Urban Ecosystems (2026) 29:97
https://doi.org/10.1007/s11252-026-01959-9

RESEARCH

Trait-mediated associations between *Ligustrum lucidum invasion* and functional diversity in urban Atlantic Alluvial Forests

Aline Cristina Stocki[1] · **Joelmir Augustinho Mazon**[2] · **Luciano Farinha Watzlawick**[3]

Received: 7 October 2025 / Accepted: 15 March 2026 / Published online: 30 March 2026
© The Author(s) 2026

Abstract

Invasive alien species are drivers of biodiversity loss and can alter forest functioning. Despite the expansion of *Ligustrum lucidum* across South America, its effects on the functional organization of tree communities in urban Atlantic alluvial forests remain poorly understood. Here, we examined how variation in *L. lucidum* abundance relates to functional trait composition and diversity across a 103-plot permanent monitoring network in southern Brazil. We quantified leaf and structural traits, calculated community-weighted means and functional diversity indices, and combined multivariate analyses with structural equation modeling to evaluate direct and indirect relationships among invasion intensity, community assembly, and functional structure. *L. lucidum* exhibited trait values distinct from those of native species, occupying one extreme of the community functional space and accumulating substantially greater biomass. Increasing invader abundance was associated with declines in native species richness and with reductions in functional dispersion (FDis) and Rao's quadratic entropy (RaoQ), indicating contraction of trait breadth and increasing similarity among native assemblages. However, invasion intensity was not directly associated with functional diversity. Instead, changes in FDis and RaoQ were mediated indirectly through shifts in species richness and dominant trait composition, demonstrating that functional reorganization emerges from trait-mediated community reassembly rather than direct suppression by the invader. Together, these findings indicate that *L. lucidum* acts as an ecological filter that reshapes trait structure, reduces functional redundancy, and may weaken ecosystem resilience in urban alluvial forests. Integrating functional metrics into monitoring and management is therefore critical for early detection, risk assessment, and restoration.

Keywords Biotic homogenization · Community assembly · Environmental filtering · Functional traits · Tree species

Introduction

Biological invasions are widely recognized as one of the leading drivers of biodiversity loss, ecosystem dysfunction, and degradation of ecosystem services worldwide (Simberloff et al. 2013). When introduced beyond their native ranges, non-native species can alter community composition, modify resource availability, and disrupt ecological processes, often generating substantial economic, environmental, and social impacts (CBD 2020; Pyšek et al. 2020). These risks are expected to intensify under accelerating climate change, urban expansion, and increasing global connectivity, which collectively enhance propagule pressure and disturbance regimes that favor the establishment of invasive species (Early et al. 2016; Seebens et al. 2021).

Alluvial and riparian forests are particularly susceptible to invasion because their intrinsic dynamics—including periodic flooding, sediment deposition, and strong

✉ Aline Cristina Stocki
stockia27@gmail.com

Joelmir Augustinho Mazon
joelmir.mazon@uniguairaca.edu.br

Luciano Farinha Watzlawick
farinha@unicentro.br

[1] Department of Agronomy, Midwestern State University (UNICENTRO), Guarapuava, Paraná, Brazil

[2] Department of Biology, University Center of Uniguairacá, Guarapuava, Paraná, Brazil

[3] Department of Agronomy, Midwestern State University (UNICENTRO), Guarapuava, Paraná, Brazil

hydrological connectivity—create recurrent disturbance and high resource turnover, conditions that facilitate colonization and rapid population growth of non-native plants (Richardson et al. 2007; Rood et al. 2020). Across continents, invasive trees frequently dominate these environments, replacing native vegetation and modifying structural and functional attributes of ecosystems. Examples include *Ailanthus altissima* in North American riverine forests, *Salix* species in Oceania, and Australian *Acacia* species in South African riparian zones, all of which alter regeneration dynamics, nutrient cycling, and biomass accumulation (Doody et al. 2014; Scott-Shaw et al. 2017; McInerney et al. 2021; Lusizi et al. 2024). Such processes may promote biotic homogenization and reduce functional stability, with consequences for ecosystem resilience and service provision (Díaz et al. 2013; Villéger et al. 2014).

Within this context, the Asian genus *Ligustrum* (Oleaceae) includes several globally invasive woody species. Among them, *Ligustrum lucidum* W.T. Aiton has become one of the most widespread tree invaders in subtropical and temperate regions due to its broad ecological tolerance, rapid growth, evergreen habit, and prolific bird-mediated seed dispersal (Nogueira et al. 2020; Fernandez et al. 2020). In invaded forests, *L. lucidum* often forms dense, persistent canopies that strongly reduce understory light availability and alter litter inputs and microclimatic conditions, leading to shifts in vegetation structure and regeneration patterns. Field studies have documented substantial increases in leaf area and structural biomass in stands dominated by this species, accompanied by declines in native tree recruitment (Paronetto et al. 2025).

Functional ecology provides a useful framework for understanding how such invasions are associated with changes in community assembly. Trait-based approaches enable the quantification of how species differ in resource-use strategies and how these differences influence coexistence, environmental filtering, and ecosystem functioning (Funk et al. 2017). In this context, two non-exclusive mechanisms may operate: invaders may occupy functional space formerly filled by native species (niche replacement), or community composition may shift toward a narrower range of strategies (trait convergence), reducing functional diversity and redundancy (Tordoni et al. 2019). Importantly, these relationships are often bidirectional. While invasive species can modify community structure and functioning, pre-existing functional characteristics—such as low diversity or particular trait syndromes—may also increase ecosystem susceptibility to invasion (Gaertner et al. 2017). Disentangling these associations remains a central challenge in invasion ecology.

Urban alluvial forests in Brazil provide a particularly suitable system for examining invasion-driven community reassembly within highly modified landscapes. These remnants function as critical components of urban green infrastructure, contributing to biodiversity conservation, carbon storage, hydrological regulation, and landscape connectivity (Naiman and Décamps 1997; Junk et al. 2014). However, they are embedded within socio-ecological settings characterized by fragmentation, edge effects, altered microclimates, and elevated propagule pressure—conditions that may simultaneously increase susceptibility to invasion and reshape community assembly processes. Despite the growing dominance of *L. lucidum* in many urban and peri-urban forest fragments, the extent to which its abundance is associated with shifts in the functional composition and diversity of native tree communities remains insufficiently quantified.

