Effects of urban, peri-urban and rural land covers on plant functional traits around Bogotá, Colombia

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Abstract
The Global South has suffered an accelerated population and urban growth. This has created multiple impacts at the regional level such as erosion, soil degradation and biodiversity loss, as well as temperature increase in the cities causing urban heat islands. Bogotá, the capital of Colombia, is one of the largest cities in the Global South and in the last five decades has undergone a rapid urban transition, impacting surrounding ecosystems. However, little is known about how urbanization affects the local flora. To understand how plants are responding and adapting to urbanization processes in the city of Bogotá, we used a land cover gradient of urban, peri-urban and rural areas, and four plant functional traits (leaf area [LA], specific leaf area [SLA], leaf dry matter content [LDMC] and wood density [WD]). We analyzed 16 species shared in at least two land covers. Although urban and peri-urban areas had higher temperatures and higher LDMC and lower SLA values than rural areas, there were no significant differences in functional traits between land covers. Some species showed significant changes between land covers, indicating that there is a species-specific response to urbanization. Considering the need for urban areas to prioritize species that promote cooling and exhibit resistance to stress, as well as the capacity to adapt to climate change, it is essential to include plants possessing different combinations of functional traits.

Keywords Global South · Heat island · Leaf traits · Wood traits · Urbanization

Introduction

The accelerated population growth has rapidly replaced natural areas favoring urban structures. In 2015, 55.3% of the world's population was in urban zones and, according to the UN's Urban Global Observatory, it is estimated that by 2050, this percentage will increase up to 68.4% (Wang et al. 2018; United Nations 2019; Litardo et al. 2020; Gonzalez-Trevizo et al. 2021). This phenomenon of urbanization has been far more rapid in the Global South, in contrast to the Global North. Currently, 70% of the largest urban agglomeration belongs to the Global South, and their populations have grown as large as twice the rate of countries from the Global North (Myers 2021). The growth of the Global South urbanizations has outpaced their own economic growth, leading to an unplanned sprawl of these cities, which cover a wider range of climate, elevation, and biomes than the ones from the Global North (Myers 2021). The increase in urbanization has been one of the most relevant topics in the global environmental agendas. This phenomenon results in multiple impacts, such as changes in the regional surroundings at a local level, erosion, decrease in water deposits and aquifers, temperature increase, loss of biodiversity and soil unproductivity (Palomeque de la Cruz et al. 2017; Gonzalez-Trevizo et al. 2021), in addition to its implications for human health.

Urban heat islands (UHI) are cities or metropolitan areas with higher temperatures than the surrounding areas. Therefore, the world's large cities are currently defined as heat islands and exotic zones with respect to their surroundings (Oke 1982). The rise in temperatures is related to the city's properties, its urban layout, and its physical,

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structural, morphological, meteorological, and environmental characteristics (Oke et al. 1991). These conditions can cause city temperature to vary between one (1) and three (3) °C over its surroundings (Peng et al. 2012; Huang et al. 2019). Additionally, UHI can create variations in air quality, heat waves, contaminant particles like PM2.5 and PM10, changes in hydrologic cycles, evaporative surfaces, and tropospheric ozone precursors (Ulpiani 2021; Gonzalez-Trevizo et al. 2021). Plants are one of the taxonomic groups most affected by the changes induced by this phenomenon, since their growth, development, reproduction, and survival depend on their environment. In addition, a key factor that will exacerbate UHI is climate change, which will affect the vegetation, including their composition, diversity, and functions (Toledo-Garibaldi et al. 2023).

As we face an exponential growth in both city size and population density (Parés-Ramos et al. 2013), we need to assess anthropic impact on the plants and the ecosystems we have fragmented as urbanization has become the norm. Several researchers have used functional traits as ecological indicators of the effects of urbanization (Lizée et al. 2011; Koch et al. 2019; Song et al. 2019a; Zhu et al. 2020). Functional traits reflect the morphological, physiological and phenological properties of organisms that may affect species' fitness and determine how they manage their resources (Nock et al. 2016; Su et al. 2021). They can explain specific physiological functions, such as resource uptake and nitrogen efficiency (Violle et al. 2007). Furthermore, these attributes have the potential to change in response to variations in the environment, thus, they can be used as indicators for community dynamics in an ecosystem (Cornelissen et al. 2003). One of the methods used to study functional trait variation response to environmental variation consists of collecting quantitative data on functional traits of key species (Koch et al. 2019) in areas with high and low levels of intervention. For instance, plants with acquisitive strategies in urban areas have larger specific leaf area (SLA), lower leaf dry matter content (LDMC), and stomatal density (Knapp 2010; Song et al. 2019b; Su et al. 2021). Meanwhile, in rural areas plants tend to have conservative strategies, such as lower SLA, leaf nitrogen (N) content and higher leaf carbon–nitrogen (C:N) ratio (Song et al. 2019b). However, most plant functional traits studies in urban environments focus on leaf traits and tend to use greenhouse-model control experiments, which do not accurately reflect variations in plant attributes in response to contrasting environmental conditions (Zhu et al. 2020).

