and did not vary from edge to interior ($p > 0.5$).

Pb in soils causes severe stress for the microbial community and plants, as well as poses a potential danger to human populations at high concentrations (Yokel and Delistraty, 2003). For the soil microbial community, elevated soil Pb is toxic and can cause enzyme inhibition and decreases in soil respiration (Doelman and Haanstra, 1979; Pan and Yu, 2011). However, the effect of Pb on soil and plant communities is highly dependent on pH. At more acidic (lower) pH values, Pb tends to be both more mobile and bioavailable, affecting its uptake by living organisms (Kushwaha et al., 2018; Martínez and Motto, 2000). Therefore, Pb toxicity at the arboretum may be tempered by increases in soil pH at the forest edge, though not in the forest interior. As also introduces toxicity stress to the soil community and has been associated with decreases in microbial biomass C and N and inhibition of enzyme activity (De Francisco et al., 2021; Ghosh et al., 2004). The elevated concentrations of these elements in arboretum soils are likely a legacy of previous land-use that likely continues to affect soil activity decades later, even in such disturbed systems as urban forest fragments; and these findings emphasize the heterogeneity of forest edges across the landscape.

3.3. Elevated soil freeze-thaw frequency at forest edges & its ramifications

We found that forest fragmentation leads to greater frequency of soil freezing and soil freeze/thaw cycles relative to the forest interior, likely due to lateral exposure and differences in vegetative cover at the forest edge and interior (Figs. 2, 5b). Using continuously-logged data from July 6, 2018 to November 22, 2019, we observed that soils at the forest edge on average spent 5 ± 2.4 days frozen and experienced 1.7 ± 0.8 freeze-thaw cycles, while soils 90 m into the forest interior never experienced mean 24 h temperatures below −0.5 °C (0 m *vs* 30–90 m freeze-thaw:

$p = 0.033$; days frozen: $p = 0.01$). Neither freeze-thaw frequency nor total days frozen were affected by urbanization class or adjacent landcover ($p < 0.4$). Soil freezing is known to increase in depth and duration when snowpack decreases (Hardy et al., 2001), but snow dynamics were not assessed at UNE sites. Forest edges adjacent to plowed roads may experience increased snow depth (depending on de-icing salt use) and therefore decreased soil freezing, though this was not supported by our findings and further investigation of winter dynamics at forest edges is needed.

Observed increases in soil freeze-thaw frequency at the forest edge compared to the forest interior regardless of urbanization class likely have implications for root turnover and decomposition (Song et al., 2017). Soil freeze-thaw cycles damage roots and reduce their ability to take up nutrients (Cleavitt et al., 2008; Sanders-DeMott et al., 2018), promote fine root turnover (Song et al., 2017), and reduce both microbial biomass and enzymatic activity (Sorensen et al., 2018). Edge root turnover dynamics are likely further affected by aboveground plant species, as well as summer edge temperatures, both of which can influence root lifespan (Chen and Brassard, 2013). Increases in soil freeze-thaw frequency at the forest edge may elevate root turnover rates at the edge where they could provide an alternative energy source for edge soil microbes, but it is critical to note that the effect of decaying (but not yet decomposed) roots would not be captured in most soil lab metrics, as like our approach most pass samples through a 2 mm sieve that excludes roots that are not fully decomposed (Soil Survey Staff, 2014). Some investigations suggest that root biomass does not change significantly from the forest edge to interior (Reinmann and Hutyra, 2017), and we theorize that given the lack of trees on the non-forested side of the edge, this would suggest greater root density per unit tree basal area at the edge, though root biomass and turnover rates at the forest edge have yet to be directly investigated. Soil freeze-thaw events are likely to increase in frequency with future global change as snow pack is lost in northern latitudes (Reinmann et al., 2019), which may further exacerbate the divergence in soil conditions from forest edge to interior.

3.4. Linking soil properties to C dynamics

Manifold differences in forest edge-to-interior conditions that are mediated by adjacent land-use necessitate a multifaceted investigation quantifying the relationships between soil C dynamics and their potential drivers. We found that soil enzyme PC1 and % SOM were significant positive predictors of mean mid-growing season soil respiration rate, while soil pH and soil [Pb] were significant negative predictors (Table 1, Fig. S3). Individual predictors explained relatively little variation in mean soil respiration rate, and soil enzyme PC1 and soil pH offered the most explanatory power (soil enzyme PC1 adj $R^2 = 0.2$; pH adj $R^2 = 0.13$). Significant positive predictors for soil % C included % SOM, soil enzyme PC1, mean soil temperature, and soluble salt content, and significant negative predictors included soil pH, [Mg] and % sand (Table 1, Fig. S3). Resulting regression models for soil % C often had greater explanatory power than those for soil respiration rates; and soil enzyme PC1, % SOM and [Mg] respectively explained up to 75 %, 69 %, and 47 % of the observed variance in soil % C.

