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RESEARCH

Heat vulnerability and leaf traits affect litter decomposition across an urban heat island in Philadelphia, Pennsylvania

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Abstract

Urbanization is rapidly transforming ecosystem processes by altering environmental conditions, including increasing temperatures due to the Urban Heat Island (UHI) effect. Changes in environmental conditions, such as temperature, may alter the rates of critical ecosystem processes and functions, including the decomposition of leaf litter. Additionally, variability in leaf litter quality may interact with changing environmental conditions, further altering rates of leaf litter decay across urban landscapes. Thus, we used a gradient of heat vulnerability (a proxy for the UHI) across the city of Philadelphia, PA, USA to evaluate how urbanization and leaf litter quality may affect leaf litter decomposition rates. Specifically, at four sites ranging in their heat vulnerability index, we deployed tea bags (i.e., green and rooibos) and natural leaf litter bags containing either *Gingko biloba* (hereafter, gingko), *Liquidambar styraciflua* (hereafter, sweetgum), *Platanus occidentalis* (hereafter, sycamore) or *Quercus rubra* (hereafter, red oak). Heat vulnerability and leaf litter species both affected the rate of leaf litter decomposition. Specifically, as site heat vulnerability increases natural leaf litter decomposition decreases; however, tea bag decomposition was unaffected by site heat vulnerability. Additionally, natural leaf litter species decompose at different rates, with species having more labile compounds (i.e., gingko and sweetgum) decomposing faster than species having more recalcitrant compounds (i.e., sycamore and red oak). Overall, our findings contribute to the growing discussion regarding the effects of urbanization on ecosystem processes and highlight the complexity of predicting decomposition processes in altered landscapes.

Keywords Anthropogenic effects · Functional traits · Litter quality · Nutrient cycling · Urban ecology · Urbanization

Introduction

Increased urbanization is driving critical environmental changes across landscapes worldwide (Grimm et al. 2008; Kowarik 2011; De Pauw et al. 2024). For instance, vegetation and tree canopy cover often decrease (Berland 2012), while the prevalence of heat-retaining impervious surfaces and heat producing human activities (e.g., power generation and use) increase in urbanized landscapes (Schueler 1994; Morse et al. 2003; Rizwan et al. 2008; Yan et al. 2019). Such changes cumulatively impact the local climate of cities through phenomena like the urban heat island effect (UHI; Kim 1992; Rizwan et al. 2008; Kim and Brown 2021), which occurs when cities have elevated temperatures and heat vulnerability (i.e., a categorical index of susceptibility to extreme heat) relative to the rural and natural areas surrounding them (Tam et al. 2015; Abrar et al. 2022). Thus, understanding the environmental consequences of urbanization is a major priority for preserving and maintaining resilient ecosystems.

Regional climatic conditions, including those associated with the UHI effect (e.g., temperature), can have important consequences for biotic and abiotic processes across landscapes, including ecosystem services like organic matter decomposition (Kroeze et al. 2013; Lin et al. 2014; De Pauw et al. 2024). For example, elevated soil temperatures

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accelerated the rate of pine needle (*Pinus sylvestris L.)* decomposition over a 1-year period (Domisch et al. 2006). Additionally, increased UV exposure can cause substantial litter mass loss through mechanisms like photodegradation, the direct breakdown of litter by UV and shortwave radiation (Hussain et al. 2023). Currently, there is limited understanding of how urbanization might mediate UV exposure, but the UHI is defined by the explicit difference in surface- and air temperature between rural and urban sites (Tam et al. 2015; Abrar et al. 2022). The elevated temperatures associated with the UHI could increase decomposition rates and variability relative to surrounding, non-urbanized, systems (Pouyat et al. 1997; Santonja et al. 2015). However, studies assessing decomposition in urban landscapes often present contradictory, and extremely variable, effects on decomposition rates (Dorendorf et al. 2015). For instance, studies in European cities (De Pauw et al. 2024), and New York City (Pouyat et al. 1997; Pouyat and Carreiro 2003), support predictions that decomposition should be elevated in urban ecosystems, while other studies suggest that urbanization can decrease decomposition rates (Pavao-Zuckerman and Coleman 2005; Meyer et al. 2020). These inconsistencies across urban decomposition studies may be attributed to multiple factors, including substrate quality (e.g., labile versus recalcitrant), the use of decomposition proxies (e.g., tea bag, corn husk, and cotton strip decomposition), and variability in abiotic conditions.

It is well established that litter quality (i.e., the variability in substrate chemical composition) can influence decomposition rates directly, by altering the availability of labile carbon, and indirectly, by influencing catabolic capacities of microbial communities (Berg et al. 1993; Aerts 1997; Gholz et al. 2000; Wang et al. 2008; Berg and McClaugherty 2020; Bourget et al. 2023). Generally, labile materials such as cellulose, hemicellulose, and soluble compounds are decomposed by fast-growing opportunistic microbes (Cortez et al. 2007; Chomel et al. 2016). Low-molecular weight phenolics like flavonoids and terpenoids also tend to be more soluble and metabolized early in the decomposition process, while more complex phenolics like tannins slow decomposition rates (Kuiters 1990; Loranger et al. 2002; Chomel et al. 2014). Similarly, leaf structural components (e.g., leaf dry matter content (LDMC), which quantifies the non-labile compounds relative to total leaf mass) is often negatively correlated with decomposition rates, especially when tannin concentrations are also high (Chomel et al. 2016; Pérez-Harguindeguy et al. 2000). For example, lignin constitutes a significant structural barrier to enzymatic degradation and tends to be decomposed after labile sources have been fully exploited (Austin and Ballaré 2010; Rahman et al. 2013; Chomel et al. 2014). At the stoichiometric level, litter with lower carbon (C): nitrogen (N) ratios tends to be more labile, and thus more easily metabolized by decomposer communities, than litter with higher C: N ratios (Pérez-Harguindeguy et al. 2000; Wang et al. 2008). These chemical properties result in distinct functional grouping of litter quality, specifically fast-decomposing (labile) and slow-decomposing (recalcitrant) litter groups (Gholz et al. 2000). Labile litter decay relates strongly to microbial activity, while abiotic conditions drive the early breakdown of recalcitrant litter material (Almagro and Martínez-Mena 2012). Thus, it is important to consider how leaf litter quality may influence decomposition rates across urban systems.

Many studies of litter decomposition across ecosystems, including urban ecosystems, have relied on proxies such as tea bag (Tresch et al. 2018; Marley et al. 2019; Mori et al. 2023; De Pauw et al. 2024), corn husk (Tresch et al. 2019), or cotton strip decomposition (Técher et al. 2024). While these approaches can provide standardized decomposition rates, they may not accurately capture the natural rates of decomposition and their variability. For example, tea and leaf litter may respond differently to changes in precipitation and soil moisture due to (1) tea's extremely high concentrations of water-soluble compounds and associated leaching processes (Blume-Werry et al. 2021), (2) tea bags retaining more moisture than the mesh used to construct larger litter bags, and (3) tea bags restricting mesofauna access. Although tea bag decay rates often respond relatively similarly to abiotic conditions when compared to natural litter species, absolute rates can differ substantially (Didion et al. 2016). For example, while rooibos tea decayed significantly slower than *P. nigra* natural litter, both substrates showed increased decay rates with increasing temperature and decreased decay rates with increasing precipitation (Didion et al. 2016). While studies have been successful in identifying site-level effects across urban-rural gradients using tea bags only (De Pauw et al. 2024), there have been few attempts to compare substrate decay rates across urban gradients. Thus, utilizing both types of substrates allows us to compare the relative decomposition rates of these substrates, while contributing to a global, standardized tea bag decomposition dataset and obtaining ecologically relevant rates of litter decay.

Here, we evaluated the combined effects of heat vulnerability (i.e., a proxy for extreme temperatures), litter quality (i.e., labile versus recalcitrant), and methodological approach on litter decomposition across an urban heat island in Philadelphia, PA. Since the UHI is explicitly defined by temperature, we collected surface temperature data to assess heat vulnerability across our sites to validate the urban heat gradient. We anticipated that increasing temperatures and

heat vulnerability would increase decomposition rates and variability for all substrates, with labile substrates decomposing faster than recalcitrant substrates. We also expected tea bags and natural litter to exhibit similar differences in substrate quality and their response to urbanization, but that natural litter would have higher absolute rates of mass loss than tea bags.

