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ECOSYSTEMS

Leaf trait divergence between *Azadirachta indica* (exotic) and native species of the northern Brazilian coast

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Abstract: The introduction of exotic plants can pose ecological threats as they may become invasive. We investigated leaf traits potentially linked to competitive advantage and invasiveness in *Azadirachta indica*, a widely used exotic tree in northeastern Brazil's urban forestry, compared to native species *Ouratea fieldingiana* and *Myrcia multiflora*. We tested the limiting similarity hypothesis, evaluating how leaf characteristics influence the ecological responses of these species and *A. indica*'s potential invasiveness. *A. indica* exhibited larger leaf area, specific leaf area (SLA), and leaf area ratio (LAR) compared to native species, but lower specific petiole length (SPL) and specific internode length (SIL). Additionally, *A. indica* displayed greater phenotypic variation in these traits. The larger leaf area, SLA, and LAR suggest a strategy in *A. indica* favoring rapid carbon gain through increased growth. The higher phenotypic variation observed may facilitate adaptation to new habitats, potentially enhancing its competitive ability and invasiveness. These findings highlight distinct functional strategies between exotic and native species, raising concerns regarding the potential invasiveness of *A. indica* in northeastern Brazil's natural ecosystems.

Key words: Exotic plants, invasiveness of plants, plant ecological strategies, phenotypic variation, specific leaf area.

INTRODUCTION

The invasion of exotic plants in natural environments poses a significant threat to global biodiversity, leading to economic losses and risks to human health (Kumschick et al. 2015, Bellard et al. 2016, Xu et al. 2006, Peyton et al. 2019). While many exotic plants are cultivated outside their native range without causing major impacts, certain species have the ability to invade and disrupt ecosystems. These species are classified as invasive plants, which are defined as species that can reproduce, expand their range in new environments, and alter the species composition, community structure, and function of invaded ecosystems (Abreu & Durigan 2011, Livingstone et al. 2020). To mitigate the risks of biological invasion, it is crucial to predict and identify potentially invasive plants, along with the factors and characteristics that promote invasion (Abreu & Durigan 2011, Livingstone et al. 2020).

Several functional attributes have been proposed to explain how plant species overcome ecological constraints in natural environments (McGill et al. 2006, Díaz et al. 2016, Maynard et al. 2022). Previous studies have focused on comparing functional traits between invasive and native species to identify key traits associated with the capacity of exotic plants to

become invasive (Kleunen et al. 2010, Gallagher et al. 2014, Zheng et al. 2018). Among the main hypotheses proposed to explain the success of exotic invasive species in natural environments, the limiting similarity hypothesis stands out. This hypothesis predicts that invasive species are more likely to establish successfully if their functional traits are sufficiently different from those of native species, thereby reducing competition for similar resources (Emery 2007, Gallien & Carboni 2017). While some studies support the limiting similarity hypothesis, suggesting that invasive species possess distinct ecological characteristics to avoid competition with native species (Ordonez et al. 2010, Zheng et al. 2018, Divíšek et al. 2018), others challenge its universality, emphasizing the importance of various factors in the invasion process that are intrinsic to the invasive species and the invaded environment (Duncan & Williams 2002, Lososová et al. 2015).

Successful invasive species often exhibit specific attributes, such as the absence of natural enemies, availability of unexploited resources, and a better adjustment of functional traits to different environmental conditions (Keane & Crawley 2002, Harvey et al. 2012, Godoy et al. 2008, Buckley et al. 2003, Davidson et al. 2011). Ecophysiological comparisons between invasive and native species have been conducted to identify the characteristics associated with the invasion potential of exotic species (Leishman et al. 2007, Feng et al. 2008, Stanisci et al. 2010). Functional traits associated with metamers—structural units of a plant composed of an internode, a petiole, and the corresponding leaf blade—play a critical role in mediating trade-offs between environmental conditions and carbon fixation strategies (Westoby et al. 2002, Ribeiro et al. 2016, Souza et al. 2018), making them valuable for comparing invasive and native species.

