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RESEARCH ARTICLE

Contribution of trees to carbon stocks in urban–rural ecosystems: Taxonomic, phylogenetic, and functional diversity in response to bioclimatic and geographic factors

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Abstract

Tree diversity plays a key role in mitigating climate change and enhancing ecosystem resilience. This study evaluated the contribution of trees across three habitats within the urban–rural gradient of Sucre, Bolivia: urban (UF), native (NF), and exotic (EF). Carbon sequestration, as well as taxonomic (TD), phylogenetic (PD), and functional (FD) diversity, were analyzed in relation to bioclimatic (temperature and precipitation) and geographic (altitude) factors. The methodology included the recording of botanical and ecological traits, along with the measurement of dendrometric classes (DBH ≥ 10 cm) in 12 temporary circular plots per habitat. Results showed higher carbon stocks in the urban forest (268.36 ± 2.76 MgC/ha), followed by the exotic (159.53 ± 0.86 MgC/ha) and the native forest (39.64 ± 0.41 MgC/ha). A total of 31 species from 19 families were identified, with marked evolutionary divergence between Pinaceae and Cupressaceae compared to Fabaceae. The urban habitat presented the highest taxonomic diversity (~51.6%), the highest phylogenetic diversity (~72%), and the greatest carbon fixation (~42%). These findings highlight the fundamental role of tree diversity in carbon sequestration, biodiversity conservation, and landscape connectivity, emphasizing the need to integrate it into sustainable urban–rural planning through adaptation and mitigation strategies that strengthen ecological resilience and ecosystem services in the urban–rural ecosystem of Sucre.

Keywords: evolutionary relationships; species composition; sub-Andean ecosystem; tree richness; traits functions.

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1. Introduction

Urban-rural ecosystems represent a continuous gradient that connects densely populated and highly modified areas with less altered rural zones, integrating urban, natural, and human elements (McDonnell & Pickett, 1990; McDonnell et al., 1997). This gradient facilitates the exchange of resources such as food, water, and biodiversity, while promoting urban-rural sustainability and climate resilience (Barrico & Castro, 2016; Marshall et al., 2018; Gebre & Gebremedhin, 2019). The transition between these ecosystems is crucial for assessing the impacts of urbanization on ecosystem services, especially carbon sequestration, and for designing sustainable urban planning strategies (Natuhara & Hashimoto, 2009; Cai et al., 2022; Guan et al., 2024; Gebru et al., 2025).

Tree diversity plays a central role in carbon storage in these systems, influenced by factors like land use, environmental conditions, and level of urbanization. In non-urban forests, greater species diversity enhances aboveground biomass and, consequently, carbon storage due to niche complementarity among species (Borges et al., 2021). In tropical regions, species richness and evenness are positively correlated with stored carbon (Shirima et al., 2015), while in urban areas, factors such as rising temperatures and pollution can limit carbon sequestration capacity (Warner et al., 2024).

Global examples illustrate the carbon-capturing potential of urban, native, and exotic forests. In Indonesia, the urban forest UI stores 468.02 t/ha, while the Rio de Janeiro botanical garden reaches 104 ± 5 MgC/ha (Febiriyanti et al., 2021; Kurtz et al., 2024). Native forests, like the Yungas in Argentina, record 162 tC/ha (Manrique et al., 2011), and exotic ones, like *Eucalyptus globulus* in Ethiopia, store 53.73 tC/ha (Solomon et al., 2024). These data underscore the importance of sustainable management to maximize climate change mitigation potential.

In Bolivia, natural ecosystems show significant variations in carbon storage capacities. The chiquitano dry forests store between 209 and 213 tC/ha (Paz-Roca & Mostacedo, 2020), while the Amazonian, Chaco, and High Andean forests range from 172.77 to 187.45 tC/ha and 17.02 to 71.09 tC/ha, respectively (Araujo-Murakami et al., 2016; Peralta-Rivero, 2022). In urban settings, open forests in Cochabamba store 35.34 tC/ha, while grasslands and streets in La Paz hold significantly lower values at 0.89 and 0.83 tC/ha (Pacheco 2020; Maldonado et al., 2023). These figures highlight the importance of evaluating and managing biological diversity in urban and rural ecosystems.

Taxonomic (TD), functional (FD), and phylogenetic diversity (PD) play key roles in carbon storage. In urban areas, species diversity improves soil carbon stocks by optimizing underground organism activity (Schittko et al., 2022), while in rural areas, traits like plant height and wood density are important predictors of carbon storage (Conti & Díaz, 2013; Mensah et al., 2024). Although phylogenetic diversity complements storage capacity in rural areas, its effect in urban environments is limited (Lososová et al., 2016; Mensah et al., 2024).

In the municipality of Sucre, Bolivia, urban-rural ecosystems comprise three main habitats: urban forest (UF), native forest (NF), and exotic forest (EF), collectively referred to as UNEF habitats. These ecosystems are crucial for mitigating climate change effects through carbon storage. Additionally, tree diversity of these habitats is influenced by bioclimatic factors (temperature and precipitation), and geographical factors (altitude gradient), which need to be investigated to implement effective conservation strategies.

