Abiotic niche partitioning among congeneric species in an Atlantic forest fragment

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Abstract

Understanding the processes that allow phylogenetically related plant species coexist is important to understand the ecological and evolutionary processes that structure biological communities. In this study, we investigated how the species *Erythroxylum simonis*, *Erythroxylum pauferrense* and *Erythroxylum citrifolium* share ecological niche dimensions according to the abiotic characteristics of their environments of occurrence. To this end, in ten pre-established plots in an Atlantic Forest remnant in northeastern Brazil, we carried out a population survey of the three species and characterised their abiotic niche by measuring light availability, humidity and the physical–chemical properties of the soil. We used generalised linear models to test whether abiotic variables influence species abundance. Our results indicate that the three species coexist along the different environmental gradients, with some level of niche overlap. The species *E. simonis* is the best competitor, showing generalist behaviour and the highest abundance in all environmental gradients. We emphasise that the adult populations of the species have adapted to various environmental and ecological challenges. Thus, the results reported are influenced by their ability to perform well in terms of physiology, growth and survival in their early-life stages.

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Introduction

Understanding how different phylogenetically close and potentially competing plant species manage to coexist is important, as it helps us to understand the ecological and evolutionary processes that structure biological communities (Cavender-Bares *et al.* 2009; Chase and Leibold 2009; Silvertown 2004a). Niche theory (Elton 1927; Grinnell 1917; Hutchinson 1957) explains how species manage to coexist over time and space by relating abiotic and biotic factors to their abundance, distribution and the intensity at which they compete and share available resources in the environment (González *et al.* 2017). Niche theory suggests that the species achieving better performance (higher rank in a continuum of species competitive ability, henceforth competitive hierarchy) under low levels of a given limiting resource may drive the competitive exclusion of lower rank species (Chesson 2000). Stable species coexistence, however, is possible considering heterogeneity in time and space of limiting resource levels, particularly if two or more resources are taken into consideration (Kobe and Vriesendorp 2011; Silvertown 2004b).

In fact, the stable coexistence of species is easier with two or more limiting conditions because the various possible combinations of these conditions over time and/or space can also allow for changes in the position of species in the competitive hierarchy (Dybzinski and Tilman 2007). Thus, species coexistence is related to the sharing of multiple niche dimensions, with each species exhibiting different strategies for using and tolerating specific aspects of each niche dimension (Dybzinski and Tilman 2007; Kim and Ohr 2020; Tilman *et al.* 1981). For example, the classic study by MacArthur and Wilson (1967) in which the coexistence of lizard species of the genus *Anolis* was observed on different islands. Each lizard species occupied different strata of the environment and exhibited distinct behaviours, which allowed for slightly different utilisation of island resources, thus promoting coexistence. Furthermore, high phenotypic plasticity may also play an important role in species coexistence, as it allows species to adjust their behaviour to reduce (or even avoid) niche overlap, especially considering the competition for multiple limiting resources (Meilhac *et al.* 2020). Over time, it can lead to evolutionary differentiation within each species ('ghost of past competition'; (Cavender-Bares et al. 2004; Meilhac *et al.* 2020), making species coexistence more likely. However, if these behavioural phenotypic plasticity adjustments are not possible or are unfavourable, one species can lead the

other to local extinction (Esch *et al.* 2018; Levine and HilleRisLambers 2009; MacArthur and Levins 1967).

Particularly for plants, environmental conditions such as light availability (Comita *et al.* 2009; Kobe 1999), water availability (Lin *et al.* 2012) and soil nutrients (Bai *et al.* 2012) are crucial for the establishment and development of many species, acting to select subsets of species capable of supporting them (Belyea and Lancaster 1999; Ettinger *et al.* 2011). Within these subsets, biotic interactions, such as interspecific competition, influence the formation of local plant communities by modulating the coexistence of species through both sharing of multiple niche dimensions and species phenotypic adjustments (Holt 2009; Wang *et al.* 2022). Consequently, although some niche overlap still occurs, plant species may occupy different positions in the multidimensional niche space, reducing competition (Belyea and Lancaster 1999; Esch *et al.* 2018) and increasing the chances of coexistence (including phylogenetically close species; Casper and Jackson 1997; Silvertown 2004b). For example, within plant communities, coexistence among congeneric species with preferences for abiotic niche gradients (such as variation in soil texture and nutrient availability) can occur through root morphological differentiations, resulting in permanence in different soil textures and differences in soil nutrient uptake potential (see Chen *et al.* 2022; Eckhart *et al.* 2017).

