



ANA CAROLINA LACERDA DE MATOS

**EXPLORING THE INFLUENCE OF URBANIZATION
INTENSITY AND HABITAT TYPES ON SPONTANEOUS
URBAN FLORA: RICHNESS, COVER, COMPOSITION, AND
FUNCTIONAL TRAITS**

**LAVRAS – MG
2023**

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Tese apresentada à Universidade Federal de Lavras, como parte dos requisitos necessários do Programa de Pós-graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Doutor.

Prof. Dr. Rafael Dudeque Zenni
Orientador

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ANA CAROLINA LACERDA DE MATOS

EXPLORANDO A INFLUÊNCIA DA INTENSIDADE DE URBANIZAÇÃO E TIPOS DE HABITAT NA FLORA URBANA ESPONTÂNEA: RIQUEZA, COBERTURA, COMPOSIÇÃO E CARACTERÍSTICAS FUNCIONAIS

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RESUMO

Compreender os efeitos da urbanização na biodiversidade é de extrema importância devido ao impacto significativo que a urbanização exerce sobre a sociedade humana. Este estudo investigou a influência da intensidade de urbanização em cidades de médio porte sobre a riqueza, cobertura vegetal e composição de espécies nativas e exóticas. Também foram analisadas diferenças nos traços funcionais das plantas nesses ambientes. Os resultados revelaram que a riqueza e a composição de plantas nativas não apresentaram relação com a intensidade da urbanização. No entanto, a riqueza de plantas exóticas e a cobertura de plantas nativas foram afetadas pela urbanização. Calçadas e lotes vagos destacaram-se como habitats importantes para a riqueza de plantas nativas e exóticas. A altura máxima das plantas foi o único traço funcional relacionado à intensidade da urbanização. A intensidade de urbanização afetou a riqueza de plantas exóticas e a cobertura vegetal de plantas nativas, enquanto a composição de espécies não foi influenciada. Estudos futuros devem considerar fatores como relação com o solo e temperatura em escalas regionais e globais para uma compreensão mais abrangente dos padrões de distribuição de plantas em áreas urbanas e suas interações com o ambiente. Além disso, a importância dos habitats urbanos para o crescimento das plantas destaca a necessidade de investigar os padrões funcionais nessas áreas, a fim de avaliar o potencial das espécies exóticas invasoras e seu impacto na biodiversidade nativa.

PALAVRAS-CHAVE: Ecologia urbana. Ecologia urbana. Habitats urbanos. Atributos funcionais. Diversidade taxonômica. Urbanização.

ABSTRACT

Understanding the effects of urbanization on biodiversity is crucial due to its significant impact on human society. This study investigated the influence of urbanization intensity of medium-sized cities on the richness, vegetation cover, and composition of native and non-native species. Differences in plant functional traits in these environments were also analyzed. The results revealed that the richness and composition of native plants were not related to the intensity of urbanization. However, the richness of non-native plants and the cover of native plants were affected by urbanization. Sidewalks and vacant lots stood out as important habitats for the richness of both native and non-native plants. The maximum height of plants was the only functional trait related to the intensity of urbanization. Urbanization intensity affected the richness of non-native plants and the vegetation cover of native plants, while species composition was not influenced. Future studies should consider factors such as soil relationships and temperature at regional and global scales for a more comprehensive understanding of plant distribution patterns in urban areas and their interactions with the environment. Furthermore, the importance of urban habitats for plant growth highlights the need to investigate functional patterns in these areas in order to assess the potential of invasive non-native species and their impact on native biodiversity.

KEYWORDS: Urban ecology. Urban ecology. Urban habitats. Functional attributes. Taxonomic diversity. Urbanization.

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PARTE 1: Introdução geral da tese

INTRODUÇÃO GERAL

A urbanização é considerada o maior agente de modificação social, econômica e ecológica na sociedade humana (MUMFORD, 1968; POTGIETER; CADOTTE, 2020). Atualmente, mais de 50% da população humana vive nas cidades, o que resulta na expansão de paisagens urbanas ao redor do mundo (KNAPP *et al.*, 2008; WILLIAMS *et al.*, 2015; ARONSON *et al.*, 2016). Em função da maioria das cidades ao redor do mundo se concentrar em áreas com alta biodiversidade, a constante expansão da urbanização tem um efeito considerável na biodiversidade global (ARONSON *et al.*, 2016). As cidades são novos ecossistemas que fornecem laboratórios naturais para examinar processos de colonização, sucessão e assembleia comunitária (ARONSON *et al.*, 2014; ARONSON *et al.*, 2016). A avaliação de tais processos em cidades é crítica, pois grande parte do conhecimento e teoria ecológica tem sido derivados de sistemas naturais ou não urbanos que podem funcionar de maneira bastante diferente (HAHS; EVANS, 2015).

Em áreas urbanas, a combinação de condições ambientais alteradas, como a diminuição da umidade média anual do ar (BRIDGMAN *et al.*, 1995) e o aumento da temperatura média anual (OKE, 1982; BOWLER *et al.*, 2010; WOLF *et al.*, 2020), além da perda ou conversão de habitats nativos resultam na formação de um ecossistema diferente das áreas naturais comumente conhecidas (ARONSON *et al.*, 2007; RICOTTA *et al.*, 2009; KOWARIK, 2011; CADOTTE *et al.*, 2017). Além disso, as áreas urbanas são um ecossistema diferente de habitats naturais, como as florestas, em função da presença de habitats exclusivamente urbanos, como calçadas, lotes vagos e praças. Estes elementos urbanos permitem que tanto plantas quanto animais possam se desenvolver, permanecer nestes locais e até mesmo expandir a área de sua ocorrência (KUHN *et al.*, 2017; POTGIETER *et al.*, 2019). Algumas espécies de plantas herbáceas, por exemplo, conseguem crescer em pequenas frestas que se formam no asfalto das calçadas e o intenso fluxo de pessoas que caminham nestas calçadas acaba facilitando a dispersão destas plantas para outros locais, aumentando ainda mais a abrangência destas espécies de plantas nas cidades (BONTHOUX *et al.*, 2019).

Alguns estudos recentes mostraram que a urbanização pode influenciar o aumento da propagação de determinadas espécies de plantas e com isso afetar diretamente a comunidade, riqueza e composição destas espécies. Por exemplo, um estudo em Blois, França, comparou pavimentos arenosos e asfaltados em termos de flora espontânea. Pavimentos arenosos

apresentaram maior cobertura vegetal e riqueza de espécies. Além disso, áreas comerciais e industriais mostraram maior diversidade de espécies e cobertura vegetal em comparação a bairros residenciais e a permeabilidade dos pavimentos também foi identificada como um fator importante para promover a biodiversidade urbana (BONTHOUX *et al.*, 2019).

Um outro estudo classificou a flora urbana em cinco tipos de flores e quatro tipos de polinizadores. Espécies adaptadas a temperaturas mais altas, maior exposição à luz e baixa umidade foram mais comuns em comunidades de plantas urbanas. As mudanças nas preferências ambientais das plantas foram mais notáveis, sugerindo que as condições urbanas específicas tiveram maior impacto em áreas extensas (DESAEGHER *et al.*, 2019). Assim, estes trabalhos exemplificam como os elementos urbanos e as condições urbanas específicas, como o aumento da temperatura, podem ser capazes de interferir na propagação de espécies de plantas nestes locais. As características urbanas específicas podem alterar parâmetros como a diversidade, composição, riqueza e até mesmo traços funcionais de espécies de plantas.

Áreas urbanizadas são caracterizadas por uma intensa indução da fragmentação do habitat e processos ambientais estressantes que filtram espécies com traços de história de vida diversificados (WILLIAMS *et al.*, 2015; HU *et al.*, 2021). Consequentemente, os traços funcionais são um aspecto essencial para compreendermos como espécies respondem aos ambientes urbanos e a forma como as espécies contribuem para o funcionamento do ecossistema (HU *et al.*, 2021). Um estudo realizado em uma cidade do sul de Minas Gerais, Brasil, investigou como a intensidade da urbanização afetou as características funcionais de dispersão de plantas espontâneas. Houve uma diminuição nos traços funcionais com o aumento da urbanização, incluindo altura das plantas, número e tamanho de frutos de plantas nativas e número de sementes de plantas naturalizadas (ALMEIDA *et al.*, 2023). Um outro trabalho realizado na mesma região de Minas Gerais com traços funcionais determinou que a altura da comunidade de plantas foi maior em lotes vagos e a área-foliar específica (SLA) das plantas aumentou com a porcentagem pavimentação (SILVA, 2023). Portanto, de acordo com os resultados dos estudos citados anteriormente, é possível afirmar que a urbanização pode afetar diretamente as características taxonômicas e funcionais de plantas em níveis distintos, como comunidades e ecossistemas, em áreas urbanas. Além disso, habitats urbanos, como calçadas e lotes vagos, podem influenciar e até mesmo determinar a presença de espécies nativas e exóticas nas cidades.

As invasões biológicas por espécies exóticas invasoras são reconhecidas como uma das mais importantes ameaças à biodiversidade e estão entre as principais causas de mudanças

globais no Antropoceno (BPBES, 2019; SHACKLETON *et al.*, 2019). O número de espécies exóticas com potencial de se tornarem invasoras e os efeitos negativos gerados pelas mesmas têm aumentado nas últimas décadas e isso tende a continuar (BPBES, 2019; VILÀ; HULME, 2017; HORVITZ *et al.*, 2017). Espécies exóticas invasoras podem ter efeitos negativos que vão desde indivíduos (sobrevivência, crescimento e reprodução) até processos ecossistêmicos (alterações na ciclagem de nutrientes, por exemplo) (PYŠEK *et al.*, 2012; ZENNI *et al.*, 2016). No Brasil, estima-se a ocorrência de pelo menos 1.214 espécies exóticas estabelecidas, das quais 460 são reconhecidas como espécies exóticas invasoras (ZENNI *et al.*, 2016). Além disso, a imigração e o intenso fluxo de atividades humanas nas cidades são características que contribuem para a entrada de diversas espécies exóticas nestas áreas, que ao longo do tempo podem tornar-se invasoras (PYŠEK *et al.*, 2010; CADOTTE *et al.*, 2017). Em função das intensas atividades humanas poderem aumentar ainda mais a ocorrência de espécies exóticas nos centros urbanos, é crucial compreender as diferenças taxonômicas e funcionais que ocorrem entre espécies nativas e exóticas.

Atualmente, uma das informações que sabemos sobre ambientes urbanizados é que a presença de espécies exóticas invasoras causa a homogeneização da cobertura vegetal e a homogeneização da cobertura vegetal afeta negativamente a biodiversidade nativa (KNAPP *et al.*, 2012; WILLIAMS *et al.*, 2015). Ainda, é válido ressaltar que áreas urbanas vêm sendo afetadas pelas pressões causadas em função do rápido crescimento da população humana, que reduzem a heterogeneidade do habitat e facilitam a invasão de espécies exóticas invasoras. Entretanto, muitos estudos acabam sendo realizados em apenas uma única cidade devido à dificuldade de execução dos trabalhos em maiores escalas, o que dificulta a determinação de padrões de ocorrência em multi-escalas e diferenças funcionais e taxonômicas entre espécies nativas e exóticas (WILLIAMS *et al.*, 2015; ARONSON *et al.*, 2016; HU *et al.*, 2021). Por isso, é necessário focar os esforços em estudos com escalas regionais que determinem os mecanismos que permitem que espécies exóticas consigam prevalecer em áreas urbanas evitando que elas se tornem invasoras e possam prejudicar a biodiversidade nativa.

Considerando a crescente expansão da urbanização e as consequências que as atividades humanas podem causar para a biodiversidade global, é extremamente relevante compreender a movimentação das espécies em áreas urbanas. Além disso, compreender as diferenças taxonômicas e funcionais de espécies nativas e exóticas em áreas urbanas e sua relação com o ambiente antropizado nos dá subsídios para focar em esforços que possam, de fato, garantir a manutenção da biodiversidade, através do conhecimento de características

funcionais de espécies de plantas exóticas que possam prejudicar as nativas. Diante disso, o presente trabalho teve como principal objetivo compreender de que maneira a urbanização de cidades com densidades demográficas distintas influencia a riqueza, cobertura vegetal e composição de plantas herbáceas nativas e exóticas. Ainda, o presente trabalho teve como objetivo determinar diferenças entre a riqueza de plantas herbáceas nativas e exóticas e habitats urbanos. Por fim, este trabalho também se propôs a compreender as diferenças nos traços funcionais de plantas herbáceas nativas e exóticas em áreas urbanas e determinar se existem diferenças nos traços ao longo de habitats urbanos distintos.