Therefore, this study evaluated the contribution of trees in urban, natural, and exotic habitats to carbon retention, as well as their taxonomic, phylogenetic, and functional diversity, considering their relationship with bioclimatic factors (temperature and precipitation) and geographic factors (altitude) in the urban–rural ecosystem of Sucre, Bolivia. The study was guided by the following research questions: (i) How do different habitat types (urban forest, native forest, and exotic forest) contribute to carbon stocks, and how are these related to bioclimatic and geographic factors? and (ii) How do habitat types influence the taxonomic, phylogenetic, and functional diversity of trees and their relationship with environmental factors? Collectively, the findings aim to provide evidence to better understand the role of tree diversity in carbon sequestration and to inform conservation strategies and sustainable urban planning.

2. Methodology

2.1. Study area

The study area encompassed three distinct habitats within the urban and rural ecosystem of the municipality of Sucre: Urban Forest (19° 2'31.22"S and 65° 15'50.51"W), covering an area of 1 176 ha, with a landscape matrix composed of both native and exotic tree species, found in parks, plazas, avenues, and integrated into the city's architectural heritage. The Native Forest (18° 50'12.00"S and 65° 6'35.30"W), spanning 11 756 ha, is recognized as the *Monte Villca Municipal Protected Area*, home to species such as *Neoraimondia herzogiana* (Caraparí) , *Anadenantera colubrina* (Willca), *Aspidosperma resonans* (perilla), and *Schinopsis lorentzii* (Soto), which are endemic to the dry inter-Andean valleys in the basins of the Grande and Pilcomayo rivers. The Exotic Forest (18° 57'29.65"S and 65° 22'19.50"W), covering 1 910 ha, is predominantly composed of tree plantations, including *Pinus pseudostrobus*, *Pinus patula*, *Pinus radiata*, *Eucalyptus globulus* and *Eucalyptus camaldulensis* (GAM-Sucre, 2021). These habitats were classified as UNEF forests (Urban Forest, Native Forest, Exotic Forest) within the urban ecosystem, based on their respective tree cover (Figure 1). The sampling unit size was calculated as 400 m² (Sampling in each plot was carried out to assess: botanical characteristics wood type, growth form, leaf type and fruit type), ecological characteristics (preferred habitat, root type, shade tolerance, pollination type), and stem diameter (≥ 10 cm DBH).

Bioclimatic data (Bio 1 and Bio 12) were obtained from WorldClim (Fick & Hijmans, 2017) with a 2.5-minute resolution using the raster package in "R". Additionally, altitude gradient data (geographical variable) were collected at each evaluated site or plot (Table S1, Supplementary Material).

Tree diversity in the UNEF habitats was assessed using predictor variables: types of UNEF habitats (UF, NF, EF), mean annual temperature and precipitation, and altitude gradients of the sampling sites. Response variables included wood density (WD), aboveground biomass (AGB), taxonomic diversity (TD), phylogenetic diversity (PD), and functional diversity (FD) for the analysis. Sampling sites consisted of 12 plots (sampling units) in each type of UNEF habitat (Table S1, Supplementary Material).

circular plot, with a radius of 11.28 m) based on the methodology of Vallejo-Joyas et al. (2005); 12 temporary circular plots in each of the three forest types of UF, NF and EF, were established, in total covering a total sampling area of 1.44 ha.