In this study, we used three congeneric species belonging to the genus *Erythroxylum* (Eryhroxylaceae) as a study model. Because they are phylogenetically related species, it is more likely that they share common traits (for example, leaf size, height, fruit size and type) or life history characteristics (Silvertown 2004b), making them excellent models for studies related to niche partitioning and species coexistence among congeneric plant. Here we investigate how three plant species belonging to the genus *Erythroxylum*, these being *Erythroxylum simonis* Plowman, *Erythroxylum pauferrense* Plowman and *Erythroxylum citrifolium* A. St.-Hil., share the dimensions of the ecological niche according to the abiotic characteristics of the environment in which they are located to allow coexistence. We hypothesise that multiple resources (light, water and mineral nutrients) or environmental conditions (soil texture) limit the three *Erythroxylum* species, and their niche space should be differentially fulfilled by individuals (differences in abundance and position in multidimensional space) along those environmental gradients, reducing competition and allowing coexistence. Thus, we expect that (1) a linear increase in the *Erythroxylum* species population as the availability of resource/ environmental conditions increases and (2) the three *Erythroxylum* species, taken in pairs, must show a lower degree of multidimensional niche overlap than expected by chance.

Material and Methods

Study area

This study was conducted in Mata do Pau Ferro State Park, located in the municipality of Areia, State of Paraíba, Northeast Brazil (Figure 1). The park is in a 600 ha Atlantic Rainforest disjuncture, regionally known as 'Brejos de Altitude' (*Barbosa et al.* 2004). 'Brejos de altitude' are enclaves of the Atlantic Rainforest within the Caatinga domain, a deciduous vegetation formation adapted to semi-arid climates (Andrade-Lima 1982; Pennington *et al.* 2009). The Mata do Pau Ferro State Park is located 600 m above sea level with an average annual temperature of 22ºC, relative humidity of around 85% and annual precipitation of 1500 mm, with a humid

climate and deep and medium fertile soils (Mayo and Fevereiro 1982; Pôrto *et al.* 2004). This State Park is home to the most representative high-altitude forest in the State of Paraíba, with about 309 species of Angiosperms, distributed in 84 families, of which Rubiaceae, Malvaceae and Solanaceae stand out as the most representative families in a number of species (Barbosa *et al.* 2004). In addition, four species of the Erythroxylaceae family occur in the study site: *Erythroxylum simonis*, *Erythroxylum pauferrense*, *Erythroxylum citrifolium* and *Erythroxylum deciduum* A. St.-Hil.

During the nineteenth century, the tropical Atlantic Forest cover located in the Northeast region of Brazil, suffered heavily from increased anthropic pressures driven by agricultural activities, which reduced it to a small fraction of its original area (Crouzeilles *et al.* 2019), resulting in a hyper-fragmented landscape (Pôrto *et al.* 2004). The creation of the Mata do Pau Ferro State Park as a protected area has reduced habitat loss in the locality, however, impacts such as illegal logging are still recorded.

Experimental design

Focal species and population survey

The genus *Erythroxylum* is characterised by woody, shrubby or arboreal plants with alternate, entire leaves, monocline flowers and fleshy (less than 1 cm in size), reddish, single-seeded fruits (Loiola *et al.* 2007). This genus is exclusively tropical and comprises about 240 species, of which 187 present a distribution exclusively in the Neotropical region (Plowman and Hensold 2004). Brazil is pointed as one of the main centres of diversity and endemism of plant species belonging to the genus *Erythroxylum* (Plowman *et al.* 1999). Of the species with a distribution in the Neotropical region, approximately 50 per cent occur in Brazil (Cordeiro et al., 2017), including species with a restricted distribution, such as *Erythroxylum pauferrense* Plowman, endemic to remnants of the Atlantic Rainforest in northeastern Brazil (Cordeiro *et al.* 2017; Loiola *et al.* 2007). The species in this group show great ecological versatility, with species found in humid and semi-arid regions, and occurring at different levels of altitudes (Loiola *et al.* 2007). In the present research, we emphasise three species belonging to this genus, *E. citrifolium*, *E. pauferrense* (endemic species in small fragments of Atlantic Forest in Northeast Brazil) and *E. simonis*, because they are well represented in terms of abundance in the study area (Araújo 2016).

The species *E. citrifolium* has a tree to shrub life form, with a height of between 1.5 and 4 m. The leaves are large and elliptical, with a pointed apex (the size of the leaves can vary according to their distribution; at our study site, the leaves of this species are larger than those of the other two focal species). The branches are 2–4 mm in diameter (colour varies from greyish to brown), the flowers are small and yellowish-white and the fruit is fleshy, single-seeded, reddish and small (less than 1 cm in size; Plowman and Hensold 2004). In the study area, flowering and fruiting usually take place between April and June. In addition, it is a species with a wide distribution in the Neotropical Region, being preferentially found in humid forest environments (Loiola *et al.* 2007).