Here, we investigate how variation in *L. lucidum* abundance is associated with the functional structure of native tree communities in an urban remnant of Atlantic alluvial forest. Specifically, we address three questions: (i) whether *L. lucidum* exhibits functional trait values that differ from those of co-occurring native species, occupying distinct regions of community trait space; (ii) whether increasing invader abundance is associated with shifts in community-weighted trait values and overall functional composition; and (iii) whether functional diversity metrics vary along the invasion gradient. By adopting a functional ecology framework, this study aims to elucidate how invasion intensity and community functional organization covary during community assembly, thereby providing insights relevant to the management and restoration of vulnerable alluvial forest ecosystems.

Materials and methods

This study was conducted in an 11.5-ha remnant of urban alluvial forest within the Cascavel River watershed, Guarapuava, Paraná, Brazil. The site lies between the Carro Quebrado Stream to the north and the Cascavelzinho River to the west (Watzlawick et al. 2021). Elevation ranges between 1,000 and 1,020 m, with a humid mesothermal subtropical climate (Cfb, Köppen classification) and predominantly alluvial-derived Latosols (Rodrigues et al. 2016; Stocki et al. 2024a, b). The site has been historically disturbed by urban waste deposition and selective logging of native trees (Watzlawick et al. 2021; Stocki et al. 2024a, b). The site was chosen because it represents a typical urban alluvial forest fragment of the southern Brazilian Atlantic Forest, making it suitable for investigating how anthropogenic disturbance and biological invasion interact to shape forest structure and functional diversity.

A total of 103 permanent plots (10 × 10 m; 100 m² each) previously established within an 11.5-ha forest remnant

were used in this study (Supplementary Figure S1). These plots are part of a long-term monitoring network that has been employed in previous research (Rodrigues et al. 2016; Watzlawick et al. 2021; Stocki et al. 2024a, b). Forty-two plots were originally installed along a toposequence to capture environmental gradients, while the remaining plots were randomly distributed throughout the fragment to represent its overall structural heterogeneity. Using this permanent inventory, we conducted the floristic and functional trait surveys for the present study. Although plots were spatially distributed along environmental gradients and across the forest fragment, they were located at sufficient distances to minimize spatial dependence, and thus were treated as independent sampling units in the analyses.

We selected ten abundant tree species (≥50 individuals per species) that together account for approximately 80.58% of the total importance value of the community, calculated as the mean of relative density, frequency, and dominance (Supplementary Table S1). The selected species were *Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl. (Sapindaceae), *Casearia decandra* Jacq. (Salicaceae), *Gymnanthes klotzschiana* Müll.Arg. (Euphorbiaceae), *Ilex theezans* Mart. ex Reissek (Aquifoliaceae), *Ligustrum lucidum* W.T.Aiton (Oleaceae), *Matayba elaeagnoides* Radlk. (Sapindaceae), *Prunus myrtifolia* (L.) Urb. (Rosaceae), *Cinnamodendron dinisii* Schwacke (Canellaceae), *Ocotea puberula* (Rich.) Nees (Lauraceae) and *Zanthoxylum rhoifolium* Lam. (Rutaceae). This selection minimized potential sampling biases associated with rare taxa and ensured that the functional characterization was based on species with a representative contribution to community structure and ecosystem functioning.

The functional traits of the selected species were measured following standardized protocols (Pérez-Harguindeguy et al. 2016). For leaf traits, twenty fully expanded leaves were collected from ten adult individuals per species. To minimize variation associated with within-crown light gradients, sampling was standardized across species. For canopy and midstory trees, leaves were taken from the outer, fully illuminated portions of the crown. For understory species naturally growing under shaded conditions (e.g., *Allophylus edulis*), leaves were sampled from the most exposed branches within their typical light environment. In all cases, only mature, fully expanded, non-senescent leaves were selected, avoiding shaded interior or recently flushed tissues. Immediately after collection, samples were stored in sealed plastic bags with moist paper and kept refrigerated until processing to maintain leaf hydration. Leaf area was quantified using ImageJ, with petioles and rachises included for compound leaves. Each leaf was weighed to obtain fresh mass, scanned, and oven-dried at 67 °C for 72 h to determine dry mass. Specific leaf area (SLA) was calculated as leaf area divided by dry mass, and leaf dry matter content (LDMC) as the ratio between dry and fresh mass. Leaf thickness (LT) was measured following Vile et al. (2005).

Structural traits were obtained directly in the field. Total tree height (H) was recorded in 2022 and again in 2024, and canopy depth (CD) was calculated as the difference between total height and the height of the primary bifurcation. Relative growth rate (RGR) was estimated from DBH measurements (DBH≥5 cm) collected in 2011 and remeasured in 2024, following Forgiarini et al. (2015). Finally, aboveground biomass (B) at both the species and plot levels was calculated using region-specific allometric equations developed for tree species in Paraná, southern Brazil (Zanette et al. 2021; adj. $R^2 = 0.928$).

To evaluate redundancy among functional traits, pairwise Spearman correlations were computed (Supplementary Figure S2). No correlations exceeded the $|\rho| \geq 0.90$ threshold typically used to indicate severe collinearity, suggesting that the selected traits represent complementary and largely independent ecological dimensions. Although some traits showed moderate-to-strong associations (e.g., SLA and LT), these relationships are expected given the underlying biological and mathematical links among leaf traits and do not indicate redundancy.

Differences in functional traits between *L. lucidum* and native species were tested using generalized linear models (GLMs). In these analyses, each functional trait (SLA, LT, LDMC, H, CD, RGR, and B) was treated as a response variable, with species identity (invasive vs. native) included as the categorical predictor. Model distributions and link functions were selected based on Shapiro–Wilk tests and visual inspection of residuals: traits meeting normality assumptions were modeled with a Gaussian distribution and identity link, whereas non-normal data were fitted with a Gamma distribution and log link. To control for multiple testing, Bonferroni-adjusted pairwise comparisons were applied ($p<0.05$). Changes in aboveground biomass between 2011 and 2024 were assessed using the Wilcoxon signed-rank test ($\alpha=0.05$). In addition, we performed a Principal Components Analysis (PCA) using all functional traits to quantify multivariate differences in functional space between *L. lucidum* and the native species.