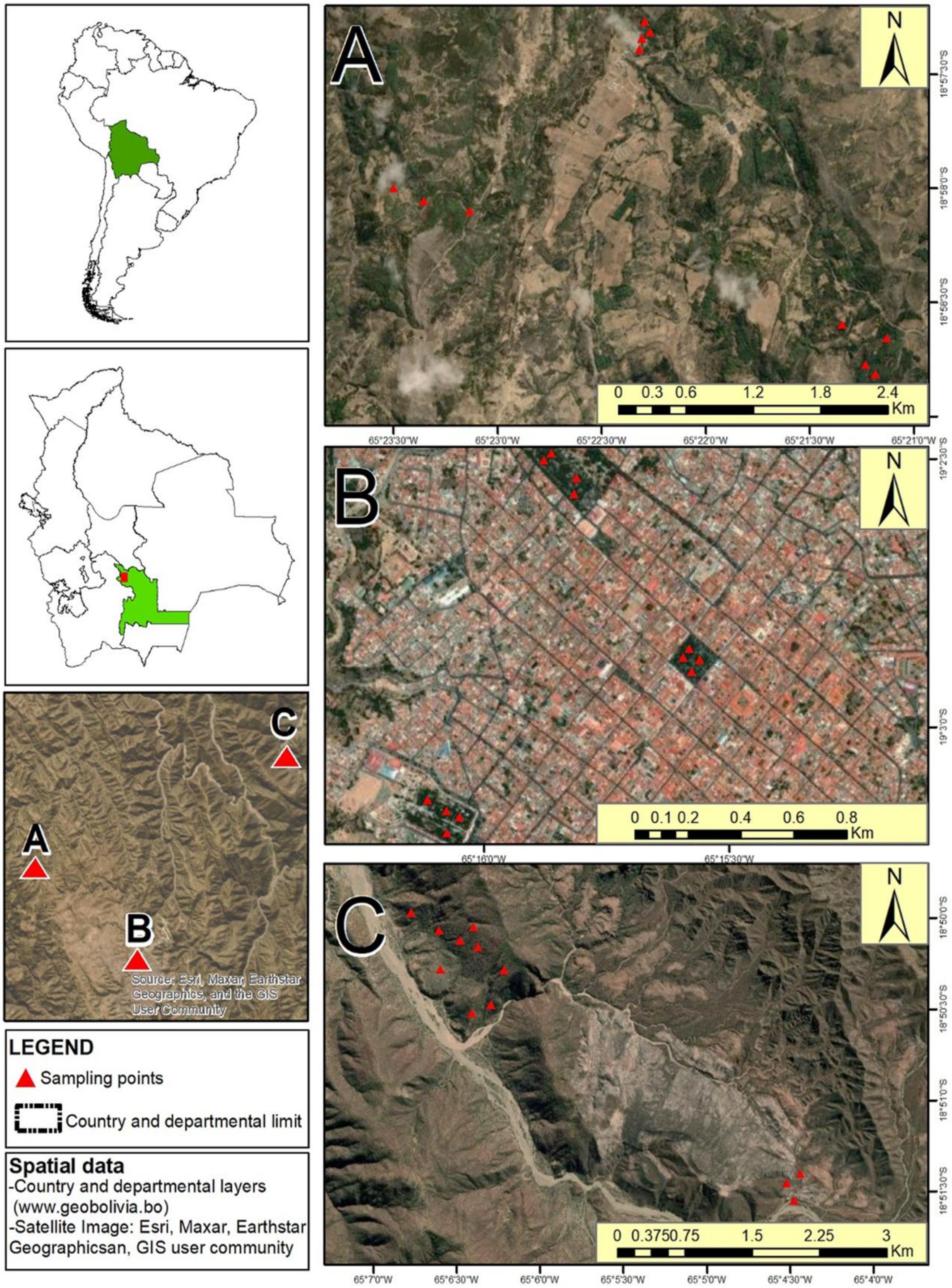

Figure 1. Map of the urban-rural ecosystem, municipality of Sucre, Bolivia, each forest type with 12 circular plots: a) Exotic forests, in peri-urban areas; b) Urban forests, with both exotic and native trees in parks and plazas; and c) Native forests, with native trees in the municipal protected area.

2.2. Taxonomic determination of species

Taxonomic identification of tree species was based on morphological characteristics of collected tree individuals at the study sites, classified using the APG IV system in the Agrobiodiversity collection of the herbarium (HSB) at the Institute of Agroecology and Food Security, Faculty of Agricultural Sciences, Universidad Mayor, Real y Pontificia de San Francisco Xavier de Chuquisaca.

2.3. Aboveground carbon reserves (AGB)

Forest biomass, the AGB of each tree, was estimated using the allometric equation (Eq. 7 of Chave et al.; 2014) defined as: $AGB_{est} = \exp[-1.803 + 0.976E + 0.976\ln(\rho) + 2.673\ln(D) - 0.0299\ln(D)^2]$ Where: AGB_{est} is the estimated aboveground biomass in Mg, E is a measure of environmental stress, ρ is wood density (g/cm^3), and D (cm) is the diameter at breast height (DBH) of the tree.

Wood density values were obtained from the Global Wood Density database (GWD), available at http://dx.doi.org/10.5061/dryad.234. The biomass estimation per tree was performed using the BIOMASS package in R (Réjou-Méchain et al., 2017). AGB results for each type of UNEF habitat were evaluated in credibility intervals based on Bayesian inference and the posterior distribution of estimated AGB parameters (Table S2, Supplementary Material). Carbon stored values for each tree species in the three types of forests (UF, NF, EF) were calculated assuming that 50% of AGB consists of carbon (Malhi et al., 2004).

2.4. Taxonomic diversity

Taxonomic tree diversity sampled in circular plots in each UNEF habitat was used to assess taxonomic diversity (TD), representing alpha diversity by analyzing each UNEF habitat separately in the three sampled forests.

2.5. Phylogenetic diversity

A phylogenetic tree was constructed, based on the species list, and classified according to the APG IV system (i.e., family/genus/species) (Chase et al., 2016). Species identification was achieved at the taxonomic level for 96.77% of all sampled species, ensuring a robust foundation for phylogenetic analysis. The list was processed using the V.PhyloMaker2 (Jin & Qian, 2022), function configured in the Leipzig Catalogue of Vascular Plants (LCVP) botanical nomenclature database (Freiberg et al., 2020). The phylogenetic diversity (PD) was calculated using the Faith's Index (Faith, 1992), based on the phylogenetic hypothesis of species, summing branch lengths according to the sampling sites or UNEF habitats on the phylogenetic tree topology (Figure S1, Table S3: Supplementary Material), representing the evolutionary history of each site or UNEF habitat.