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PARTE 2: Artigo para submissão na revista *Urban Ecosystems*

(<https://www.springer.com/journal/11252>)

Unveiling the Influence of Urbanization Intensity on Spontaneous Urban Flora: Cover, Richness, and Composition

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Abstract

Over the 20th century, the urban human population has grown from 20 million to 2.8 billion; today, more than half of the human population lives in urban areas. The scale and speed of urban growth have multifaceted impacts on the global environment and urbanization is now considered a major driving force of biodiversity loss and biological homogenization. Considering that cities continue to expand, and more urban elements, such as sidewalks, vacant lot and public parks, will appear within these urban areas, it is essential to comprehend how urbanization can affect spontaneous plant communities in different cities. For that, the current work sought to answer the following questions: (I) How does intensity of urbanization affect the richness of native and non-native herbaceous species in cities? (II) How does intensity of urbanization affect the plant cover of native and non-native herbaceous species in cities? (III) How does intensity of urbanization affect the composition of native and non-native herbaceous species in cities? (IV) How does urban habitats affect native and non-native herbaceous species richness? Our results revealed that the richness and composition of native plants were not related to the intensity of urbanization. However, the richness of non-native plants and the cover of native plants were affected by urbanization intensity. Sidewalks and vacant lots stood out as important habitats for the richness of both native and non-native plants.

Keywords: Urban ecology; urban community; non-native; native; plant.

Introduction

Over the 20th century, the urban human population has grown from 20 million to 2.8 billion; today, more than half of the human population lives in urban areas (UNFPA, 2007). The scale and speed of urban growth have multifaceted impacts on the global environment (ELMQVIST *et al.*, 2013) and urbanization is now considered a major driving force of biodiversity loss and biological homogenization (BLOUIN *et al.*, 2019). Thus, biodiversity crisis resulting from rising levels of anthropogenic impacts on ecosystems has been extensively discussed over the last decades (ELLIS *et al.*, 2010; CARDINALE *et al.*, 2012; ISEHARD *et al.*, 2019). However, the impact of human populations on biodiversity patterns is still poorly understood (RAMÍREZ-RESTREPO; MACGREGOR-FORS, 2017; ISEHARD *et al.*, 2019). As cities continue to expand, changing and fragmenting landscapes from agricultural and native areas to areas covered primarily by impermeable surfaces, there is a growing concern about the loss of natural habitats, extinction of native species, and spread of invasive non-native species (ARONSON *et al.*, 2017; WILLIAMS *et al.*, 2015; RICOTTA *et al.*, 2017).

In urban areas, anthropogenic land use, such as land subdivision, roads, and human-made activities, have been implicated as a cause of increasing non-native species richness and abundance (LOCKWOOD *et al.*, 2005; GALLARDO *et al.*, 2015; EL-BAROUGY *et al.*, 2021). Considering this, a study evaluated how plant species richness and beta diversity differ in vacant lots between two urban areas. They found a lower beta diversity for plant communities in vacant lots in the most urbanized landscape compared to the least urbanized one, but no effect of local level of urbanization intensity in either of the landscapes. Non-native richness was higher than native richness at each local level of urbanization intensity (BLOUIN *et al.*, 2019). Another study determined urbanization by comparing plant diversity and proportion of non-native/endemic plant species with the percentage of total impervious surface area. An increase in impervious surface area reduced plant diversity and the ratio of non-native to endemic plant species increased as impervious surface area increased (YAN *et al.*, 2019). Thus, the results of these studies indicate that urban elements, such as vacant lots, can play a role in determining species richness and composition and biotic homogenization (which leads to loss of beta-diversity) occurred in many urbanized landscapes.

Urban elements such as vacant lots and squares, can play a role in determining species richness and composition of spontaneous plant species in urban areas. Other urban elements, such as streets and sidewalks can be a significant component of urban landscapes, with multiple ecological roles and social-economic functions (CANEVA *et al.*, 2020). Native and non-native

urban spontaneous vegetation can be found in any type of green space within a city as well as growing on surfaces such as walls, pavements and rooftops. Spontaneous vegetation range in extent from large vacant lots (MILLARD, 2004) to very small, such as in pavement cracks or sidewalks. Some works have shown that spontaneous vegetation can contribute to important ecosystem services in urban areas, such as habitat for insects and other arthropods (ROBINSON; LUNDHOLM, 2012), and utilitarian value as medicine, food and ceremonial objects (GUERRERO-LEIVA *et al.*, 2021). Besides that, urban green spaces provide refuges for species that are unintentionally introduced by humans, and which do not inhabit to the remnants of natural habitats in urban areas. Cities can harbor a significant number of non-native plant species that can find good condition in places like vacant lots, sidewalks, public squares (BLOUIN *et al.*, 2019; BONTHOUX *et al.*, 2019; FIGUEROA *et al.*, 2020). Within time, introduced non-native plant species in urban areas can reproduce, spread, and become invasive species, bringing negative consequences to urban native flora since invasive species can compete for space and resources (CELESTI-GRAPOW *et al.*, 2006). A recent study determined the contribution of native and non-native species in urban parks of a temperate biome, recording 550 species, 16.2% of which native and 83.8% non-native (FIGUEROA *et al.*, 2020). Therefore, these studies show the importance of understanding how urban elements drivers of can be facilitating biological invasions. It is important to understand the patterns and differences between native and non-native plant species to ensure that urban areas can be places capable of conserving native biodiversity.

Urbanization is one of the most homogenizing of all major human activities (MCKINNEY, 2006; KNAPP *et al.*, 2012; WILLIAMS *et al.*, 2015), which can lead to the loss of biodiversity. Besides that, urban elements, can play a role in facilitating the spread of plant species (BLOUIN *et al.*, 2019; BONTHOUX *et al.*, 2019; FIGUEROA *et al.*, 2020). Understanding the relationship between urban elements and native and non-native species can bring us a more comprehensive idea about the patterns of spontaneous plant community parameters, such as species richness, composition and plant cover. Comprehend the differences between native and non-native community parameters can guide us to thoroughly understand of how urban elements can shape and facilitate the spread of native and non-native species. Enhancing our comprehension of the distinctions in community parameters between native and non-native species holds the potential to bolster the conservation efforts of native species in urban areas, while concurrently deepening our understanding of the intricate relationship between urbanization and biodiversity.

Considering that cities will continue to expand, and more urban elements will potentially alter the composition and distribution of spontaneous plant communities as urbanization encroaches upon natural habitats, it is essential to comprehend how urbanization can affect spontaneous plant communities in different cities. For that, the current work sought to answer the following questions: (I) How does intensity of urbanization affect the richness of native and non-native herbaceous species in cities? (II) How does intensity of urbanization affect the plant cover of native and non-native herbaceous species in cities? (III) How does intensity of urbanization affect the composition of native and non-native herbaceous species in cities? (IV) How does urban habitats affect native and non-native herbaceous species richness?

Methods

Our study area comprised of six medium-sized cities in the southern region of Brazil: Alfenas (21° 25' 46" S, 45° 56' 50" W), Lavras (21° 14' 45" S, 44° 59' 59" W), Poços de Caldas (21° 47' 18" S, 46° 33' 45" W), Pouso Alegre (22° 14' 3" S, 45° 55' 60" W), Três Corações (21° 42' 29" S, 45° 16' 10" W) and Varginha (21° 32' 47" S, 45° 25' 51" W) (Fig. 1). The cities have around 80,973, 105,756, 169,838, 154,293, 80,561, and 137,608 of total human population, respectively, with demographic densities of 86.75 hab/km², 163.26 hab/km², 278.54 hab/km², 240.51 hab/km², 87.88 hab/km² and 311.29 hab/km² (IBGE, 2019). The region's climate is characterized as subtropical, with a dry winter (Cwa classification according to Köppen and Geiger), with an annual average temperature of 20.6° C and an average annual rainfall of 1508 mm (SÁ JÚNIOR, 2009).

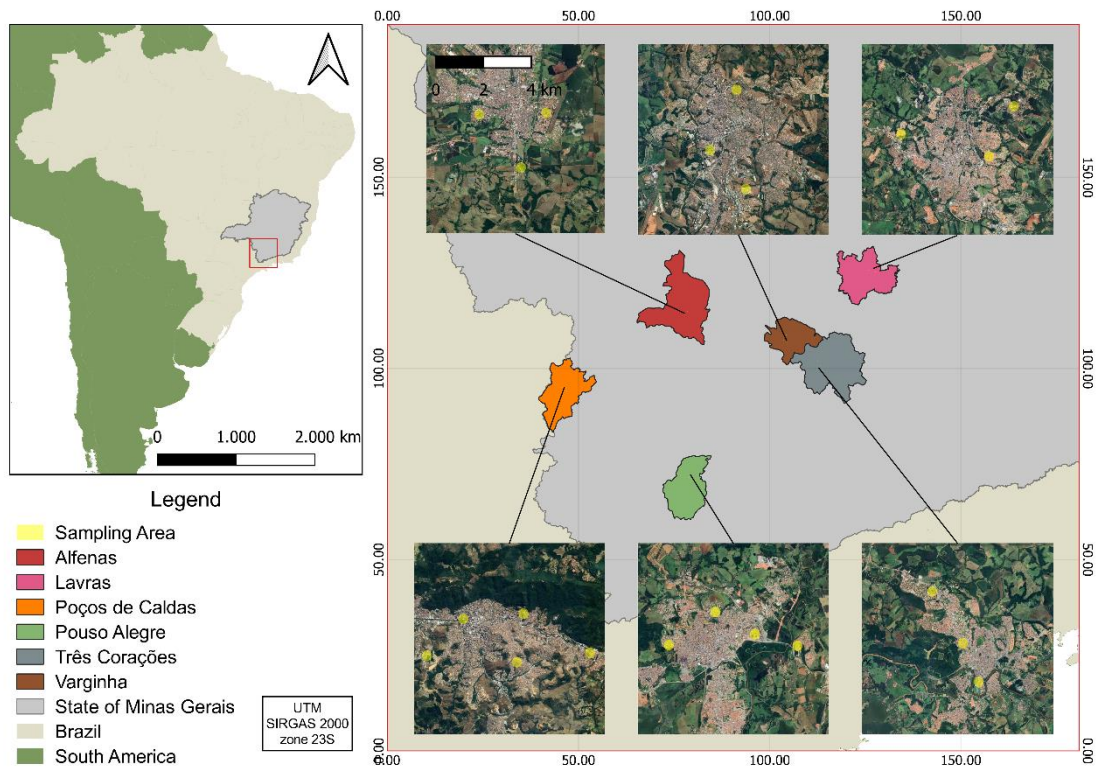


Fig. 1. Map of the study area location in Minas Gerais, Brazil, and distribution of classified areas within the urban perimeter of the municipalities of Alfenas (red), Lavras (pink), Poços de Caldas (orange), Pouso Alegre (green), Três Corações (blue), and Varginha (brown). The square areas of 1 km² define the intensity of urbanization in the landscape, and the yellow circular areas with a radius of 200 m define the locations of the sample units.

Firstly, we used Sentinel-2 images of the study cities (obtained in September 2019) with a resolution of 10 m to characterize the landscape around each study area. We used the Semiautomatic Classification (SCP) plugin (CONGEDO, 2016) to classify the images in QGIS software version 3.10.0 (QGIS Development Team, 2019). We considered four classes of land cover: water bodies, impervious surfaces, trees, and grasses. We considered all urban areas, such as roads, buildings, and industrial areas, as impervious surface cover. For the grass cover class, we included exposed soil, natural open fields, areas covered with ruderal plants, and managed grassland. Finally, we manually post-processed the land use map resulting from the classification to correct minor errors of the semiautomatic classification.

Using the LeCos plugin (JUNG, 2016), we calculated each class's coverage percentages and the landscape's Shannon diversity index along four radii (200 m, 500 m, 750 m, and 1,000 m). The percentages of land cover represented the class cover concerning the total landscape

area, and the Shannon diversity index described the environmental heterogeneity of the landscape, considering the patch number of each landscape class (BOSCOLO *et al.*, 2017; NERY *et al.*, 2018). The Shannon index of the landscape increased when the number of different land cover units increased, or the proportional area of these units became more equitable (MCGARIGAL *et al.*, 2012). We considered the percentage of impervious surface cover, which varied between 38.31 and 93.22%, to characterize the urbanization gradient.