Consequently, this study aims to use plant functional traits as proxies to understand how plants respond and adapt to urbanization processes in the city of Bogotá, a large city of the Global South (the fourth largest in Latin America). We hypothesize that trait variation along an urbanization gradient (from urban to peri-urban to rural areas) is due to

the UHI effect. This effect could be reflected in acquisitive strategies in urban zones (i.e., higher SLA and leaf area [LA]; lower LDMC and wood density [WD]), and conservative strategies in rural zones (i.e., lower SLA and LA; higher LDMC and WD). However, this general trend could vary due to the high plant diversity in the study area, indicating a species-dependent response.

Materials and methods

Study area

Bogotá is located on the eastern Colombian mountain range in the Andean region and is Colombia's most densely populated city (Angel et al. 2010; Rojas et al. 2010). Like several urban centers in South America, it has suffered an accelerated urban transition in the last five decades, going from a population of 700,000 in the 1950's to more than 7,181,469 in 2018 (DANE 2018; Rodríguez et al. 2019; Bernal and Orcid 2021). The urban area has also increased. In the 70's the city's area was 13,985 ha; in the 80's it increased to 22,775 ha; and in the 2000's to 36,232 ha. The influence of the city is so pronounced that the urban expansion overlaps with nearby municipalities and rural areas through a process of metropolization (Bernal and Orcid 2021). The city is located at an altitude of ca. 2650 m, with an average annual temperature of 14 °C (Fig. 1a), annual rainfall of ca. 1,000 mm (Fig. 1b) and average relative humidity of 73%. Bogotá is the largest urban settlement in the world with these climatic conditions and its metropolitan area one of the largest urban areas in Latin America (Angel et al. 2010; Rodríguez et al. 2019; Mixed Migration Centre 2020).

Previous studies have indicated that UHI is a result of the city's increased density (Angel et al. 2010). Therefore, we divided our study area into three zones: urban, peri-urban and rural, following the land classification of Bogotá described in the land management plan (Secretaría Distrital de Planeación 2022) (Fig. 1c). We classified samples collected within a distance of less than 10 km from the urban area as peri-urban. Samples collected at distances of 10 km or more were categorized as rural. (Fig. 1c).

