



Original Paper

Environmental factors driving plant trait distributions in coastal zones of Atlantic Forest

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Abstract

Environmental filtering has been defined as the effect of environmental gradients on species in a plant community and can be the dominant driver of community assembly. Here, we evaluate the relationship between plant communities and the environment in the Restinga vegetation. For this, we measured 11 functional traits of plant species present along transects covering a marked edaphic environmental gradient. This gradient was characterized through Principal Component Analysis of soil characteristics. The relationships between the edaphic gradient and functional traits were evaluated using linear models. Finally, we compared the contributions of species turnover and intraspecific variation to among-site variation in functional traits. The gradients associated with soil nutrients (PCA axis 1) and soil acidity and organic matter (PCA axis 2) were then used to test the observed changes in community composition and were significant predictors of the distribution of water potential, leaf dry matter content and K content, height and chlorophyll index. Decomposing the total variation in the distribution of functional traits between species turnover and intraspecific variation revealed that species turnover explains a greater proportion of the observed variation. We conclude that community assembly is strongly limited by environmental filters and mediated by functional traits at the species level.

Key words: assembly rules, community composition, dune, functional trait, Restinga, turnover.

Resumo

A filtragem ambiental é o efeito dos gradientes ambientais nas espécies e pode ser o principal fator de montagem de comunidades de plantas. Aqui, avaliamos a relação entre comunidades vegetais e o solo na vegetação Restinga do nordeste do Brasil. Para isso, medimos 11 características funcionais das espécies vegetais presentes ao longo dos transectos, cobrindo um gradiente ambiental marcado. Este gradiente foi caracterizado através da Análise de Componentes Principais (PCA) da composição química do solo. As relações entre o gradiente edáfico e as características funcionais foram avaliadas usando modelos lineares. Finalmente, comparamos as contribuições da substituição de espécies e variação intraespecífica na comunidade vegetal. Os gradientes associados aos nutrientes do solo (eixo 1 da PCA) e acidez do solo e matéria orgânica (eixo 2 da PCA) foram então utilizados para testar as mudanças observadas na composição da comunidade e uma relação significativa foi encontrada com o eixo 2. Os eixos foram preditores significativos da distribuição da altura, teor de clorofila, potencial hídrico, massa seca e teor de K. A decomposição da variação total na distribuição de características funcionais entre a rotatividade de espécies e a variação intraespecífica revelou que a rotatividade de espécies

See supplementary material at <https://doi.org/10.6084/m9.figshare.16879834.v1>

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explica uma proporção maior da variação observada. Concluímos que a montagem da comunidade é fortemente limitada por filtros ambientais e mediada por características funcionais no nível das espécies.

Palavras-chaves: regras de montagem, estrutura da comunidade, duna, atributos funcionais, Restinga, variação interespecífica.

Introduction

A central goal of ecology is to understand the processes that influence community assembly and that control species distributions across environmental gradients (McGill *et al.* 2006; Fortunel *et al.* 2014). Two contrasting deterministic processes have been implicated in structuring plant communities: environmental filters (Weiher & Keddy 1995; Cornwell *et al.* 2006) and limiting similarity (MacArthur & Levins 1967; Stubbs & Wilson 2004). In relation to the former, community assemblage can be conceptualized as consequence of successive environmental filters which exclude species lacking certain functional traits (adaptations to local abiotic/biotic conditions) from the species pool (Kraft *et al.* 2015). As a consequence, species within a filtered community tend to have similar functional attributes that allow them to survive within the environment. In contrast, the concept of limiting similarity suggests that co-occurring species need to have somewhat different ecological strategies (and traits) in order to avoid high levels of interspecific competition (MacArthur & Levins 1967).

Functional traits can represent ecological strategies and determine how plants respond to environmental factors (Pérez-Harguindeguy *et al.* 2013). The distribution of traits in the community should therefore broadly reflect processes that structure plant communities (Bochet & García-Fayos 2015). It follows that trait distributions should change along environmental gradients because of environmental filtering, adaptive phenotypic plasticity [*e.g.*, individuals of many plant species are taller in fertile habitat (Lepš *et al.* 2011)], or a combination of these two effects (Lepš *et al.* 2011; Siefert *et al.* 2014; Zuo *et al.* 2017).