Methods

Site descriptions

To evaluate the relative effects of urbanization on leaf litter decomposition, we established four field sites across the Philadelphia urban heat island (UHI). While the city has actively worked to expand urban tree canopy cover (Philadelphia & Recreation 2023), recent mapping efforts have identified distinctive UHIs throughout the city (The Nature Conservancy 2023). We leveraged these maps to identify four sites that represented a gradient in temperature and Heat Vulnerability Index. To further validate this heat gradient, we deployed temperature loggers (HOBO Pendant MX Temperature/Light Data Logger) at each site for the duration of the study and compared mean temperature and daily cumulative UV by site (see Fig. 1). Philadelphia is one of the largest cities in the United States, with a metro area spanning 348 km^2 and a population of 1.55 million people. The city is located within a temperate climatic zone with a mean annual temperature of 13.7 °C and mean monthly temperatures ranging from 1.1 °C in January to 26.2 °C in July (GLISA 2025). Precipitation is distributed approximately evenly across the year in Philadelphia, with a mean annual total of 112.1 cm (GLISA 2025).

Bog's Alley (hereafter, BA) is a narrow concrete alleyway with a thin layer of accumulated soil located behind a block of rowhouses in south Philadelphia (39° 55' 56.64" N, 75° 11' 6.36' W). While the site is generally devoid of larger vegetation, there were two large trees of heaven (*Ailanthus altissima*) located within the center of the alley, which attracted numerous invasive spotted lanternflies (*Lycorma delicatula*). BA represents the most extreme levels of urbanization within our study, with the highest mean temperature (23.6 °C), occurrence of non-native species, and accumulation of pollutants (e.g., plastics). Additionally, BA is located within Census Tract 32, which ranks *high* (hottest 20% of tracts) on the Philadelphia Heat Vulnerability Index.

The Summer Winter Community Garden (hereafter, G) is an urban garden located in Powelton Village, just north of Drexel University's campus (39° 57' 32.80" N, 75° 11' 20.60' W). Specifically, we placed our study within a large ~2 m x 1.5 m plot filled with soil that had previously contained vegetables (e.g., celery) and various native and non-native annuals. This plot had limited canopy cover, but a single White Mulberry (*Morus alba*) tree that stood approximately 3 m from the plot and provided some afternoon shade. The G site is located within Census Tract 90, which ranks *very low* on the Philadelphia Heat Vulnerability Index.

Woodland's Cemetery and Arboretum (39° 56' 54.3" N 75° 12' 09.8" W) is a historic cemetery and green space originally built in the 1700's along the west bank of the Schuylkill River just south of the University of Pennsylvania campus. Woodlands (hereafter, W) contains an assortment of native, exotic, and invasive plant species. Specifically, the location we used for this study was covered by orchard grasses (*Dactylis* spp.) and Poverty oat grass (*Danthonia spicata*). Additionally, canopy cover was provided by nearby Norway maple (*Acer platanoides*) and common hackberry (*Celtis occidentalis*) trees. W is located within Census Tract 369, which ranks *very low* on the Philadelphia Heat Vulnerability Index.

Cobb's Creek Park (hereafter, CC) is an 851-acre urban park that features extensive riparian habitat running adjacent to Cobb's Creek on the western border of the Philadelphia metropolitan area. The park contains multiple diverse habitats, including restored freshwater wetlands and forests. Specifically, the location used in our study was in forested riparian habitat approximately 10 m from the bank of Cobb's Creek (39° 57' 07.6" N 75° 15' 05.0" W). The site was covered with natural debris (e.g., sticks and leaves) as well as wildrye (*Elymus* spp.), and American pokeweed (*Phytolacca americana*). Canopy cover was provided by nearby chestnut oak (*Quercus bicolor*) and American sycamore (*Platanus occidentalis*) trees. CC is located within Census Tract 82, which ranks *high* on the Philadelphia Heat Vulnerability Index. Despite this high Heat Vulnerability Index, the interior regions of the park, where we placed the study, create a forested microclimate that likely reduced local heat stress.

Natural leaf litter decomposition bags

To evaluate the effects of heat vulnerability and leaf quality on litter decomposition, we constructed 80 leaf litter bags (5 cm x 5 cm, length x height) using 1 mm mesh. This mesh size allowed for the entry of mesofauna such as mites, nematodes, pot worms, and springtails, as well as juvenile earthworms and millipedes (Swift et al. 1979). All leaves for litter bags were collected in Fall 2023 on Drexel

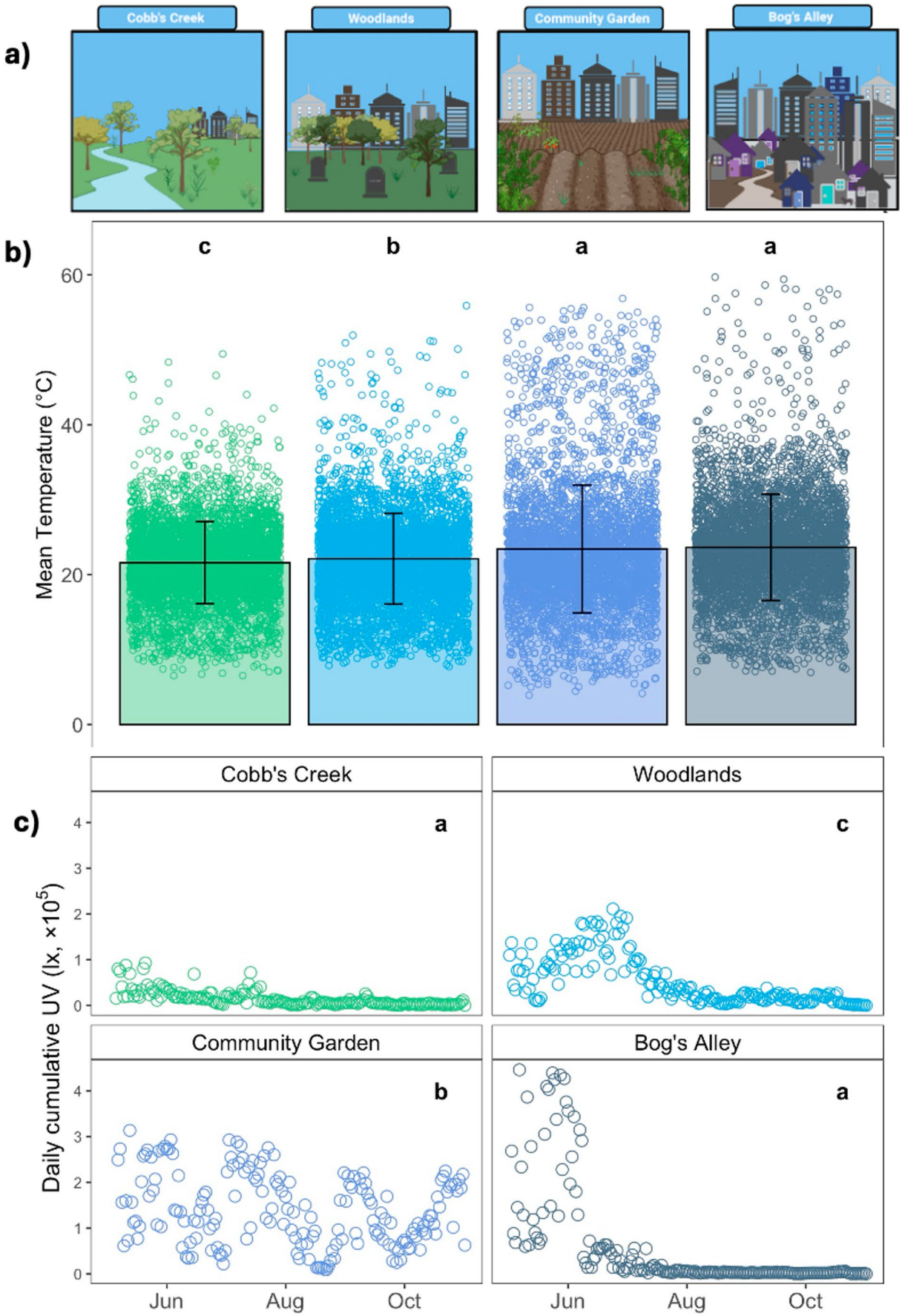

a)
Cobb's Creek
Woodlands
Community Garden
Bog's Alley
b)
c
b
a
a
Mean Temperature (°C)
0
20
40
60
c)
Cobb's Creek
Woodlands
Community Garden
Bog's Alley
a
c
b
a
Daily cumulative UV (lx, ×10^5)
0
1
2
3
4
Jun
Aug
Oct