Trait data

We obtained plant functional trait data for the urban and peri-urban areas mainly from Rodríguez-Alarcón et al. (2020). We completed the data for peri-urban (i.e., Torca) and rural areas (i.e., Guasca, Guatavita, Tabio) from data collected in municipalities near Bogotá, obtained from the Rastrojos Project. Four functional traits were analyzed due to their relationship with light and water use, and their sensitivity to abiotic disturbance (Zambrano et al. 2019; Su et al.
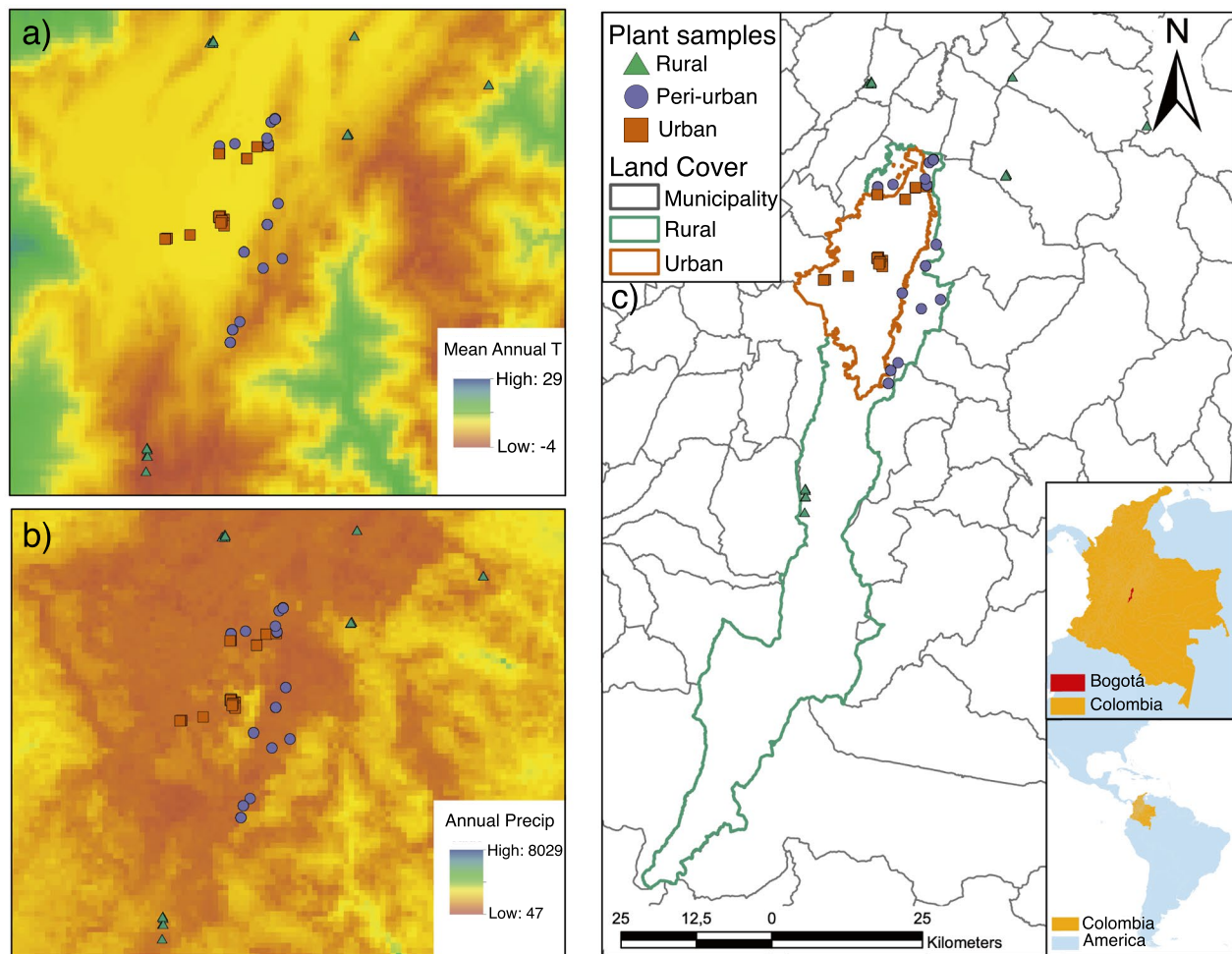
Fig. 1 Sampling locations in the different land covers (urban, peri-urban, and rural). **a** Map of mean annual temperature (Mean Annual T) (°C) in the study area. **b** Map of annual precipitation (Annual Pre-cip) (mm) in the study area. **c** Land cover types in Bogotá and surrounding areas, and classification of the sampling locations according to their proximity to urban Bogotá

2021). We used wood density (WD, g cm^{-3}) from branch samples due to their relationship with water transport (Chave et al. 2009). We also analyzed three foliar traits which are highly sensitive to environmental and land use changes, and may reflect aspects related to adaptability (Zambrano et al. 2019; Zhu and Xu 2021; Su et al. 2021). These foliar traits are leaf area (LA, cm^2), specific leaf area (SLA, cm^2 g^{-1}) and leaf dry matter content (LDMC, mg g^{-1}). All leaf traits were measured in healthy looking leaves including the petiole, following standard protocols (Pérez-Harguindeguy et al. 2013; Salgado-Negret et al. 2015).

Data analysis

Bioclimatic variables were downloaded from the World-Clim version 2 database with a spatial resolution of 30 s (~ 1 km^2) (Fick and Hijmans 2017). We used annual mean temperature (BIO1) and annual precipitation (BIO12) to

describe the climatic conditions in Bogotá city and surrounding areas using ArcMap 10.4.1 (ESRI inc.) (Fig. 1). The WorldClim variables temperature seasonality (TS), maximum temperature of warmest month (Tmax), minimum temperature of coldest month (Tmin), precipitation of wettest month (Pmax), precipitation of driest month (Pmin) and precipitation seasonality (PS) were also used to characterize the urban, peri-urban and rural areas.

For the analyses, we used species that were present in at least two land cover types, with more than three individuals per cover. In addition, a principal component analysis (PCA) was performed to reduce the dimensionality of the environmental variables of the collected individuals and to define if there were climatic differences between coverages (urban, peri-urban and rural). For these analyses, we used the R packages factoextra and FactoMineR (Lê et al. 2008; Kassambara and Mundt 2020).