Numerous studies examining community assembly have focused on trait variation due to changes in species composition along environmental gradients, because it typically involves clear and easily measurable differences in trait values among species (Lepš *et al.* 2011; Kichenin *et al.* 2013). However, recent studies have shown that intraspecific variation may also play an important role in community trait responses

to environmental variation (Jung *et al.* 2010; De Bello *et al.* 2011; Siefert *et al.* 2015; Zorger *et al.* 2019). While some researchers have proposed that competition for limited resources is the main driver of intraspecific trait variation of co-occurring species (Lepš *et al.* 2011; Auger & Shipley 2013), others have suggested that environment filtering is the dominant driver of community assembly (Barros *et al.* 2017; Zhang *et al.* 2018).

In heterogeneous environments such as sand dune ecosystems, vegetation mosaics are often associated with environmental filtering imposed by strong edaphic gradients (Cardoso & Lomônaco 2003). The mosaic of plant communities of the coastal zones of Brazil, generally known as Restinga, is a good example of such a heterogeneous habitat subject to intense biophysical selection pressures. Specifically, Restinga communities are subject to a wide array of environmental conditions, such as high temperatures, flooding, high salinity and lack of nutrients (Assumpção & Nascimento 2000; Scarano 2002). Plant survival and reproduction is therefore closely associated with levels of soil exposure, edaphic factors, and vegetation critical mass required to stabilize nutrient relations of the system (Reinert *et al.* 1997). Thus, the Restinga ecosystem provides an interesting opportunity to evaluate the role of environmental filtering in plant community composition, and to compare the relative importance of intraspecific variation and species turnover in determining functional trait distributions.

Several studies have already focused on functional trait variation and distribution contributes to structure the diverse communities of species rich tropical plant communities through differential niche-based processes (Kraft *et al.* 2008; Malhado *et al.* 2009; Neyret *et al.* 2016). Although some studies carried out on sandy soil and Restingas have demonstrated functional responses of plants to different environmental conditions (see Mahdavi & Bergmeier 2016; Rosado & De Mattos 2010; Scarano 2002; Scarano *et al.* 2001), information on how species turnover and intraspecific variation contribute to these responses is still lacking. Preliminary observations suggest

that the distribution of plant traits in Restinga systems may be strongly influenced by edaphic factors, such as pH, aluminium content, organic matter and salinity (Giaretta *et al.* 2013; Santos-Filho *et al.* 2013). Given the strong environmental gradients present in the Restinga, we hypothesized that environmental filters play a significant role in community composition, mediated by the distribution of functional traits associated with survival-related pathways. Specifically, we predict that: 1) there will be significant changes in community composition in response to observed environmental gradients; 2) changes in community composition will reflect the distribution of plant functional traits along the same environmental gradients, and; 3) observed functional changes will be mostly driven by community turnover rather than intraspecific variation.

Materials and Methods

Study area and collection

We conducted this study in six plots (50 × 200 m) distributed in two Restingas areas (09°42'S, 35°47'W; 09°47'S, 35°52'W) in the Santa Rita Sustainable Development Reserve, Northeast Brazil. This reserve is within an area has a typical tropical climate, with a mean annual temperature around 24.7 °C and mean annual precipitation of

1,726 mm. The natural vegetation is characterized by a mosaic of plant communities that occupy sandy plains formed by marine deposits of the late Quaternary which lie between the sea and the tabuleiros (large, flat areas formed from Tertiary deposits of crystalline rock) occupied by Atlantic Forest (Scarano 2002). The first vegetation encountered along the beach-to-inland gradient is a narrow strip of beach vegetation, in which creeping psammophytes grow on the shifting sands of the upper part of the beach. Behind these embryo dunes is the foredune, a slightly higher and older beach ridge dominated by grasses (Castanho *et al.* 2012).

Based on Reinert *et al.* (1997) and Souza *et al.* (2008), we divided Restingas areas into four plots/zones (50 × 200 m each) characterized according edaphic factors and non-vegetation types: zone a- areas nearest to the sea, where psammophilous and halophyte species dominate, particularly rhizomatous, cespitose, and creepy herbaceous; zone b- intermediate zones, 2 kilometres from the sea, composed of dense 0.5 to 1 m high shrub mosaics; zone c- zones located furthest from the sea (3 kilometres), composed by shrubs and trees between 2 and 5 m high, and; (zone d) flooded areas (3,5 kilometres from the sea) (Fig. 1).