Using a stepwise regression model selection framework, respiration was best predicted by soil temperature, VWC, pH, [Ca], [Na], [Mg], and [Pb] (adj $R^2 = 0.46$). For soil % C, stepwise selection resulted in a model with soil temperature, % SOM, [Ca], [Na] and soil enzyme PC1 as predictors (adj $R^2 = 0.89$; Table S2). We note that due to collinearity between SOM and soil % C, we investigated model fit excluding % SOM and found minimal impacts on model performance. Soil temperature, [Na], soluble salt content and soil enzyme PC1 were ultimately selected as predictors of % C (adj $R^2 = 0.86$). Final models were also compared with: 1) individual, additive, and multiplicative models using distance from the edge and urbanization class as predictors, 2) additive and multiplicative models using both temperature and VWC. We found that for both soil respiration and soil % C, the models created through stepwise selection perform significantly better than all others by metrics of both parsimony and explanatory power (Tables 1, S2).

While most models for soil dynamics are strongly driven by soil temperature and moisture, our results underscore that these factors alone are insufficient to explain the observed trends in soil C cycling at the forest edge. Furthermore, by far outperforming more simplistic models that lack quantifiable soil attributes, models of explicit soil properties demonstrate that moving beyond qualitative classifications like 'urban' and 'rural' is both possible and necessary to understand soil C dynamics at the forest edge. We found that direct consequences of nearby human land management (*e.g.*, soluble salt content, [Na], [Pb]) have significant effects on soil CO_2 efflux and soil % C. Inclusion of soil enzyme PC1 suggests further perturbations to the soil microbiome that contribute to decreases in soil % C at the edge. In conjunction with low correlation between soil respiration and soil % C, differences in both single-predictor significance and stepwise model selection suggest a decoupling between soil C fluxes and the soil C pool that is absent from our current understanding of the effects of global change.

4. Conclusions & future directions

Given widespread acknowledgement of the importance of soils in global carbon cycling and ecosystem health, it is imperative to understand forest edge effects on belowground processes. The inherent complexity of forest edges is amplified by the widely varying influence of abutting human activity and land management, but these confounded systems have largely been avoided until recently. The range of forest edges characterized through the UNE project expose a wide spectrum of soil conditions and activity. We demonstrate that forest fragmentation and urbanization effects on soil C cycling go beyond elevated soil temperatures and dryness at the forest edge. Increases in edge soil pH, metal and cation concentrations and sand content, alongside distinct decreases in edge soil % C and % SOM, have cascading effects on soil activity, thus supporting our initial hypothesis. Our collective findings suggest that soil C cycling is slowed at the urban forest edge and underscore the link between edge soil properties and soil C cycling. Soil enzyme activity, % SOM and pH were significant predictors of both soil respiration and % C, and our investigations revealed that in addition to temperature, other conditions mediated by human activity (*e.g.*, Pb and cation levels, soluble salt content) can further explain observed soil C dynamics at temperate forest edges. While our field campaign spanned a distance of 100 km, forest fragmentation is ubiquitous and urbanization continues to drive land-use change worldwide. We expect that our findings about the influence of adjacent land use on forest edge soil C dynamics are relevant throughout the fragmented, urbanized forest landscapes of the temperate forest biome.

Substantial knowledge gaps remain regarding the link between fragmented forests above- and belowground, including the role of roots (*e.g.*, sugar concentrations, biomass, turnover rates), tree and understory species composition, and increases in aboveground biomass at the temperate forest edge. Quantifying the resulting differences in root distribution, litter dynamics, mycorrhizal fungal associations, and soil C inputs will be key in further elucidating soil dynamics at the forest edge. Trees at the edge have also been shown to be at increased risk of heat stress associated with climate change (Reinmann and Hutyra, 2017), and coupled with increased vulnerability due to lateral exposure and more frequent freeze-thaw cycling, this suggests that soil communities and properties at the forest edge may play an outsized role in future forest edge resiliency.

In addition to continued study of forest edges *in situ* across urbanization and other gradients, there is a clear need to investigate the connection between forest edges and global change manipulation experiments. Specifically, there is a need for controlled manipulation experiments that address multiple manipulations/global change drivers simultaneously. The complex, and sometimes synergistic, interactions of simultaneous stressors (Rillig et al., 2019) make it difficult to assess how multidimensional global change drivers at the forest edge are affecting soils and their C stores across contexts, biomes and time. Urban expansion is a pivotal driver of present forest fragmentation, and by 2030, urban land cover is projected to nearly triple compared to global urban land area

circa 2000 (Seto et al., 2012). Forest edge conditions are increasingly prevalent across the landscape, and failure to account for unique soil activity at the edge leads to critical errors in our understanding of C and other biogeochemical cycling (Garvey et al., 2022). Soils at the forest edge record the legacy of adjacent and historical land-use in ways that we are only beginning to understand. Future efforts to model soil and forest C dynamics must acknowledge altered soil carbon fluxes and dynamics at the forest edge. These collected findings highlight the ongoing challenges in characterizing decomposition and other soil dynamics, as well as their drivers, in these fragmented and confounded systems.

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CRediT authorship contribution statement

Sarah M. Garvey: Conceptualization, Methodology, Investigation, Data curation, Funding acquisition, Writing – original draft, Visualization. **Pamela H. Templer:** Conceptualization, Methodology, Resources, Funding acquisition. **Jennifer M. Bhatnagar:** Conceptualization, Methodology, Resources. **Lucy R. Hutyra:** Conceptualization, Methodology, Resources, Funding acquisition.

Data availability

Data available on request from the authors and is being processed for archival at the Harvard Forest LTER data archive.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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