We included a total of 16 species in the study (Table S1). First, we calculated the mean and standard deviation for each species and for each functional trait in the different land covers. Then, we tested if plant functional traits were significantly different between land covers with an analysis of variance (ANOVA) or Kruskal–Wallis (depending on normality and homoscedasticity), using the R nortest package (Gavrilov and Ruslan 2015), and the car package (Fox and Weisberg 2019) (Table S2).

Finally, we examined species comparisons between land covers using a t-test or Mann–Whitney-Wilcoxon test (Table S3). Plots were made with ggplot 2 (Wickham 2016) and the statistical analyses were performed using R 4.2.1 (R Core Team 2022).

Results

The PCA shows differential climatic characteristics among areas. As expected, urban land cover exhibited extreme temperatures (Fig. 2), but interestingly, the climate envelope had a lower range of dispersion than the two other land coverages. Temperature was also an important factor for the peri-urban coverage, and there was higher variation (more dispersion) compared to the urban area. In contrast, we found a more relevant correlation with precipitation and seasonality for rural areas.

We did not find any significant differences between the mean trait values for each cover type (urban, peri-urban, and rural) regarding the four functional traits analyzed (LDMC, SLA, LA, WD), when pooling all species together ($p > 0.05$) (Fig. 3; Table S2). However, there were some interesting trends. Peri-urban and urban areas tend to have lower SLA and higher LDMC values than the rural land cover (Fig. 3).

We obtained significant differences for some of the traits (Fig. 4; Table S3), when analyzing species separately. LA was significantly different for *M. parviflora* ($U = -3.79$, $p = 0.035$) and values increased in individuals from peri-urban to rural areas (Fig. 4). LDMC was significantly different for *Abatia parviflora*, *Duranta mutisii* and *Miconia squamulosa* between peri-urban and rural areas ($p < 0.05$). In the first two species LDMC values increased, while in *M. squamulosa* they decreased. For *Eucalyptus globulus* values significantly increased from urban to peri-urban land covers ($t = -3.12$, $p = 0.015$); for *Myrcianthes leucoxyla* there was a significant decrease, while in *Varronia cylindrostachya* a significant increase from urban to rural areas ($t = 8.76$, $p = 0.002$; $t = -3.51$, $p = 0.032$; respectively). For SLA, we found significant differences between peri-urban and rural areas for *Morella parviflora* (increase) and *A. parviflora* (decrease) ($t = -2.75$, $p = 0.037$; $U = 3.40$, $p = 0.025$; respectively), and between urban and rural coverages for *V. cylindrostachya* (decrease; $t = 3.66$, $p = 0.013$). WD was significantly higher for *Cedrella montana* and *V. cylindrostachya* between the urban and rural areas ($t = -2.88$, $p = 0.037$; $t = -2.93$, $p = 0.021$; respectively), and lower for *M. leucoxyla* ($t = 3.82$, $p = 0,008$). In contrast, WD values were higher from peri-urban to urban areas in *M. squamulosa*, ($t = -2.74$, $p = 0.018$). All p-values can be found in Table S3.