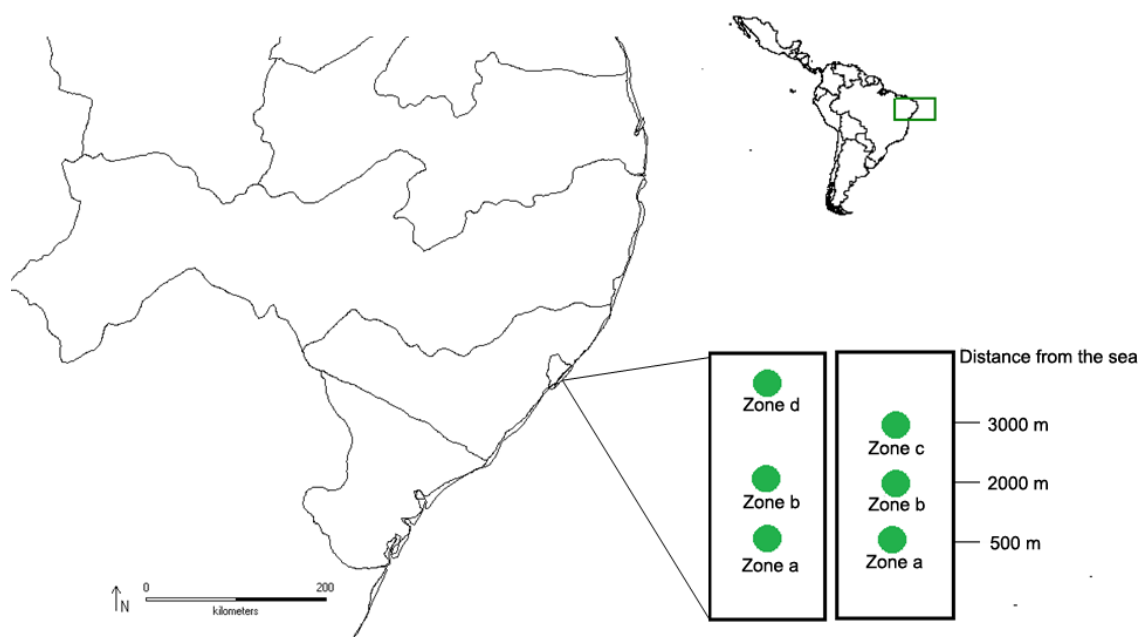


Figure 1 – Representation of sampling in zones of Restingas.

Plant morphophysiological traits were measured between March and June 2016, in order to sample the plant community at peak standing biomass during the rainy season. In Restinga environments, nurse plants promote facilitation by enhancing fitness, survival and/or growth of associated species (Callaway *et al.* 2002). This often results in the process of nucleation, i.e. the formation of vegetation clumps or islands, and the vegetation becomes organized in small islands separated by sandy stretches with clumps (Pimentel *et al.* 2007). Because of this, for each type of zone, two transects (200 m) were established perpendicular to the seashore. We collected all individuals in each transect.

Selection and measurements of functional traits

Trait-based community analysis requires the selection of traits that are critical to the community processes of interest (Cornelissen *et al.* 2003; Baraloto *et al.* 2010). Our selection of traits thus represented the leaves and the overall life form of each species, covering a wide range of traits frequently deemed essential for plant survival and establishment in extreme environments (Tab. 1) (Pérez-Harguindeguy *et al.* 2013). We selected adult individuals and minimum and preferred number of replicates for different traits according Pérez-Harguindeguy *et al.* (2013).

Specifically, we measured leaf area (cm²) -10 leaves per individual- with LAI 3000 (Li-Cor). Leaf dry matter content (LDMC) (g) was measured following drying to constant mass at 60 °C (around 72 h), and specific leaf area -SLA- was calculated for each lamina as the ratio of leaf area to leaf dry matter content (cm²/g). We considered the rachis as part of the leaf for the SLA calculation (Pérez-Harguindeguy *et al.* 2013). Chlorophyll index was estimated from five measurements per lamina using a portable, non-destructive chlorophyll meter Minolta SPAD 502DL (Spectrum Technologies, Plainfield, IL, USA). Maximum quantum efficiency of PSII (Fv/Fm) was determined after 20 min of leaf dark adaptation period using the saturation pulse of actinic light (8000 lmol/ m²) through a modulated fluorometer (PAM 2500). Leaf water potential (MPa) was measured around 12:00 PM using a Scholander pressure chamber. Leaf phosphorus (P), sodium (Na⁺) and potassium (K⁺) were measured in mg/g according to the methodology recommended by EMBRAPA (Carmo *et al.* 2000).