The species *E. pauferrense*, like *E. citrifolium*, has a life form of tree to shrub, with a height of between 1.5 and 4 m. However, its leaves are small, slightly discoloured and generally elliptical (sometimes rounded). The branches can be 2–3 mm in diameter and vary in colour from greyish to brown, the flowers are also small and yellowish-white, the fruit fleshy, with a single seed (with grooves), reddish and small (less than 1 cm in size; Plowman 1986). Unlike *E. citrifolium*, its flowering and fruiting in the study area
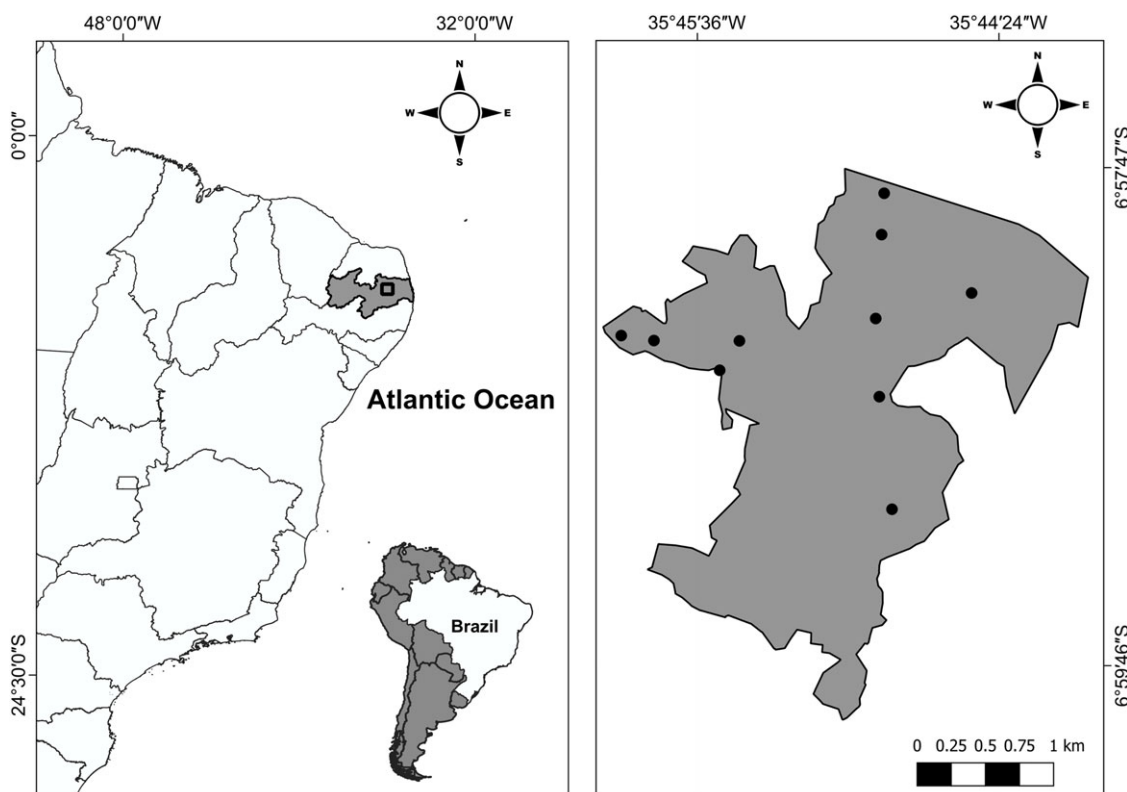
Figure 1. Map with the location of the Mata do Pau Ferro State Park in the Municipality of Areia – PB, highlighting the sampling units (dark circles).

takes place over a longer period, from March to July. *E. pauferrense* is endemic to the Northeastern Region of Brazil and is found in remnant areas of the Atlantic Rainforest (Loiola *et al.* 2007). In addition, it is worth mentioning that this species has a great affinity in terms of characteristics and habitat with *E. simonis* and can be distinguished by the following features: *E. simonis* has a height of between 2 and 2.5 m, thick, elliptical leaves with a pointed apex, a bright green colour on the adaxial side and fruits with smooth seeds (Loiola *et al.* 2007). Its flowering and fruiting in the study area may be in two periods, the first between March and June and the second between October and November. The distribution of *E. simonis* is restricted to north-eastern Brazil, with occurrence in fragments of the Atlantic Forest in the states of Paraíba, Pernambuco, Ceará, Sergipe and Rio Grande do Norte (Cordeiro *et al.* 2017).

To survey the species, we used ten 20 m × 50 m plots, previously established in the study area. The plots were distributed throughout the Mata do Pau Ferro State Park in order to cover its surface as much as possible. Within the plots, we marked and counted the individuals belonging to the three species of the genus *Erythroxylum* that were at least 10 cm in diameter at breast height (Felfili *et al.* 2011).