Fig. 1 (a) Illustration depicting each site used in the incubation experiment (Created in https://BioRender.com, agreement number #: TO28SW6929) **(b)** Bar plots showing the associated mean temperature (°C, across the entire experiment duration) and the standard deviation for each study site. Individual data points (collected hourly) are overlayed. The sites are listed along the x-axis in the following order from left to right: Cobbs Creek, Woodlands, Community Garden, and Bog's Alley. Different letters indicate significant differences between sites as determined by ANOVA and Tukey HSD ($F=90.34$, $df=3$, $p<0.001$) **(c)** Individual time series depicting daily cumulative UV exposure (lux) across the incubation duration. Daily cumulative UV was calculated by summing all hourly UV values ($n=24$) for each day and site. Different letters indicate significant differences between sites as determined by the Kruskal-Wallis test and subsequent pairwise Wilcox tests (BH adjustment, $\chi^2=282.96$, $df=3$, $p<0.001$), chosen due to right-skewed distribution (zero inflated) and unequal variance

University's campus (39° 57' 16.1"N 75° 11' 17.8"W) and in green spaces in northern Philadelphia (40° 5' 37.5"N, 75° 8' 19.4"W and 40° 5' 37.7"N, 75° 8' 1.8"W) and sorted by species before being left to air dry to a constant weight. We focused on four main species: (1) gingko (*Gingko biloba*), (2) sweetgum (*Liquidambar styraciflua*), (3) sycamore (*Platanus occidentalis*), and (4) red oak (*Quercus rubra*). These species display chemical characteristics that can be assigned functionally as either labile-dominant or recalcitrant-dominant, corresponding to distinct decomposition potential (Gholz et al. 2000; Cotrufo et al. 2013). Gingko and sweetgum contain relatively high concentrations of soluble flavonoids, terpenoids, and polysaccharides and lower lignin content, while sycamore and red oak are lignin- and tannin-dominated with a lower proportion of labile compounds (see Table 1). Additionally, their elemental stoichiometry differs, with gingko (53.2 ± 11.4; mean ± SD) and sweetgum (50.9 ± 13.31) having similar carbon to nitrogen (N) ratios, compared to a lower ratio for sycamore (31.0 ± 5.36) and a higher ratio for red oak (80.9 ± 10.82). Therefore, gingko and sweetgum were considered predominantly labile relative to the predominantly recalcitrant structure of sycamore and red oak. These four species also represent a broader community-level shift in street trees through Philadelphia's recent history (LaNoce et al. 2022).

In each litter bag, we added 4 g whole leaves of either gingko, sweetgum, sycamore, or red oak. Leaves were layered and edges gently folded where necessary to fit into litter bags. We deployed five litter bags of each leaf species (i.e., gingko, sweetgum, sycamore, red oak) on the soil surface at each of our four field sites and let them decompose for six months (May – November 2024). Within our sites, we intentionally placed bags on soil patches without surrounding trees matching our litter species to avoid potential confounding effects of home-field advantage (Ayres et al. 2009). When deploying and collecting litter bags, we placed each individual litter bag in its own plastic bag to allow us to account for any potential litter loss that occurred during transport. At the start of the study, we also 'deployed' five handling controls per leaf species at each site to account for impacts of transport and handling during deployment on initial leaf litter biomass and observed minimal biomass loss. Upon collection of all litter bags, we rinsed the remaining leaf litter to remove any soil or debris before drying the litter in the oven at 65 °C to a constant weight. We calculated the mass loss of leaf litter (initial biomass – final biomass) then divided the total mass loss by the total days that the litter bags were deployed to obtain the decay rate (mass loss day^{-1}).

All dried litter (including from handling controls) was ground using electric grinders (Cuisinart® Coffee Grinder, Model no. DCG-20), and then ashed in a muffle furnace (four hours at 550° C) to estimate litter OM via loss-on-ignition (Appendix Fig. S1). Additionally, we analyzed samples for total carbon and total nitrogen content (%) using a Carlo Erba 1112 Flash Elemental Analyzer operated by the Patrick Center for Environmental Research at the Academy of Natural Sciences in Philadelphia (Appendix Fig. S1).

Tea bag decomposition bags

To further evaluate the effects of litter quality on decomposition rates across a gradient of heat vulnerability, we assessed the decay rate of green tea (Lipton Green Tea Sencha) and rooibos tea (Lipton Rooibos Tea) at each of our four sites using a modified version of the Tea Bag Index (TBI; Keuskamp et al. 2013). Specifically, we constructed 48 dual-compartment leaf litter bags (5 cm x 5 cm, length x height) using 1 mm mesh then placed one green tea bag and one rooibos tea bag in each litter bag (one tea bag per compartment). The tea bags themselves are made of 0.25 mm synthetic mesh. This non-standard approach was utilized to minimize the loss of replicates in our public field sites. We deployed nine dual compartment litter bags containing tea bags at all four sites in May 2025, concurrently with our natural litter bags. We then retrieved three dual compartment litter bags every two months (July, September, November) until the study concluded. This meant that we had tea bags that were deployed for two, four, and six months. When collected, we placed each dual compartment litter bag in a separate plastic bag to account for any tea loss during transport. In the laboratory at Drexel University, we removed tea bags from the mesh bags before rinsing them and drying them at 65 °C to a constant weight. We calculated the mass loss (initial biomass- final biomass) of each tea bag, then divided the mass loss by the number of days that tea bags were deployed to obtain the decay rate (mass loss day^{-1}).

Statistical analysis

Natural leaf litter decomposition

To evaluate the effects of heat vulnerability and leaf litter species on mass loss day^{-1}, we used a two-way ANOVA, with field site (i.e., BA, G, W, and CC) and leaf species (i.e., gingko, sweetgum, sycamore, red oak) as fixed factors. We tested assumptions of normality and homogeneity of variance with descriptive statistics (Shapiro-Wilk test, Levene's test) and visual inspection of residuals (histogram, quantile-quantile plots). We followed our ANOVA with a Tukey's Honest Significant Difference (HSD) post-hoc test ($\alpha = 0.05$). Using the temperature logger data, we calculated the mean temperature over the study period at each of our four field sites (i.e., BA, G, W, and CC). We then ran a simple linear regression to mechanistically evaluate how mean site temperature affects the site decay rate (mean decay rate of all litter bags deployed at a given site). To determine potential influences of UV exposure, we calculated the daily cumulative UV exposure per site and ran a linear regression between mean daily cumulative UV and mean site decay rate. All statistical analyses were conducted in R (R Core Team 2024).

Tea bag decomposition

To evaluate the decay of tea bags during the study, we used a linear mixed model with site (i.e., BA, G, W, and CC) and tea bag type (i.e., green tea versus rooibos tea) as fixed factors, the interaction terms (i.e., site*tea bag type), and collection timepoint (i.e., July, September, November) as a random effect. The resulting likelihood ratio test indicated that the fixed factor, site ($\chi^2 = 4.51$, df = 3, $p = 0.21$), and the interaction term ($\chi^2 = 3.97$, df = 3, $p = 0.26$) did not significantly affect tea bag decomposition, thus we decided to remove them from the model and proceed with a model containing only tea bag type (i.e., green tea versus rooibos tea) as a fixed factor and collection timepoint (i.e., July, September, November) as a random effect. We then used a Type II Wald chi-squared test to assess model significance and calculated estimated marginal means to provide comparisons of tea types (Tukey-adjusted), accounting for variation across time. All analyses were performed using the lme4, car, and emmeans packages in R (Bates et al. 2023; Fox and Weisberg 2023; Lenth 2023).

Tea bag and natural leaf litter comparison

To further explore how litter quality may affect litter decay rates, we pooled our natural leaf litter species into two groups: predominantly labile (i.e., gingko and sweetgum; $n = 40$) and predominantly recalcitrant (i.e., sycamore and red oak; $n = 37$; Table 1) and compared these values to the decay rates (after six months; collected November 2025) that we obtained for green tea (i.e., labile group; $n = 23$) and rooibos tea (i.e., recalcitrant group; $n = 18$) using a Kruskal-Wallis Test and subsequent Dunn's test with the Bonferroni correction for p-value adjustment. Tea bags and natural litter were incubated concurrently for the same duration, therefore justifying comparison of substrate decomposition. Additionally, to qualitatively assess how heat vulnerability (i.e., site) impacts the heterogeneity of litter decay rates, we calculated the coefficient of variation (CV) for each leaf litter species (i.e., gingko, sweetgum, sycamore, red oak) and tea type (i.e., green and rooibos) at each site.