When invading a new ecosystem, invasive plant species often encounter environmental conditions that differ from their natural range, leading to significant changes in ecophysiological characteristics in response to these novel selective pressures (Niinemets et al. 2003, Molina-Montenegro & Naya 2012, Konarzewski et al. 2012). These changes allow the invasive species to grow, survive, and reproduce in habitats with different environmental filters. For example, studies have shown that invasive species modify petiole length and internode spacing to optimize light capture and water transport efficiency (Guo et al. 2013). Additionally, they adjust their specific leaf area (SLA) to optimize resource acquisition and enhance competitive ability. Higher SLA values, as observed in invasive species, facilitate rapid growth and resource use efficiency compared to native species (Feng et al. 2008, Sandel & Low 2019). Such adjustments enhance their competitive ability and adaptability in novel ecosystems. Consequently, invasive species can modify and adapting their ecological strategies through notable differences in functional traits related to environmental stress, competitive ability, and disturbance tolerance (Huxman & Smith 2001, Niinemets et al. 2003, Zou et al. 2007, Funk 2008). Variations in functional traits of a species can result from several factors, including phenotypic plasticity and/or genetic variation (Valladares & Pearcy 1997, Matesanz et al. 2010, Gianoli & Valladares 2012, Lázaro-Nogal et al. 2015, Ribeiro et al. 2016). The capacity to adjust functional traits according to different environmental conditions can significantly contribute to the niche breadth, thereby expanding the biogeographic range of a plant species (Primack 1979, Delerue et al. 2013).

Azadirachta indica A. Juss (Meliaceae), commonly known as "Indian-neem," is an evergreen tree species native to India. It has

been introduced in Brazil since 1984 and is economically important for its agricultural, medicinal, and cosmetic uses (Neves & Carpanezzi 2009, Soares et al. 2009, Jack et al. 2020). *A. indica* has been widely used in urban forestry due to its adaptability to different climate and soil types, resulting in its uncontrolled spread and potential competition with native species, particularly in northeastern Brazil (Espínola & Júlio 2007, Moro et al. 2013). However, limited knowledge exists regarding the functional traits that contribute to the invasive potential of *A. indica*, especially in tropical environments. Therefore, this study aimed to compare the leaf functional traits of two abundant native species, *Ouratea fieldingiana* (Gardner) Engl. (Ochnaceae) and *Myrcia multiflora* (Lam.) DC (Myrtaceae), with the exotic plant *A. indica*, evaluating the influence of metamers' characteristics on the ecological responses and invasive potential of *A. indica*.

We tested the hypothesis of limiting similarity by comparing the metamer traits of the exotic plant with those of the native species. Our expectation was that the exotic plant would present metamer characteristics that would favor faster growth and greater carbon accumulation, such as a higher leaf area and specific leaf area (SLA), when compared to native species. The latter, in turn, would tend to exhibit more conservative strategies, more adequate to the semi-arid environment of our study (Leishman et al. 2007, Feng et al. 2008). Furthermore, we investigated the phenotypic variation of metamer traits among the studied species, with the expectation of finding greater variation in the exotic plant. This would serve as an indication of its greater adaptability and potential to colonize new habitats.

MATERIALS AND METHODS

Study area

The study was conducted in a 13-ha fragment of coastal savannah vegetation, characterized by shrub-tree sized vegetation (Castro et al. 2012), located at the Instituto Federal de Educação, Ciência e Tecnologia do Ceará, in Acaraú, Ceará, Brazil (2°53'20.64" S, 40°6'47.52" W). The region features a seasonal tropical warm semi-arid climate classified as AW, with average temperatures ranging from 26 °C to 28 °C. Rainfall is concentrated between January and May (summer-autumn), with a historical annual average precipitation of 1200 mm (INMET 2019).