Characterising the abiotic multidimensional niche overlap

Luminosity
In June 2019, we took hemispherical photographs of the canopy using a Digital Plant Canopy Imager – CID-110 analyzer (CID, Inc) to obtain the light availability through photosynthetically active radiation (PAR) present in the understory (Table S1). The photographs were taken 1 m above the ground, in the four corners and centre of the plots, at moments with diffuse light conditions (in

our case, early in the morning) to allow the maximum possible contrast between the forest canopy and the sky (Whitford *et al.* 1995). After the photographs were taken, the value of photosynthetically active radiation for each plot was obtained by calculating the average of the five photos taken in each plot.

Chemical composition and soil granulometry
In each plot, with the help of a Dutch auger, we collected six simple soil samples (depth between 0 and 20 cm), after this process, we mixed all the samples and took a 300 g aliquot for the chemical and granulometric analyses of the soils. Following the protocol described in (Donagema *et al.* 2011), the granulometric ratios and chemical composition of the soils were measured. In total, 13 soil chemical and physical variables were collected: clay, sand, silt, C, H+Al, Al, Na, K, P, pH, Mg, Ca and organic matter. The clay, sand and silt values were converted into percentages to be used in the statistical analysis.

Soil moisture
We collected soil twice, before and after the rainy season, to obtain the average moisture content of each plot. In each collection, we took a 100 g aliquot from the composite sample of each plot. We weighed the samples (fresh weight – FW) and dried them in an oven (temperature of 60ºC) until constant weight, which was considered as the sample dry weight (DW). With this, we calculated the moisture content (h, measured in percentage) of the soil following the formula (Donagema *et al.* 2011; Klar *et al.* 1966; Papadakis 1941):

$$h = \frac{FW - DW}{DW} \times 100$$

We calculated Spearman's cross-correlation matrix to check (Figure S1) for multicollinearity among the 15 potential predictors (abiotic variables) of the study. Through the correlation matrix, we found that the 15 variables were highly correlated. Thus, we selected only those variables that had correlation values between −0.7 and 0.7 to ensure some degree of independence among the variables. The six continuous explanatory variables selected for inclusion in the models were PAR, moisture, sand, silt, potassium and calcium. Subsequently, we performed a variance inflation factor (VIF) analysis of each predictor using the car and MuMin statistical packages for R software version 3.6.0 (R Development Core Team 2020). In the analysis, the highest VIF obtained was 2.2, which indicates low collinearity between the predictor variables (Neter *et al.* 1990) thus allowing them to be included in our statistical model.

Analysis of data

We constructed generalised linear models (GLM) to understand how the three species of the *Erythroxylum* genus share the multidimensional niche space according to the abiotic variables considered in our study. We build three individual models (one model for each of the three *Erythroxylum* species) to see how each species responds separately to the environmental variables. In these models, the response variable is the abundance of the *Erythroxylum* species itself in each plot. The basic GLM model was $AbunSp \sim PAR + moisture + sand + silt + K + Ca$, where $AbunSp$ is the abundance of species, PAR is photosynthetically active radiation, *moisture* is the variable related to the availability of water in the plots under study *sand* and *silt* represent the percentage concentration of sand and silt in the soils, K and Ca are the concentrations of potassium and calcium in the soils of the plots studied. As the abundance of the species is count data, we modelled it as a Poisson distribution with a logarithmic link function. In addition, the predictor variables used in the analyses were Z-transformed to ensure comparability between the variables.

We assessed the degree of abiotic niche overlap considering the three species taken in pairs. We produced relative density surfaces for each species based on the Kernel index, using the ecospat.-grid.clim.dyn function provided by the 'ecospat' package (Di Cola *et al.* 2017). Subsequently, we determined the equivalence (and statistical significance) of their niches using the 'ecospat.niche.equivalency.test' function from the same package, based on the niche overlap index D (Warren *et al.* 2008). We adopted the hypothesis of niche separation and set the 'overlap.alternative' parameter to the 'lower' option. To check the validity of the hypothesis, the model was adjusted for 100 randomisations, and the observed D value was compared with the randomised values (Broennimann *et al.* 2012).

All the analyses were carried out in the R statistical software (R Development Core Team 2020).