Table 1 Chemical characteristics of each of the leaf species used in the decomposition experiment. Numerical values are means (± 1 SD; see Appendix)

Species	Initial C: *N*	Litter Quality	Chemical Profile	References
Gingko biloba	53.15 (11.4)	Highly labile	Rich in soluble phenolics (like flavonoids) and terpenoids, low lignin and structural compounds	Jin et al. 2002; van Beek 2002; Liu et al. 2021
Liquidambar styraciflua	50.88 (13.3)	Moderately labile	High concentration of volatiles, simple phenolics and polysaccharides; moderate lignin	Ardón et al. 2009; Pozzobon et al. 2023; Zhao et al. 2025
Platanus occidentalis	31.01 (5.4)	Moderately recalcitrant	Low labile flavonoids and volatiles, High cellulose structural fiber, low tannins, moderate lignin	Al-Naib and Rice 1971; Ribeiro et al. 2022
Quercus rubra	80.91 (10.8)	Highly recalcitrant	Low soluble phenolics, moderate cellulose, high tannins (complex phenolic) and lignin	Seikel et al. 1971; Rowe and Conner 1979; Ardón et al. 2009; Dyderski et al. 2020

Results

Natural leaf litter decomposition

Field site (i.e., BA, G, W, and CC; $F = 14.89$, df = 3, $p < 0.001$) and leaf species (i.e., gingko, sweetgum, sycamore, red oak; $F = 15.15$, df = 3, $p < 0.001$) affect the

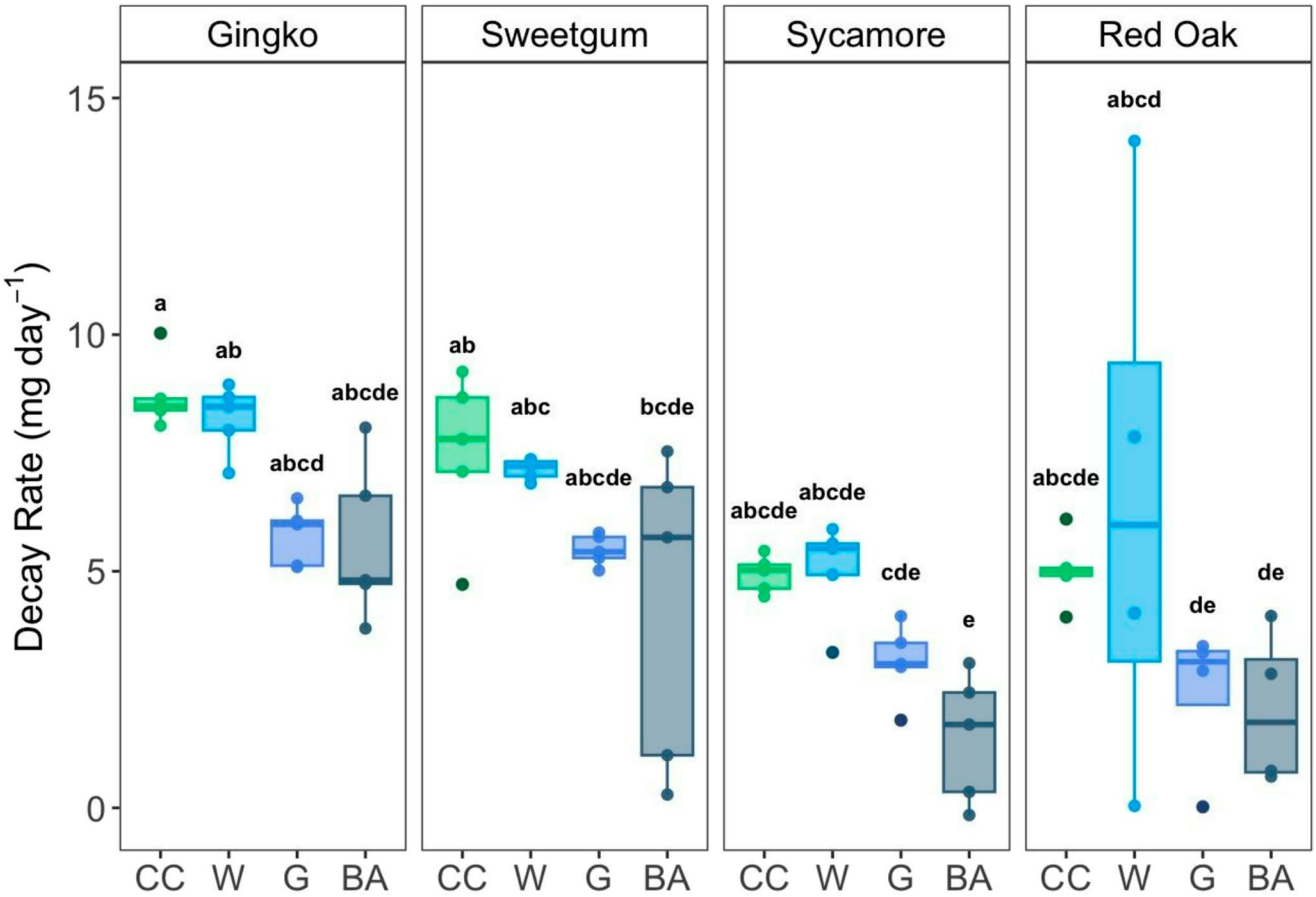


Fig. 2 Boxplots showing differences in mass loss decay rate (mg day^{-1}) by site and species. The horizontal line within each boxplot shows the median, with the box spanning the interquartile range (IQR; 25th-75th percentiles). Whiskers extend to the smallest and largest values within 1.5 * IQR from the hinges, and points beyond this range are plotted as outliers (grey). Different letters indicate significant differences between treatments as determined by ANOVA and Tukey HSD ($\alpha = 0.05$)

rate of leaf litter decay across an UHI in Philadelphia (Fig. 2). Specifically, leaf litter decay rate declined with increasing field site heat vulnerability (Fig. 3a), with leaf litter at our low heat vulnerability sites (i.e., W and CC; 6.65 ± 2.36 mg day^{-1}, mean ± 1SD) decomposing 72.7% faster than litter at our high heat vulnerability sites (i.e., BA and G; 3.85 ± 2.23 mg day^{-1}). This relationship between leaf litter decay rate and site heat vulnerability is likely associated with site temperature, as mean leaf litter decay rate is negatively correlated with mean field site temperature ($R^2 = 0.92$; Fig. 3b). There was no strong association between mean daily cumulative UV exposure and mean litter decay rate ($R^2 = 0.29$; Appendix: Fig. S1).

Leaf species composed predominantly of labile compounds decomposed faster than leaf species composed predominantly of recalcitrant compounds (6.59 ± 2.02 mg day^{-1} and 3.83 ± 2.58 mg day^{-1}, respectively; Fig. 4a). Labile leaf species consistently decayed at a faster rate (≥35%) than recalcitrant leaf species (Fig. 4b). There was interaction between leaf species and field site on leaf litter decay ($F = 0.36$, df = 9, $p = 0.95$; Fig. 2).

Tea bag decomposition

The inclusion of collection timepoint as a random effect significantly improved model fit ($\chi^2 = 123.7$, df = 1, $p < 0.001$) and the tea bag types decayed at different rates ($\chi^2 = 127.06$, df = 1, $p < 0.001$), with green tea decomposing approximately 72.3% faster than rooibos tea, based on model-adjusted mean rates (10.63 ± 2.54 SE mg day^{-1} and 6.17 ± 2.54 SE mg day^{-1}, respectively). This pattern was consistent with raw arithmetic means (5.64 ± 0.63 SD mg day^{-1} vs. 3.64 ± 0.9 SD mg day^{-1}), reflecting a 54.9% difference in decay rate.