On the edge of the studied fragment, individuals of exotic *A. indica* are found. The oldest individuals of *A. indica* were anthropically introduced to the area for landscape purposes, however it is already possible to observe the natural recruitment of the species in the study area. Among the native species in the studied fragment are found: *Byrsonima crassifolia* (L.), *Chrysophyllum arenarium* Allemão, *Eugenia punicifolia* (Kunth) DC, *Myrcia multiflora* (Lam.) DC., *Ouratea fieldingiana* (Gardner) Engl. and *Randia armata* (Sw.) DC. Due to the greater abundance and ease of access for this study, we selected individuals of *M. multiflora* (Myrtaceae) and *O. fieldingiana* (Ochnaceae). The description of the biology of native species *M. multiflora* e *O. fieldingiana* and the exotic *A. indica* can be seen in (Supplementary Material - Data SI).

Morphological metamer traits

Between December 2019 and January 2020, 10 adult individuals of each species with height greater than 1.5 m were randomly selected within the study area. Individuals in good phytosanitary conditions were selected, without the presence of parasites and shading, at least 10 m apart. From each individual of the sampled species, we collected a total of 5 metamers (internode,

petiole and the corresponding leaf) in the last nodes with mature and fully expanded leaves. After collected, the metameres were digitalized on a millimeter scale and using the Image J software, the leaf area (LA in cm^2), length of the petiole (PL in cm) and length between nodes (IL in cm) were determined. Metamers were stored in paper bags and placed in an oven at 70 ° C by 72 hours until they reached constant dry weight, where each part of the metamer was weighed separately. After obtaining the dry mass of the different parts of the metamers, we calculated the specific leaf area (SLA - leaf blade area per unit dry leaf mass; in cm^2g-1), the ratio of the leaf area to the total mass of the metamer. (LARm - area of the leaf blade per dry mass unit of the metamer; in cm^2g^{-1}), the specific length of the petiole (SPL - length of the petiole per unit of mass of the petiole; cm g^{-1}) and the specific length of the internode (SIL, length of the inter-node per unit mass of the get in on; in cm g^{-1}) (Poorter 2009, Souza et al. 2018). Data on metamer traits are presented in Supplementary Material - Table SI.

Statistical analysis

To assess whether leaf metamer traits differ among the studied species, potentially indicating variations in their ecological strategies, we performed a principal component analysis (PCA) using six variables (Souza et al. 2021). The PCA was performed using the Past software-Version 1.99 (Hamer et al. 2001). To assess whether the metamer traits differ between species, generalized linear models (GLM) were performed, following the guidelines described by Crawley (2013) and applied in a similar study by Souza et al. (2018). In this case, the metamer traits of each individual were used as the response variables, and species were included as the explanatory variable in the GLMs. The models were constructed using a Gaussian distribution, appropriate for the continuous nature of the response variable data. An F-test was applied to compare the models and assess differences in metamer traits among species. Post hoc contrast analysis was performed to group species with similar metamer traits (Crawley 2013).

To test if phenotypic variation within individuals in leaf metamer traits varies among species we performed GLM. The phenotypic variation within individuals was used as response variable and the height of individuals as explanatory variable. The phenotypic variation within individual (PV) was expressed in percentage, so PV = (SD/X)100 where SD is the standard deviation of a particular trait in an individual and X is the average of a particular trait in an individual (Valladares et al. 2006, Souza et al. 2019). Due to all metamers of a same individual have the same genotype, the phenotypic variation within individuals can be thought of as partly due to phenotypic plasticity (Buzatti et al. 2019).

All models were built using the appropriate error distribution considering the nature of each response variable, following by model criticism via residual analysis (Crawley 2013).