Results

We sampled a total of 1027 individuals belonging to the three species of the genus *Erythroxylum* in the ten plots under study. Of this number, 781 individuals belonged to the species *E. simonis* (occurring in all plots, occurrence frequency = 1), 177 to

E. pauferrense (0.8 occurrence frequency) and 69 to *E. citrifolim* (0.5 occurrence frequency) (Table S2).

Effect of predictor variables on the abundance of *Erythroxylum* species

Our abundance models for the three *Erythroxylum* species suggested that the availability of photosynthetically active radiation exerted different effects on the abundance of the three focal plant species in our study. The abundance of *E. simonis* increased in response to the light gradient, unlike *E. citrifolium*, which responded negatively to increased light availability. *E. pauferrense* on its turn, showed no consistent response across our gradient of PAR incidence (Table 1; Figure 2A).

The species *E. citrifolium* and *E. simonis* exhibited similar patterns of monotonic increasing abundance as soil moisture rises (as illustrated in Figure 2B). In contrast, *E. pauferrense* showed a slightly negative response (driven by a single dry plot harbouring about 40 individuals), but with a higher concentration of occupied plots (consequently, higher proportion of relative abundance) in wetter plots (Table 1; Figure 2B). The proportions of sand and silt played different roles on the abundance of the three plant species. Our results show that *E. citrifolium* showed no influence of the sand gradient on its abundance but responded negatively to increasing silt proportion (Table 1; Figure 2C and 2D). The abundance of *E. pauferrense* was positively correlated to the proportion of sand but showed no response to silt proportion, while *E. simonis* showed increased abundance as the concentration of sand and silt increased (Table 1; Figure 2C and 2D).

The availability of potassium in the soil had a positive effect on the population of *E. citrifolium* and a marginally significant effect on the abundance of the species *E. pauferrense* but did not affect *E. simonis* abundance (Table 1, Figure 2E). In addition, the populations of *E. simonis* and *E. pauferrense* were positively affected by soil calcium concentrations, with a higher slope; consequently, a stronger effect on the species *E. simonis* (Table 1, Figure 2F).

Abiotic niche overlap of Erythroxylum species along environmental gradients

The relative abundance distribution of the three species of the genus *Erythroxylum* showed different responses along the gradients of environmental variables describing their observed ecological niche (Figure 3). The species *E. simonis* showed the highest relative abundance along all environmental gradients (Figure 3; Figure S2), with abundance peaking in wet environments under low to intermediate luminosity. In addition, *E. simonis* occurred at higher abundances on soil texture of about 60% of sand and 10% silt, with low potassium concentration, and showed high abundance across the whole calcium gradient (Figure 3C to 3F and Figure S2). *E. pauferrense* showed preferences for environments with low to intermediate incidence of photosynthetically active radiation (it is absent in sites with high luminosity), low to high water availability, soils with intermediate proportion of sand and silt and low concentrations of potassium and calcium (Figures 3A to 3F and Figure S2). *E. citrifolium* showed the lowest relative abundance along the gradients, exhibiting a conspicuous peak of relative abundance in sites with lower incidence of photosynthetically active radiation, higher water availability, soils with a significant presence of sand, low concentrations of silt, high availability of potassium and low calcium availability (Figures 3A to 3F and Figure S2).

Table 1. Effect of abiotic variables of the ten study plots on the abundance of *E. citrifolium*, *E. pauferrense* and *E. simonis* in a landscape Brazilian Atlantic Tropical Rainforest

Model	Df	Deviance	Resid. Df	Resid. Dev	p
Erythroxylum citrifolium					
PAR	1	25.75	8	147.41	<0.001
Moisture	1	98.99	7	48.42	<0.001
Sand	1	0.30	6	48.13	0.586
Silt	1	25.03	5	23.10	<0.001
K	1	23.10	4	0.00	<0.001
Ca	1	0.00	3	0.00	1.000
Erythroxylum pauferrense					
PAR	1	0.79	8	194.38	0.372
Moisture	1	11.99	7	182.39	<0.001
Sand	1	49.98	6	132.41	<0.001
Silt	1	0.17	5	132.24	0.677
K	1	3.73	4	128.50	0.053
Ca	1	4.54	3	123.96	0.033
Erythroxylum simonis					
PAR	1	20.48	8	110.11	<0.001
Moisture	1	22.26	7	87.85	<0.001
Sand	1	22.51	6	65.34	<0.001
Silt	1	14.69	5	50.65	<0.001
K	1	0.04	4	50.61	0.836
Ca	1	41.86	3	8.74	<0.001

Notes: PAR, photosynthetically active radiation; K, potassium; Ca, calcium.

Taken together, species-specific response to each abiotic niche dimension produces its multidimensional abiotic niche, which showed different levels of niche overlap with the multidimensional abiotic niche of the remaining species. Two pairs of species showed lower niche overlap (D) than randomly expected. The species *E. citrifolium* and *E. pauferrense* presented D-value 2.18 times lower than the expected by chance (observed D = 0.395 *vs.* random D = 0.859 ± 0.041; p = 0.009), while *E. simonis* and *E. pauferrense* showed D-value 1.42 times lower than random D (0.508 *vs.* 0.721 ± 0.071; p = 0.009). *E. simonis* and *E. citrifolium*, however, showed D-value 1.04 times higher than randomly calculated (0.594 *vs.* 0.571 ± 0.059), but differences did not depart from expected by chance (p = 0.712).