Fig. 2 Principal component analysis (PCA) of environmental variables for the samples included in this study. Environmental variables: Tmax, maximum temperature of the warmest month; Tmin, minimum temperature of the coldest month; TS, temperature seasonality; PS, precipitation seasonality; Pmax, precipitation of the wettest month; Pmin, precipitation of the driest month
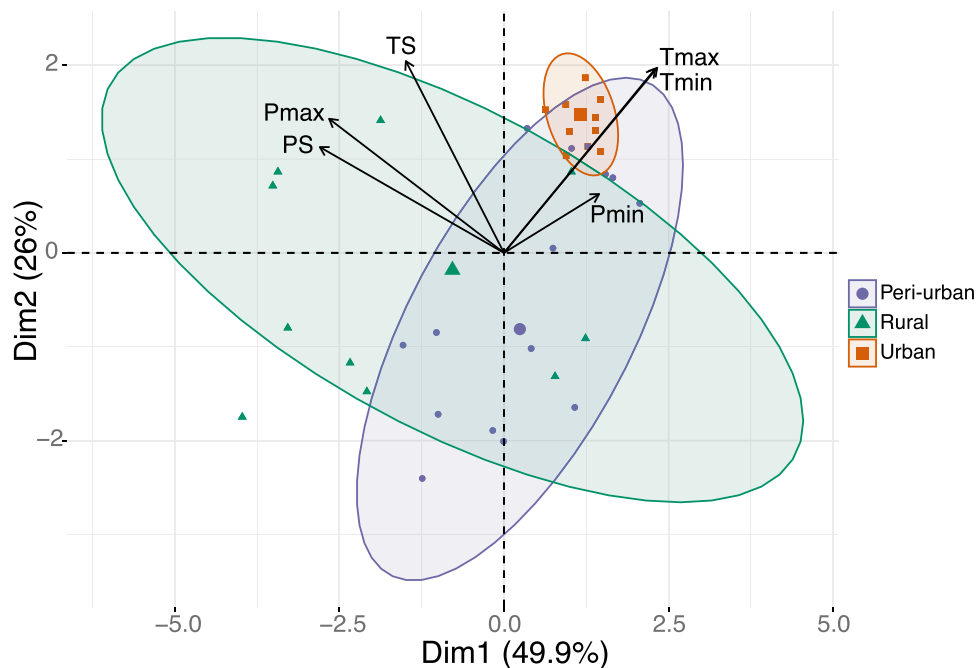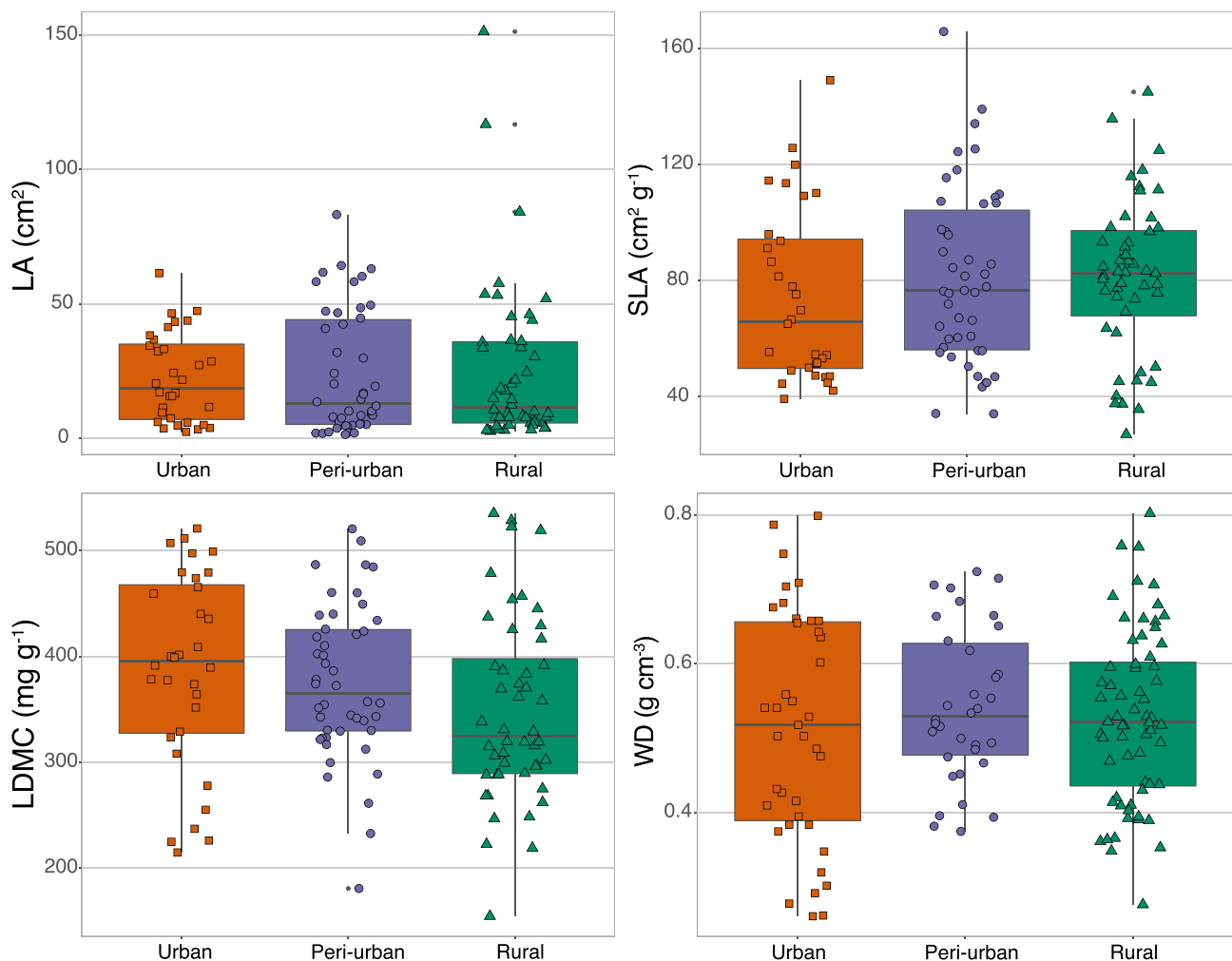
Fig. 3 Boxplots and individual values for the functional traits between urban, peri-urban, and rural coverage. The graph shows the dispersion and deviation of the data corresponding to functional traits of leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and wood density (WD) for urban, peri-urban and rural coverage. The bottom and top of the boxplot indicates the 25th and 75th percentiles (respectively); the horizontal line within the box indicates the median value