Measurement of environments variables

We collected ten soil samples in each zone at a depth of 15 cm. We mixed the sample soil to obtain a composite sample per zone. Organic matter content (OM, g/Kg), ion exchange capacity (IEC, cmol_c/dm³), pH in water, Calcium (Ca²⁺, cmol_c/dm³), magnesium (Mg²⁺, cmol_c/dm³), phosphorus (P, mg/dm³), sodium (Na⁺, mg/dm³) and potassium (K⁺, mg/dm³) were extracted according to a methodology recommended by EMBRAPA (2013).

Data analysis

We used a Principal Component Analysis (PCA) with soil composition variables to characterize the edaphic gradients present in the study site. The first two PCA axis explained a large proportion of the variation and were thus used to represent the environmental gradients in subsequent analyses. Community composition changes along the environmental gradient were detected using a multivariate model (ManyGLM) in the R package *mvabund* (Wang *et al.* 2012; Warton *et al.* 2012). This methodology was specifically developed for complex community composition data and was used for parameter estimates for generalised linear models simultaneously fitted to each of many variables, critically, takes into account the interactions between species commonly that are absent in standard GLM approaches (Milazzo *et al.* 2016). According Warton *et al.* (2012) this approach detects differences in communities of less abundant species that may be more poorly represented by distance-based approaches. Subsequently, we also analysed the relationships between edaphic gradients and functional traits using linear models. Trait averages were calculated from 'specific average' using trait values for individual species that are specific to each habitat where the species are found (Lepš *et al.* 2011) (Table S1, available on supplementary material <<https://doi.org/10.6084/m9.figshare.16879834.v1>>). Linear models were performed separately for each sampled trait and considered as explanatory variables the two main axis resulting from the PCA described above.

Finally, we compared the relative contribution of species turnover and intraspecific variation in explaining among-site variation in functional traits by partitioning the variance explained by each component. For this, we used the method proposed by Lepš *et al.* (2011) based on the decomposition

Table 1 – Measured functional traits, their respective biological significances and expected relation with different environmental factors

| Trait | Functional role | References |
|----------------------|---|---|
| Height | Competitive vigour, resource availability. Taller plants are likely to settle in areas with nutrient-rich soils. | (Lammerts <i>et al.</i> 1999; Cornelissen <i>et al.</i> 2003) |
| Leaf area | Changes in the leaf area represent a functional strategy associated with the availability of water and/or soil nutrients. For example, small leaf size maintain leaf temperature and greater photosynthetic and water use efficiency under the combination of high solar radiation, low availability of water and nutrients and Salinity. | (Sharma 1996; Ackerly <i>et al.</i> 2002) |
| Dry mass | Is a predictor of nutrient availability in the soil. The increase in the availability of P and K in soils promotes a gradual biomass allocation | (Marschner 1995; Lawrence 2001) |
| SLA | Reports on leaf longevity, photosynthetic rate and growth rate, Positively related with leaf nitrogen (N) concentration. Low SLA values have been associated with low soil N and P | (Wright <i>et al.</i> 2004; Maire <i>et al.</i> 2015) |
| Chlorophyll index | Chlorophylls absorb light energy and transfer it to the photosynthetic apparatus. In this way, its quantification can provide valuable information about the physiological performance of the leaves. Communities with greater abiotic stress tend to have less chlorophyll content. | (Sims & Gamon 2002; Spasojevic & Suding 2012) |
| Fv/Fm | Indicative of efficiency in the use of radiation by photochemistry and, consequently, the assimilation of carbon. Saline stress causes a complex effect on metabolism, resulting in ionic toxicity that interfere with the physical conditions of the soil or the availability of other elements, indirectly affecting the development of plants. | (Tester & Bacic 2005) |
| Leaf water potential | Is a simple indicator of the leaf's water status; the more negative the value, the more dehydrated the leaf. The water potential of the leaf tends to decrease as the evaporative demand increases. The hydraulic deficit results in decreased growth and development. | (Bréda <i>et al.</i> 2006) |
| P | Leaf P concentration and leaf N:P were related to soil total P alone. The sequence of responses suggests that increased available P promoted an increase in photosynthetic area which led to increased wood production | (Herbert & Fownes 1995; Ordoñez <i>et al.</i> 2009) |
| Na+ | Salinity reduced leaf area and number of tillers, and increased Na+ and Cl ⁻ concentrations in leaves. | (Sharma 1996) |
| K+ | The uptake of K by the leaves can increase the turgor and contribute to a greater water potential | (Tanguilig <i>et al.</i> 1987). |
| N | Leaf N concentration was related to both soil C:N and soil total P | (Ordoñez <i>et al.</i> 2009) |