Community functional composition was quantified as community-weighted means (CWMs), representing the average trait value weighted by species abundance (Malysz et al. 2019). Community-weighted means were calculated using only native species, excluding *L. lucidum*. This decision avoids mathematical inflation of trait means caused by the invader's own trait values and allows us to quantify how native functional composition shifts along the invasion gradient. Functional diversity was assessed using five complementary indices that capture distinct aspects of community

trait structure: functional richness (FRic), which measures the volume of functional space occupied by the community; functional evenness (FEve), reflecting the regularity of trait value distribution within that space; functional divergence (FDiv), indicating how trait values are distributed toward extreme versus central positions; functional dispersion (FDis), expressing the mean distance of species from the community centroid weighted by abundance; and Rao's quadratic entropy (RaoQ), which integrates trait dissimilarity and species abundance to quantify overall functional variance (Villéger et al. 2008; Laliberté and Legendre 2010; Malysz et al. 2019). These metrics were chosen because together they provide a comprehensive representation of trait complementarity, redundancy, and resource-use differentiation within the community.

Thus, CWMs and functional metrics represent the functional structure of the native component of the community as a function of *L. lucidum* abundance. Invasion intensity was quantified as the relative abundance of *L. lucidum (*% of individuals per plot), which we used as a proxy for invasion stage. We did not directly measure invasion time; therefore, low relative abundance may indicate either early stages of invasion or environmental constraints that limit the dominance of the invader. To assess the effects of *L. lucidum* abundance on ecosystem functioning, we fitted generalized additive mixed models (GAMMs) with thin-plate regression splines (Fernandez et al. 2021). In these models, functional diversity indices (FRic, FEve, FDiv, FDis, and RaoQ) and CWMs of each trait were used as response variables, and the relative abundance of *L. lucidum* (percentage of individuals per plot) as the predictor. Plot identity was included as a random effect to account for repeated measures and spatial dependence.

To explicitly evaluate potential direct and indirect relationships among invasion intensity, functional traits and community functional diversity, we fitted structural equation models (SEM). This approach allows the simultaneous estimation of multiple causal pathways and is particularly suitable when bidirectional or mediated effects are expected. In the SEMs, the relative abundance of *L. lucidum* was included as an exogenous variable representing invasion intensity. Community-weighted means of functional traits were specified as intermediate predictors, and functional diversity indices (functional dispersion – FDis, and Rao's quadratic entropy – RaoQ) were included as response variables. Models were fitted using the lavaan package in R with standardized coefficients (β), and statistical significance was assessed using z-tests ($\alpha = 0.05$). SEM diagrams were visualized using the semPlot package. All statistical analyses were conducted in R (R Core Team 2025), using the packages vegan (Oksanen et al. 2019), FD (Laliberté et al. 2015), gamm4 (Pedersen et al. 2019), FSA (Ogle et al. 2023), and lavaan (Rosseel 2012).

Results

The comparison of functional traits between *L. lucidum* and native tree species (Supplementary Table S2) revealed significant differences across all traits analyzed (Fig. 1a - Supplementary Table S3). *L. lucidum* had lower values of specific leaf area (SLA) and leaf dry matter content (LDMC), but higher leaf thickness (LT) than natives. For structural traits, the invasive species showed lower mean values of canopy depth (CD), height (H), and relative growth rate (RGR) ($p < 2 \times 10^{-16}$). Between 2011 and 2024, there was a statistically significant increase in total community biomass ($V = 67{,}787$, $p < 2.2 \times 10^{-16}$). In 2011, aboveground biomass did not differ significantly between *L. lucidum* and native species ($p = 0.291$). However, by 2024 the invasive species exhibited values more than twice those of native species ($p < 0.001$; Fig. 1b).

Principal component analysis (PCA) showed that *L. lucidum* did not form a completely distinct cluster and instead occupied one extreme of the functional trait space defined by native species. In the foliar trait PCA (Fig. 2a), PC1 explained 70.1% of the variance and contrasted higher SLA values with higher LDMC and leaf thickness, whereas PC2 (26.3%) was mainly associated with variation in leaf thickness. Individuals of *L. lucidum* were located toward the LDMC–LT end of PC1. In the structural trait PCA (Fig. 2b), PC1 explained 49.7% of the variance and was associated with height, crown depth, and biomass, while PC2 (21.7%) was primarily related to relative growth rate. *L. lucidum* individuals were positioned toward the positive side of PC1. Across both ordinations, substantial overlap was observed between invasive and native species.

Greater abundance of *L. lucidum* ranged from 0 to 80% of individuals and was treated as a continuous measure of invasion intensity (Fig. 3; Supplementary Table S4). Native species richness declined sharply at low invasion levels and reached a plateau at approximately 40% invasion, remaining consistently lower thereafter (Fig. 3a). Leaf dry matter content (LDMC) increased slightly with invasion intensity, whereas specific leaf area (SLA) decreased (Fig. 3b). Structural traits showed variable responses: crown depth decreased along the invasion gradient, while mean height and relative growth rate exhibited weak or non-linear patterns (Fig. 3c). Among functional diversity metrics, only functional dispersion (FDis) and Rao's quadratic entropy (RaoQ) were negatively associated with *L. lucidum* abundance, with both indices declining at low to intermediate invasion levels and remaining reduced across the gradient