RESULTS

Variation in metamer traits among native and exotic plants

The principal component analysis (PCA) of leaf metamer data data highlighted variations in ecological strategies among the three studied species (Figure 1). The first two axes explained 91.31% of the total variation, with PC1 primarily separating the exotic *A. indica* from the native *M. multiflora* and *O. fieldingiana* (Table I). PC1 loadings indicated negative correlations between leaf area (LA), petiole length (PL), internode length (IL), leaf area ratio (LAR), and

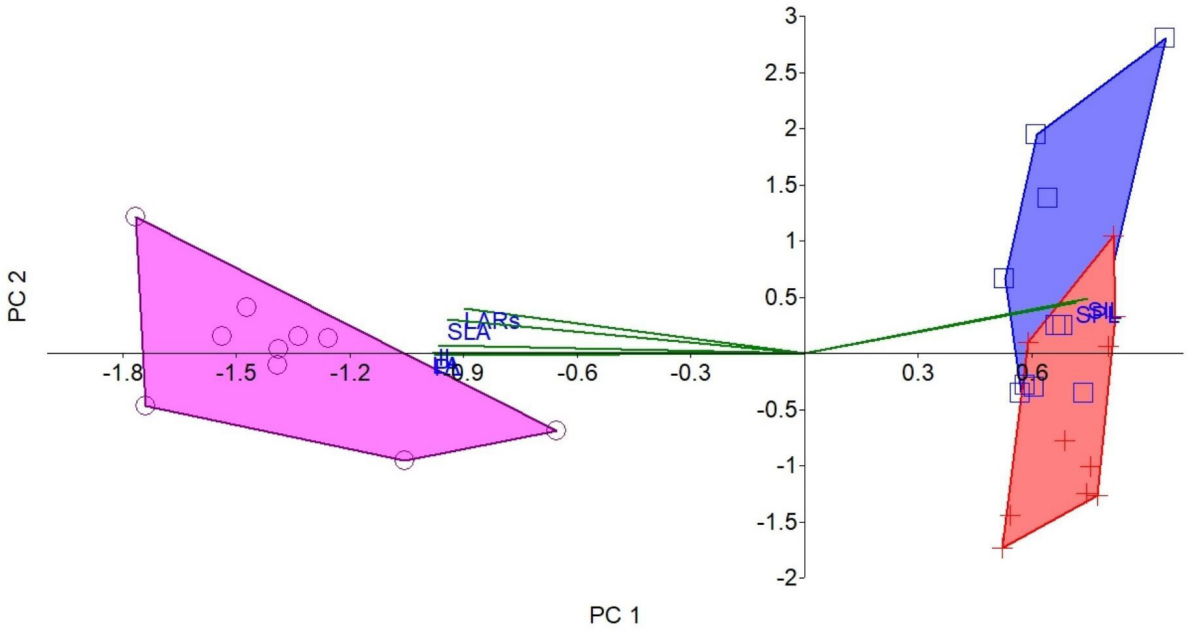

Figure 1. Biplot representation of the scores on the first two axes of the principal component analysis (PCA) of leaf metamer traits for *Azadiracta indica* in circles, *Myrcia multiflora* in square, *Ouratea fieldingiana* in cross.

specific leaf area (SLA) with specific petiole length (SPL) and specific internode length (SIL).

Consistent with the PCA, generalized linear models (GLMs) confirmed significant differences ($p < 0.05$) for all measured traits between the exotic and native species (Figure 2). *A. indica* exhibited higher LA, PL, IL, LAR, and SLA compared to the native species (Figure 2a-e). Conversely, *A. indica* displayed lower SPL and SIL (Figure 2f-g). Native species *M. multiflora* and *O. fieldingiana* displayed variation in PL, IL, LARs, SLA, and SIL (Figure 2b-g).

Phenotipic variation of traits among native and exotic plants

The species exhibited high phenotypic variation in all morphological traits of metamer, with the overall phenotypic variation from 25.3% in *A. indica* and 18.4% and 21.8% to *M. multiflora* and *O. fieldingiana*, respectively (Figure 3). All traits showed significantly greater phenotypic variation in the exotic species *A. indica*, except for internode length that was higher in *O. fieldingiana* (Figure 3). The petiole length (F= 0.74 P> 0.05), SLP (F= 0.46 P> 0.05) and SIL (F= 0.74 P> 0.05), which did not vary among species.