Secondly, we selected a total 21 sampling areas in the six municipalities. We selected our sampling areas based on the Sentinel-2 images we obtained to characterize the landscape around each study area. The number of sampling areas per municipality varied according to the urban area of each city excluding areas deemed unsafe after a first visit and areas that were not completely within the urban perimeter of the city. After all potential sampling areas were mapped and evaluated *in situ*, we selected three areas in Alfenas (26.8 km²), Lavras (24.4 km²), Três Corações (18.4 km²), and Varginha (30.7 km²), four areas in Pouso Alegre (27.5 km²), and five areas in Poços de Caldas (37.1 km²) for a total of 21 sampling areas. In each city we defined a 1 km buffer around each sampling area, so the buffers would not overlap within each other in the cities, and we could obtain the maximum quantity of buffers per city as possible. For that reason, we had the variation from 3 to 5 sampling areas in the cities. We characterized our 21 sampling areas by a 200 m radius buffer around areas, which was inside the 1 km buffer. Our sampling area selection followed closed the one used by Tavares-Brancher *et al.* (2023). Within each sampling area, we haphazardly placed ten 1 m² plots to sample spontaneous herbaceous plants. To characterize our sampling areas, we selected three types of the urban habitats: sidewalks, vacant lots, and public parks. Our criterion for urban elements guaranteed that each street within the buffer had at least one plot (we chose the place of each plot according to the presence of urban elements) so that we could sample the entire length of the 200 m buffer. To understand how richness of native and non-native species can vary along urban elements, we collected the spontaneous plants we found on sidewalks, vacant lots and public parks within our plots.

We conducted the fieldwork between February 2020 and February 2021 (with six sampling months during Summer and Spring). We sampled only spontaneous herbaceous plants and did not include cultivated flora. In each 1 m² plot, we measured the percentage of plant cover of all species by a single observer in each sampling unit and collected five individuals of each species inside the plot. In the laboratory, we used the APG system (Angiosperm Phylogeny Group) IV (2016), published identification guides and the support from a botanist (see

acknowledgements) to identify to the species level. To classify each species into native and non-native of the study region, we used information available at the ReFlora - Virtual Herbarium <https://reflora.jbrj.gov.br/reflora>. We conducted a species accumulation curve analysis to assess if the species accumulation curves stabilized across all six cities and to determine if our sampling effort was sufficient to adequately capture the species diversity in each city included in the study.

To determine which variables, we could use as a proxy for urbanization, we did a Pearson correlation test. Since all the variables were correlated, we decided to use the one that best described intensity of urbanization, which was the proportion of impervious surface. To answer how intensity of urbanization affects the richness and plant cover of native and non-native herbaceous species in cities, we did linear models (LM) and generalized linear models (GLM). In one of the models, we used the richness of native species as our response variable, and in the other model, we used the richness of non-native species. For both models we used the proportion of impervious surface as our explanatory variable. For the GLM, we used the Gamma (GLM) family distribution for our models with richness and plant cover. To verify if native and non-native species richness varied across the urban habitats (sidewalks, vacant lots and public parks) we did linear models (LM). To verify the relationship between urban habitats and species richness we did a post-hoc analysis (Tukey).

Finally, to answer if the intensity of urbanization could affect the composition of native and non-native species in six different cities, we did a Redundancy analysis (RDA) (function “rda”, package “vegan” - OKSANEN *et al.*, 2021), which is a method to extract and summarize the variation in a set of response variables that can be explained by a set of explanatory variables. In the first RDA analysis, we utilized the set of native species present in the 21 sampling areas to define the composition of the native species as the response variable. In the second RDA analysis, we utilized the set of non-native species present in the 21 sampling areas to define the composition of non-native species as the response variable. For both models we used the proportion of impervious surface, as our operational variables. All analyses were performed using R Statistical Software (v4.0.5; R Core Team, 2021).

Results

We identified a total of 104 plant species in the six cities belonging to 75 genera and 29 botanical families (Sup. Table 1). We classified 55 species as native and 49 as non-native species according to the region where the study occurred (Sup. Table 1). The city with the greatest

number of species was Poços de Caldas (62 species, 31 for either native and non-native species), followed by Pouso Alegre (40 species, where 21 were native species and 19 were non-native species), Alfenas (39 species, where 19 were native species and 20 were non-native), Três Corações (36 species, where 19 were native and 17 were non-native species), Varginha (36 species, 18 for either native and non-native species) and Lavras (35 species, where 20 were native and 15 were non-native species) (Table 1). The most common species across all six cities were: *Conyza bonariensis*, *Euphorbia hirta*, *Euphorbia prostrata* and *Urochloa decumbens*. We classified *C. bonariensis*, *E. hirta* and *E. prostrata* as native species and *U. decumbens* as a non-native species.

The urbanization intensity did not explain native species richness ($R^2 = 0.012$; $p = 0.6$) (Fig. 2) (Table 1). However, the non-native species richness increased with increases in urbanization intensity ($R^2 = 0.3$, $p = 0.02$) (Fig. 2). We found differences in both, native ($F = 12.51$; $p < 0.001$) and non-native ($F = 45.43$; $p < 0.001$) species richness between urban habitats (Fig. 3). Comparing the three urban habitats, sidewalks are richer than parks ($p = 0.004$), vacant lots are richer than sidewalks ($p < 0.0001$). We found differences for the analysis between non-native species richness and urban habitats (Fig. 3). Non-native species richness was greater in sidewalks than parks ($p < 0.001$) but did not vary between vacant lots and parks ($p = 0.05$). Finally, non-native species richness was greater in sidewalks than vacant lots ($p < 0.001$). Finally, non-native species richness was greater in sidewalks than vacant lots ($p < 0.001$).

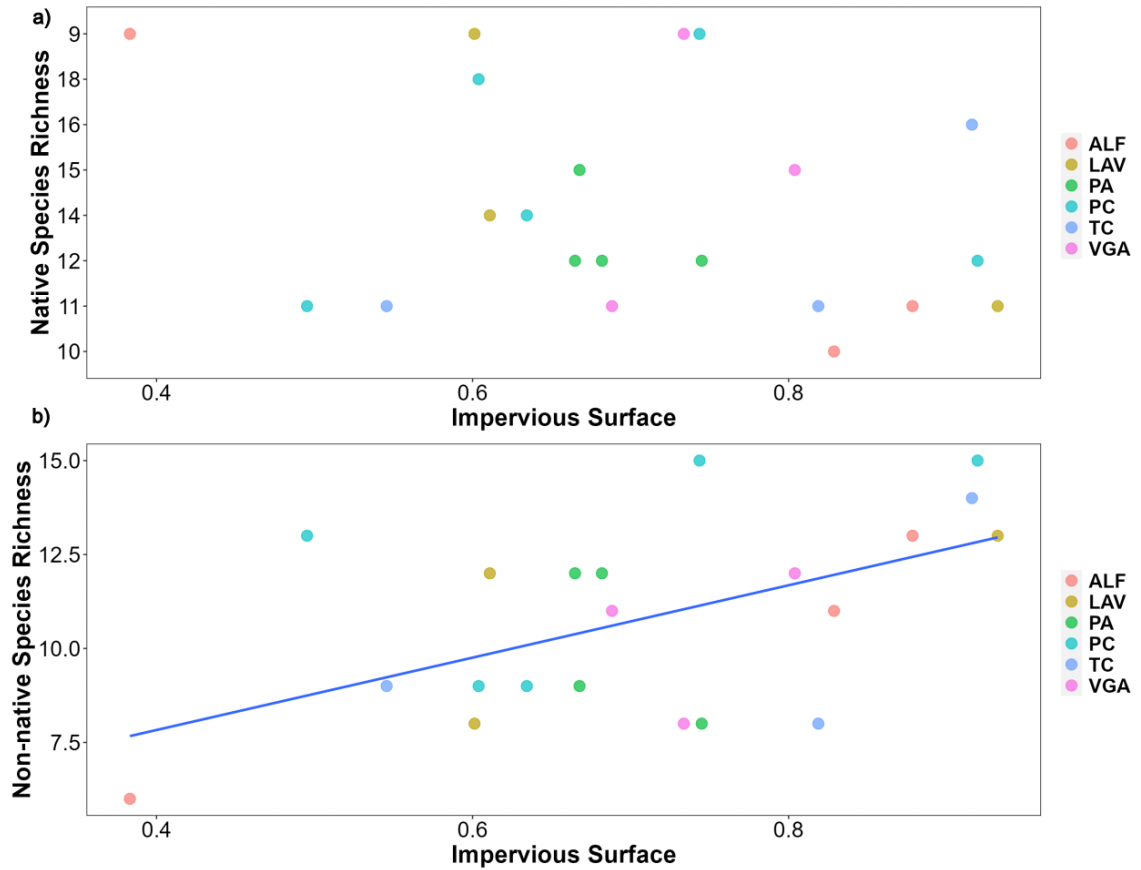


Fig. 2. Variation in (a) native and (b) non-native plants richness as a function of urbanization (proportion of impervious surface). Red dots on the graph represent the city of Alfenas (ALF), yellow dots the city of Lavras (LAV), green dots the city of Pouso Alegre (PA), blue dots the city of Poços de Caldas (PC), gray dots the city of Três Corações (TC) and purple dots the city of Varginha (VGA).

Table 1. Mean and standard deviation (SD) values of the dependent variables for species richness and cover.

Dependent variables	Mean	SD
Total species richness	17.71154	± 49.20211
Native species richness	18.52727	± 52.0174
Non-native species richness	16.79592	± 46.3582
Alfenas total species richness	5.923077	± 9.243446
Alfenas native species richness	6.894737	± 10.70771
Alfenas non-native species richness	5	± 7.773098
Lavras total species richness	8.228571	± 11.80749
Lavras native species richness	7.55	± 12.11991
Lavras non-native species richness	9.133333	± 11.73436
Poços de Caldas total species richness	6.483871	± 15.11567
Poços de Caldas native species richness	6.387097	± 13.37081
Poços de Caldas non-native species richness	6.580645	± 16.90518
Pouso Alegre total species richness	9,825	± 14.63555
Pouso Alegre native species richness	10.19048	± 15.60967
Pouso Alegre non-native species richness	9.421053	± 13.89371
Três Corações total species richness	6.694444	± 9.313031
Três Corações native species richness	7.631579	± 10.56309
Três Corações non-native species richness	5.647059	± 7.873541
Varginha total species richness	7.972222	± 14.32976

Varginha native species richness	10	± 18.33672
Varginha non-native species richness	5.944444	± 8.821579
Total species cover	11.75841	± 15.8985
Native species cover	40.76471	± 29.96079
Non-native species cover	65.72906	± 51.96029
Alfenas total species cover	10.31602	± 12.10029
Alfenas native species cover	8.396947	± 11.85274
Alfenas non-native species cover	12.83	± 12.01771
Lavras total species cover	12.16319	± 15.1291
Lavras native species cover	9.635762	± 12.85275
Lavras non-native species cover	14.94891	± 16.90907
Poços de Caldas total species cover	13.23632	± 18.25891
Poços de Caldas native species cover	9.635762	± 12.85275
Poços de Caldas non-native species cover	18.90686	± 22.41297
Pouso Alegre total species cover	10.00763	± 14.09706
Pouso Alegre native species cover	7.084112	± 7.73034
Pouso Alegre non-native species cover	13.50279	± 18.53584
Três Corações total species cover	12,639	± 16.5617
Três Corações native species cover	9.103448	± 8.455541
Três Corações non-native species cover	17.97917	± 23.16621
Varginha total species cover	12.10105	± 17.31224
Varginha native species cover	8.116667	± 7.607902