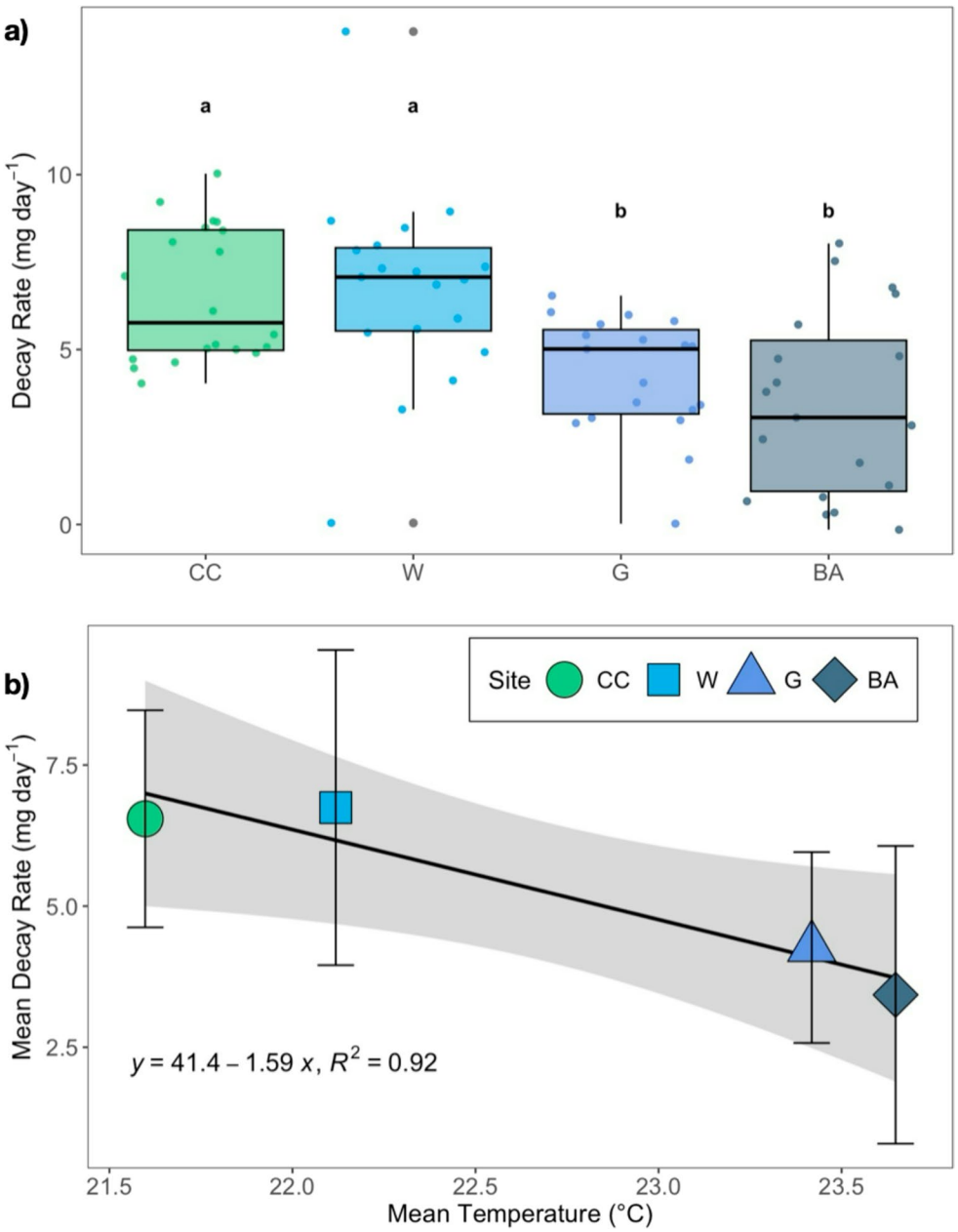


Fig. 3 **(a)** Boxplots showing differences in mass loss decay rate (mg day^{-1}) by site. The horizontal line within each boxplot shows the median, with the box spanning the interquartile range (IQR; 25th-75th percentiles). Whiskers extend to the smallest and largest values within 1.5 * IQR from the hinges, and points beyond this range are plotted as outliers (grey). Actual data points are plotted as well to show detailed distribution. Different letters indicate significant differences between treatments as determined by ANOVA and Tukey HSD ($\alpha = 0.05$) **(b)** Linear regression displaying mean mass loss decay rate (mg day^{-1}) as a function of mean temperature (°C, across the entire experiment duration) for each site. Standard deviation of mean mass loss is shown with error bars, and the equation of the line and R^2 value is presented. Shaded area represents 95% CI

Tea bag and natural leaf litter comparison

When comparing the decay rates of our tea bags and natural leaf litter, we found that substrates characterized by labile compounds (i.e., green tea, gingko, and sweetgum) decomposed approximately 64% faster than substrates characterized by recalcitrant compounds (i.e., rooibos tea, sycamore and red oak; $\chi^2 = 53.71$, df = 3, $p < 0.001$, Fig. 5b). The coefficients of variation for decay rate tended to be greatest at BA, the site with the highest heat vulnerability and mean temperature (Appendix: Table S1). This trend was observed more in the natural leaf litter than the tea bags. The decay rates of all natural leaf litter species showed considerable heterogeneity across field sites, while the decay rates of tea bag types were relatively homogeneous across sites (Appendix: Table S1).

Discussion

Leaf litter decomposition rates decreased with increasing heat vulnerability across sites along an urban heat island in Philadelphia, PA. In fact, leaf litter decay rates rapidly

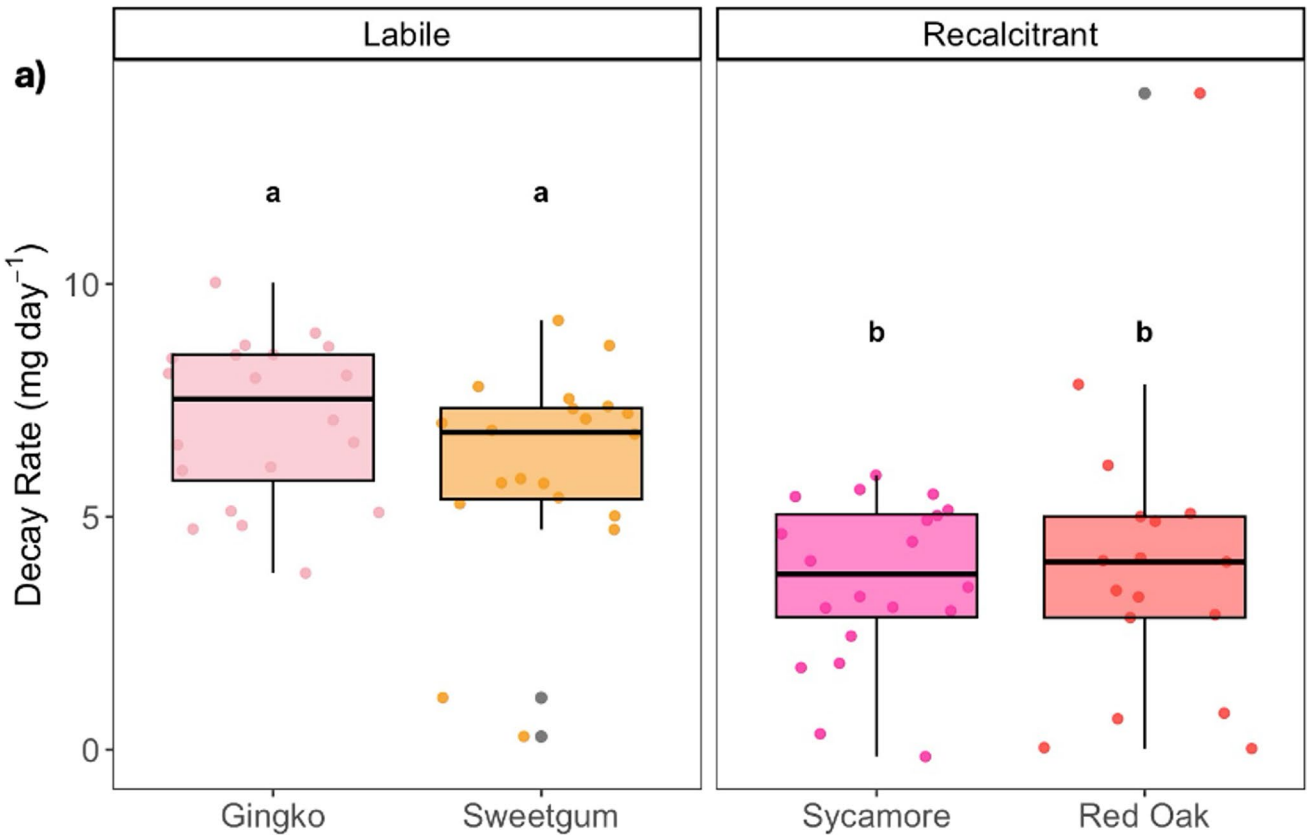
declined with increasing mean site temperature. While site-level differences were detected using natural leaf litter, there were no site-level effects on tea bag decomposition, suggesting a discrepancy in decomposition dynamics between natural litter and tea bag substrates. Regardless of site temperature, heat vulnerability and substrate type, substrates containing predominantly labile compounds decompose faster than those containing predominantly recalcitrant compounds, which corroborates the importance of litter quality as a predictor of leaf litter decomposition. Overall, our findings suggest that decomposition dynamics are strongly influenced by climatic conditions, including those associated with the UHI effect, with implications for urban nutrient cycling and land management (Fig. 6).

Natural leaf litter of all species tended to decay slower in sites with higher heat vulnerability and mean temperature than sites with low heat vulnerability and mean temperature. Additionally, variability in decomposition rate increased with increasing heat vulnerability (Table S1). These results support prior studies in Asheville, NC, Basel, Switzerland, and the French Mediterranean (Pavao-Zuckerman and Coleman 2005; Santonja et al. 2015; Meyer et al. 2020), that also found leaf litter decomposition decreased with increasing urbanization or became more variable with increasing heat stress. However, many foundational studies assessing leaf litter decomposition across urban landscapes (e.g., New York City, Helsinki, and Zurich; Pouyat et al. 1997; Pouyat and Carreiro 2003; Nikula et al. 2010; Tresch et al. 2019) suggest that leaf litter decomposition should increase with increasing urbanization due to the UHI elevating air and soil temperatures (Pouyat et al. 1997; Pouyat and Carreiro 2003; Tresch et al. 2019).