Discussion

Our results indicate that the three species belonging to the genus *Erythroxylum* coexist along the different environmental gradients, with some level of ecological niche overlap. We found that, based on species abundance and occurrence frequency across plots, *E. simonis* is the best competitor, showing a generalist behaviour and the highest abundance across all environmental gradients. The species *E. pauferrense*, on its turn, appeared as the second stronger competitor. Its behaviour across environmental gradients is similar to *E. simonis*, but *E. pauferrense* showed a less generalist character and exhibited lower niche overlap than expected by chance with both remaining species. The species *E. citrifolium* occupies the lowest rank in the competitive hierarchy and showed a narrow pattern in resource use and habitat preference (specialist behaviour), although it presents high level of niche overlap with *E. simonis*. *E. citrifolium*, exhibited very conspicuous peaks of relative abundance concentration, achieving higher population density in sites with lower light incidence, higher water availability, moderate amounts of sand, low amounts of silt, higher levels of potassium and lower concentration of calcium in the soil. Additionally, it is important to emphasise that the adult population of the species studied has been able to adapt to various environmental and ecological challenges. Thus, the outcomes we report here are influenced by the species' ability to perform well in terms of physiology, recruitment, growth and survival during their early life stages. Finally, we recognise that despite the considerable effort put into data collection, the sample size of the plots ($n = 10$) can be considered small. A larger sample could provide a more robust and detailed view of species dynamics and their ecological interactions. Therefore, future studies with a larger number of sample plots would be valuable to confirm and expand our results, offering a more comprehensive understanding of niche sharing between the three focal species of our study.

The monotonic increase in the population of a plant species in a resource gradient indicates that the plant's performance is limited by that resource (Farrior *et al.* 2013; Gleeson and Tilman 1992; Liebig 1855), our data suggests light, water and calcium as limiting resources. It is also known from literature (Dybzinski and Tilman 2007; McPeek 2019; Tilman 1990; Tilman *et al.* 1981) that increases in the availability of limiting resources must foster performance of the best competitor species, *E. simonis* in our case. The other two *Erythroxylum* species had more variable behaviour, showing opposite responses to the moisture gradient, and alternating from no-responsive to slightly responsive (either increasing or decreasing) to the other resource gradients (light, potassium and calcium). It suggests that *E. citrifolium* and *E. pauferrense* tend to segregate their ecological niche space and use resources differently, highlighting a possible fierce competition in the past. Additionally, gradients of environmental conditions, soil texture in our study, may modulate population size of the three species, with *E. simonis* achieving higher population density across the whole gradient, which points to high phenotypic plasticity. *E. citrifolium* and *E. pauferrense*, however, showed opposite trends concerning soil texture, indicating that these species are better adapted, respectively, to sandy and silty soils. This complex set of responses to resource availability and environmental conditions allows the three plant species to coexist, and the whole picture points to different levels of niche overlap amongst them.