of the sum of squares of the trait variation along the gradient. To assess the respective contribution of species turnover and intraspecific variability, we used function “trait.flex.anova” developed by the authors for the R software (R Development Core Team <<https://www.r-project.org>>).

Results

We found a marked environmental gradient characterized by chemical changes in soil. The first two PCA components explained 93% of the total variance of environmental attributes according to soil composition variables (Fig. 2). PCA axis 1 was mainly associated with soil nutrients (P, Na, K, Mg and IEC) and explained 59.2% of the variation observed between sampled sites, while the PCA axis 2 related mainly to pH, H+Al, OM

and Ca variables, and explained 33.8% of the total observed variance (Fig. 2). Both axes were then used to test the observed changes in community composition between zones, and a significant relationship was found with axis 2 (Tab. 2).

Plant functional traits were measured in 200 individuals of 18 wood plant species (Tab. 3) and the environmental gradients represented by the two PCA axes were significant predictors of the distribution of five out of the eleven study traits (Fig. 3; Tab. 4). There was a relationship with both predictors for water potential, LDMC and K content, while two other traits (height and chlorophyll index) only showed a significant relationship with axis 2. Effect sizes (standardized estimates) were generally higher for axis 2 than for axis 1 (Tab. 4). Higher values of PCA axis 2 were

Table 2 – ManyGLM testing the relationship between predictors (axis1 and axis 2 from PCA) and community composition. Significant results are in bold.

| Predictor | Deviance | P value |
|-----------|----------|--------------|
| Axis 1 | 1.413 | 0.599 |
| Axis 2 | 3.805 | 0.028 |

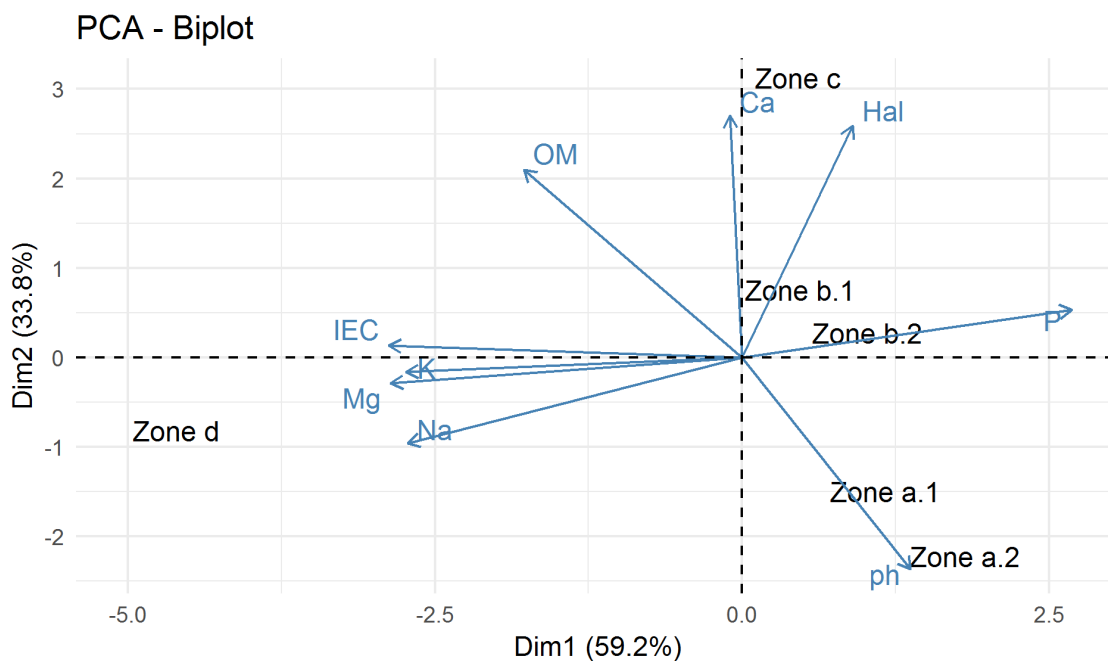


Figure 2 – Principal component analysis for edaphic attributes (Na, K, Mg, IEC, OM, Ca, Hal, pH) from two Restinga study sites.

positively associated with height, but negatively associated with chlorophyll index, water potential and LDMC. In contrast, higher values of PCA axis 1 were associated with increasing water potential, LDMC and K content (Fig. 3).