2.6. Functional diversity

A functional trait matrix, was constructed based on the examination of eight traits related to: a) wood type (wood, semi-wood), b) growth form (tree, shrub, palm, climber), c) leaf type (broad, scale-like, needle-like), d) fruit type (berry, bracts, capsule, cone, date, drupe, follicle, legume, syconium), e) preferred growth habitat (dry, wet, semi-wet), f) root type (deep, shallow), g) shade tolerance (low, medium, high), and h) pollination type (birds, insects, wind) (Table S4, Figure S2:Supplementary Material). These functional ranges were collected from the Plant Trait Database (https://www.try-db.org/) (Díaz et al., 2016) for each species and compared with data collected during the sampling process.

Subsequently, a functional dendrogram was built from the species and functional traits matrix using the Gower distance method for continuous and categorical data, and the UPGMA clustering method. Finally, we used the "as.phylo" function from the APE package in R (Paradis & Schliep, 2019) to generate the topological phylogenetic tree into a dendrogram representing functional diversity (FD) based on botanical and ecological species traits (Pavoine & Bonsall, 2011), by summing branch lengths according to the UNEF habitats (Faith, 1992).

2.7. Forest composition

The tree composition in the 36 plots evaluated in the UNEF habitats was analyzed using a non-metric multidimensional scaling (NMDS) of species abundance in each plot. NMDS analysis was performed using PAST software with the Bray-Curtis dissimilarity measure (Hammer et al., 2011). The NMDS axis scores were used as a dissimilarity measure between habitat type. The Whittaker diagram was used to determine species dominance in the habitats, related species diversity and abundance distribution in each community. Species were classified according to their relative abundance, with the most abundant on the X-axis and the abundances represented on a logarithmic (log10) scale on the Y-axis.

2.8. Statistical analysis

The carbon reserve estimation adjustment was conducted by combining the total height of each tree and individuals with GWD estimates. A vector of height (H) and relative standard error (RSE) was constructed assuming a 0.5 m error in directly measured trees. Additionally, AGBmonteCarlo was applied, setting height values and errors considering direct or estimated tree measurements. A negative binomial generalized linear model (GLM.NB) was used to investigate variations among habitats and carbon reserves. After model construction, the model's normality and residue distribution, significance probability (p-values), and dispersion parameter indicating slight data over dispersion, was checked. ANOVA was applied to the model, and the significance of the differences between habitat effects was estimated using Tukey's post hoc tests in the multcomp package in R (Bretz et al., 2016). Multiple linear regression models were also applied to examine the variation among habitat types (UF, EF, EF) and bioclimatic variables (mean annual temperature and precipitation), geographical variables (altitude), carbon reserve, and biotic variables (taxonomic, phylogenetic, and functional diversity).

The modelling structure included: i) specifying the model type according to the data types (continuous, count, categorical), ii) performing basic model residual diagnostics considering variance homogeneity, residue normality, over dispersion, and zero inflation using the ape library in R, iii) conducting advanced model residual diagnostics using the DHARMa library in R (Hartig & Hartig 2017). The most appropriate models were: Gaussian GLM for taxonomic diversity (TD) (DP: 1.272727, AIC: 115.7), negative binomial GLM for phylogenetic diversity (PD) (DP: 1.101017, AIC: 472.87), and Gaussian GLM for functional diversity (FD) (DP: 0.03986208, AIC: -8.9727). The dispersion parameter values indicate nearness to 1 suggesting no over dispersion, 1.5 indicating over dispersion, and the Akaike Information Criterion (AIC) refers to the model quality, where lower AIC values indicate better model fit and complexity balance.

3. Results and discussion

3.1 Carbon stocks in UNEF habitats

The three habitat types identified in this study maintain carbon stocks, with UF showing the highest average carbon stock (276.35 ± 2.30 MgC/ha), followed by EF (159.53 ± 0.86 MgC/ha), and NF (39.64 ± 0.41 MgC/ha) (Figure 2a). Carbon stock is significantly associated with habitat type ($F_{(2,33)} = 17.49$, $p < 0.001$). Tukey post-hoc tests revealed significant differences in carbon stocks between NF-EF ($p < 0.001$) and UF-NF ($p < 0.001$), with lower significance for UF-EF ($p < 0.035$) (Figure 2a; Table S5, S6: Supplementary Material).

Carbon stock (0–41 MgC/ha) is highest in temporary plots with a mean temperature of 15 ºC (Figure 2b), showing a negative but significant relationship ($F_{(1,34)} = 9.046$, $p < 0.004$) (Table S7, Supplementary Material). Similarly, carbon stock is greatest with an annual mean precipitation between 650–700 mm, exhibiting a highly significant positive relationship ($F_{(1,34)} = 15.034$, $p < 0.001$) (Figure2c). Additionally, there is a significant direct positive relationship ($F_{(1,34)} = 8.4887$, $p < 0.0062$) between carbon stock (0–41 MgC/ha) and altitudinal gradient (2700–3000 m.a.s.l.) in the evaluated plots (Figure 2d).