Discussion

There were differences in the climatic conditions of the three land covers in this study: urban, peri-urban and rural. In urban and peri-urban areas, maximum and minimum temperatures were the most influencing climatic factors, while in rural zones, the main influence was driven by maximum precipitation and precipitation seasonality. Even though no significant differences were found in functional trait values when combining all species, urban and peri-urban areas tend to have lower SLA and higher LDMC values. The nonsignificant trend may indicate phenotypic plasticity in the species evaluated and the different strategies plants have to cope with stressful environments.

The variations along the urbanization gradient of different traits such as SLA may suggest that urban plants can be stress-tolerant ruderals, which allows them to endure

changing conditions (Ilyas et al. 2021). Nevertheless, different species have shown multiple strategies to deal with urban heat islands, UHI (e.g., Ilyas et al. 2021). For example, species with high LDMC, leaf carbon content (LCC) and C:N ratio tend to have a conservative strategy, while species with high SLA, LA and leaf width (LW) tend to present an acquisitive strategy (Huang et al. 2022). In this study we had hypothesized that species growing in urban and peri-urban areas would have traits related to an acquisitive strategy. This was not the case (Fig. 3). Only two species, *V. cylindrostachya* and *M. leucoxyla*, had an acquisitive strategy in these land covers.

Heat island effects on functional traits

Several studies have found that leaf traits tend to have significant variations in populations present in urbanized
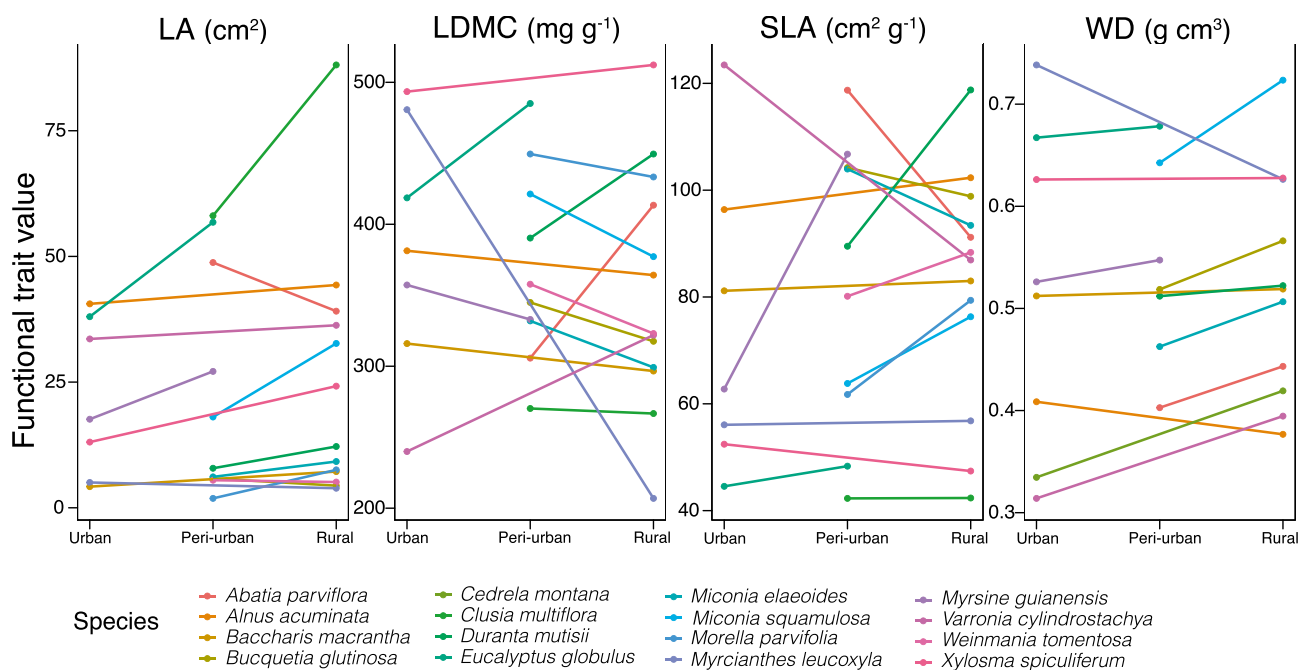
Fig. 4 Trends in functional trait means of shared species in urban, peri-urban and rural coverages. The functional traits of leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), and wood density (WD) are presented for each species measured in the different land covers: urban, peri-urban and rural