One critical factor that may explain some of the global variability in urban decomposition rates is precipitation and consequently, soil moisture, which can interact with temperature to affect decomposition (Aerts 2006). While we did not directly collect moisture data at our field sites, Philadelphia experienced unusual drought conditions, ranging from 'abnormally dry' (D0) to 'severe drought' (D2), for five of the six months that our study was deployed (U.S. Drought Monitor 2025). Such drought conditions may have hampered litter decomposition (Santonja et al. 2015; Xie et al. 2020). For instance, a global meta-analysis suggests that decreased precipitation reduces decomposition by an average of 21% (Su et al. 2023). Thus, while higher temperatures usually stimulate microbial biomass and activity, under moisture limited conditions microbial activities, including decomposition, may be suppressed (Tiunov and Scheu 2005; Christiansen et al. 2017; Petraglia et al. 2019). Indeed, multiple empirical and synthesis studies identify moisture as a key limiting factor constraining decomposition in urban ecosystems and have noted that moisture effects can override temperature effects in these systems (Aerts 2006; Meyer et al. 2020).

Photodegradation by UV exposure may also contribute to litter loss; however, we did not find a clear relationship between decay rate and mean cumulative UV exposure across our sites. The lack of UV effect may be due to other factors, not quantified directly in our study, such as differences in vegetation cover. Additionally, distinct micro- and macrofauna communities may have also driven differences in decomposition rates across our sites. For example, we only observed macrofauna in natural litter bags collected from Bog's Alley. Additionally, phenomena like the home-field advantage effect, while potentially at play in our study, should have been limited due to our intentional efforts to place all litter bags in areas devoid of our four leaf species (i.e., gingko, sweetgum, sycamore, and red oak). Overall, our findings support the notion that temperature, as associated with the UHI, is an important driver of decomposition in urban ecosystems; however, the impacts of temperature on decomposition are likely mediated by moisture and precipitation.

While we detected differences in decay rate by site and mean site temperature for natural leaf litter, no site effects were detected for either tea type (Fig. 5a). This is especially surprising, as the decay rates of green tea bags and rooibos tea bags at six months were comparable to natural leaf litter species of similar quality (i.e., labile and recalcitrant, respectively; Fig. 5b). Tea bags may not respond as strongly to site-level differences in temperature as natural leaf litter for multiple reasons. First, tea contains high concentrations of water-soluble compounds relative to other plants (Blume-Werry et al. 2021), which may have led to slower decomposition across our drought stressed sites, due to substrate inaccessibility to microbes. Indeed, leaching constitutes a major pathway of substrate mobilization for tea bags (Marley et al. 2019), which was likely suppressed under moisture limited conditions. Second, the tea bags themselves, due to their fine mesh, may alter microclimate conditions, slightly altering decomposition rates. For instance, the finer mesh of the tea bags may slightly increase air temperature and moisture, while decreasing detritivore access to litter (Bokhorst and


a)
Labile
Recalcitrant
Decay Rate (mg day^{-1})
10
5
0
a
a
b
b
Gingko
Sweetgum
Sycamore
Red Oak

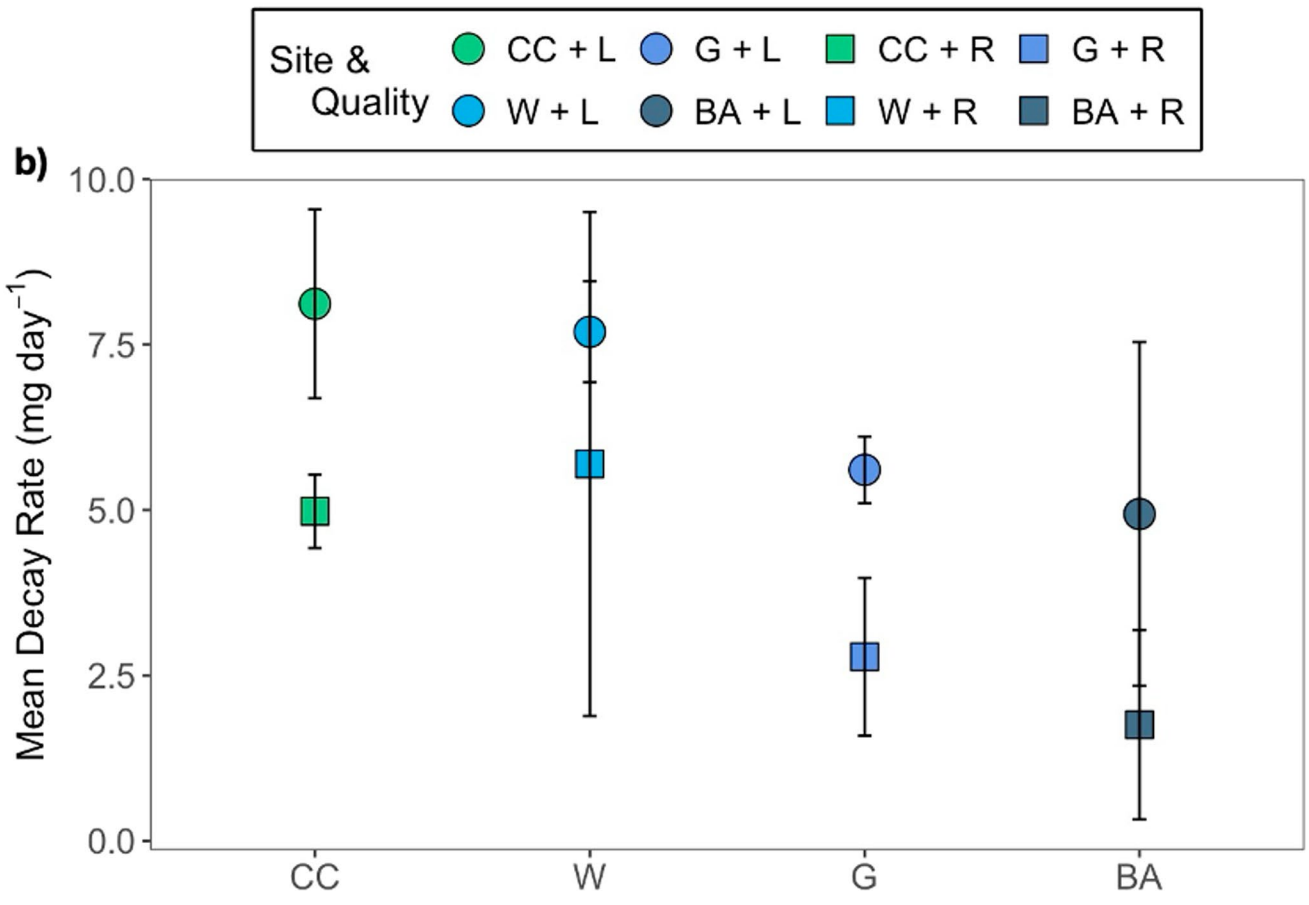

Site & Quality
CC + L
G + L
CC + R
G + R
W + L
BA + L
W + R
BA + R
b)
Mean Decay Rate (mg day^{-1})
10.0
7.5
5.0
2.5
0.0
CC
W
G
BA