The results of this study demonstrate the influence of habitat types on carbon stocks. Urban forests (UF = 276.35 ± 2.30 MgC/ha) exhibited the highest carbon storage compared to exotic forests (EF) and native forests (NF). This elevated value is attributed to the dasometric characteristics of the diverse tree species (native and exotic), the advanced age of the trees, which exceeds 100 years, and municipal management of green areas. However, the carbon stock reported in 14 plots in the Achumani area of La Paz, Bolivia (0.83 MgC/ha; Pacheco, 2020), is significantly lower than the average in the present study (1.77 MgC/ha). This discrepancy may be explained by factors such as the number and type of plots, tree height, diameter, age, and species composition.

In contrast, studies in other regions report higher carbon stocks in urban forests. In Chapultepec Park, Mexico, total carbon stock was estimated at 11,226 MgC/ha (López-López et al., 2018), whereas the urban forest in UI, Indonesia, recorded storage up to 468.02 t/ha (Febiriyanti et al., 2021). Conversely, the arboretum of the Rio de Janeiro Botanical Garden reported lower aboveground carbon density, at 104 ± 5 MgC/ha (Kurtz et al. 2024). In eight U.S. cities, urban forests store between 214 and 267 MgC/ha (Jevon et al. 2024). These differences can be attributed to variations in tree density, species diversity, and specific habitat characteristics.

The native habitat (NF) exhibited the lowest carbon stock (39.64 ± 0.41 MgC/ha) among the habitats in the Sucre municipality. This value reflects the characteristics of the Andean ecosystem, with native tree species of smaller height and diameter compared to other ecosystems, such as the Tucuman-Bolivian Forest. In Cochabamba, Bolivia, an analysis of 122 plots of natural urban habitats reported an average storage of 35.34 MgC/ha over approximately 20 years (Maldonado et al., 2023), a value close to the lower limit (35.3 MgC/ha) of the present study. Conversely, the dry Chiquitano forests of Bolivia exhibited variations from 209 to 213 MgC/ha (Paz-Roca & Mostacedo, 2020), differences explained by the average tree height (15 – 19 m) compared to that of the present study habitat (4 – 11 m). Additionally, other native forests show high carbon storage values. The Yungas in Argentina retain 162 tC/ha (Manrique et al., 2011), while natural urban forests in the United States store between 214 and 267 MgC/ha (Jevon et al., 2024). These variations reflect the influence of forest structure, where larger and more mature trees significantly contribute to total biomass (de Paula et al., 2011). This analysis highlights the importance of sustainable management of native forests to maximize their carbon storage capacity and mitigate the effects of climate change.

3.2. Taxonomic diversity

A total of 558 tree individuals belonging to 31 species were recorded in all habitats (Table 1). UF had the highest species TD (16 ± 0.3956), followed by NF (15 ± 0.3760) and EF (2 ± 0.1421) (Figure 3a). Species TD was significantly related to habitat type ($F_{(2,33)} = 10.825$, $p < 0.001$). Tukey means tests between habitat pairs and species diversity showed significant differences, particularly between NF-EF ($p < 0.0008$), UF-EF ($p <$ 1e-04), and no significant differences UF-NF ($p = 0.7494$) (Table S8, Supplementary Material). There was a low significant positive relationship between species richness and temperature ($F_{(1,34)} = 6.911$, $p < 0.012$), a non-significant negative relationship between species richness and precipitation ($F_{(1,34)} = 1.9699$, $p < 0.1695$), and a significant negative direct relationship between species richness and altitude gradient ($F_{(1,34)} = 7.7353$, $p < 0.008$) (Table S9, Supplementary Material). The taxonomic diversity (TD) of 31 tree species presents in the three habitats studied in the Sucre municipality spans a forested area of 14 842 ha, distributed among urban forests (UF), rural forests (NF), and exotic forests (EF). Over the past four decades, the management of tree species in this urban-rural ecosystem has reflected a taxonomic contribution of 51.6% in UF, 48.3% in NF, and 6.5% in EF, with only two species shared between habitats (UF-EF and UF-NF). In contrast, the vascular plant diversity recorded in Chuquisaca between 1999 and 2009 includes 3 279 species (Serrano & Vildozo, 2015), many of which belong to ecosystems such as the Tucuman-Bolivian Forest and the Inter-Andean Valleys, where the 16 native species identified in this study are found. However, the species richness in other urban ecosystems in Bolivia, such as Cochabamba (9 native species; Maldonado et al., 2023) and La Paz (18 native and exotic species; Pacheco, 2020), differs from the results of the present study. Internationally, cities such as Berlin (Germany) report 68 tree species (Richter et al., 2020), while Beijing (China) registers 26 species (Sun et al., 2019). These differences in TD can be attributed to factors such as sampling effort, species composition, and habitat delineation. In the present study, the influence of temperature and altitudinal gradients conditions TD across habitats, where NF species are predominantly native, while EF species are exotic. Moreover, at higher altitudinal gradients, no native tree species were recorded. In this context, greater species diversity in urban environments enhances soil carbon stocks by stimulating subterranean organism activity (Schittko et al., 2022), whereas in rural ecosystems, species richness positively correlates with carbon sequestration (Richards & Méndez, 2014; Ali & Yan, 2017).