Table I. Principal component analysis for eight leaf metamer traits in native plant of coastal vegetation and the exotic *Azadirachta indica*.

	PC1	PC2
Eigenvalues	5.62	0.70
Percent (%)	80.35	9.97
Cumulative Percent (%)	80.35	90.32
Metamer Traits	**Eigenvectors**	
Leaf area (cm^2)	-0.98	0.01
Petiole length (cm)	-0.98	-0.02
Internode length (cm)	-0.97	0.07
LARs ($cm^2\ g^{-1}$)	-0.90	0.40
SLA ($cm^2\ g^{-1}$)	-0.94	0.30
SPL ($cm^2\ g^{-1}$)	0.72	0.46
SIL ($cm^2\ g^{-1}$)	0.75	0.49

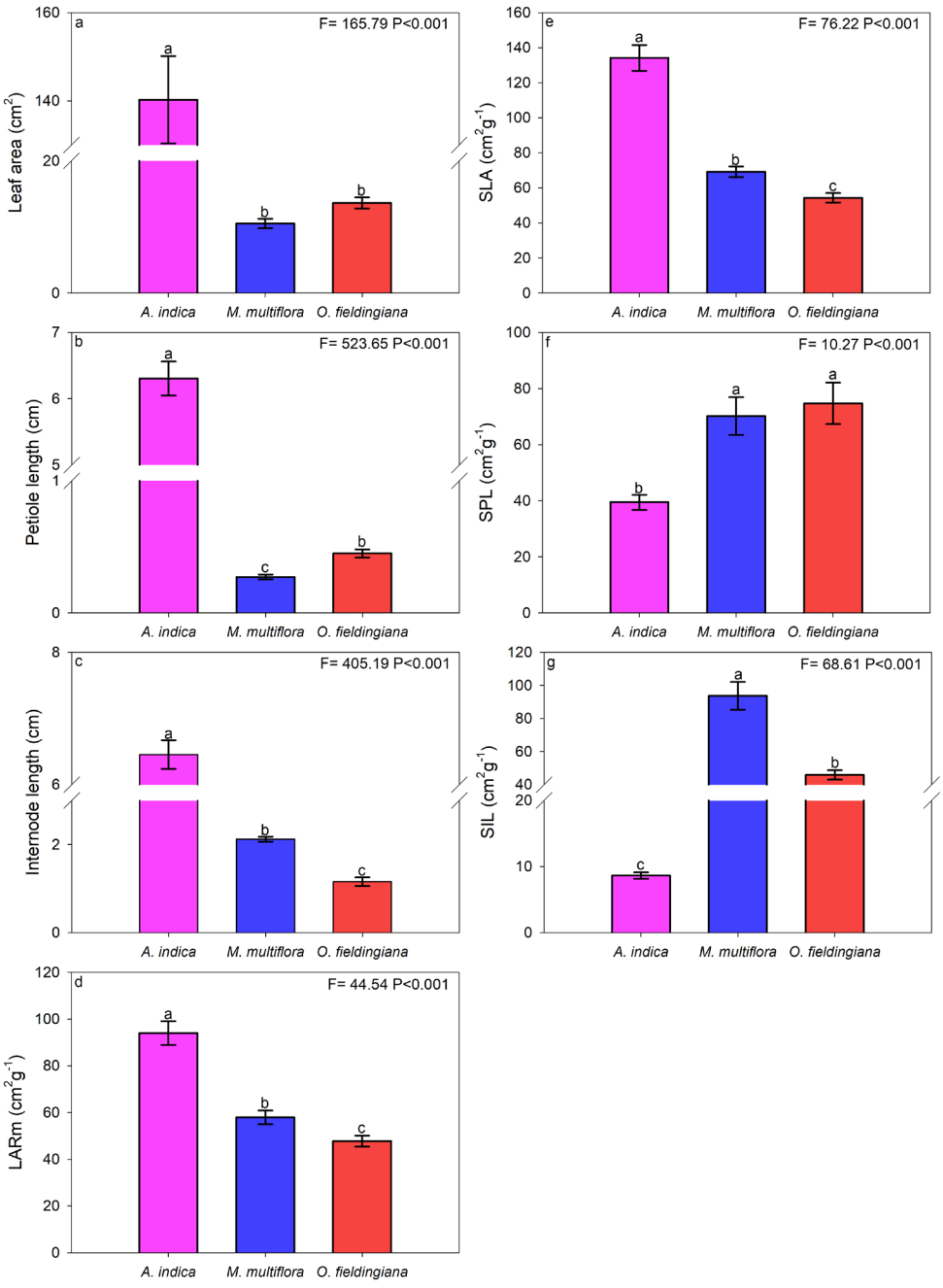

Figure 2. Variation of leaf metamer traits among native plant of coastal vegetation and the exotic *Azadirachta indica* for; a) leaf area (cm²); b) petiole length (cm); c) internode length (cm); d) LARs, leaf area ratio of the metamer ($cm^2\ g^{-1}$); e) SLA, specific leaf area ($cm^2\ g^{-1}$); f) SPL , specific petiole length($cm\ g^{-1}$); g) SIL, specific internode length ($cm\ g^{-1}$). Average and standard deviation values of each species are shown.

DISCUSSION

Our results indicate significant differentiation in the functional traits of metamers between exotic and native species. The native species *M. multiflora* and *O. fieldingiana* displayed greater similarity in their leaf trait responses across metamers, characterized by low values of leaf area, LARs, and SLA, along with higher values of SPL and SIL. In contrast, the exotic species *A. indica* exhibited an inverse response, with higher values of leaf area and SLA, and reduced SPL and SIL compared to the native species. This supports our hypothesis our hypothesis of limiting similarity, which posits that the exotic species would display metamer traits favoring faster growth and greater carbon accumulation,