The coexistence of phylogenetically close species requires some differentiation in the acquisition and use of available resources to minimise competitive pressures (Dybzinski and Tilman 2007; Martin and Mallik 2023; Tilman *et al.* 1981), which can drive niche overlapping or segregation (Weber and Strauss 2016). Our results show that the three species, in the absence of their close competitors, can occupy the whole resource and environmental condition gradients, but they alleviate competitive pressures by shifting their observed niche. For example, species pairs *E. citrifolium* with *E. pauferrense* and *E. simonis* with *E. pauferrense* fulfill different parts of the possible multidimensional niche space,
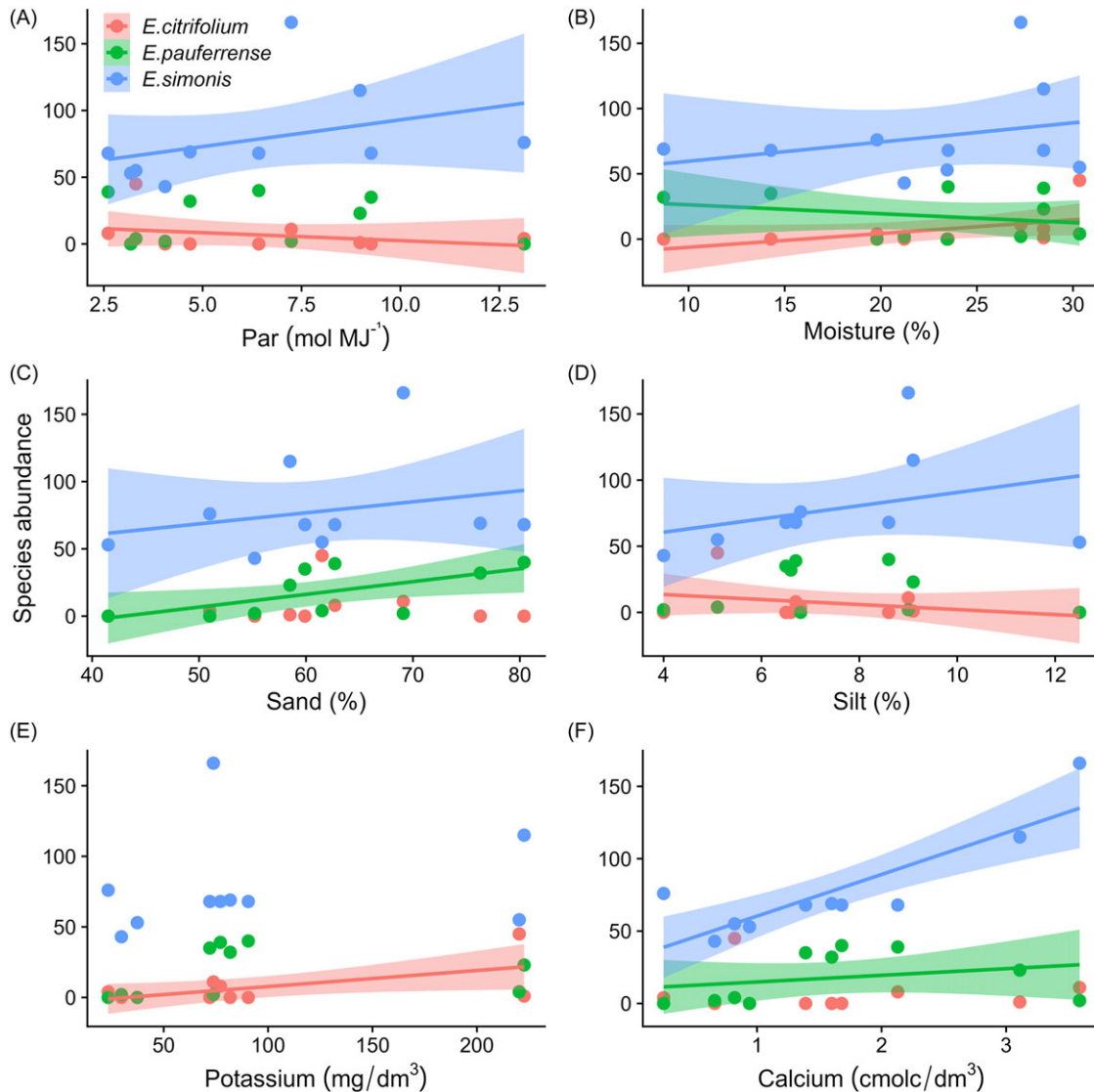
Figure 2. Response of the abundance of *E. citrifolium*, *E. pauferrense* and *E. simonis* along gradients of environmental variables in the ten study plots in a landscape Brazilian Atlantic Tropical Rainforest. Par: photosynthetically active radiation.

with a coexistence strategy of reducing niche overlap and decreasing competition. Concerning *E. simonis* and *E. citrifolium*, however, the coexistence strategy seems different. In this case, the species *E. citrifolium*, concentrates its population in a restricted part of the multidimensional niche space, presumably around the optimal values for each resource and condition evaluated, which favours its persistence in the system, although this niche space still shared with *E. simonis*. From this, we believe that phenotypic plasticity plays a central role as it is involved in both coexistence strategies, either allowing species to modify their phenotype in order to segregate their niches, either allowing a species to restrict its population to sites where it achieves higher performance in order to maximise their survival likelihood. Additionally, the role of species characteristics such as root depth and resource use efficiency can collaborate in the efficient use of water, modulate population size and competitive strategy. For example, the species *E. simonis* has a deep root system that allows it to reach water and mineral deposits inaccessible to the other two remaining species

(Briones *et al.* 1996; Silvertown 2004b), thus gaining access to these extra resources.