3.3. Phylogenetic diversity

Phylogenetic diversity was related to habitat type ($F_{(2,33)} = 8.7496$, $p < 0.0008939$), with the highest PD index (in millions of years) in UF (2385.4506 ± 60.76), followed by NF (1484.5453 ± 29.33) (Table S3; Figure 3b), and the lowest PD in EF (725.8377 ± 46.2). Pairwise mean "t" tests between habitat types and PD showed significant differences between UF-NF ($p < 0.00018$), UF-EF ($p <$ 1e-04), and no significant differences between NF-EF ($p < 0.9585$) (Table S10, Supplementary Material). PD had a significant correlation with species richness (SR) ($r = 0.650$, $p < 0.001$) (Figure S3). Phylogenetic species richness (PSR) showed a high correlation with PD ($r = 0.956$, $p < 0.001$) (Figure S3). Precipitation was positively and significantly related to PSR ($F_{(1:29)} = 19.138$, $p < 0.001$), as was the altitude gradient with PSR ($F_{(1,29)} = 11.509$, $p < 0.002$) (Tables S11, S12: Supplementary Material). Phylogenetic endemism (PE) had a high correlation with species richness (SR) ($r = 0.909$, $p < 0.001$) and with PD ($r = 0.642$, $p < 0.008$) (Figure S3). Altitude gradient showed a significant negative relationship with PE ($F_{(1,34)} = 4.9032$, $p < 0.033$) (Table S13, Supplementary Material). Species evolutionary distinctiveness (ED) highlighted *Hesperocyparis macrocarpa* (400.788 Mya) and *Pinus pseudostrobus* (362.919 Mya) as the most evolutionarily distinct species, while *Senegalia praecox* and *Senegalia gilliesii* (37.743 Mya) were among the least distinct.

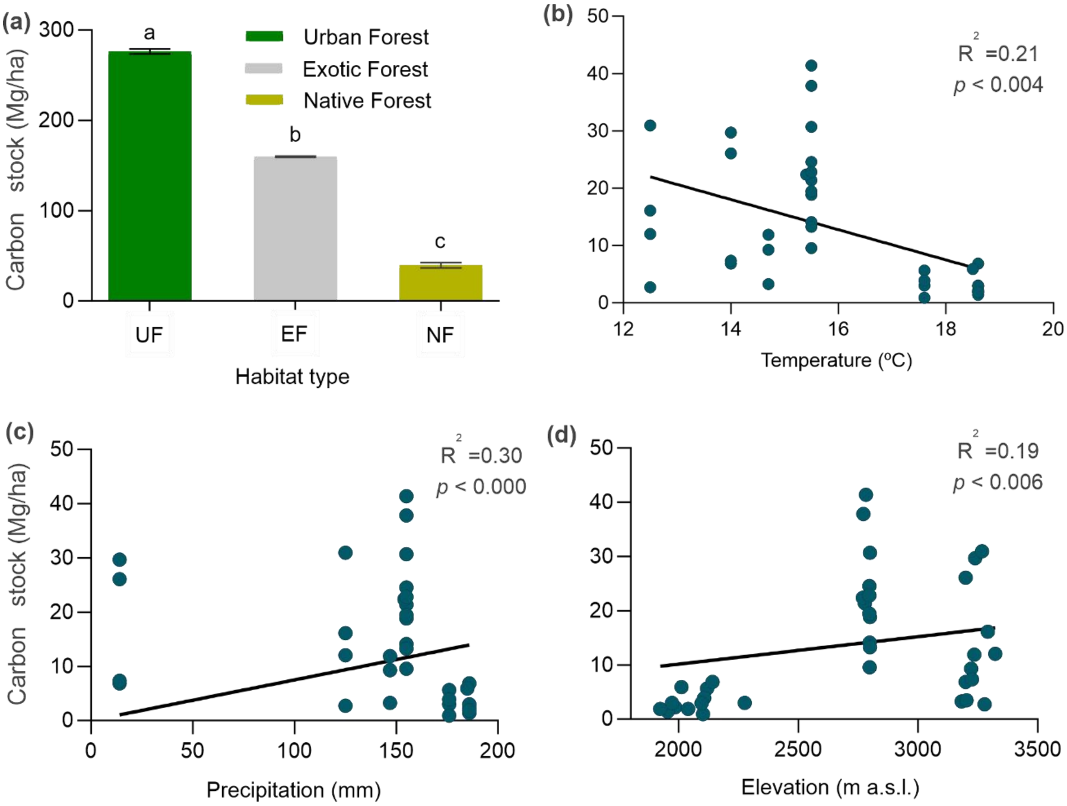

Figure 2. Contribution of habitat types to carbon reserves and their bioclimatic and geographic influence: (a) Carbon reserves in habitats: urban forest (UF), native forest (NF), and exotic forest (EF). Different letters indicate significance at $p \leq 0.05$, and the bars represent the standard error (±SE). (b) Effect of mean annual temperature on carbon reserves. Colored points represent the distribution of carbon stock for each sampling site (n = 36) in relation to the temperature range (12-19 ºC), with values corresponding to the regression model (R^2 = coefficient of determination; p = significance). (c) Influence of mean annual precipitation on carbon reserves. Colored points indicate the distribution of carbon reserves (n = 36) in relation to the precipitation range (536-708 mm). (d) Effect of elevation on carbon reserves along the altitudinal gradient. Colored points illustrate the distribution of carbon reserves (n=36) in relation to the elevation range (1923-3323 m.a.s.l.).