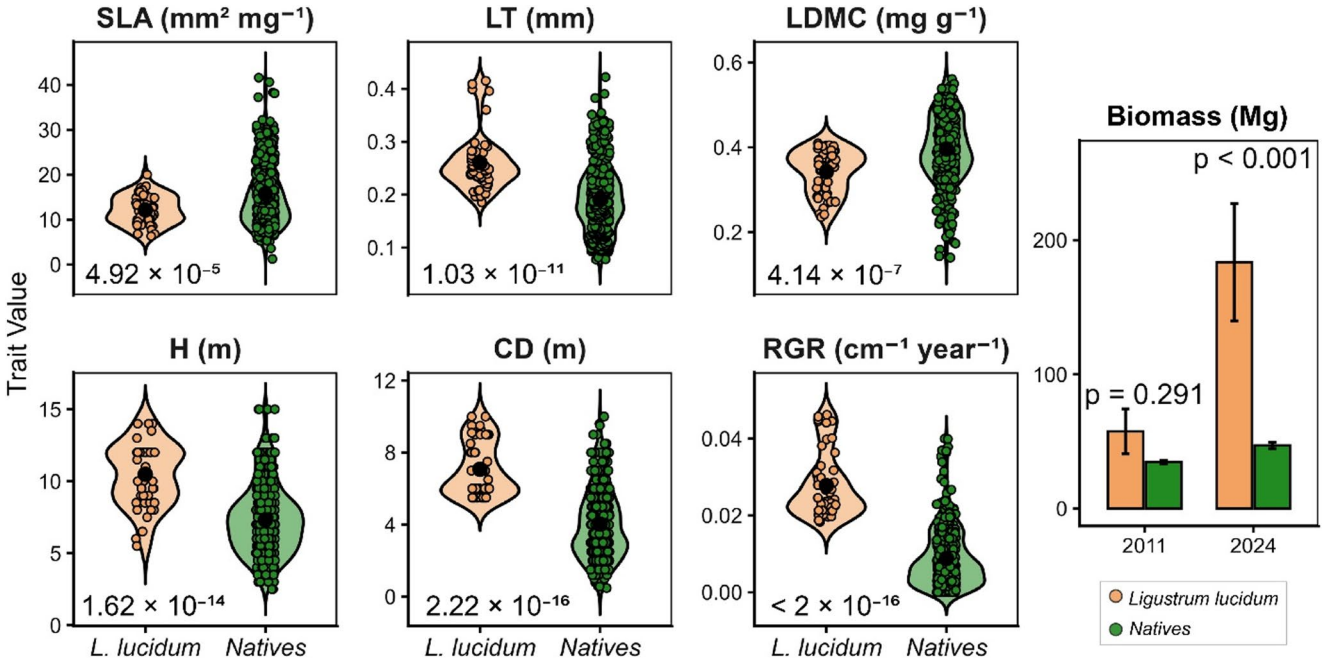


Fig. 1 (**a**) Distribution of functional traits: SLA (specific leaf area), LT (leaf thickness), LDMC (leaf dry matter content), H (total height), CD (crown depth), and RGR (relative growth rate). Violin plots represent the probability density of values for each group. Points indicate individual observations, black dots denote group means, and vertical lines represent the median and interquartile range. P-values were obtained from generalized linear models (GLMs) comparing *L. lucidum* and native species. (**b**) Aboveground biomass (Mg) of *L. lucidum* and native species in 2011 and 2024 (log scale). Bars represent mean biomass ± SE. P-values correspond to Wilcoxon tests comparing groups within each year. Native species included in the study: *Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl. (Sapindaceae), *Casearia decandra* Jacq. (Salicaceae), *Gymnanthes klotzschiana* Müll.Arg. (Euphorbiaceae), *Ilex theezans* Mart. ex Reissek (Aquifoliaceae), *Ligustrum lucidum* W.T.Aiton (Oleaceae), *Matayba elaeagnoides* Radlk. (Sapindaceae), *Prunus myrtifolia* (L.) Urb. (Rosaceae), *Cinnamodendron dinisii* Schwacke (Canellaceae), *Ocotea puberula* (Rich.) Nees (Lauraceae) and *Zanthoxylum rhoifolium* Lam. (Rutaceae)

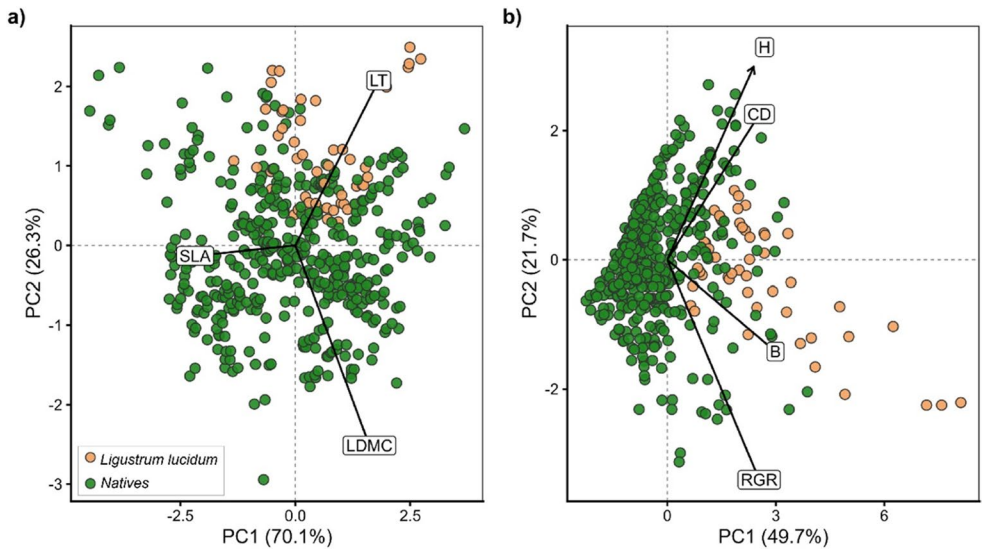


Fig. 2 Principal component analysis (PCA) of functional traits of native species and *Ligustrum lucidum*. (**a**) Foliar traits: specific leaf area (SLA), leaf dry matter content (LDMC), and leaf thickness (LT). **b**) Structural traits: mean height (H), aboveground biomass (B), crown depth (CD), and relative growth rate (RGR). Black arrows indicate trait loadings on the principal axes. Percentages in parentheses denote variance explained. Native species included in the study: *Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl. (Sapindaceae), *Casearia decandra* Jacq. (Salicaceae), *Gymnanthes klotzschiana* Müll.Arg. (Euphorbiaceae), *Ilex theezans* Mart. ex Reissek (Aquifoliaceae), *Ligustrum lucidum* W.T.Aiton (Oleaceae), *Matayba elaeagnoides* Radlk. (Sapindaceae), *Prunus myrtifolia* (L.) Urb. (Rosaceae), *Cinnamodendron dinisii* Schwacke (Canellaceae), *Ocotea puberula* (Rich.) Nees (Lauraceae) and *Zanthoxylum rhoifolium* Lam. (Rutaceae)