Varginha non-native species cover 18.80374 ± 25.27077

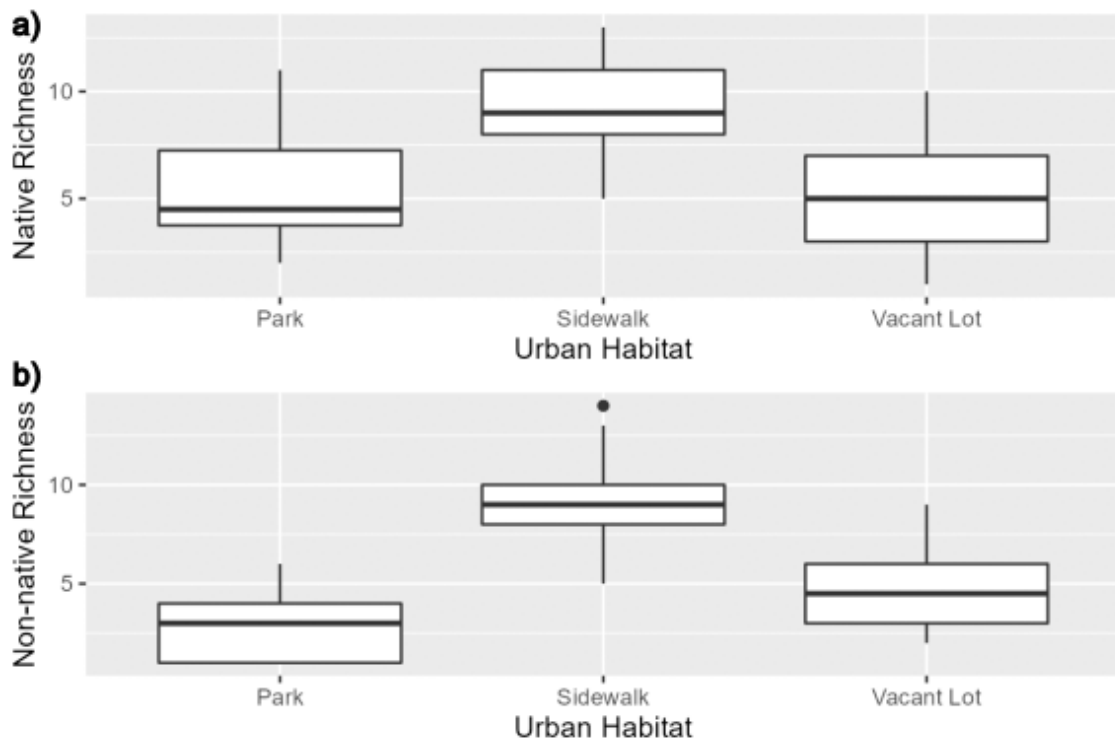


Fig. 3. Variation in (a) native plant richness and (b) non-native plant richness as a function of urban habitats (parks, sidewalks and vacant lots).

Native plant cover showed a significant relation with the proportion of impervious surface ($R^2 = 0.07$; $p = 0.002$), revealing that native plant cover increased with the increasing of the intensity of urbanization (proportion of impervious surface) (Fig. 4). For non-native plant cover we did not find a relation between the proportion of impervious surface and non-native plant cover ($R^2 = 0$; $p = 0.95$), which means that Our findings did not reveal any correlation between the presence of non-native plant cover and the rising proportion of impervious surfaces (Fig. 4).

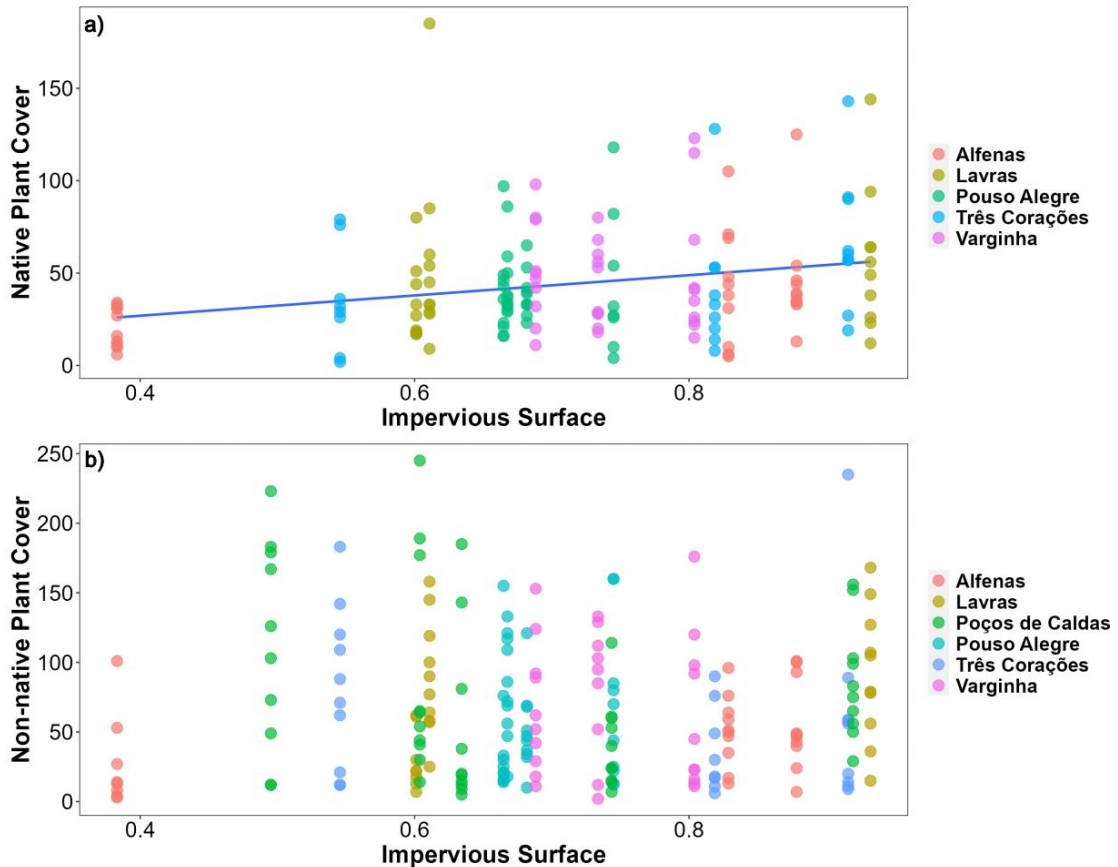


Fig. 4. Variation in native plant cover (a) and non-native plant cover (b) as a function of urban variables and Shannon Index. Red dots on the graph represent the city of Alfenas, yellow dots the city of Lavras, green dots the city of Pouso Alegre, blue dots the city of Poços de Caldas, gray dots the city of Três Corações and purple dots the city of Varginha.

The RDA analysis conducted to investigate the relationship between intensity of urbanization and the composition of native species explained 1.8% of the data variation (Fig. 5), suggesting that the proportion of impervious surface had little association with the variation in native species composition. The ANOVA performed to further assess the relationship between native species composition and the proportion of impervious surface, also did not show any significant relationship ($F = 1.09$; $p = 0.34$), which means that the proportion of impervious surface did not influence the variation in native species composition. Similarly, the model developed for the RDA analysis to understand the relationship between the proportion of impervious surface and the composition of non-native species explained only 1.2% of the variation in the data (Fig. 5). Results for the ANOVA also indicated no significant relationship between the proportion of impervious surface and the composition of non-native species ($F = 1.1044$; $p = 0.3$), which means that the proportion of impervious surface did not determine the

considering the richness for all the species in the six cities. Urban habitats showed a significant relationship with native and non-native richness species, where for both native and non-native species richness we found differences between parks, sidewalks and vacant lots. Urbanization intensity had a positive effect on native plant cover, whereas the proportion of impervious surface increased, native plant cover also increased. However, we could not determine any relation between non-native plant cover and urbanization intensity. Finally, urbanization intensity did not determine the variation in both native and non-native species composition.

We found a positive relationship between urbanization intensity and non-native species richness, whereas no significant relationship was observed between native species and urbanization intensity. We expected that with the increase of urbanization we would find fewer non-native species. However, we found that non-native species richness increased with the increasing of urbanization intensity. Our results rely on the characteristics of the sampling areas we collected. Herbaceous species, such as *Oxalis corniculata* and *Pilea microphylla* (both non-native species found in all six cities), can grow in small gaps in sidewalks and spaces on streets due to their botanical characteristics that enable their proliferation in paving areas with limited space for growth (MOREIRA; BRAGANÇA, 2011). Moreover, we consistently noticed a prevalent trend among people to cultivate small gardens in front of their houses, especially along sidewalks. This practice significantly contributed to the greater likelihood of encountering a wider array of species in regions characterized by a higher proportion of impervious surfaces. Furthermore, the global prevalence of ornamental plant markets and landscaping practices in urban areas has led to a preference for non-native plant species that differ from the native flora typically found in residential environments, where most of our urban plots were located (FIGUEROA *et al.*, 2020; GUERRERO-LEIVA *et al.*, 2021).

Previous studies have long recognized the effect of habitat on species richness in urban environments, including human-made habitats such as public parks, sidewalks, vacant lots, and home gardens, which can harbor considerable species richness (CELESTI-GRAPOW *et al.*, 2006; SUKOPP, 2002; PYŠEK *et al.*, 2004a). Moreover, a high diversity of habitats in urban areas has been linked to high overall biodiversity of cities (PYŠEK, 1989; HELDEN; LEATHER, 2004; SATTTLER *et al.*, 2010; LOKATIS *et al.*, 2023). Here, our results showed differences for native and non-native species richness and urban habitats. Native and non-native species richness presented the same pattern across urban habitats. In general, we found that sidewalks presented a greater species richness than the other urban habitats. These results follow the other result we had for the relation between urbanization intensity and species

richness, where species richness increased with the increasing of urbanization intensity. Sidewalks exhibit a higher plant species richness compared to other urban habitats, including public parks, due to several key factors. While parks are carefully designed and manicured to create aesthetically pleasing landscapes, sidewalks are typically left to natural processes with minimal human intervention (FIGUEROA *et al.*, 2020; GUERRERO-LEIVA *et al.*, 2021). This allows for a greater diversity of plant species to establish and thrive, as they are not subjected to pruning, mowing, or herbicide treatments that may limit their growth (GUERRERO-LEIVA *et al.*, 2021). Secondly, the microhabitats present on sidewalks provide unique opportunities for plant colonization. Sidewalks feature small cracks, crevices, and gaps between paving rocks that act as miniature ecosystems. These microhabitats offer sheltered environments where plant seeds can become lodged, germinate, and establish themselves (BONTHOUX *et al.*, 2019). The urban environment surrounding sidewalks, with its diverse sources of seeds and dispersal agents like wind and animals, further contributes to the potential colonization. Moreover, sidewalks benefit from a constant influx of organic matter and nutrients from nearby vegetation and urban runoff. Fallen leaves, seeds, and other organic debris accumulate on sidewalks, providing a fertile substrate for plant growth. This continuous input of nutrients supports a greater variety of plant species compared to public parks, where nutrient levels may be more carefully managed or supplemented through artificial means (LANDRY; CHAKRABORTY, 2009; ARONSON *et al.*, 2016; GERRISH; WATKINS, 2018). Lastly, the human factor plays a role in sidewalk plant diversity. As pedestrians traverse sidewalks, they inadvertently transport seeds on their shoes or clothing, dispersing them along their path (APOLLO, 2021). This unintentional seed dispersal mechanism contributes to the introduction of new plant species and further enhances the species richness of sidewalk flora. Overall, the combination of less intensive management, unique microhabitats, nutrient availability, and human-mediated seed dispersal make sidewalks surprisingly rich in plant species compared to other urban habitats, such as public parks (FIGUEROA *et al.*, 2020; GUERRERO-LEIVA *et al.*, 2021). Recognizing and appreciating the ecological value of sidewalks can inform urban planning and management strategies aimed at enhancing biodiversity in cities.

Urbanization intensity and native plant cover presented a positive relation in our analysis, where native plant cover increased with the increasing of the proportion of impervious surface. One of the things that can explain our results is the fact that in our study the areas with more proportion of impervious surface were also the ones which comprise the richest neighborhoods (LANDRY & CHAKRABORTY, 2009). In the region of our study, the neighborhoods that have

high incomes are also the ones that most invest in gardening, and our results follow the same pattern found by previous studies of the scientific literature (LANDRY; CHAKRABORTY, 2009; GERRISH; WATKINS, 2018). According to it, a study demonstrated that the wealthier neighborhoods of a Brazilian city had both the highest tree biodiversity and number of trees, whereas the poorer neighborhoods presented a low biodiversity level and fewer tree species. Even though our work did not quantify tree cover, we can assume that socioeconomic aspects play a crucial role in determining plant species cover since plant species cover is strongly associated by human preferences (LANDRY; CHAKRABORTY, 2009; ARONSON *et al.*, 2016; GERRISH; WATKINS, 2018).

Our findings indicated that the presence of native species varied across the sampling areas of the study, whereas the overall composition of non-native species remained relatively consistent. These results follow what previous studies have already shown related to biotic homogenization that non-native species can lead in urban areas (KNAPP *et al.*, 2008; BLOUIN *et al.*, 2019; LOKATIS *et al.*, 2023). Our findings and the results of previous work clarify that species composition of different cities are becoming more similar as urbanization intensity increases (GROFFMAN *et al.*, 2014; LOKATIS *et al.*, 2023).