Decomposition of total variation in the distribution of each functional trait demonstrated that species turnover accounts for a much larger proportion of total trait variation than intraspecific variation (Tab. 5). The percentage of variation explained by the turnover component varied between ~87 and 100 whereas that of intraspecific variability varied between 0 and 22%. For foliar area, chlorophyll index, nitrogen, sodium and potassium concentration, all observed variation was due to species turnover (Tab. 5). There was a positive covariation between species turnover and intraspecific variation for height, Fv/Fm, leaf area, LDMC and SLA, indicating that the effects of species turnover and intraspecific variation reinforced each other (i.e., sites dominated by species with high values of those traits also tended to have individuals with high trait values for their species). Co-variation between intraspecific

variation and turnover was negative for chlorophyll index, water potential and phosphorus.

Discussion

Our results showed that the previously established vegetation zones are characterized by a significant difference in the chemical soil characteristics, framing an environmental gradient. Furthermore, the observed changes in community composition and environmental gradients correlated strongly with plant functional traits, generating additional insights into mechanisms behind the observed environmental filtering. Plant community composition and associated functional traits are known to be affected by a combination of environmental factors whose relative influence may be difficult to tease apart (Fortunel *et al.* 2014). However, our results showed that some edaphic factors have a significant effect on community composition in Restinga habitats.

Soil pH is a factor that is known to affect the establishment of plant communities in Restingas (Santos-Filho *et al.* 2013), because acidic pH reduces the rates of decomposition in the soil

Table 3 – Plants found in the six plots of Restinga

| Family | Specie |
|------------------|--|
| Anacardiaceae | <i>Schinus terebinthifolius</i> Raddi. |
| Apocynaceae | <i>Hancornia speciosa</i> Gomez. |
| Burseraceae | <i>Protium heptaphyllum</i> (Aubl.) Marchand. |
| Capparidaceae | <i>Capparis cynophallophora</i> L. |
| Chrisobalanaceae | <i>Chrysobalanus icaco</i> L. |
| Dilleniaceae | <i>Tetracera breyniana</i> Schldtl. |
| Erythroxylaceae | <i>Erythroxylum citrifolium</i> A. St. –Hill. <i>Erythroxylum</i> sp. |
| Euphorbiaceae | <i>Croton polyandrus</i> Spreng. |
| Fabaceae | <i>Canavalia rosea</i> (Sw.) DC. <i>Senna</i> sp. <i>Crotalaria</i> sp. |
| Goodeniaceae | <i>Scaevola plumeri</i> Vahl. |
| Nyctaginaceae | <i>Guapira</i> sp. |
| Ochnaceae | <i>Ouratea nitida</i> Aubl. |
| Rubiaceae | <i>Chiococca alba</i> (L.) Hitchc. <i>Tocoyena selleana</i> Schum. <i>Guettarda angelica</i> Mart. |

and consequently decreases soil organic matter (OM). Areas with higher OM availability are more favourable to the development of taller woody plants (Lammerts *et al.* 1999), which explains the relationship between plant height and PCA axis 2. Plant height is often related with water potential

(van der Weele *et al.* 2000). Leaf water potential is an indicator of the leaf's water status and shows the balance between water availability in the soil. It tends to decrease as evaporative demand (evapotranspiration potential) increases (Bréda *et al.* 2006), potentially explaining our observation of

Table 4 – Linear models testing the relationship between predictors (axis1 and axis 2 from PCA) and functional traits. Significant results are in bold.