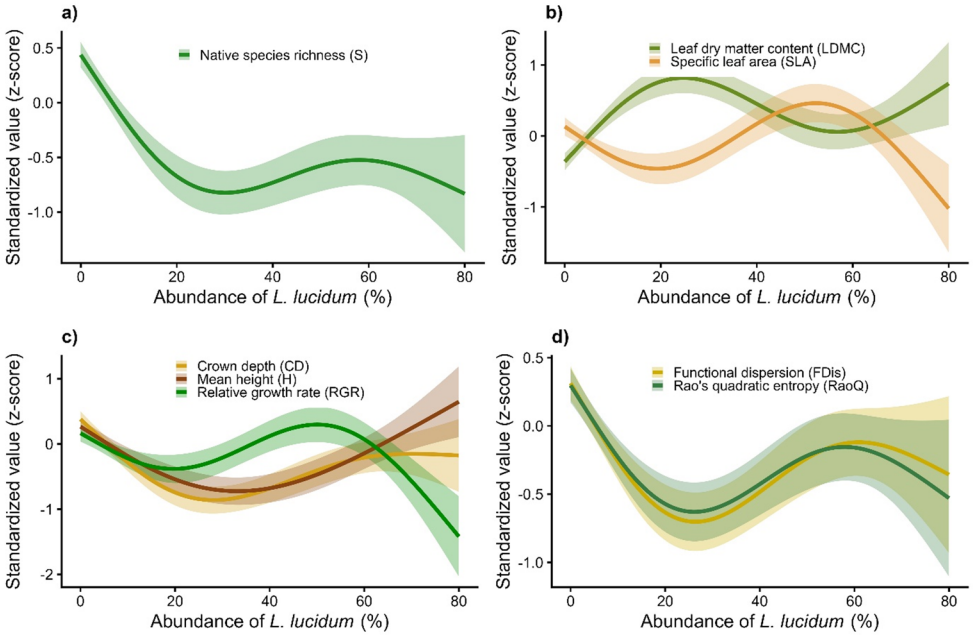


Fig. 3 Relationships between *Ligustrum lucidum* abundance and standardized (z-score) native community attributes estimated using GAMMs. (a) Native species richness (S). (b) Foliar traits: leaf dry matter content (LDMC) and specific leaf area (SLA). (c) Structural traits: canopy depth (CD), mean height (H), and relative growth rate (RGR). (d) Functional diversity indices: functional dispersion (FDis) and Rao's quadratic entropy (RaoQ). Solid lines indicate GAMM-fitted smooth functions, and shaded areas represent 95% confidence intervals. All variables were standardized (z-scores). Community-weighted means and functional diversity metrics were calculated using only native species, excluding *L. lucidum*

(Fig. 3d). Functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) showed no significant relationships with invasion intensity.

Because the structural equation models were saturated (df = 0), global fit indices were not evaluated, and interpretation focused on path coefficients. The models explained a substantial proportion of variance in functional diversity, accounting for 71.5% of variation in functional dispersion (FDis) and 68.6% in Rao's quadratic entropy (RaoQ). Structural equation models revealed significant direct effects of species richness, specific leaf area (SLA), and mean height on functional dispersion, with FDis increasing with species richness ($\beta = 0.52$, $p < 0.001$), SLA ($\beta = 0.51$, $p < 0.001$), and mean height ($\beta = 0.27$, $p = 0.036$). Leaf dry matter content (LDMC), relative growth rate (RGR), crown depth (CD), and invasion intensity did not show significant direct effects ($p > 0.05$). For Rao's quadratic entropy, significant positive effects were detected for SLA ($\beta = 0.68$, $p < 0.001$), species richness ($\beta = 0.51$, $p < 0.001$), and mean height ($\beta = 0.27$, $p = 0.036$), whereas LDMC, crown depth, relative growth rate, and invasion intensity were not significant predictors. No direct effects of invasion intensity were detected for either functional diversity metric (Fig. 4; Supplementary Table S5).

Discussion

Our results indicate that increasing *L. lucidum* abundance is associated with declines in native species richness and a reorganization of community functional structure, suggesting that invasion intensity is tightly linked to community assembly processes in urban alluvial forests. Along the invasion gradient, functional diversity exhibited non-linear responses: functional dispersion (FDis) and Rao's quadratic entropy (RaoQ) declined at low to intermediate invasion levels and exhibited a modest recovery at higher invasion intensity, although values remained below those observed at low invasion levels. Similar non-monotonic patterns have been documented in invaded ecosystems, where biological invasions restructure—rather than uniformly reduce—functional diversity (Villéger et al. 2014; Tordoni et al. 2019). Rather than reflecting a simple contraction of functional space, these dynamics are consistent with a reconfiguration of trait distributions, whereby initial environmental filtering is followed by the persistence of fewer, functionally distinct species occupying more extreme regions of trait space.

Trait-based contrasts between *L. lucidum* and native species help clarify the mechanisms underlying this functional reorganization. The invader occupied one extreme of the multidimensional trait spectrum and consistently diverged in both foliar and structural attributes. Across the invasion gradient, community-weighted means shifted toward lower specific leaf area (SLA), higher leaf dry matter content (LDMC), and lower relative growth rates. Because community-weighted means emphasize the traits of the most abundant species, these shifts are consistent with the mass-ratio hypothesis (Grime 1998), which proposes that ecosystem functioning is largely governed by dominant taxa. Moreover, these coordinated changes align with the conservative–acquisitive leaf economics spectrum (Wright et al. 2004; Funk et al. 2017), indicating directional adjustments in dominant strategies rather than stochastic species turnover.