In conclusion, urbanization intensity alone did not explain both native and non-native species composition, which we can assume that there are other factors influencing native and non-native species composition besides the proportion of impervious surface. In urban areas, the number of factors that can influence species composition is extensive; land use, soil type, climate, human activity and habitat fragmentation are some factors that can affect plant species composition (ARONSON *et al.*, 2016; DESAEGHER *et al.*, 2019). Since in urban areas there are so many factors acting on plant species composition, it is challenging to find what characteristics are driving species composition. Urban habitat types can affect species composition (BONTHOUX *et al.*, 2019), and more complex stressors that operate through biological and biophysical interactions, such as changes to dispersal vectors, would be expected to vary depending on local factors including the biotic composition and its spatial distribution (WILLIAMS *et al.*, 2015). Thus, there is a need for further studies to evaluate other factors that are determining plants species composition besides urban habitats and the proportion of impervious surface. In addition, clearly patterns related to urban factors affecting plant species composition will help us to improve cities as places for biodiversity conservation.

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Supplementary material

STable 1 – Species list, family and information about the invasion status of the species.

Scientific name	Family	Status
<i>Amaranthus blitum</i>	Amaranthaceae	Non-native
<i>Amaranthus deflexus</i>	Amaranthaceae	Non-native
<i>Amaranthus spinosus</i>	Amaranthaceae	Non-native
<i>Amaranthus viridis</i>	Amaranthaceae	Non-native
<i>Boerhavia diffusa</i>	Nyctaginaceae	Non-native
<i>Capsicum annuum</i>	Solanaceae	Non-native
<i>Celosia argentea</i>	Amaranthaceae	Non-native
<i>Commelina benghalensis</i>	Commelinaceae	Non-native
<i>Commelina diffusa</i>	Commelinaceae	Non-native
<i>Cosmos sulphureus</i>	Asteraceae	Non-native
<i>Cynodon dactylon</i>	Poaceae	Non-native
<i>Desmodium incanum</i>	Fabaceae	Non-native
<i>Drymaria cordata</i>	Caryophyllaceae	Non-native
<i>Echinochloa crus-galli</i>	Poaceae	Non-native
<i>Eleusine indica</i>	Poaceae	Non-native
<i>Emilia fosbergii</i>	Asteraceae	Non-native
<i>Eragrostis pilosa</i>	Poaceae	Non-native
<i>Galinsoga parviflora</i>	Asteraceae	Non-native
<i>Galinsoga quadriradiata</i>	Asteraceae	Non-native
<i>Geranium robertianum</i>	Geraniaceae	Non-native
<i>Hedera helix</i>	Araliaceae	Non-native
<i>Lantana camara</i>	Verbenaceae	Non-native

<i>Lepidium virginicum</i>	Brassicaceae	Non-native
<i>Leucas martinicensis</i>	Lamiaceae	Non-native
<i>Matricaria chamomilla</i>	Asteraceae	Non-native
<i>Melinis minutiflora</i>	Poaceae	Non-native
<i>Melissa officinalis</i>	Lamiaceae	Non-native
<i>Momordica charantia</i>	Cucurbitaceae	Non-native
<i>Oxalis corniculata</i>	Oxalidaceae	Non-native
<i>Parthenium hysterophorus</i>	Asteraceae	Non-native
<i>Pilea microphylla</i>	Urticaceae	Non-native
<i>Poa annua</i>	Poaceae	Non-native
<i>Polygonum capitatum</i>	Polygonaceae	Non-native
<i>Portulaca oleracea</i>	Portulacaceae	Non-native
<i>Praxelis pauciflora</i>	Asteraceae	Non-native
<i>Pteridium arachnoideum</i>	Dennstaedtiaceae	Non-native
<i>Rapistrum rugosum</i>	Brassicaceae	Non-native
<i>Sigesbeckia orientalis</i>	Asteraceae	Non-native
<i>Sinapis arvensis</i>	Brassicaceae	Non-native
<i>Solanum lycopersicum</i>	Solanaceae	Non-native
<i>Taraxacum officinale</i>	Asteraceae	Non-native
<i>Tridax procumbens</i>	Asteraceae	Non-native
<i>Urochloa decumbens</i>	Poaceae	Non-native
<i>Urochloa plantaginea</i>	Poaceae	Non-native
<i>Urtica dioica</i>	Urticaceae	Non-native
<i>Veronica chamaedrys</i>	Plantaginaceae	Non-native
<i>Veronica persica</i>	Plantaginaceae	Non-native

<i>Veronica serpyllifolia</i>	Plantaginaceae	Non-native
<i>Zoysia matrella</i>	Poaceae	Non-native
<i>Ageratum conyzoides</i>	Asteraceae	Native
<i>Alternanthera pungens</i>	Amaranthaceae	Native
<i>Ambrosia artemisiifolia</i>	Asteraceae	Native
<i>Astraea lobata</i>	Euphorbiaceae	Native
<i>Bidens alba</i>	Asteraceae	Native
<i>Bidens gardneri</i>	Asteraceae	Native
<i>Bidens pilosa</i>	Asteraceae	Native
<i>Bidens subalternans</i>	Asteraceae	Native
<i>Borreria capitata</i>	Rubiaceae	Native
<i>Borreria verticillata</i>	Rubiaceae	Native
<i>Calopogonium mucunoides</i>	Fabaceae	Native
<i>Chaetogastra gracilis</i>	Melastomataceae	Native
<i>Chaptalia nutans</i>	Asteraceae	Native
<i>Conyza bonariensis</i>	Asteraceae	Native
<i>Conyza canadensis</i>	Asteraceae	Native
<i>Croton glandulosus</i>	Euphorbiaceae	Native
<i>Cuphea carthagenensis</i>	Lythraceae	Native
<i>Cuphea racemosa</i>	Lythraceae	Native
<i>Desmodium barbatum</i>	Fabaceae	Native
<i>Dichondra macrocalyx</i>	Convolvulaceae	Native
<i>Elephantopus mollis</i>	Asteraceae	Native
<i>Eragrostis airoides</i>	Poaceae	Native
<i>Euphorbia heterophylla</i>	Euphorbiaceae	Native
<i>Euphorbia hirta</i>	Euphorbiaceae	Native
<i>Euphorbia hyssopifolia</i>	Euphorbiaceae	Native
<i>Euphorbia peperomioides</i>	Euphorbiaceae	Native
<i>Euphorbia prostrata</i>	Euphorbiaceae	Native
<i>Euphorbia thymifolia</i>	Euphorbiaceae	Native
<i>Ipomoea cairica</i>	Convolvulaceae	Native
<i>Ipomoea purpurea</i>	Convolvulaceae	Native
<i>Laportea aestuans</i>	Urticaceae	Native
<i>Macroptilium lathyroides</i>	Fabaceae	Native
<i>Macroptilium martii</i>	Fabaceae	Native
<i>Marsypianthes chamaedrys</i>	Lamiaceae	Native
<i>Mimosa pudica</i>	Fabaceae	Native
<i>Mitracarpus hirtus</i>	Rubiaceae	Native
<i>Mollugo verticillata</i>	Molluginaceae	Native
<i>Phyllanthus niruri</i>	Phyllanthaceae	Native
<i>Phyllanthus tenellus</i>	Phyllanthaceae	Native
<i>Pterocaulon virgatum</i>	Asteraceae	Native

<i>Richardia brasiliensis</i>	Rubiaceae	Native
<i>Setaria parviflora</i>	Poaceae	Native
<i>Sida acuta</i>	Malvaceae	Native
<i>Sida ciliaris</i>	Malvaceae	Native
<i>Sida rhombifolia</i>	Malvaceae	Native
<i>Sida spinosa</i>	Malvaceae	Native
<i>Solanum americanum</i>	Solanaceae	Native
<i>Sonchus oleraceus</i>	Asteraceae	Native
<i>Sphagneticola trilobata</i>	Asteraceae	Native
<i>Stachytarpheta cayennensis</i>	Verbenaceae	Native
<i>Stemodia verticillata</i>	Plantaginaceae	Native
<i>Stylosanthes viscosa</i>	Fabaceae	Native
<i>Turnera melochioides</i>	Turneraceae	Native
<i>Turnera subulata</i>	Turneraceae	Native
<i>Waltheria indica</i>	Malvaceae	Native

PARTE 3: Artigo para submissão na revista *Journal of Applied Ecology*

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The type of urban habitat matters to functional traits of native and non-native spontaneous urban flora

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Abstract

Anthropogenic activities, including road traffic, airport operations, and shipping logistics, continually drive the dynamic transformation of urban landscapes, shaping the cityscape and impacting its residents. Urban areas consist of diverse habitats with varying capacities to harbor biodiversity, and herbaceous plants, for example, can grow on sidewalks, vacant lots, public parks, and roadsides. Considering that non-native species cause the homogenization of vegetation in urban areas and the lack of information about all the potential impacts these species can cause on native biodiversity, it is crucial to explore how traits can play a role in determining species' competitive strategies to persist in urban areas. Hence, the current work sought to determine how urbanization intensity affects functional traits of native and non-native plants. For this work we asked the following questions: (I) How can urbanization intensity affect native and non-native species height, SLA and leaf mean length? (II) How can urban habitats determine the establishment of native and non-native species in urban ecosystems? Our results determined that sidewalks and vacant lots stood out as important habitats for the height of both native and non-native plants. The maximum height of plants was the only functional trait related to the intensity of urbanization.

Keywords: Functional diversity; urbanization; non-native plants traits; native plant traits.

Introduction

Anthropogenic activities, including road traffic, airport operations, and shipping logistics, continually drive the dynamic transformation of urban landscapes, shaping the cityscape and impacting its residents. (DESAEGHER *et al.*, 2019; AHMED *et al.*, 2020). Urban areas consist of diverse habitats with varying capacities to harbor biodiversity, and herbaceous plants, for example, can grow on sidewalks, vacant lots, public parks, and roadsides. Furthermore, human movements can facilitate the arrival of non-native species in urban areas and the consequences for biodiversity are still unclear since the ecological knowledge and theory has been derived from natural or non-urban systems that can function quite differently from urban areas (HAHS; EVANS, 2015). When non-native species are introduced in new ecosystems, they persist spontaneously (KNAPP *et al.*, 2012). Thus, urban areas are the starting point of colonization for many non-native species and drive the global homogenization of floras (OLDEN *et al.*, 2006; KNAPP *et al.*, 2012).

Previous research has suggested that biotic homogenization, or the process of ecological similarity increasing across different locations, is likely influenced by two separate mechanisms (ZHU *et al.*, 2019). The first mechanism involves species that thrive in urban environments, which can lead to increased similarity among urban floras. The second mechanism suggests that urbanization may favor certain traits and niches, resulting in a non-random selection of specific groups of species that drive the homogenization process. A study on floras in four Russian cities found higher phylogenetic diversity among native species compared to non-native species. The mean phylogenetic distance (MPD) for natives was positively standardized, indicating their dissimilarity from each other, while it was negatively standardized for non-natives, suggesting phylogenetic clustering (TRETAKOVA *et al.*, 2021). Another study examined yard management's impact on taxonomical, phylogenetic, and functional plant community homogenization compared to natural areas. Residential yards were functionally more homogeneous in terms of α - and β -diversity compared to natural areas. Within yards, taxonomic, phylogenetic, and functional diversity showed weak correlation. Hence, urban biotic homogenization is anticipated to be particularly significant, as shared human preferences and management practices in environmentally diverse regions may lead to the selection of similar plant species or closely related species with similar trait sets.

Urban ecosystems feature intense anthropogenic activities and environmental stressors that filter species with varying life-history traits. Therefore, traits can be essential to understanding how species respond to urban environments (HU *et al.*, 2021). For example, a

study in China found that most traits' values spanned a wide range across the 70 spontaneous species, and seed size and leaf element composition played a crucial role in contributing to the functional differentiation among species (HU *et al.*, 2021). In Egypt, a study found that non-native species' traits were significantly related to human-made pressures and soil resources in urban areas but not in non-urban areas. Native plants, on the other hand, consistently showed trait-environment relationships in urban and non-urban areas (EL-BAROUGY *et al.*, 2021). Lastly, a review synthesized the results of 29 studies that examined plant traits of urban floras. Some plant traits (e.g., woodiness, seed mass, and height) increased in response to urbanization. In contrast, other traits have mixed responses, and many other traits were understudied (WILLIAMS *et al.*, 2015). Hence, despite the important findings from these studies, there still needs to be more clarity on which urban characteristics facilitate the spread of non-native species and which species' traits are most responsive to the effects of urbanization.