The phylogenetic diversity (PD) in the present study is directly related to TD. The UF habitat exhibits a higher evolutionary rate (2 385.45 ± 60.76) compared to NF and EF. This result may be influenced by the coexistence of native and exotic species, tree age, municipal conservation policies, and phylogenetic criteria assigned to taxa (Faith, 1992). Lower PD values observed in NF (~62.23%) and EF (~30.42%) reflect both the specific composition of the habitats and the conservation status of TD. The phylogenetic tree topology of the 31 analyzed species indicates a high evolutionary rate in species such as *Hesperocyparis macrocarpa* (400 Mya) and *Pinus pseudostrobus* (362 Mya), in contrast to *Senegalia gilliesii* and *Senegalia praecox* (37.743 Mya). Conversely, the presence of 233 native and exotic species along an urbanization gradient in Minneapolis-Saint Paul (USA) shows a PD variation between habitats (563.73 – 610.78 Mya; Knapp et al., 2012), values lower than those obtained in the present analysis. These differences likely arise from species composition rather than TD. Although PD plays a complementary role in rural ecosystems, it does not always capture the functional mechanisms driving carbon storage in urban environments (Lososová et al., 2016; Mensah et al., 2024).

3.4. Functional diversity

Functional diversity (Figure 3c) was found to be significantly related to habitat types ($F_{(2,33)}$ = 13.626, p < 0.001), with UF showing the highest expression of functional traits (0.866 ± 0.061), followed by NF (0.7297 ± 0.073) and EF (0.449 ± 0.028) (Table S14 Supplementary Material; Figure 3c). Pairwise mean "t" tests indicated significant differences between NF-EF (p < 0.001), UF-EF (p < 0.001), and no significant differences between UF-NF (p = 0.213) (Table S15, Supplementary Material). FD had a high correlation with species richness (SR) (r = 0.939, p < 0.001), functional richness (FRIC) (r = 0.749, p < 0.001), and functional dispersion (FDIS) (r = 685, p < 0.001). Additionally, FD had a significant positive relationship with temperature ($F_{(1,34)}$ = 4.931, p < 0.033), while the altitude gradient had a significant negative relationship with FD ($F_{(1,34)} = 5.534$, $p < 0.024$) (Table S14).

Functional diversity (FD), in turn, is closely linked to TD. In the present study, UF habitat exhibits the highest expression of functional traits (0.866 ± 0.061) compared to NF and EF. This result may be influenced by factors such as tree structure, climate, conservation efforts, and species' morphological and physiological traits. Collective functional traits of plant communities are key determinants of carbon accumulation in terrestrial ecosystems (Conti & Díaz, 2013). Characteristics such as height, density, and leaf type are fundamental in carbon fixation (Díaz et al., 2016). In the present analysis, functional traits of NF (84.26%) and EF (51.84%) are lower compared to UF (100%), a difference associated with TD, PD, and habitat-specific composition. Additionally, FD provides critical insights into the distribution range, abundance, ecological guilds, and productive characteristics of ecosystems (Morelli et al., 2018). Thus, functional traits of arboreal diversity in specific habitats are essential indicators of carbon fixation and ecosystem functioning in urban and rural settings. In urban areas, these traits enhance soil multifunctionality, while in rural areas, traits such as plant height and wood density are key predictors of carbon storage (Conti & Díaz, 2013; Mensah et al., 2024).

3.5. Tree species composition

In the overall composition of tree species (Figure 3d), a significant difference was observed among habitat types, as evidenced by ANOSIM analysis (R = 0.715, p = 0.0001) (Figure 3d). Pairwise comparisons revealed significant differences between all habitat pairs (all $p = 0.0001$). The species dominance in the habitats included a total of 31 species (Table S16, Supplementary Material). In the EF habitat, the abundance proportion and species range highlighted *Pinus pseudostrobus* (proportion = 74.1%, range = 1) and *Eucalyptus globulus* (proportion = 25.9%, range = 2). In contrast, the NF habitat presented 15 species, with *Senegalia gilliesii* (proportion = 34.5%, range = 1) and *Senegalia praecox* (proportion = 15.1%, range = 2) as the dominant species. In the UF habitat, comprising 16 species, *Hesperocyparis macrocarpa* (proportion = 51.9%, range = 1) was found to be the species with the tallest and largest individuals, while *Ligustrum lucidum* (proportion = 16%, range = 2) emerged as the most abundant species.