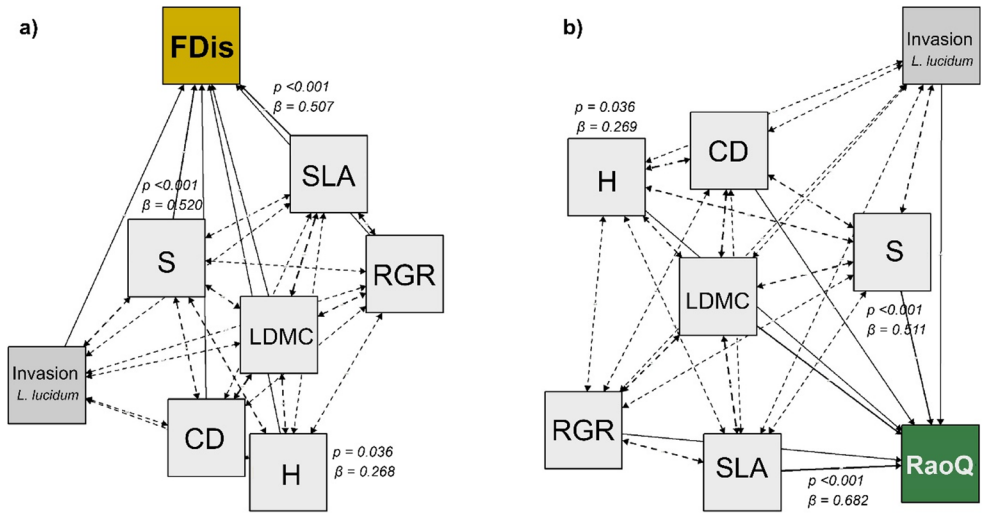


Fig. 4 Structural equation models describing the direct and indirect effects of invasion intensity and plant functional traits on functional diversity. Panels show effects on (a) functional dispersion (FDis) and (b) Rao's quadratic entropy (RaoQ). Boxes represent observed variables and arrows indicate hypothesized causal relationships. Standardized coefficients (β) and p-values are shown only for significant effects. Abbreviations: S = native species richness; SLA = specific leaf area; LDMC = leaf dry matter content; CD = crown depth; H = mean height; RGR = relative growth rate; Invasion = relative abundance of *Ligustrum lucidum*

Patterns observed in functional diversity metrics provide complementary evidence of trait filtering along the invasion gradient. Declines in FDis and RaoQ at early invasion stages indicate reduced trait dispersion and increased similarity among native species, a pattern commonly associated with environmental filtering and competitive exclusion constraining viable strategies (Díaz et al. 2013; Diniz et al. 2024). Under higher invader dominance, however, the persistence of a few functionally distinct taxa increased pairwise trait distances, leading to a partial recovery of dispersion metrics despite continued taxonomic loss. Comparable dynamics have been linked to the joint effects of species loss and limiting similarity among the remaining taxa (Loiola et al. 2018). Importantly, functional diversity indices describe how traits are distributed within communities but do not specify which strategies dominate, whereas community-weighted means more directly capture shifts in prevailing functional strategies (Bello et al. 2021; Ohlert et al. 2024; Kilgore and Restrepo 2025). Together, these metrics indicate that invasion is associated with both contraction and redistribution of trait space.

Structural shifts further reinforce these trait-based patterns. Reductions in crown depth and changes in height distributions are consistent with increased light limitation beneath dense *L. lucidum* canopies. Such canopy-driven environmental modifications are known to favor shade-tolerant, slow-growing species (Hoyos et al. 2010; Ferreras et al. 2019; Laughlin 2024). In this context, canopy-mediated conditions may act as biotic environmental filters, constraining regeneration niches and disadvantaging species with more acquisitive strategies. Similar mechanisms have been described in riparian forests, floodplains, and Mediterranean systems, where invasive dominance is associated with reduced functional redundancy and convergence in resource-use strategies (Tordoni et al. 2019; Lázaro-Lobo et al. 2021). Our results are consistent with these assembly processes operating in urban alluvial forests.

Although invasion intensity was strongly associated with changes in species richness and dominant trait values, structural equation modeling revealed no significant direct effects of invasion on functional diversity metrics. Instead, these associations appeared to be mediated indirectly through reductions in species richness and shifts in dominant trait values. Trait-mediated frameworks in invasion ecology predict that invaders influence ecosystem organization primarily by altering community composition and environmental conditions rather than exerting direct effects on diversity indices per se (Petchey and Gaston 2002; Gaertner et al. 2017). Accordingly, our findings are consistent with invasion-related community reassembly operating through compositional and dominance pathways, rather than through direct mechanistic effects on functional diversity metrics.

These patterns align with broader theoretical expectations in invasion ecology. Biological invasions often act as ecological filters that reorganize communities around a narrower set of viable strategies, potentially reducing functional redundancy and increasing the dominance of traits suited to altered environmental conditions (Díaz et al. 2013; Castro-Díez et al. 2021). In dynamic and disturbance-prone systems such as alluvial forests, hydrological variability and urban fragmentation may further facilitate invader establishment and spread (Gaertner et al. 2017). Consistent declines

in functional breadth and increased trait convergence have been reported across floodplain and riparian ecosystems worldwide (Tordoni et al. 2019; Lázaro-Lobo et al. 2021), patterns that mirror those observed here.

Under projected climate change scenarios, these associations may intensify. Increasing frequencies of floods, droughts, and thermal extremes are expected to favor species with broad ecological tolerance and high establishment capacity (Early et al. 2016). Given its evergreen habit, rapid growth, and tolerance to hydrological variability, *L. lucidum* may benefit from such conditions, potentially expanding across connected floodplain networks and reinforcing invasion-related shifts in community structure and functional organization.

From a management perspective, the strong associations between invasion intensity, declining species richness, and altered functional organization underscore the importance of early detection and rapid control. Trait-based and functional diversity approaches can strengthen monitoring programs by identifying ecosystem-level impacts that extend beyond taxonomic change (Petchey and Gaston 2002; Gladstone-Gallagher et al. 2019; Bullock et al. 2022) Targeted removal of *L. lucidum*, combined with the reintroduction of native species representing complementary trait syndromes, may help restore functional redundancy and enhance ecosystem resilience.

Finally, our results have important policy implications. Although national initiatives such as CONABIO Resolution No. 05/2009 provide a strategic framework for invasive species management, *L. lucidum* is not currently included in official federal lists, which may limit coordinated preventive and corrective actions. Recent syntheses of invasive flora in Brazil emphasize the need for stronger integration between science and policy (Zenni et al. 2024). At the state level, Paraná classifies the genus *Ligustrum* as invasive (Portaria IAP No. 59/2015), prohibiting its transport and commercialization. Expanding federal recognition and incorporating functional diversity indicators into risk assessment frameworks could better align regulatory policies with ecological evidence. Collectively, our findings indicate that invasion-associated community reassembly alters both taxonomic and functional organization, reinforcing the importance of integrating trait-based approaches into conservation and restoration planning.