A study explored the impact of urbanization on functional traits of native and non-native plants. Habitat type had a stronger influence on the plant community than the level of urbanization. Community height was greater in lots, and specific leaf area increased with more impervious surfaces. Few traits showed variation with urbanization, whereas vacant lots contained a higher abundance of community traits (SILVA *et al.*, 2023). As cities continue to grow and expand, human activities will persist, making it imperative to understand how species can thrive in urban areas. The introduction of non-native species in cities can lead to the homogenization of vegetation, which can directly impact global biodiversity. One effective approach to gaining insight into plant responses to urbanization is using functional traits. These traits can aid in biodiversity conservation and provide a deeper understanding of the consequences of urbanization on plant communities.

Considering that non-native species cause the homogenization of vegetation in urban areas and the lack of information about all the potential impacts these species can cause on native biodiversity, it is crucial to explore how traits can play a role in determining species 'competitive strategies to persist in urban areas. Hence, the current work seeks to determine how urbanization can affect functional traits of native and non-native plants. For this work we asked the following questions: (I) How does urbanization affect native and non-native species height, SLA and leaf mean length? (II) How does urban habitats determine the establishment of native and non-native species in urban ecosystems?

Methods

We conducted the study in six medium-sized cities located in southern Minas Gerais, Brazil: Alfenas (21° 25' 46" S, 45° 56' 50" W), Lavras (21° 14' 45" S, 44° 59' 59" W), Poços de Caldas (21° 47' 18" S, 46° 33' 45" W), Pouso Alegre (22° 14' 3" S, 45° 55' 60" W), Três Corações (21° 42' 29" S, 45° 16' 10" W), and Varginha (21° 32' 47" S, 45° 25' 51" W) (Fig. 1). The climate in the region is classified as subtropical with a dry winter, according to the Köppen and Geiger classification (Cwa). The average annual temperature is 20.6°C, and the average annual rainfall is 1508 mm (SÁ JÚNIOR, 2009). The estimated population of these cities was 80,973, 105,756, 169,838, 154,293, 80,561, and 137,608, respectively (IBGE, 2019).

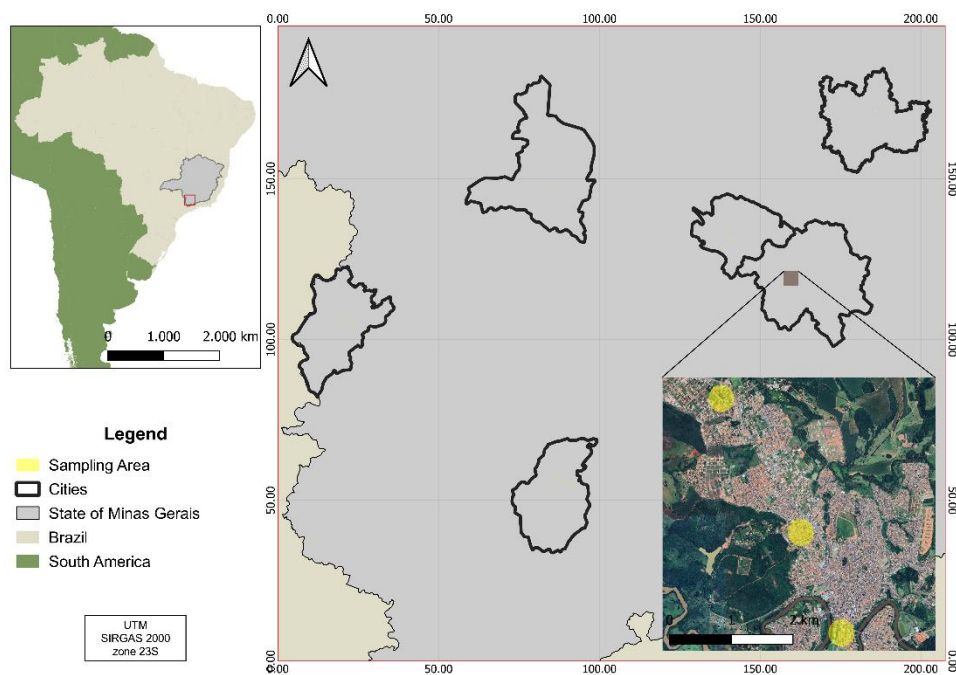


Fig. 1. Map of the study area location in South America, Brazil, Minas Gerais, and distribution of classified areas within the urban perimeter of the municipalities of Alfenas, Lavras, Poços de Caldas, Pouso Alegre, Três Corações, and Varginha. The square areas of 1 km² define the intensity of urbanization in the landscape, and the yellow circular areas with a radius of 200 m define the locations of the sample units.

We used Sentinel-2 satellite images of the designated cities, which were acquired in September 2019 and had a resolution of 10 meters, to characterize the landscape surrounding each study site. We employed the Semiautomatic Classification (SCP) plugin (CONGEDO, 2016) in QGIS software version 3.10.0 (QGIS Development Team, 2019) for image classification. We considered four land cover classes, including water bodies, impervious surfaces, trees, and grasses. Impervious surface cover included all urban areas such as roads,

buildings, and industrial areas. The grassland cover class encompassed exposed soil, natural open fields, areas with ruderal plants, and managed grass. Subsequently, we conducted manual post-processing of the land use map to rectify minor errors resulting from the semiautomatic classification.

We used the LeCos plugin (JUNG, 2016) to calculate the coverage percentages for each class, as well as the Shannon diversity index of the landscape at four different radii (200 m, 500 m, 750 m, and 1,000 m). We calculated the class coverage percentages in relation to the total landscape area, providing insights into the representation of various land cover types (BOSCOLO *et al.*, 2017; NERY *et al.*, 2017). We utilized the Shannon diversity index to quantify the environmental heterogeneity of the landscape, considering both the number and proportion of different landscape classes (MCGARIGAL *et al.*, 2012). Subsequently, we quantified the environmental heterogeneity of the landscape, considering the number and proportion of landscape classes, using the Shannon diversity index. (BOSCOLO *et al.*, 2017; NERY *et al.*, 2017). To capture the urbanization gradient, we also considered the percentage of impervious surface cover, which ranged from 38.31% to 93.22%.

Furthermore, we identified a total of 21 sampling areas across the six municipalities. We determined the number of sampling areas per municipality based on the size of the urban area, with areas that were considered unsafe or located outside the city's urban perimeter excluded after an initial assessment. Following an on-site evaluation of all potential sampling areas, we selected three areas each in Alfenas (26.8 km²), Lavras (24.4 km²), Três Corações (18.4 km²), and Varginha (30.7 km²), four areas in Pouso Alegre (27.5 km²), and five areas in Poços de Caldas (37.1 km²), resulting in a total of 21 sampling areas. Our sampling area selection followed closed the one used by Tavares-Brancher *et al.* (2023). Within each city, we established a 1-kilometer buffer around each sampling area, which accounted for the variation in the number of sampling areas per city, ranging from three to five. To characterize the 21 sampling areas, we defined a 200-meter radius buffer within the 1-kilometer buffer. Within each sampling area, we randomly placed ten 1 m² plots to sample spontaneous herbaceous plants. We specifically targeted three types of urban habitats for characterization, namely sidewalks, vacant lots, and public parks. Our approach ensured that each street within the buffer had at least one plot, selected based on the presence of urban elements, enabling us to sample the entire length of the 200-meter buffer.

We conducted our fieldwork over six sampling months during Summer and Spring, spanning from February 2020 to February 2021. Our focus was on spontaneous herbaceous plants, excluding cultivated flora from our sampling. Within each 1 m² plot, we collected five individuals of each species found within the plot. In the laboratory, we employed the APG system (Angiosperm Phylogeny Group) IV (2016), published identification guides, and received expert assistance from a botanist (see acknowledgements) to accurately identify the species. To determine whether each species was native or non-native to the state of Minas Gerais, we relied on information available at the Re flora - Virtual Herbarium, accessible at <https://reflora.jbrj.gov.br/reflora>.

We used the work published by PÉREZ-HARGUINDEGUY *et al.* (2013) as a reference for carrying out the measurements of each functional trait. With the aid of a tape measure, we measured the height of the tallest individual of each species present in the plot. Also, we made the measurements of leaf area, specific leaf area (SLA) and leaf length in the laboratory. We calculated SLA by having the mean of all five individuals of each species we found in the plots. We calculated SLA considering the ratio of mean wet leaves area and the mass of the same dry leaves (cm²/g). We obtained leaf area through the software ImageJ by digitalizing all wet leaves that we sampled, including leaves stalk. After digitalizing, we put the leaves in aluminum containers and dried out them in a stove for 48 hours in an oven at 60°C (Table 1).

Table 1. Description of the functional attributes selected for sampling.

Trait	Value	Unity	Ecological function
Height	Maximum measure	cm	Competitive skill
Leaf length	Mean	cm, mm	Response to climate conditions, response to soil conditions, the effects of biogeochemical cycles, competitiveness and protection/defense
Leaf area	Mean;Standard deviation	mm ²	Climatic response to soil conditions, CO ₂ concentration, effects of biogeochemical cycles, effects of disturbance and protection/defense regimes
Specific Leaf Area	Mean;Standard deviation	mm ² /mg	Climatic response to soil conditions, CO ₂ concentration, effects of biogeochemical cycles, effects of disturbance and protection/defense mechanisms

To understand if urbanization intensity could affect native and non-native species traits, we calculated the Community-Weighted Mean (CWM) for height, SLA and mean leaf length, since we used community weighted average values for our variables. We calculated CWM by the inverse relationship between the sum of the multiplication of the trait value of each species occurrence by its respective coverage value, and the sum of the coverages of all species that occur in the sampling site for each plot. We used general and generalized linear models (LM and GLM, respectively). We used Gamma and Gaussian Family distributions. To answer how urban habitats can determine the establishment of native and non-native species in urban areas we used generalized linear models with Gamma error distribution. To verify the relationship between urban habitats and species richness we did a post-hoc analysis (Tukey). We also did a Pearson correlation to verify what variables we could use as a proxy for urbanization. Since all the variables were correlated, we decided to use the one that best described urbanization, which was the proportion of impervious surface. All analyses were performed using R Statistical Software (v4.2.1; R Core Team, 2021).

Results

The urban intensity did not explain the CWM height ($R^2 = 0.001$; $p = 0.88$), the CWM SLA ($R^2 = 0.003$; $p = 0.8$) or the CWM mean leaf length of native species ($R^2 = 0.009$; $p = 0.6$) (Fig. 2, Table 2).

Table 2. Mean and standard deviation (SD) values of the dependent variables for total, native and non-native species traits.