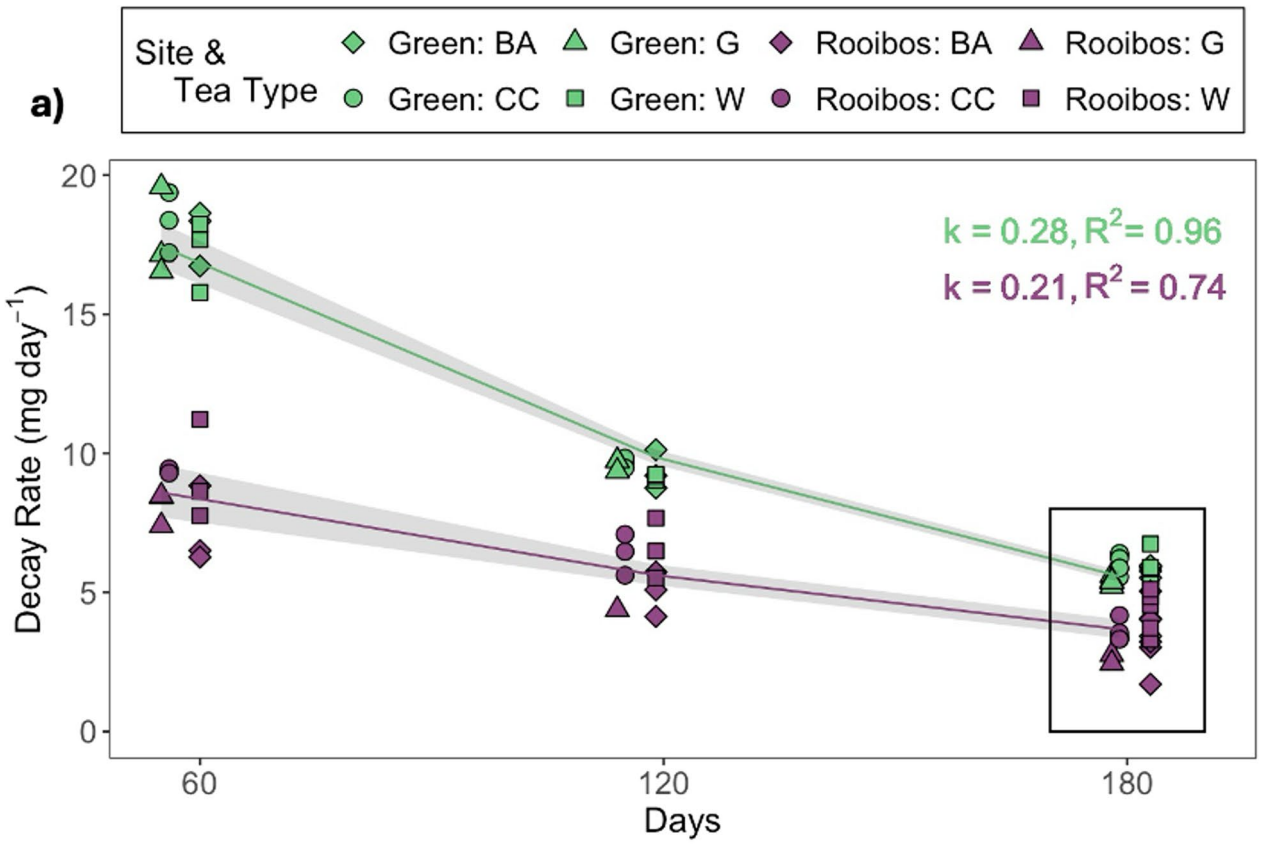
Fig. 4 **(a)** Boxplots illustrating differences in mass loss decay rate (mg day^{-1}) by species. The horizontal line within each boxplot shows the median, with the box spanning the interquartile range (IQR; 25th-75th percentiles). Whiskers extend to the smallest and largest values within 1.5 * IQR from the hinges, and points beyond this range are plotted as outliers (grey). Actual data points are plotted as well to show detailed distribution. Different letters indicate significant differences between treatments as determined by ANOVA and Tukey HSD ($\alpha = 0.05$) **(b)** Mean decay rate (mg day^{-1}) and standard deviation plotted for binned labile group and recalcitrant group at each site. Across sites, labile litter species decomposed 71.8% faster than recalcitrant litter species, with specific site differences including 62.9% (CC), 35.1% (W), 101.6% (G), and 181.7% (BA)

Wardle 2013). This is especially noteworthy since detritivores such as earthworms have been suggested to be key drivers of decomposition rates along urban gradients (Pouyat et al. 1997). Juvenile earthworms and other mesofauna were able to access the natural litter (Swift et al. 1979), while smaller mesofauna species likely penetrated even the fine mesh of the tea bags, but potentially on a delayed time scale (Setälä et al. 1996). Indeed, this additional fine-mesh layer of the tea bags could have influenced decomposition timelines and access, resulting in an absence of site-level effects. Nevertheless, the potential differences in site-level responses between natural leaf litter and tea bags should caution other researchers against relying solely on tea bags when designing field experiments, especially along subtle spatial gradients such as urbanization gradients. Our data suggests that deploying both natural leaf litter and tea bags constitutes an ideal approach, which can facilitate a greater understanding of drivers of decomposition, while also contributing to a standardized, global decomposition data set.

Decomposition rates of both natural litter and tea bags depended on litter quality. Specifically, natural leaf species and tea bags characterized by labile compounds (i.e., gingko, sweetgum, green tea) decomposed faster than species characterized by recalcitrant compounds (i.e. sycamore, red oak, rooibos tea), with a relatively similar magnitude across sites (Figs. 4b and 5a). This is consistent with previous studies suggesting that substrate chemical composition can have important consequences for decomposition (Gholz et al. 2000; Bourget et al. 2023). For example, the concentration of labile compounds in decaying plant material is often positively correlated with decay rate (Carreiro et al. 1999), while the concentration of recalcitrant compounds (e.g., acid-unhydrolyzable residue, or lignin) is often negatively correlated with decay rates (Berg and McClaugherty 2020). Recalcitrant plant materials slow decomposition because lignified plant materials produce stronger physical barriers to decomposition, inhibiting leaching and fragmentation (Liu et al. 2006), and other specialized compounds (e.g., secondary metabolites) can inhibit microbial activity (Chomel et al. 2016). In fact, it has been suggested that the chemical characteristics of leaf litter may be a better predictor of decomposition rates than microbial communities and abiotic conditions (Petraglia et al. 2019). Additionally, our study shows that leaf C and N content alone do not predict these outcomes (see Appendix), suggesting more complex relationships between leaf chemical composition and decomposition rates. Thus, understanding the generality of the effects of leaf litter chemical characteristics (i.e., labile versus recalcitrant) on decomposition rates is critical for understanding how nutrients are recycled across urban landscapes (Vauramo and Setälä 2011).

Sycamore species and northern red oak constitute some of the most dominant species by leaf area in Philadelphia (2012: 8.7% and 7.6% respectively; USDA Forest Service, Northern Research Station 2023), likely due to their extensive planting history. For example, species in the *Platanus* genus (e.g., sycamore) were the most planted street tree in Philadelphia during the 1930s (32.06%) but declined to only 0.91% by the 1950 s (LaNoce et al. 2022). Northern red oak and gingko each constituted around 4% of total street tree plantings in the 1930 s, but gingko plantings increased by 11.25% in the 1950 s (LaNoce et al. 2022). Sweetgum has also been planted mainly in the 1950 s but represented only 1.38% of all street tree plantings in the city. Since the 2000 s, planting efforts across the city have prioritized higher species and functional diversity, with none of our four species being commonly planted today. These historical shifts in planted tree species composition likely have significant consequences for local biogeochemical dynamics. Indeed, urbanization tends to increase aboveground productivity, which in turn constitutes the primary input to soil organic matter (SOM; Cotrufo et al. 2013; Enloe et al. 2015). Generally, more stable SOM is formed from high-quality, labile litter input through higher microbial substrate-use efficiency (Cotrufo et al. 2013). Thus, urban tree management decisions should critically evaluate species selection, based on chemical properties, and their associated decomposition dynamics to select species that promote ecosystem resilience and functions (Enloe et al. 2015).

Overall, our study contributes to the ongoing discussion on leaf litter decomposition dynamics in urban landscapes, particularly in the context of the UHI and


a)
Site & Tea Type
Green: BA
Green: G
Rooibos: BA
Rooibos: G
Green: CC
Green: W
Rooibos: CC
Rooibos: W
k = 0.28, R2= 0.96
k = 0.21, R2 = 0.74
Decay Rate (mg day-1)
Days
60
120
180