| Trait | Axis 1 | | Axis 2 | |
|-------------------|----------------|-------------|-----------------|--------------|
| | Estimate ± SE | P value | Estimate ± SE | P value |
| Height | -0.137 ± 0.046 | 0.06 | 0.200 ± 0.061 | 0.04 |
| Chlorophyll index | 0.333 ± 0.357 | 0.41 | -1.712 ± 0.472 | 0.03 |
| Water potential | 0.070 ± 0.0193 | 0.03 | -0.202 ± 0.025 | 0.004 |
| Fv/Fm | -0.015 ± 0.009 | 0.20 | 0.014 ± 0.012 | 0.32 |
| Foliar Area | 55.56 ± 29.37 | 0.15 | -107.65 ± 38.88 | 0.06 |
| Dry mass | 0.53 ± 0.128 | 0.02 | -0.753 ± 0.169 | 0.02 |
| SLA | 11.605 ± 6.912 | 0.19 | -5.44 ± 9.152 | 0.59 |
| N | 1.160 ± 0.656 | 0.17 | -2.192 ± 0.869 | 0.08 |
| P | 0.332 ± 0.329 | 0.38 | 0.421 ± 0.436 | 0.40 |
| Na | -0.066 ± 0.495 | 0.90 | -0.872 ± 0.655 | 0.27 |
| K | 1.739 ± 0.478 | 0.03 | -1.935 ± 0.632 | 0.05 |

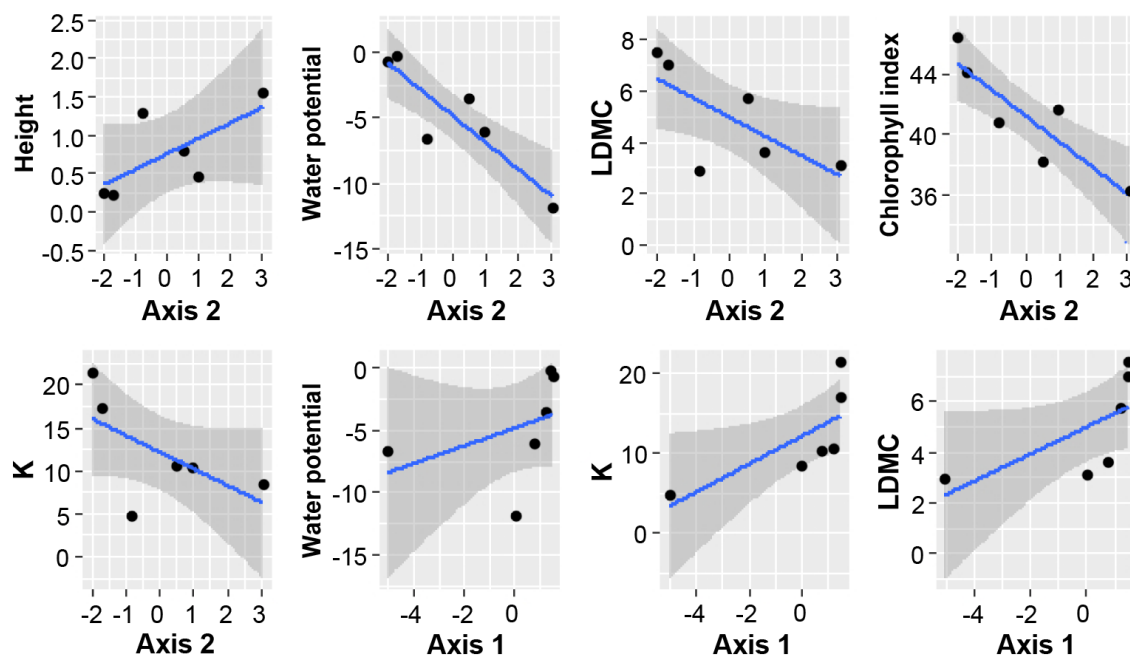


Figure 3 – Relationship between PCA derived environmental gradients (axis 1 and 2) and height, chlorophyll, water potential, LDMC and K contend.

higher water potential in leaves with lower levels of OM and pH in soil.

A growing availability of P and K in soils promotes a gradual biomass allocation (Marschner 1995; Lawrence 2001), as observed in the positive relationship between the availability of such nutrients and LDMC. Nutrient availability is also an important indicator of strategies of habitat preferences and of productivity of plants related to environments under stress (Niklas & Christianson 2011). Under conditions of water stress, such as found in Restinga (Scarano 2002; Neves *et al.* 2009), the survival of plants may be partly due to their ability to maintain turgor as a result of the slow decline in leaf water potential brought about by low transpiration rate and continued uptake of nutrients, especially K (Tanguilig *et al.* 1987). Increased K uptake suggests that, under water stress conditions, K may be absorbed preferably and may result in an osmotic adjustment which contributes to higher leaf-water potential (Tanguilig *et al.* 1987). We observed a similar pattern in the positive relationship between K availability and water potential.