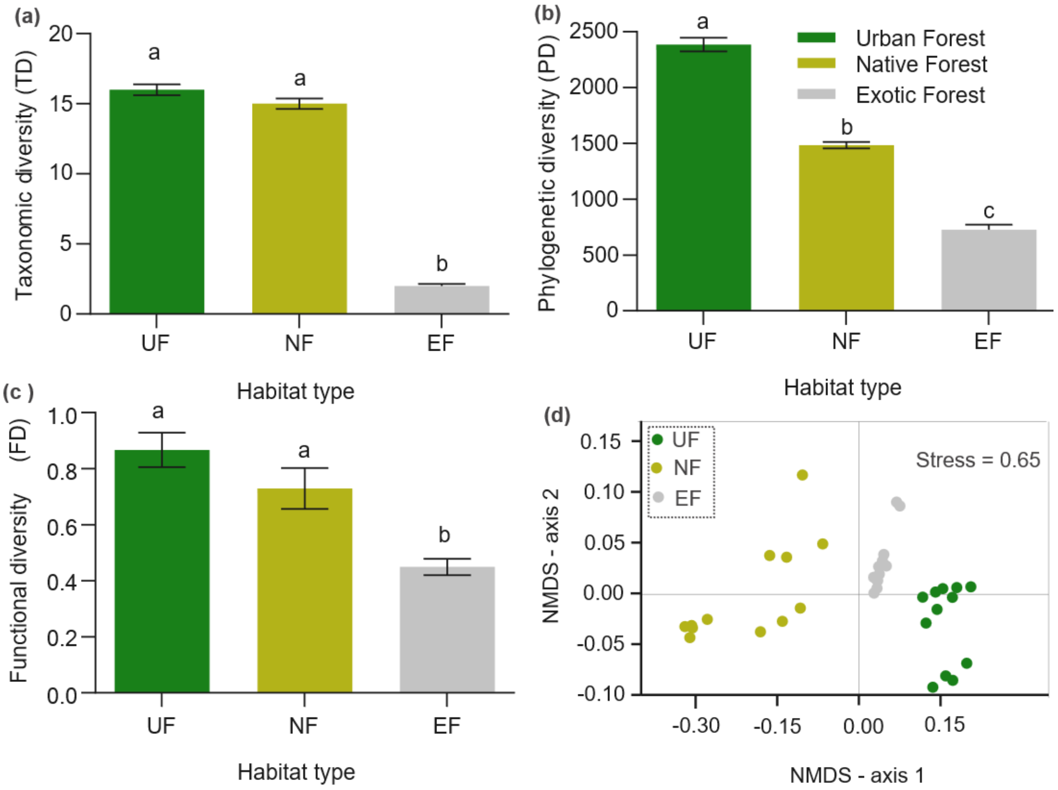

Figure 3. Effects of habitat type on tree diversity and species composition: (a) Taxonomic diversity (TD; i.e., species richness) among urban forest (UF), native forest (NF), and exotic forest (EF). Different letters indicate significance at $p \leq 0.05$, and the bars represent the standard error (±SE). (b) Phylogenetic diversity (PD) in millions of years among habitat types. (c) Functional diversity (FD) among habitat types. (d) Non-metric multidimensional scaling (NMDS) ordination of community structure (NMDS axis 1; NMDS axis 2) among urban forest (UF), native forest (NF), and exotic forest (EF).

The carbon storage capacity, determined by vegetation, tree density, and species composition (Lwasa et al., 2022), highlights the potential of the forest habitats in the municipality of Sucre to mitigate climate change and promote environmental sustainability. This municipality, with an urban-rural ecosystem covering 172 169.17 ha, comprising 4.6% urban area, 95.18% rural area, and 0.21% forest area and a population density of 152 inhabitants/km^2 (GAMS, 2020), has strengthened this potential through approximately 40 years of afforestation and conservation strategies implemented by the former Regional Development Corporation of Chuquisaca and the Autonomous Municipal Government of Sucre. These efforts have optimized the taxonomic, phylogenetic, and functional diversity of trees in response to bioclimatic and geographic factors, solidifying their contribution to sustainable urban management and ecosystem health.

4. Conclusions

The research evidences the contribution of trees in urban-rural ecosystems in the municipality of Sucre, Bolivia, which play a decisive role in carbon retention and taxonomic, phylogenetic, and functional diversity, modulated by bioclimatic (temperature and precipitation) and geographical (altitude) factors. Urban forests have the greatest carbon capture capacity, resulting from the coexistence of native and exotic trees species, their longevity, and the management strategies implemented in the urban-rural ecosystem. Tree diversity, conditioned by environmental gradients, is a key factor in maximizing carbon sequestration and maintaining ecosystem functionality. These findings highlight the need to integrate tree diversity conservation with sustainable urban-rural planning, strengthening ecological resilience and ecosystem services in urban-rural environments.

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Author contributions

M. Serrano and **W. Felipez**: Conceptualized the study, coordinated research activities, and prepared the manuscript. **J. Bejarano**: Contributed to data collection, analysis, and drafting. **R. Lozano**. and **M. H. Jimenez**: Supervised fieldwork and validated the data **W. Felipez** and **R. Lozano**: Provided statistical support and reviewed the manuscript.

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Data availability

The data generated and analyzed during this study are available in the Supplementary Materials. Additionally, the datasets have been deposited in Zenodo with the following DOI: https://doi.org/10.5281/zenodo.17179882.

Declarations

The authors declare no competing interests.

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