Collectively, our findings indicate that invasion-associated community reassembly in urban alluvial forests is characterized not merely by species loss, but by a directional redistribution of functional strategies mediated through shifts in dominance and environmental filtering. By integrating functional diversity metrics, community-weighted means, and structural equation modeling, our results support the view that invasion effects on ecosystem organization operate primarily through trait-mediated pathways. These findings reinforce the importance of incorporating trait-based approaches into both ecological theory and management frameworks to better anticipate the long-term consequences of biological invasions under ongoing environmental change.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11252-026-01959-9.

Acknowledgements This work was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil, through the Social Demand Program (DS), which provided a doctoral fellowship to Aline Cristina Stocki. The authors are grateful to UNICENTRO for institutional support. We also thank the anonymous reviewers for their valuable comments and suggestions, which greatly improved the quality of this manuscript.

Author contributions All authors contributed to the study conception and design. ACS wrote, reviewed, and edited the manuscript, and prepared the figures and tables. JAM reviewed the manuscript. ACS and JAM performed the fieldwork and collected the data. LFW supervised the research and carried out the formal analysis. All authors read and approved the final version of the manuscript.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). This work was supported by the Social Demand Program (DS) of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil, which provided a doctoral fellowship to ACS.

Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics Approval Not applicable.

Consent for publication All authors have read and approved the final version of the manuscript for publication.

Consent to Participate All authors have read and agreed to participate in this study.

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright

holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Bello F, Lavorel S, Hallett LM et al (2021) Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. Trends Ecol Evol 36:822–836. https://doi.org/10.1016/j.tree.2021.05.001

Bullock JM, Fuentes-Montemayor E, McCarthy B et al (2022) Future restoration should enhance ecological complexity and emergent properties at multiple scales. Ecography 2022:e05780. https://doi.org/10.1111/ecog.05780

Castro-Díez P, Alonso Á, Saldaña-López A, Granda E (2021) Effects of widespread non-native trees on regulating ecosystem services. Sci Total Environ 778:146141. https://doi.org/10.1016/j.scitotenv.2021.146141

CBD (2020) Global Biodiversity Outlook 5. Montreal

Díaz S, Purvis A, Cornelissen JHC et al (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. Ecol Evol 3:2958–2975. https://doi.org/10.1002/ece3.601

Diniz ÉS, Dias FS, Borda-de-Água L, González PMR (2024) Anthropogenic disturbance and alien plant invasion drive the phylogenetic impoverishment in riparian vegetation. Biodivers Conserv 33:4237–4256. https://doi.org/10.1007/s10531-024-02949-z

Doody TM, Lewis M, Benyon RG, Byrne G (2014) A method to map riparian exotic vegetation (*Salix* spp.) area to inform water resource management. Hydrol Process 28:3809–3823. https://doi.org/10.1002/hyp.9916

Early R, Bradley BA, Dukes JS et al (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. Nat Commun 7:12485. https://doi.org/10.1038/ncomms12485

Fernandez RD, Ceballos SJ, Aragón R et al (2020) A global review of *Ligustrum Lucidum* (Oleaceae) invasion. Bot Rev 86:93–118. https://doi.org/10.1007/s12229-020-09228-w

Fernandez RD, Castro-Díez P, Aragón R, Pérez-Harguindeguy N (2021) Changes in community functional structure and ecosystem properties along an invasion gradient of Ligustrum lucidum. J Veg Sci 32:e13098. https://doi.org/10.1111/jvs.13098

Ferreras AE, Whitworth-Hulse JI, Tecco PA et al (2019) Environmental constraints to native woody species recruitment in invaded mountain woodlands of central Argentina. For Ecol Manage 440:189–201. https://doi.org/10.1016/j.foreco.2019.03.022

Forgiarini C, Souza AF, Longhi SJ, Oliveira JM (2015) In the lack of extreme pioneers: trait relationships and ecological strategies of 66 subtropical tree species. J Plant Ecol 8:359–367. https://doi.org/10.1093/jpe/rtu028

Funk JL, Larson JE, Ames GM et al (2017) Revisiting the holy grail: using plant functional traits to understand ecological processes. Biol Rev 92:1156–1173. https://doi.org/10.1111/brv.12275

Gaertner M, Wilson JRU, Cadotte MW et al (2017) Non-native species in urban environments: patterns, processes, impacts and challenges. Biol Invasions 19:3461–3469. https://doi.org/10.1007/s10530-017-1598-7

Gladstone-Gallagher RV, Pilditch CA, Stephenson F, Thrush SF (2019) Linking traits across ecological scales determines functional resilience. Trends Ecol Evol 34:1080–1091. https://doi.org/10.1016/j.tree.2019.07.010

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Hoyos LE, Gavier-Pizarro GI, Kuemmerle T et al (2010) Invasion of glossy privet (*Ligustrum lucidum*) and native forest loss in the Sierras Chicas of Córdoba, Argentina. Biol Invasions 12:3261–3275. https://doi.org/10.1007/s10530-010-9720-0

Junk WJ, Piedade MTF, Lourival R et al (2014) Brazilian wetlands: their definition, delineation, and classification for research, sustainable management, and protection. Aquat Conserv 24:5–22. https://doi.org/10.1002/aqc.2386

Kilgore A, Restrepo C (2025) Integrating hyperspectral imaging, plant functional diversity, and soil-lithology to uncover mountainscape disturbance dynamics induced by landsliding. Remote Sens (Basel) 17:1806. https://doi.org/10.3390/rs17111806

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. https://doi.org/10.1890/08-2244.1

Laliberté E, Legendre P, Shipley B (2015) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1:0–12

Laughlin DC (2024) Unifying functional and population ecology to test the adaptive value of traits. Biol Rev 99:1976–1991. https://doi.org/10.1111/brv.13107

Lázaro-Lobo A, Lucardi RD, Ramirez-Reyes C, Ervin GN (2021) Region-wide assessment of fine-scale associations between invasive plants and forest regeneration. For Ecol Manage 483:118930. https://doi.org/10.1016/J.FORECO.2021.118930

Loiola PP, de Bello F, Chytrý M et al (2018) Invaders among locals: alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. J Ecol 106:2230–2241. https://doi.org/10.1111/1365-2745.12986

