

Universidade Federal de São Carlos
Programa de Pós Graduação em Ciências Ambientais
Departamento de Botânica

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RELAÇÕES ENTRE TRAÇOS FUNCIONAIS ECOLOGICAMENTE
IMPORTANTES DE ESPÉCIES ARBUSTIVO-ARBÓREAS DE
CERRADO

Orientador: Prof. Dr. Marco Antonio Batalha

São Carlos
Março de 2016

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Resumo

Os chamados “Esquemas de Estratégias Ecológicas Vegetais” agrupam as espécies em categorias ao longo do espectro de seus traços funcionais. Quando dois ou mais traços funcionais importantes estão correlacionados entre espécies coocorrentes, eles definem uma dimensão estratégica. Há quatro principais dimensões de estratégias ecológicas para estabelecer relações entre os traços: altura máxima da planta, tamanho dos ramos e das folhas, estrutura e fisiologia foliar, e produção de sementes. Os traços que podem definir essas dimensões são: altura máxima da planta, densidade da madeira, área foliar, área foliar específica, tamanho do fruto, e tamanho da semente. Nessa dissertação, apresentamos os resultados em um único capítulo, escrito em inglês. Coletamos os seis traços para 28 espécies arbustivo-arbóreas no Parque Estadual de Vaçununga, sudeste do Brasil. Analisamos as relações entre esses traços para espécies lenhosas de cerrado e comparamos nossos resultados com os encontrados para florestas tropicais. Encontramos duas correlações significativas: entre tamanho do fruto e tamanho da semente e entre tamanho do fruto e área foliar. Identificamos, também, duas estratégias ecológicas: espécies com baixas áreas foliares específicas, e espécies altas áreas foliares específicas. Espécies lenhosas de cerrado e florestas parecem ter estratégia ecológicas distintas, provavelmente pelas diferentes pressões a que estão submetidos.

Palavras-chave: estratégias ecológicas, traços funcionais, savana, modelo de equações estruturais.

Abstract

The so-called "Plant Ecology Strategy Scheme" groups species into categories along the spectrum of their functional traits. When two or more important functional traits are correlated between concurrent species, they define a strategic dimension. There are four main dimensions of ecological strategies for establishing the relationships among functional traits of plants: maximum plant height, size of branches and leaves, leaf structure and physiology, and seed production. Traits that may define these dimensions include: maximum plant height, wood density, leaf area, specific leaf area, fruit size, and seed size. We analysed the relationships among the traits in cerrado woody species and compared the results with those found in tropical forests. In this dissertation, we presented our results in a single chapter, written in english. We measured these traits from 28 woody species at the Vaçununga State Park, southeastern Brazil. We found two significant relationships: between fruit size and seed size and between fruit size and leaf area. We also identified two ecological strategies: species with high specific leaf area and species with low specific leaf area. Cerrado and forest woody species seem to have distinct ecological strategies, probably due to the different environmental pressures to which they are submitted.

Key-words: ecological strategy, functional trait, savanna, structural equation model.

Introdução Geral

Um dos principais desafios da Ecologia é se distanciar de descrições de estudos de caso e chegar a princípios e modelos mais gerais (Duckworth et al. 2000). Desse modo, começaram a ser propostos, no século XIX, sistemas de classificação de vegetação, que agrupavam as espécies de acordo com determinados atributos. Humboldt, em 1807, propôs o agrupamento das plantas tendo como base a fisionomia. Sem muitos esforços para tal classificação, a fisionomia teria a forma predominante da vegetação, podendo ser um cacto ou uma bananeira (Cain 1950). Em 1838, Grisebach, adotou a ideia de Humboldt e acrescentou que o clima influenciaria na vegetação, criando assim, outro sistema de classificação (Cain 1950).

Dentre outros sistemas definidos na época, o de Raunkiaer (1934) foi o mais abrangente. Ele revisou os modelos propostos e estabeleceu critérios, que, segundo ele, estavam faltando para avaliar a influência do clima sobre as formas de vida. Sendo assim, recomendou três regras para selecionar as características que seriam utilizadas no agrupamento de espécies: os atributos deveriam ser estruturais, o que representaria uma adaptação morfológica; os atributos deveriam ser óbvios, de modo a garantir que a forma de vida pudesse ser facilmente reconhecida e as formas de vida deveriam ser de natureza homogênea, representando um único aspecto a ser considerado (Raunkiaer 1934). Assim, as formas de vida eram delimitadas pelo grau de proteção das gemas vegetativas frente às estações adversas (Raunkiaer 1934).

A partir dessa perspectiva, Grime (1979) e Tilman (1980) introduziram a ideia

do desempenho funcional das plantas em resposta aos diferentes gradientes ambientais, ou seja, o conceito de estratégias ecológicas ganhou destaque (Grace 1991). O triângulo de Grime agrupa as espécies em três estratégias distintas: plantas que habitam locais com baixa fertilidade, pouca perturbação ambiental e têm desenvolvimento lento são chamadas de plantas "tolerantes ao estresse"; as que habitam locais com alta fertilidade, ainda com pouca perturbação, e que tinham altas taxas de crescimento são as espécies "competidoras" e as espécies que vivem em ambientes com alta fertilidade, toleravam alta perturbação e têm altas taxas de crescimento eram as espécies "ruderais" (Craine 2005). Tilman, por sua vez, apresentou um modelo mecanicista que prevê o sucesso competitivo das espécies em relação aos recursos disponíveis e às taxas de absorção dos mesmos (Grace 1991).