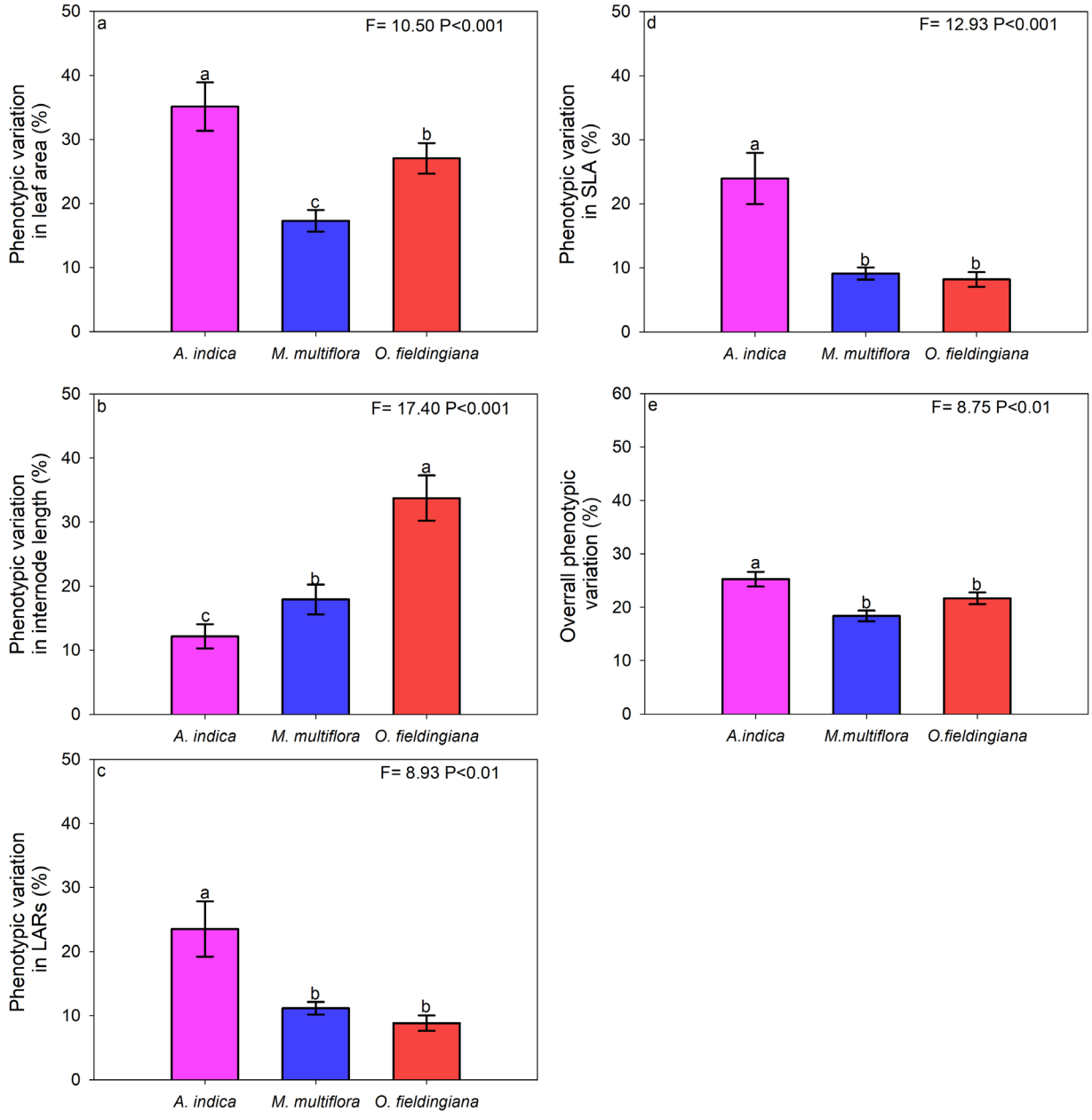

Figure 3. **Trait phenotypic variation within individuals (measured as percentage of change) among native plant of coastal vegetation and the exotic *Azadirachta indica* for; a) leaf area (cm²); b) internode length (cm); c) LARs, leaf area ratio of the metamer ($cm^2\ g^{-1}$); d) SLA , specific leaf area ($cm^2\ g^{-1}$); e) overall leaf metamer trait phenotypic variation (measured as the arithmetic mean of the percentage of change for all leaf metamer traits). Average and standard deviation values of each species are shown.**

while the native species, adapted to the semi-arid environment, would exhibit more conservative strategies. These findings align with previous studies that have observed distinct functional trait differences between exotic and native plant species, generally showing that invasive exotic species tend to have higher values of LARs and SLA compared to native species (Leishman et al. 2007, Feng et al. 2008, Sandel & Low 2019). Species with high SLA values are

typically associated with faster growth rates, rapid leaf material turnover, and higher seed productivity compared to species with low SLA values (Gallagher et al. 2014, Bogdziewicz et al. 2023). This set of characteristics can contribute to the transition of exotic species *A. indica* from naturalized to invasive in a wide range of environmental contexts.

The exotic species *A. indica* exhibited LARs and SLA approximately twice as high as those of the native species studied. Species with high leaf area, LARs, and SLA tend to have a higher photosynthetic rate, enabling them to rapidly accumulate carbon and promote rapid growth (Poorter & Evans 1998, Feng et al. 2008, Liu et al. 2017). This advantage holds true even in seasonal environments, such as the coastal vegetation studied, where a higher efficiency in water use or increased water supply to leaf structures is expected (Krishnamurthy et al. 2007, Mitchell et al. 2008). In fact, *A. indica* exhibited low values of SPL and SIL, which can favor a greater supply of water to the leaves. Larger leaves with a higher SLA require more hydraulic and biomechanical support, which can be achieved through low SPL and SIL values, enhancing the efficiency of biomass investment for foraging (Poorter & Rozendaal 2008). Shorter internodes and petioles reduce resistance to water flow, and lower SPL values increase the number of conducting vessels per unit length, resulting in increased water supply to the leaf blade (Noda et al. 2004, Zach et al. 2010, Guo et al. 2013, Sun et al. 2016).