The processes underlying species coexistence in space and time rise in importance in the current scenario of increasing anthropogenic disturbances, like natural resources hyper-exploitation, land cover change and global climate change (Åkesson *et al.* 2021; Descombes *et al.* 2020). Such anthropogenic disturbances could favour the replacement of disturbance-sensitive organisms, the loser species *sensu* Filgueiras *et al.* (2021) by habitat-generalist and disturbance-adapted ones, the winner species *sensu* Filgueiras *et al.* (2021). Such replacement can be fostered by changes in species competitive hierarchy driven by anthropogenic disturbances, leading to increased taxonomic, functional and phylogenetic similarity among ecological communities (i.e. biotic homogenisation; Tabarelli *et al.* 2012). Thus, investigating and understanding how environmental changes act on the responses of species with different limited resource utilisation strategies is fundamental for building appropriate conservation protocols (Daru *et al.* 2021),
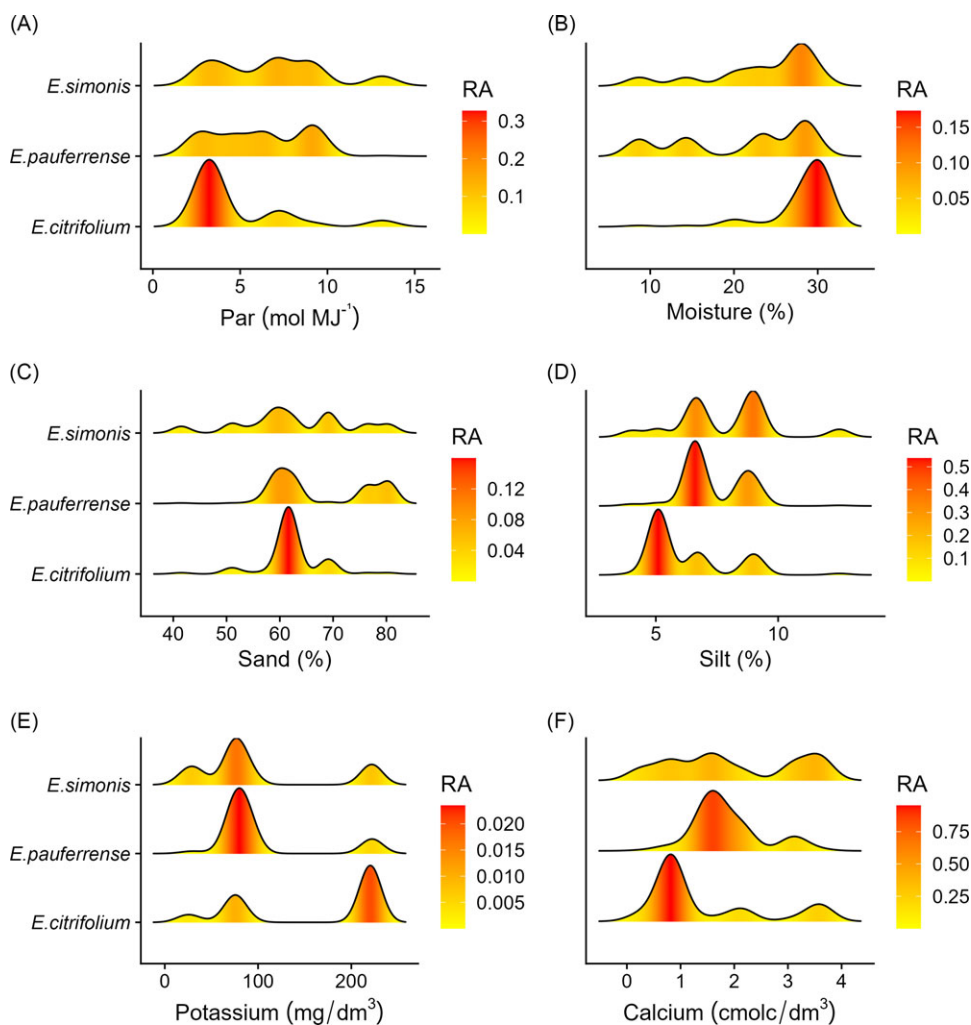
Figure 3. Population distribution of the *E. citrifolium*, *E. pauferrense* and *E. simonis* along gradients of photosynthetically active radiation (PAR) (A), moisture (B), soil and (C) and silt (D) ratios, potassium (E) and calcium (F) in a landscape Brazilian Atlantic Tropical Rainforest. Abbreviations: RA, the proportion of relative abundance. The sum of the area under the curve equals 1 (or 100% of the individuals).

especially when it comes to species that are more restricted to certain environmental conditions, phylogenetically close, or rare, as is the case of *E. pauferrense* (Loiola *et al.* 2007). Our results also suggest that phenotypic plasticity plays an important role in species coexistence as it could allow, on one side, niche segregation leading to character displacement and, on the other side, constraining observed ecological niche to the optimal zones even though it elicits a reduction in population size as a handicap. Finally, we acknowledge that the processes behind the niche partitioning among the three species may be related to other mechanisms, such as biotic interactions (i.e. seed dispersal or pollination), which can reverberate across local communities' assembly processes, deserving further investigation in the future.

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