locations, and these traits influence the success of plants in urban ecosystems (Palma et al. 2017). Plant responses to environmental variation are associated with their adaptive strategies, which include efficient use of nutrients, water and light resources, dispersal strategies, and renewal strategies (Raevel et al. 2012; Song et al. 2019b). High SLA values indicate more resource uptake, while low SLA values are related to drought tolerance (Nautiyal et al. 2002). Different studies have shown a negative correlation between SLA and increasing temperature (Zhu et al. 2020; Zhu and Xu 2021), which is the overall pattern observed in the urban area of Bogotá (Figs. 2–3).

Urban areas also have more runoff than rural areas, indicating that water drains quicker, and less water is ultimately available for evapotranspiration (Taha 1997). Low urban and peri-urban SLA values compared to rural, are related to urban plant responses to water stress and high temperatures in the area (Zhou et al. 2020). High SLA values in rural areas are related to a greater resource absorption. According to some authors, leaf traits related to nutrient use and maintenance determine the distribution of species along the urban–rural gradient (Wright et al. 2004; Osnas et al. 2013; Song et al. 2019b). This could explain the species-dependent response observed in our study, and the lack of a significant overall pattern.

Similarly, LA values are related to allometric factors specific to each plant (Pérez-Harguindeguy et al. 2013) and to the ecological strategy of nutrient acquisition with respect to the environmental conditions (Searle et al. 2011; Pérez-Harguindeguy et al. 2013; Su et al. 2021). Despite not finding significant differences between land covers, we found that plants are responding differently and individually to the climatic factors (Fig. 4). This has also been found in other studies (e.g., Alotaibi et al. 2020). Additionally, Searle et al. (2011) and van Rensburg et al. (1997) found that *Quercus rubra* responded differently in an urban–rural gradient depending on the city: New York in the USA or Potchefstroom in Africa, respectively.

High LDMC values indicate high nutrient retention efficiency (Zhu et al. 2021), which correlates with SLA for nutrient availability (Smart et al. 2017). This functional trait varies according to the conditions to which the plant is exposed, in addition to the species. For instance, when *L. quihoui* is exposed to a dust-polluted environment, there is an increase in dry matter content (Zhu et al. 2021). This result could reflect that variations in functional traits and strategies employed to tolerate urban conditions are influenced not only by temperature changes but also by urban atmospheric particulate matter (Zhu and Xu 2021). Accordingly, dry matter content is expected to vary depending on each species and its plasticity. A response to increased dry matter content has been particularly evident in exotic species (El-Barougy et al. 2021). In our study, the only exotic species that showed this pattern was *E. globulus* (Fig. 4; Table S1).

Wood density is a determining factor in xylem transport and establishes the storage properties and water relationships of plants. Species with higher WD may experience more fluctuations in water deficits in dry seasons, while species with low WD suffer cavitation (Gartner and Meinzer 2005). As for our results, there is considerable variation in WD values, especially in urban areas. However, most species tended to increase WD from urban to rural land covers (Fig. 4), which could reflect the higher precipitation seasonality in these areas (Figs. 1–2).

Urban planning, management implications and climate change

Estimations for 2050 global population growth trends show that 68.4% of the population will be in urban areas, which leads to the expansion of urban heat islands (Gonzalez-Trevizo et al. 2021). Therefore, urban arborization planning arises as an effective mitigation strategy for heat island effects, given the cooling potential of vegetation (Xu et al. 2017). However, this planning must be adequate and account for local environmental conditions, because trees articulate the main ecological structure of cities such as Bogotá (Mahecha et al. 2010).