Conversely, the native species studied exhibited leaf traits that were opposite to those observed in the exotic species, mainly with low values of LARs and SLA. While lower SLA values may limit the photosynthetic capacity of the plant, they can also reduce water loss through transpiration, increasing water use efficiency (Lázaro-Nogal et al. 2015). Similar patterns have been observed in various ecosystems worldwide, where plants in arid environments with limited water availability tend to have lower LARs and SLA (Ackerly et al. 2000, Reich et al. 2003, Uribe-Salas et al. 2008, Ribeiro et al. 2016, Souza et al. 2018).

Furthermore, our study found that the exotic species *A. indica* exhibited greater phenotypic variation in most functional traits compared to the native species analyzed. This increased phenotypic variation can promote invasion by enhancing the species' ability to respond positively to the environmental conditions of the invaded ecosystem (Niinemets et al. 2003, Molina-Montenegro & Naya 2012, Konarzewski et al. 2012). The greater phenotypic variation observed in *A. indica* for leaf area, LARs, SLA, and overall mean of phenotypic variation suggests that the exotic species can adjust its functional traits to maximize carbon gain under favorable conditions. This phenotypic variation may contribute to the species' competitive and invasive capacity, enabling it to occupy new habitats (Forsman 2014, Liao et al. 2016).

Considering the coastal savannas' characteristics, which are predominantly characterized by shrub-herbaceous vegetation with few large trees and no continuous canopy formation (Castro et al. 2012, Oliveira et al. 2012), the arboreal nature of *A. indica*, with the traits favoring rapid growth and competition observed in our study, raises concerns about its potential to become invasive and form dense monospecific stands in coastal savannas (Jelbert et al. 2015). Furthermore, it is important to highlight that the botanical family Meliaceae, to which the exotic species *A. indica* belongs, is not recorded in floristic studies in this specific environment (Castro et al. 2012, Oliveira et al. 2012). The considerable phylogenetic distance between the exotic species *A. indica* and the other native species that make up the plant community

of coastal savannas may favor the success of the invasion. This is due to the reduction of niche overlap between *A. indica* and the native species, as well as the absence of natural enemies, providing competitive advantages for the exotic species during the invasion process (Zheng et al. 2018, Omer et al. 2022). Such invasions could have widespread ecological impacts on the ecosystem, including reductions in biodiversity, changes to disturbance regimes (e.g., fire), alterations in biogeochemical cycles, and decreased water availability, as documented in the literature on biological plant invasions in similar coastal savanna ecosystems (Maitre et al. 2011, Richardson & Rejmánek 2011, Rundel et al. 2014, Morris et al. 2020).

In conclusion, our findings reveal distinct functional strategies between the exotic species *A. indica* and the native *O. fieldingiana* and *M. multiflora*. The higher values of leaf area, LARs, and SLA in *A. indica* suggest a strategy that promotes carbon accumulation and rapid growth, while the native species demonstrate a more conservative growth approach, aligning with our initial predictions. Moreover, the exotic species exhibited greater phenotypic variation in leaf functional traits, potentially enhancing their adaptive capacity and competitive ability, thereby increasing its invasive potential. Although our study examined a limited number of native species, our results serve as a warning regarding the potential invasiveness of *A. indica*. Given its widespread use in urban forestry (Moro & Westerkamp 2011, Rufino et al. 2019, Costa et al. 2019), allelopathic characteristics (França et al. 2008, Rickli et al. 2011), unimpeded reproduction (Moro et al. 2013), phylogenetic distance from the native plant community (Castro et al. 2012, Oliveira et al. 2012), and functional differences with ecophysiological traits favoring competition, *A. indica* represents a potential invader of natural coastal environments in northeastern Brazil. Monitoring the spread of *A. indica* in natural environments is necessary to mitigate potential damage to local biodiversity.

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SUPPLEMENTARY MATERIAL

Data SI.
Table SI.

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