Dependent variables	Mean	SD
Total species height	33.28786	± 18.23396
Total species SLA	100.3959	± 38.77917
Total species mean leaf length	6.69274	± 4.131116
Native species height	20.56422	± 13.07409

Native species SLA	94.30958 ± 37.85898
Native species mean leaf length	3.318299 ± 1.224632
Non-native species height	39.54095 ± 20.60718
Non-native species SLA	96.76406 ± 39.31013
Non-native species mean leaf length	8.703201 ± 4.717529

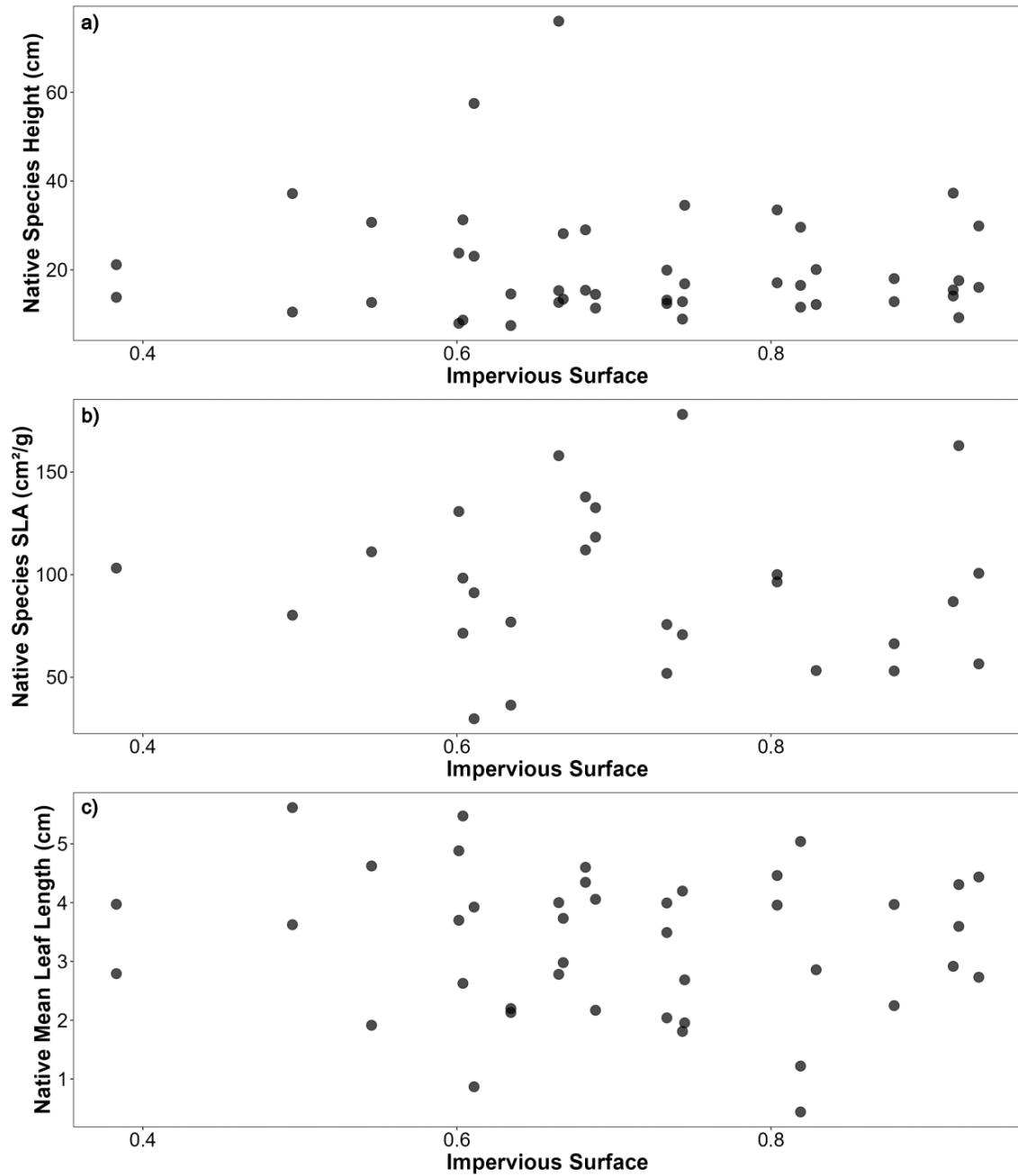


Fig. 2. Variation of native species height (a), SLA (b) and mean leaf length (c) across urbanization intensity. Native species height, SLA and mean leaf length are in axis y and proportion of impervious surface is in axis x.

The proportion of impervious surface only explained 3.73% of the CWM of height of non-native species ($R^2 = 0.03$; $p = 0.3$) (Fig. 3), so the height of non-native species did not vary within the increasing of the proportion of impervious surface. Also, the proportion of impervious surface only explained 5.44% of the variation of the CWM of SLA of non-native species ($R^2 = 0.05$; $p = 0.26$) (Fig. 3), determining that CWM of SLA of non-native species did

not increase neither decrease within the increasing of urbanization intensity. Lastly, the proportion of impervious surface only explained 2.04% of the variation of CWM of mean leaf length of non-native species ($R^2 = 0.02$; $p = 0.5$) (Fig. 3), which means that CWM of mean leaf length of non-native species did not vary according to the increase of the proportion of impervious surface.

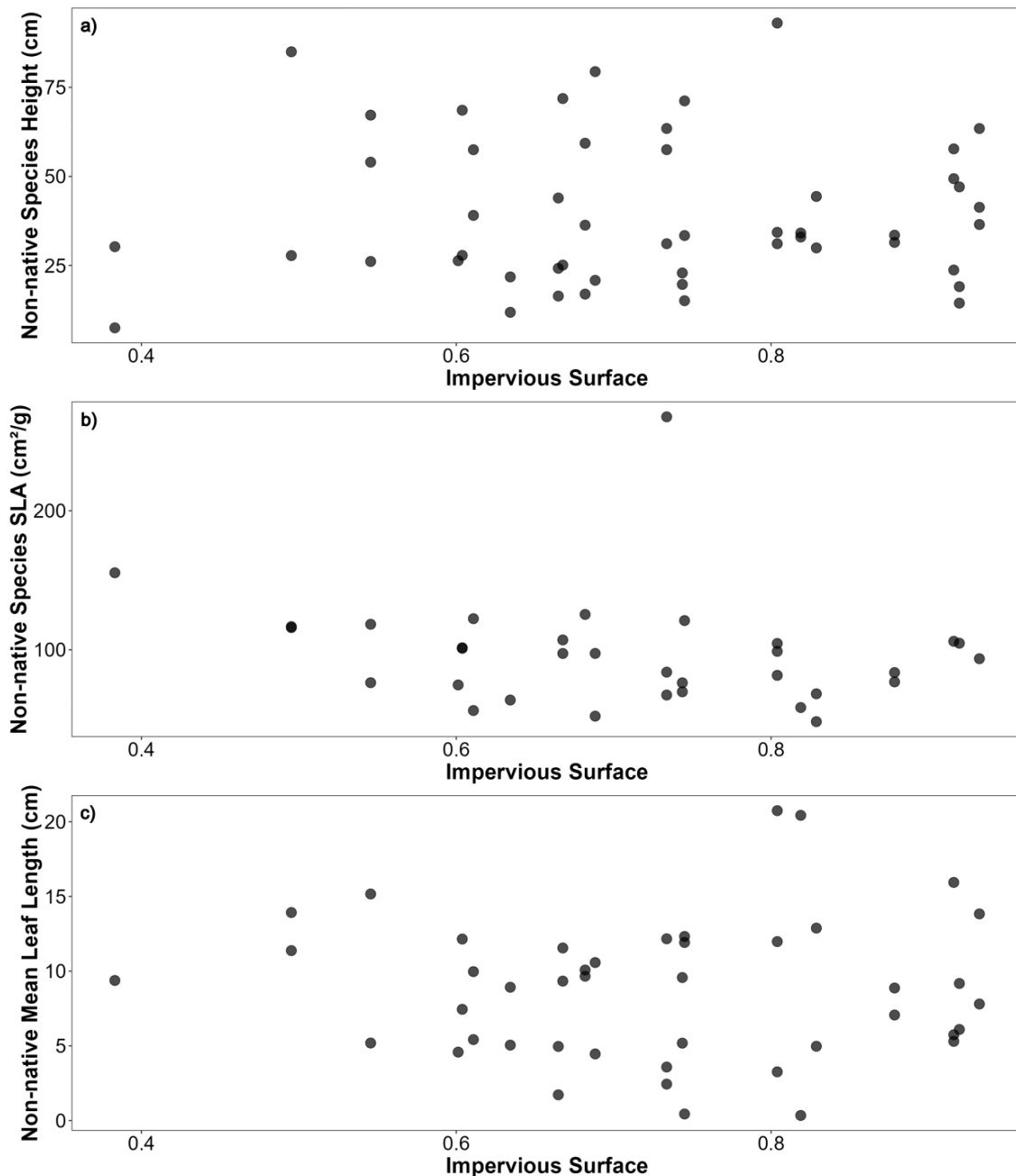


Fig. 3. Variation of non-native species height (a), SLA (b) and mean leaf length (c) across urbanization intensity. Non-native species height, SLA and mean leaf length are in axis y and proportion of impervious surface is in axis x.

Urban habitats affected the CWM of height of native species ($F = 12.15$; $p < 0.001$). We found differences for CWM of height of native species between vacant lots and parks ($p = 0.0007$) and between vacant lots and sidewalks ($p = 0.0002$), but we did not find any differences for sidewalks and parks ($p = 0.7$) (Fig. 4). These results highlighted that CWM of height of native species was greater in vacant lots than in parks and sidewalks. For CWM of SLA of native species, we did not find any differences between urban habitats ($F = 0.855$; $p = 0.437$) (Fig. 4). Therefore, we could not find any variation related to CWM of SLA of native species between sidewalks and parks ($p = 0.809$), vacant lots and parks ($p = 0.9335$) and vacant lots and sidewalks ($p = 0.4277$). Finally, our results showed that for CWM of mean leaf length of native species we could not find any differences between urban habitats ($F = 1.36$; $p = 0.268$) (Fig. 4). Thus, there was no variation between sidewalks and parks ($p = 0.9167$), no variation between vacant lots and parks ($p = 0.6672$) and no variation between vacant lots and sidewalks ($p = 0.2408$).

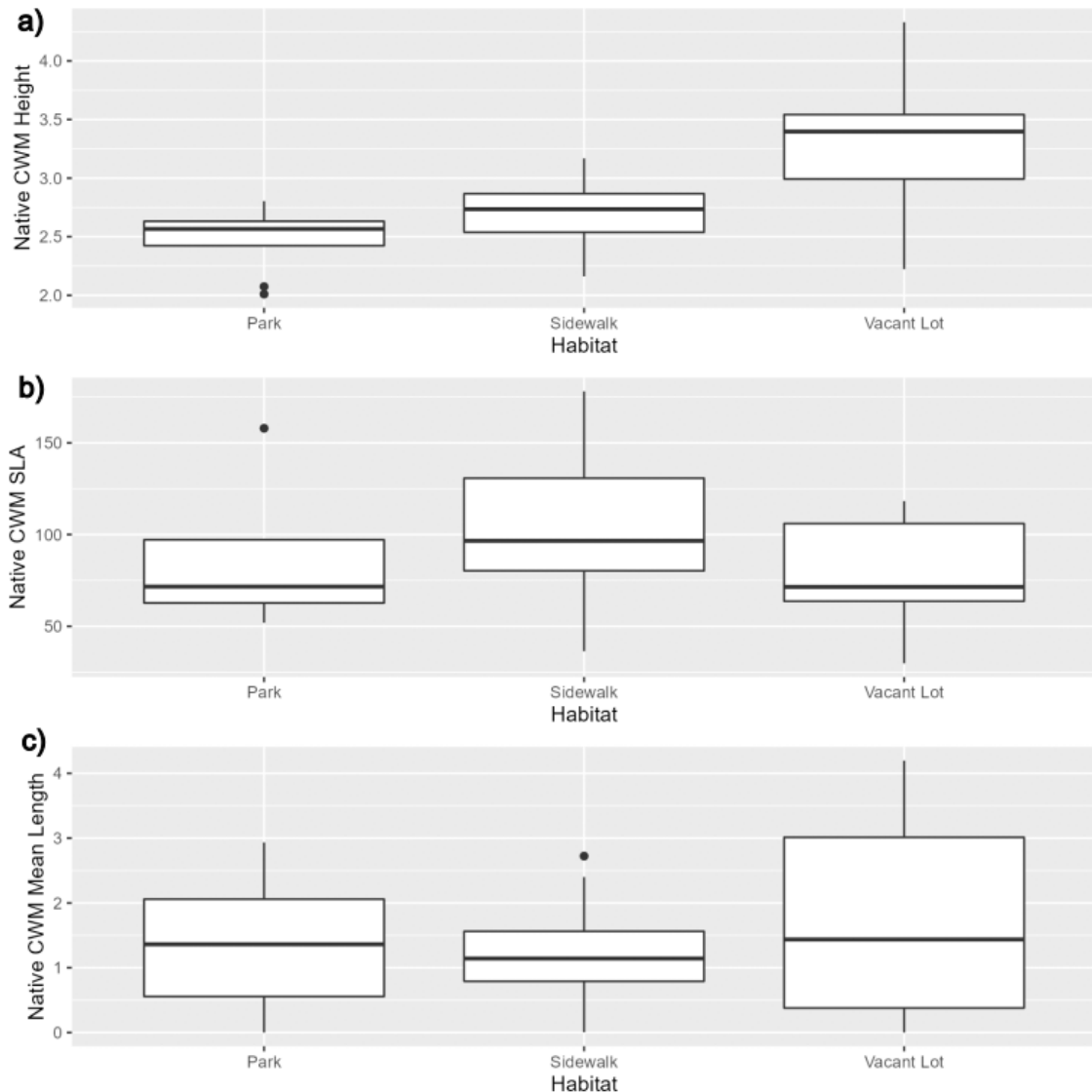


Fig. 4. Variation of native species height (a), SLA (b) and mean leaf length (c) across urban habitats. Native species height, SLA and mean leaf length are in axis y and urban habitats (parks, sidewalks and vacant lots) is in axis x.