Urban air cooling is highly dependent on LA and SLA. Greater LA promotes shading effects and increased evapotranspiration rates (Vargas and Molina 2014; Ferrini et al. 2020; Ngao et al. 2021). In the case of Bogotá, the species that would present this pattern for LA and SLA are *A. parviflora* and *V. cylindrostachya* (Fig. 3). However, if urban planning selects tree species with larger LA, it is essential to reduce exposure to pollutants and attend to nutrient availability (Pourkhabbaz et al. 2010; Grote et al. 2016; Deva et al. 2020). In contrast, low LA and SLA reduce evapotranspiration rates and decrease water stress in plants. In the common bean (*Phaseolus vulgaris*), the most heat-tolerant individuals exhibited lower SLA (Deva et al. 2020). This trend would be found in species such as *M. parviflora* and could be related to resistance to high temperatures in heat islands. This demonstrates that species may respond differently to stress in UHI and could explain why there is no significant pattern of increasing or decreasing functional trait values in the urban-to-rural gradient in Bogotá (Fig. 3).

Leaf dry matter content and WD are important traits for urban air cooling (Cortes and Matias 2019). It has been shown that CO_2 capture contributes directly to mitigating UHI (Solecki et al. 2005; Gartland 2008; Vargas and Molina 2014; Zhang et al. 2014; Blachowski and Hajnrych 2021). In this study, higher LDMC values were found in urban areas compared to peri-urban and rural (Fig. 3). This could indicate that the species that have the highest LDMC (i.e., *X. spiculiferum* and *M. parviflora*) and/or WD (i.e., *M. leucoxyla*) are the ones that contribute the most to air cooling.

In order to favor cooling, species with high WD, SLA and LA should be chosen in urban planning. These would need to be placed in areas where water availability and air quality can be guaranteed. However, plants with low SLA and LA, and high LDMC are more resistant to the stressful conditions of the city. Both options are important in large cities, but we still need more research on how plants are responding and adapting to UHI. This is a particularly important in cities in the Global South which should aim to maintain the species diversity associated to the original land covers.

In addition, there is another significant challenge that will exacerbate the current impacts of the UHI: the compounding effect of climate change. Urban forests (including trees, shrubs, lawns and other vegetation) have been one of the most widely used strategies to mitigate extreme heat in cities (Khan and Conway 2020; Huang 2022). Beyond their role in temperature moderation, urban forests offer a variety of ecosystem services including air purification, greenhouse gas mitigation, runoff reduction, and noise abatement. Additionally, they contribute to global climate regulation, carbon sequestration, and avian habitats (e.g., Escobedo et al. 2011; Kowarik 2011; Gómez-Baggethun et al. 2013; Nowak et al. 2014; Livesley et al. 2016). In the context of diverse tropical landscapes, urban and peri-urban forests also serve as essential reservoirs of biodiversity (Toledo-Garibaldi et al. 2023).

Despite these benefits, urban forests remain susceptible to the impacts of climate change (e.g., Gauthier et al. 2014; Ordóñez and Duinker 2014; Brandt et al. 2016; Khan and Conway 2020). The escalating effect of climate change is projected to amplify temperatures within urban areas, potentially exceeding the tolerable range for plant species. This phenomenon could be exacerbated by the UHI, particularly affecting plants and their water-related processes, such as evapotranspiration. This intricate interplay is further influenced by shifts in precipitation, solar radiation, and cloud cover (Barradas and Esperon-Rodriguez 2021; Huang 2022; Esperon-Rodriguez et al. 2022). Water availability emerges as a critical determinant of tree survival under heat stress, alongside the anticipated surge in extreme weather events including heat waves and droughts (Barradas and Esperon-Rodriguez 2021; Esperon-Rodriguez et al. 2022). A recent study by Esperon-Rodriguez et al. (2022) examined 3,129 tree species in 164 cities (78 countries). 56–65% of these species exceed safe limits under current temperature and precipitation, surviving due to management (e.g., irrigation) and/or trait plasticity (Esperon-Rodriguez et al. 2022). Our results underscore considerable trait variation within species (Fig. 4; Table S3), which could explain how, in addition to management, plants survive even when exceeding their safety limits.

By 2050, an estimated 70% of species will be affected by climate change, as projected under the RCP 6.0 scenario (Esperon-Rodriguez et al. 2022). The implications are more

pronounced in lower latitudes (in cities like New Delhi and Singapore), where all species are vulnerable. This susceptibility to changing conditions emphasizes the urgency of increasing our understanding of urban forests, especially in poorly studied cities such as those in the Global South. Climate change amplifies the UHI effect and increases global tree mortality (Brandt et al. 2016). However, despite plant susceptibility, considerations for species selection have not been systematically integrated into urban forest planning within future climate change scenarios (Khan and Conway 2020). To safeguard the ecosystem services already provided by urban forests, a paradigm shift is needed. This shift should prioritize the integration of climate-resilient species, focusing on both species and functional diversity.

Declarations

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