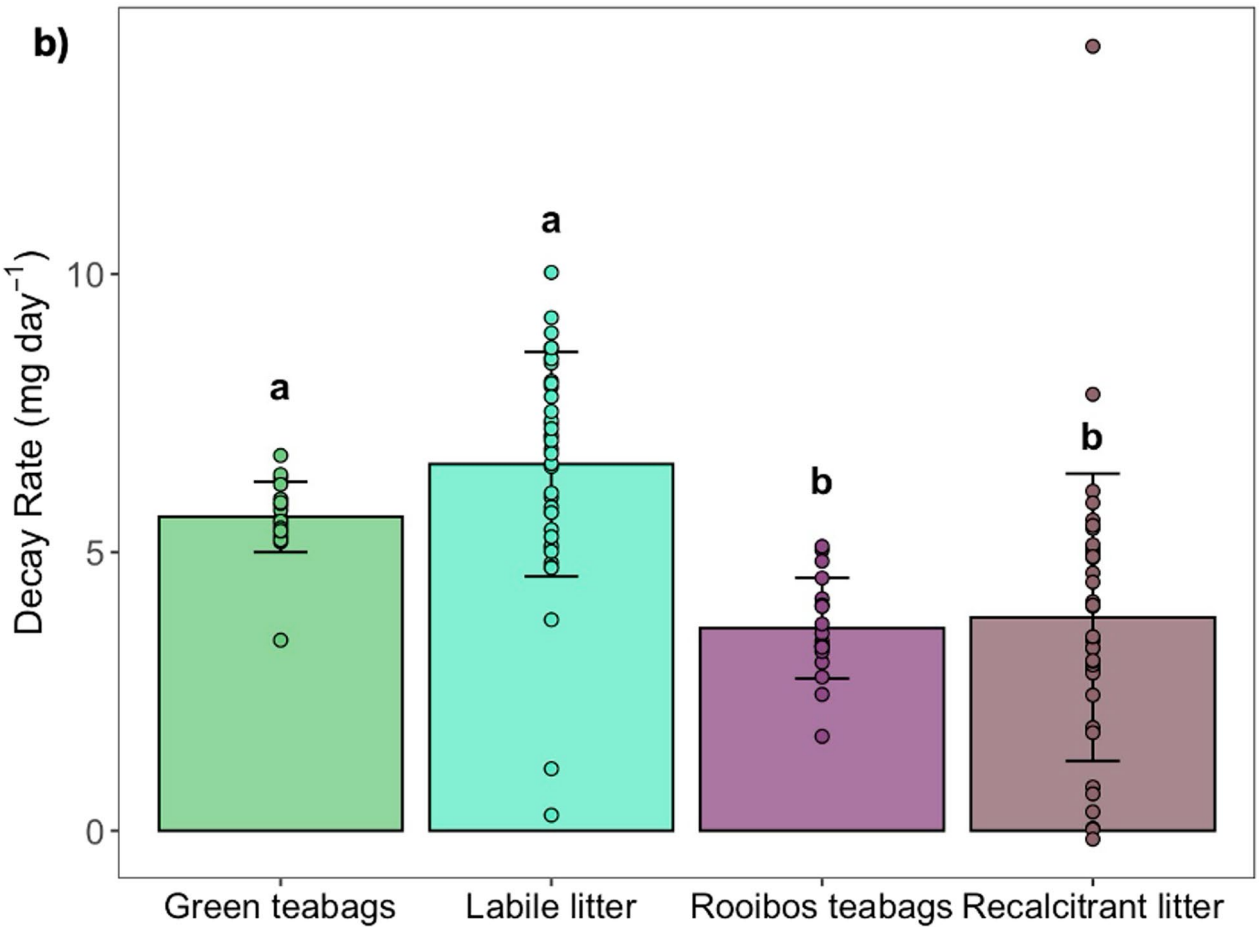

b)
Decay Rate (mg day-1)
a
a
b
b
Green teabags
Labile litter
Rooibos teabags
Recalcitrant litter

Fig. 5 **(a)** Time series of decay rate (mg day^{-1}) by tea type and site. Tea bags were collected in 2-month intervals after the initial deployment. To support visualization purposes, we fit separate generalized linear models (GLMs) for each tea type to estimate the decomposition rate constant (k, where -k = slope), predicted values, confidence intervals (95% CI), and deviance-based pseudo-R^2 (where $R^2 = 1$ – model deviance/null deviance). A rectangle is drawn to indicate data used in panel (b) **b)** Bar plots showing mean decay rate (mg day^{-1}) for labile litter group (gingko, sweetgum), recalcitrant litter group (sycamore, red oak) and associated green (labile) and rooibos (recalcitrant) teabags pooled across all sites. Decay rate was averaged across the entire experiment duration (6 months) for both teabags and litter samples. Standard deviation is shown with black bars, while different letters indicate significant differences between treatments. Data points are plotted as overlay

changing climatic conditions. While past studies suggest that increasing temperatures in urban areas should increase decomposition rates, we found that increasing temperatures across a Philadelphia UHI decreased decomposition rates, likely due to confounding effects of severe and prolonged drought conditions in the region. However, these site-level differences were only observed for natural leaf litter, not tea bags, suggesting that substrate choice and litter bag preparation should be considered carefully when designing decomposition studies. Across all sites, natural leaf litter and tea bag decomposition rates were impacted by their chemical composition, with labile substrates consistently decomposing faster than recalcitrant substrates. Together, our study highlights the importance of considering the interaction of multiple environmental stressors (i.e., temperature, UV, soil moisture) on decomposition rates in urban landscapes and suggests that city tree planting efforts should consider the chemical composition of planted species to effectively manage nutrient cycling and promote carbon retention in urban ecosystems.

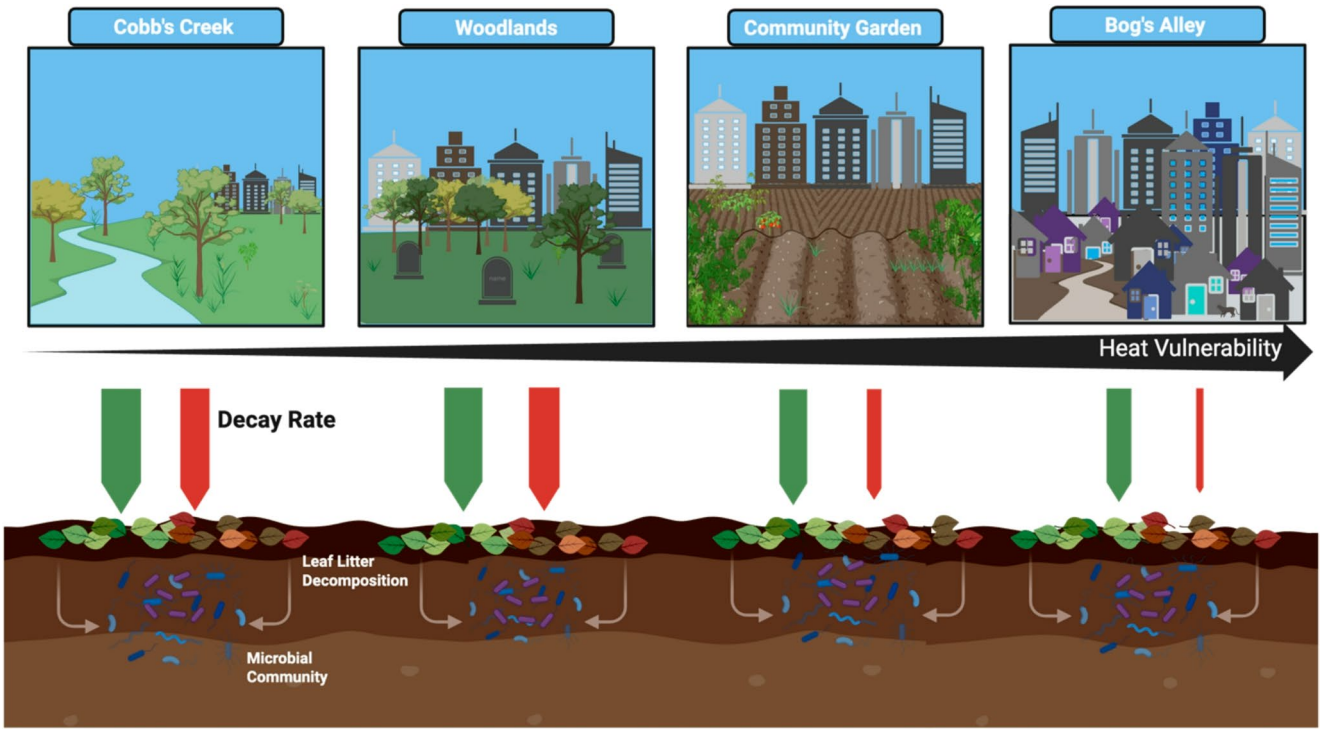


Fig. 6 Conceptual diagram illustrating decay rate differences by site and litter quality. Green shaded leaves designate labile leaf species (gingko, sweetgum), while red shaded leaves represent recalcitrant leaf species (sycamore, red oak). Width of arrows is indicative of relative magnitude differences in decay rate between quality groups within and across sites. No data was collected regarding the microbial community and thus no assumptions regarding community composition or biomass are made. Likewise, no assumptions about background litter input are made. Created in https://BioRender.com (agreement number #: TO28SW6929)

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Author contributions All authors contributed to study conception, design, material preparation, and data collection. DF and SR performed the data analysis. DF, SR, and DP wrote the first draft of the manuscript and all authors reviewed and approved the final manuscript.

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Data availability The experimental data and the R code used for this project are available in Shelby Rinehart's OSF account available at https://osf.io/sv3qh/?view_only=b0a97704a7b846d8ba14c3b7960b2b01.

Declarations

Competing interests The authors declare no competing interests.

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