Our analysis determined that urban habitats affected the CWM of height of non-native species ($F = 32.06$; $p < 0.001$) (Fig. 5). We found no differences for CWM of height of non-native species between sidewalks and parks ($p = 0.29$). However, we found differences between vacant lots and parks ($p < 0.01$) and vacant lots and sidewalks ($p < 0.01$). These results highlighted that CWM of height of non-native species was greater in vacant lots than in parks and sidewalks. For CWM of SLA of non-native species, we did not find any differences between urban habitats ($F = 0.469$; $p = 0.63$) (Fig. 5). Therefore, we could not find any variation related to CWM of SLA of non-native species between sidewalks and parks ($p = 0.9461$), vacant lots and parks ($p = 0.6547$) and vacant lots and sidewalks ($p = 0.7318$). Finally, our results showed

that for CWM of mean leaf length of non-native species we could not find any differences between urban habitats ($F = 2.039$; $p = 0.141$) (Fig. 5). Thus, there was no variation between sidewalks and parks ($p = 0.5$), no variation between vacant lots and parks ($p = 0.75$) and no variation between vacant lots and sidewalks ($p = 0.125$).

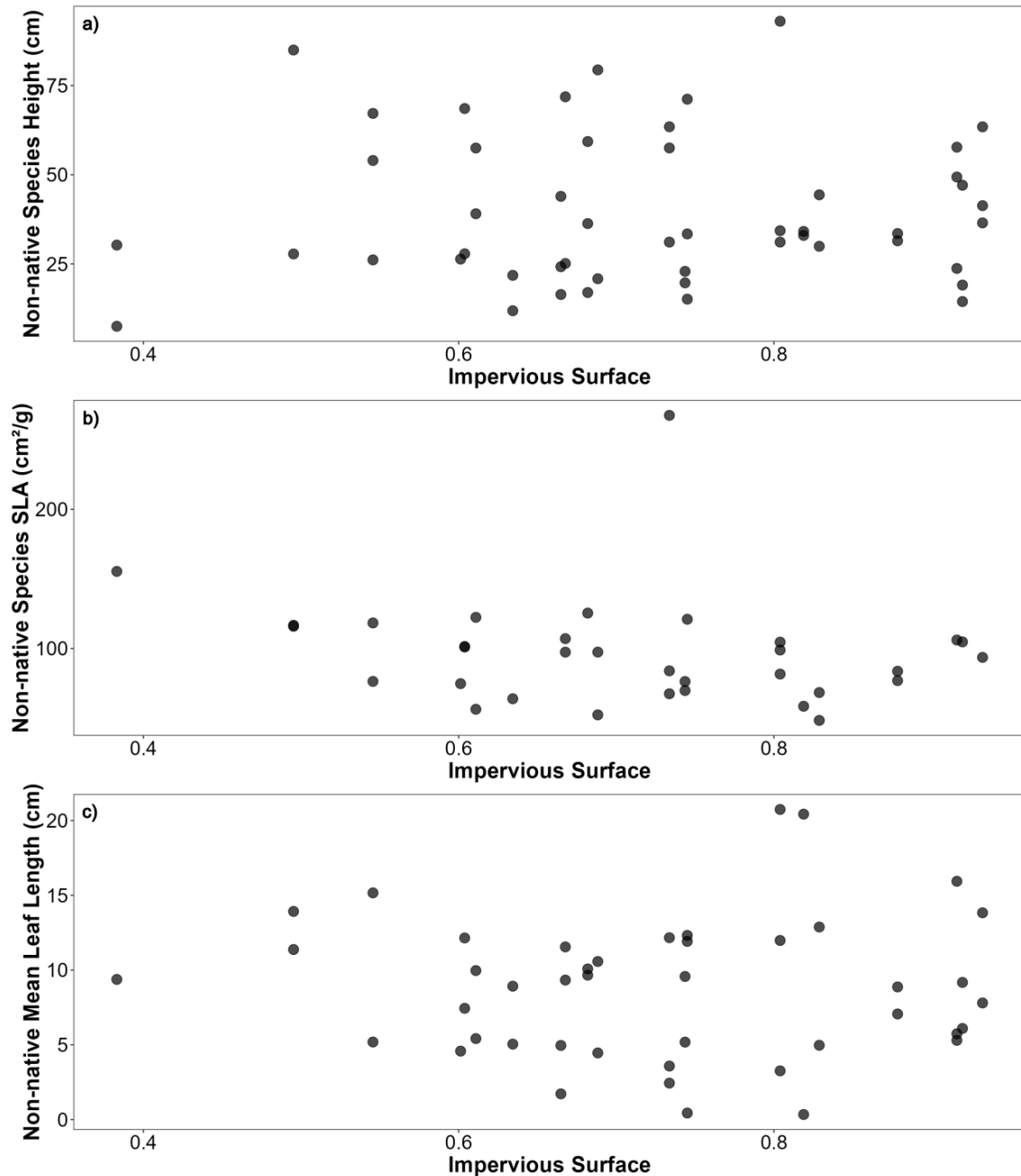


Fig. 5. Variation of non-native species height (a), SLA (b) and mean leaf length (c) across urban habitats. Non-native species height, SLA and mean leaf length are in axis y and urban habitats (parks, sidewalks and vacant lots) is in axis x.

Discussion

Our work sought to comprehend how the intensity of urbanization affected native and non-native species CWM of height, CWM of SLA and CWM of leaf mean length and how urban habitats determined the establishment of native and non-native species in urban ecosystems. The level of intensity of urbanization did not affect native and non-native traits across our study areas. However, when comparing urban habitats and their effects on native and non-native traits, we identified significant differences for one of the traits. Specifically, our results revealed variations in native and non-native height based on urban habitats, with native height being greater in vacant lots compared to other urban habitats, and non-native height being shorter in sidewalks compared to other urban habitats. These findings suggest that urban habitats, rather than other urban elements, play a crucial role in shaping native and non-native traits in urban ecosystems.

Our results did not find significant relationships between the traits of native and non-native species and urbanization intensity. Another study found that non-native plant traits had weak associations with the environment in nonurban habitats, whereas these associations were strong in urban habitats. By contrast, native plants revealed consistency in their trait–environment associations along the urbanization gradient (EL-BAROUGY *et al.*, 2021). Therefore, due to the strong influence of frequent human-induced disturbances in urban areas (e.g., public parks, pollution, changes in landscape composition) that overshadow the plant functional type effects observed in natural ecosystems (KOTZE *et al.*, 2021), it is challenging to find patterns that clearly show the relationship between urbanization intensity and species traits. Besides that, to find patterns across species traits in urban areas, it is essential to work in more than one city, but since it is costly and challenging, most of the studies make their work in only one city (EL-BAROUGY *et al.*, 2021; HU *et al.*, 2021). For that reason, we chose an approach that encompassed a more comprehensive range of cities (six in total), so we could check trait patterns across all the cities of this present study. Considering that we based our results on a regional scale, we applied a more robust analysis for our data between urbanization intensity and species traits. Therefore, we can assume that for a regional scale, traits such as height and mean leaf length are not good predictors for variations related to urbanization intensity.

According to previous works (KNAPP *et al.*, 2008; ARONSON *et al.*, 2014; ARONSON *et al.*, 2016) anthropogenic filters, such as urban form and development history, socioeconomic and cultural factors (ARONSON *et al.*, 2016) can filter both native and non-native species. In

addition, in our study we could not find any differences for both native and non-native traits and urbanization intensity. Therefore, urbanization intensity did not explain the variation among native and non-native traits. Possibly, there are other factors influencing native and non-native traits, but since we only used the proportion of impervious surface to determine traits variation, further works need to be done to evaluate the relation between traits and urbanization intensity.

Urban habitats showed an important relation for CWM of height of non-native and native species, since for both native and non-native height we determined differences among parks, sidewalks and vacant lots. Native and non-native heights were greater in vacant lots compared to our results related to sidewalks and public parks. Urban flora is constituted by a rich diversity of vascular plants found in varied urban habitats (parks and public squares, sidewalks/pavement, vacant lots, and others) which are environmentally and floristically heterogeneous (FIGUEROA *et al.*, 2020). Areas like vacant lots facilitate plants' growth due to the availability of space and more soil nutrients (BLOUIN *et al.*, 2019; FIGUEROA *et al.*, 2020) when compared to sidewalks and other urban habitats. Other studies have already shown that vacant lots can function as an important urban habitat in terms of native conservation. A study determined that non-native species were functionally more homogenous than natives both within and between vacant lots (BLOUIN *et al.*, 2019), and since our results showed that native height was higher in vacant lots, we can assume the importance of these urban habitats for biodiversity and conservation in urban ecosystems.

Sidewalks are urban habitats with limited space for plant growth and have been studied about permeability level and soil availability as crucial factors influencing plant distribution on pavements, as suggested by previous research (DE CAUWER *et al.*, 2014a, 2014b). Our findings align with these studies, as we observed smaller heights for native and non-native traits compared to vacant lots and public parks. Furthermore, sidewalks often undergo intensive herbicide use and pruning to control weeds, resulting in a reduced potential for biodiversity conservation in urban environments (BONTHOUX *et al.*, 2019). In our study region, pruning and herbicide usage are commonly practiced, and these actions, combined with the limited space for plant growth on sidewalks, can directly impact plant traits in urban ecosystems. The application of herbicides and pruning practices hinder the proper growth of plant species, directly influencing their height and overall development. A previous study found that taller plants were more common in urban areas (THOMPSON; MCCARTHY, 2008), whereas another study found that shorter species had high urbanity, probably because urban floras contain many short-lived ruderal species (KNAPP *et al.*, 2009). The near consistency of the response of plant

height to urbanization intensity in different studies and across cities (DUNCAN *et al.*, 2011) is likely to be because plant height is expected to respond positively to many of the effects of urbanization (e.g., Urban Heat Island, higher nutrients) while negative impacts may be hidden by an urban extinction debt as taller species are generally longer lived (HAHS *et al.*, 2009, WILLIAMS *et al.*, 2015).

In conclusion, our study revealed that native and non-native species' height were the only trait that showed a significant difference related to urbanization intensity. We identified urban habitats as important determinants of how urbanization intensity affects species persistence, and we found that plant traits can be valuable tools in explaining such variations in urban ecosystems. Considering that urbanization intensity is driven by a complex array of factors that can interact to influence plant traits, variations in the relative strengths of these drivers may contribute to the variability in trait responses to urbanization, as suggested by previous studies (MCDONNELL; HAHS, 2013; WILLIAMS *et al.*, 2015). Future research should focus on investigating specific urbanization processes and accurately measuring plant functional trait responses.

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Conclusão geral

Nossos resultados mostraram que a urbanização afetou apenas a riqueza de plantas exóticas e em contrapartida, a urbanização afetou somente a cobertura vegetal de plantas nativas. Já para os nossos resultados em relação à composição de espécies, tanto a composição de espécies de plantas nativas quanto a de plantas exóticas não foram afetadas pela urbanização. Em relação aos resultados comparando a variação de riqueza de plantas nativas e exóticas nos diferentes habitats urbanos, determinamos os mesmos padrões entre plantas nativas e exóticas. Estes resultados mostraram que embora a urbanização tenha afetado as comunidades de plantas nativas e exóticas, existem muitos fatores em um ecossistema urbano que podem direcionar a permanência destas espécies nestes locais. Por isso, é necessário que estudos em diferentes escalas (regionais e globais) incorporem fatores como, relação das espécies com o solo e temperatura, para que tenhamos uma compreensão mais clara acerca dos padrões de distribuição de comunidades de plantas e suas interações com o ambiente. Em uma abordagem funcional, nenhum dos traços funcionais utilizados neste estudo mostraram relação com a urbanização. Entretanto, os habitats urbanos mostraram relações importantes com a altura tanto de plantas nativas quanto de plantas exóticas. Este último resultado demonstra a importância de habitats urbanos para o crescimento das plantas em geral e que mais esforços são necessários para determinarmos os padrões funcionais de plantas nos diferentes habitats presentes em áreas urbanas. Desta forma, poderemos compreender se a urbanização pode favorecer que espécies exóticas se tornem invasoras e afetem a biodiversidade nativa regional.