These mechanisms suggest that the environmental gradients observed in Restinga areas ultimately structure the distribution of local plant communities and their associated traits. Different environmental conditions result in an increase of number of ecological niches within each site reflecting in a great variation in the

richness of local species and a species turnover among plots. The dominance of interspecific trait variation for all eleven traits suggests that that changes in the relative abundances of species are caused by habitat changes (Lepš *et al.* 2011; Zuo *et al.* 2017). It has been suggested that intraspecific effects are more important in short environmental gradients, where changes in species composition are small (Wright *et al.* 2004; Albert *et al.* 2011). However, in resource-poor environments the effect of environmental filters tends to be more intense and the plant communities are correspondingly more influenced by species selection and show higher levels of functional convergence (Kraft *et al.* 2008; Lohbeck *et al.* 2014).

Environmental filter should weaken the intraspecific variation, because rather than being excluded from a habitat species can adjust their characteristics to the environment (Kichenin *et al.* 2013). Nevertheless, in our study it is likely that intraspecific trait plasticity is insufficient to buffer against environmental filtering. The greatest contribution of intraspecific variation was observed in water potential (22%). The intraspecific variation observed in this characteristic show negative covariation indicating that areas dominated by species with high water potential values tend to contain individuals with low trait values for their species (Siefert *et al.* 2014). It follows that species turnover and intraspecific variation compensate for each other,

Table 5 – Percentage of total variation in community-weighted mean trait values explained due to species turnover, intraspecific variation, and their covariation.

| Trait | Turnover | Intraspecific | Covariation |
|-------------------|----------|---------------|-------------|
| Height | 88% | 5% | 7% |
| Chlorophyll index | 100% | 10% | -10% |
| Water potential | 87% | 22% | -9% |
| Fv/Fm | 91% | 2% | 7% |
| Foliar Area | 99% | 0% | 1% |
| Dry mass | 91% | 4% | 5% |
| SLA | 92% | 2% | 6% |
| N | 100% | 0% | 0% |
| P | 97% | 14% | -11% |
| Na | 99% | 0% | 0% |
| K | 99% | 1% | 0% |

leading to an absence of response of community-average trait values (Lepš *et al.* 2011).

The effect of environmental filtering observed in our study implies similar ecological needs of co-occurring species. Others studies have observed that species in dunes from the same habitat type have similar traits as result of exposure to the same environmental stress (Scarano *et al.* 2001; Mahdavi & Bergmeier 2016). These results do not support the action of limiting similarity in dunes as proposed by Stubbs & Wilson (2004). According to these authors species can more readily coexist if they differ in their resource use patterns. Rosado & De Mattos (2010) also observed that traits of the leaf economic spectrum showed small interspecific variation. However, these authors also noted that traits with physiological significance for the Restinga, such as water potential, showed considerable interspecific variation and recommend considerable caution when selecting functional traits to describe whole-plant responses to environmental drivers. In summary, the ability of a given species to colonize the dune habitat depends on integrative traits resulting from multiple trait arrays, not necessarily captured by the leaf economic spectrum (Rosado & De Mattos 2017).

This study provides important insights about how environmental factors influence the distribution of plant traits in the Restinga. The strong environmental gradients observed are clear and intuitive. Still, it would be interesting to explore similar questions in other tropical systems where, like the Restinga, vegetation is established in sandy soils. Such habitats are likewise somewhat poorly studied and may provide important insights into plant community dynamics under strong environmental gradients.

Acknowledgements

We also thank Francesco de Bello, for suggestions for data analysis; and Richard Ladle, for the English language review. RAC is currently funded by a post-doctoral scholarship from FCT - Fundação para a Ciência e Tecnologia (SFRH/BPD/118635/2016). ACMM is funded by CNPq-Conselho Nacional de Desenvolvimento Científico e Tecnológico (#309980/2018-6).

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Area Editor: Dr. Mário Luís Garbin

Received in February 12, 2020. Accepted in December 08, 2020.



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