Lusizi Z, Motsi H, Nyambo P, Elephant DE (2024) Black (*Acacia mearnsii*) and silver wattle (*Acacia dealbata*) invasive tree species impact on soil physicochemical properties in South Africa: a systematic literature review. Heliyon 10:e24102. https://doi.org/10.1016/j.heliyon.2024.e24102

Malysz M, Milesi SV, Dos Santos AS, Overbeck GE (2019a) Functional patterns of tree communities in natural Araucaria forests and old monoculture conifer plantations. Acta Bot Bras 33:777–785. https://doi.org/10.1590/0102-33062019aabb0249

McInerney PJ, Doody TM, Davey CD (2021) Invasive species in the Anthropocene: help or hindrance? J Environ Manage 293:112871. https://doi.org/10.1016/j.jenvman.2021.112871

Naiman RJ, Décamps H (1997) The ecology of interfaces: riparian zones. Annu Rev Ecol Syst 28:621–658. https://doi.org/10.1146/annurev.ecolsys.28.1.621

Nogueira GS, Seger GDS, Boeger MRT, Muschner VC (2020) The phenology of *Ligustrum lucidum* (Oleaceae): climatic niche conservatism as an important driver of species invasion in Araucaria forest. Biol Invasions 22:2975–2987. https://doi.org/10.1007/s10530-020-02302-9

Ogle D, Doll JC, Wheeler AP, Dinno A (2023) FSA: Simple Fisheries Stock Assessment Methods

Ohlert T, Kimmel K, Avolio M et al (2024) The impact of trait number and correlation on functional diversity metrics in real-world ecosystems. PLoS One 19:e0306342. https://doi.org/10.1371/journal.pone.0306342

Oksanen J, Blanchet FG, Kindt R et al (2019) vegan: Community Ecology Package

Paronetto JS, Díaz Villa MVE, Cagnone MF et al (2025) Impact of *Ligustrum lucidum* invasion on the structure and functioning of coastal dry forests: a case study from Argentina. Can J Forest Res 55:1–12. https://doi.org/10.1139/cjfr-2025-0045

Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models in ecology: an introduction with mgcv. PeerJ 7:e6876. https://doi.org/10.7717/peerj.6876

Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. Ecol Lett 5:402–411. https://doi.org/10.1046/j.1461-0248.2002.00339.x

Pérez-Harguindeguy N, Díaz S, Garnier E et al (2016) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234. https://doi.org/10.1071/BT12225

Pyšek P, Hulme PE, Simberloff D et al (2020) Scientists' warning on invasive alien species. Biol Rev 95:1511–1534. https://doi.org/10.1111/brv.12627

R Core Team (2025) A language and environment for statistical computing. https://www.r-project.org/

Richardson DM, Holmes PM, Esler KJ et al (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Divers Distrib 13:126–139. https://doi.org/10.1111/j.1366-9516.2006.00314.x

Rodrigues AL, Watzlawick LF, Genú AM et al (2016) Atributos de um solo florestal em uma topossequência e relações com a comunidade arbórea. Floresta 46:145–154. https://doi.org/10.5380/rf.v46i2.36219

Rood SB, Scott ML, Dixon M et al (2020) Ecological interfaces between land and flowing water: themes and trends in riparian research and management. Wetlands 40:1801–1811. https://doi.org/10.1007/s13157-020-01392-4

Rosseel Y (2012) lavaan: An Package for Structural Equation Modeling. J Stat Softw 48. https://doi.org/10.18637/jss.v048.i02

Scott-Shaw BC, Everson CS, Clulow AD (2017) Water-use dynamics of an alien-invaded riparian forest within the Mediterranean climate zone of the Western Cape, South Africa. Hydrol Earth Syst Sci 21:4551–4562. https://doi.org/10.5194/hess-21-4551-2017

Seebens H, Bacher S, Blackburn TM et al (2021) Projecting the continental accumulation of alien species through to 2050. Glob Chang Biol 27:970–982. https://doi.org/10.1111/gcb.15333

Simberloff D, Martin JL, Genovesi P et al (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66. https://doi.org/10.1016/j.tree.2012.07.013

Stocki AC, Mazon JA, Jadoski SO, Watzlawick LF (2024a) Environmental variables, floristics, diversity, and species distribution in an urban alluvial forest. Cienc Nat 46:e74098. https://doi.org/10.5902/2179460X74098

Stocki AC, Mazon JA, Watzlawick LF (2024b) Forest dynamics and invasion of *Ligustrum Lucidum* in an urban alluvial Atlantic Forest fragment. Ambiente e Água - An Interdisciplinary Journal of Applied Science 19:1–17. https://doi.org/10.4136/ambi-agua.2976

Tordoni E, Petruzzellis F, Nardini A et al (2019) Make it simpler: alien species decrease functional diversity of coastal plant communities. J Veg Sci 30:498–509. https://doi.org/10.1111/jvs.12734

Vile D, Garnier É, Shipley B et al (2005) Specific leaf area and dry matter content estimate thickness in laminar leaves. Ann Bot 96:1129–1136. https://doi.org/10.1093/aob/mci264

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301. https://doi.org/10.1890/07-1206.1

Villéger S, Grenouillet G, Brosse S (2014) Functional homogenization exceeds taxonomic homogenization among European fish assemblages. Glob Ecol Biogeogr 23:1450–1460. https://doi.org/10.1111/geb.12226

Watzlawick LF, Guilhermeti PGC, Jadoski SO, Mazon JA (2021) Growth analysis of *Gymnanthes Klotzschiana* Müll.Arg. in different sociological positions and soil water conditions. Ciência E Natura 43:e71. https://doi.org/10.5902/2179460X63370

Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827. https://doi.org/10.1038/nature02403

Zanette VH, Watzlawick LF, Silva RAR, Mazon JA (2021) Identidade de modelos para estimativa de biomassa aérea na Floresta Ombrófila Mista. Scientia Forestalis 49:e3472. https://doi.org/10.18671/scifor.v49n131.09

Zenni RD, Ziller SR, da Rosa CA et al (2024) Invasive non-native species in Brazil: an updated overview. Biol Invasions 26:2397–2405. https://doi.org/10.1007/s10530-024-03302-9

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.