Posteriormente, Wright et al. (2004) propuseram o "espectro de economia foliar", que compreende espécies com alto e baixo retorno no investimento em nutrientes e em massa seca. Mais recentemente, Díaz et al. (2016) analisaram variações em seis traços funcionais críticos ao crescimento, sobrevivência e reprodução de plantas amostradas em todo o mundo e verificaram que a ocupação desse espaço multidimensional está fortemente concentrada, indicando coordenação e comprometimentos. A maior parte da variação se concentrou em duas dimensões, uma refletindo o tamanho e a outra representando o espectro econômico foliar (Díaz et al. 2016).

Com isso, a classificação das espécies por meio da funcionalidade dos seus traços se mostra bastante importante. Os traços funcionais, portanto, são características morfológicas, fisiológicas e fenológicas que envolvem aspectos-chave da história de vida dos organismos e refletem as interações destes com o

ambiente (Violle et al. 2007). Sendo assim, as estratégias ecológicas podem ser pensadas como um balanço entre os traços funcionais e o ambiente, gerado por restrições físicas, fisiológicas ou ontológicas ou por seleção natural favorecendo certas combinações de atributos (Wright et al. 2007). As plantas, ainda, devem possuir estratégias relacionadas a três principais fatores: capacidade de tolerância às condições em que se encontram; capacidade de aquisição de nutrientes, água e luz; e capacidade de resposta a distúrbios (Wilson et al. 1999).

Nesse contexto, Wright et al. (2007) utilizaram seis traços funcionais comumente utilizados na literatura para testar as correlações entre os traços funcionais das espécies de florestas tropicais: altura máxima da planta, densidade da madeira, área foliar, área foliar específica, tamanho do fruto, e tamanho da semente. Esses traços são importantes pois englobam as quatro principais dimensões de estratégias que já foram identificadas: altura máxima da planta, tamanho dos ramos e das folhas, estrutura e fisiologia foliar, e produção de sementes (Westoby et al. 2002).

A partir desse trabalho, procuramos investigar as estratégias ecológicas das espécies arbustivo-arbóreas do cerrado, levando em consideração os mesmos seis traços funcionais e as mesmas relações propostas para as florestas tropicais. Esperávamos que resultados poderiam diferenciar-se, em algum grau, devido às particularidades ambientais que o cerrado apresenta como solos pobres em nutrientes e com altos níveis de alumínio, regime de fogo e sazonalidade. No capítulo I dessa dissertação apresentaremos, pois, os resultados encontrados para o cerrado e as possíveis discussões.

Referências Bibliográficas

- Cain SA. 1950. Lifeforms and phytoclimate. *Botanical Review* 16: 1-32.
- Craine JM. 2005. Reconciling plant strategy theories of Grime and Tilman. *Journal of Ecology*, 93, 1041–1052.
- Díaz S, Kattge J, Cornelissen JH, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Gillison AN, Zanne AE, Chave Z, Wright SJ, Sheremet'ev SN, Jactel H, Baraloto C, Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A, Falczuk V, Rüger N, Mahecha MD & Gorné LD. 2016. The global spectrum of plant form and function. *Nature* 529: 167-171.
- Duckworth JC, Kent M & Ramsay PM. 2000. Plant functional types: an alternative to taxonomic plant community description in biogeography? *Progress in Physical Geography* 24: 515-542.
- Grace JB. 1991. A clarification of the debate between Grime and Tilman. *Functional Ecology* 5:583–587.
- Raunkiaer C. 1934. *The life forms of plants and statistical plant geography*. Clarendon, Oxford.
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I & Garnier E. 2007. Let the concept of trait be functional! *Oikos* 116:882–892.
- Westoby M, Falster DS, Moles AT, Vesk PA & Wright IJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology, Evolution and Systematics* 33:25-59.
- Wilson PJ, Thompson K & Hodgson JG. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* 143:155–

162.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R. 2004. The worldwide leaf economics spectrum. *Nature* 428:821-827.

Wright IJ, Ackerly DD, Bongers F, Harms KE, Ibarra-Manriquez G, Martínez-Ramos M, Mazer SJ, Müller-Landau HC, Paz H, Pitman NCA, Poorter L, Silman MR, Vriesendorp CF, Webb CO, Westoby M & Wright SJ. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99:1003-1015.

**Relationships among ecologically important traits in woody species of the
Brazilian cerrado**

Abstract

The so-called "Plant Ecology Strategy Scheme" groups species into categories along the spectrum of their functional traits. When two or more important functional traits are correlated between concurrent species, they define a strategic dimension. There are four main dimensions of ecological strategies for establishing the relationships among functional traits of plants: maximum plant height, size of branches and leaves, leaf structure and physiology, and seed production. Traits that may define these dimensions include: maximum plant height, wood density, leaf area, specific leaf area, fruit size, and seed size. We analysed the relationships among the traits in cerrado woody species and compared the results with those found in tropical forests. We measured these traits from 28 woody species at the Vaçununga State Park, southeastern Brazil. By using Pearson correlation analyses and structural equation modelling, we found two significant relationships: between fruit size and seed size and between fruit size and leaf area. Based on the traits, we identified two ecological strategies: (1) short species with high specific leaf area and small leaves, fruits, and seeds; (2) tall species with low specific leaf area and large leaves, fruits, and seeds. Cerrado and forest woody species seem to have distinct ecological strategies, probably due to the different environmental pressures to which they are submitted.

Key-words: ecological strategy, functional trait, savanna, structural equation model.

Introduction

Ecological strategies can improve our ability to predict the functioning of communities, the impacts of environmental changes, and the provision of environmental services (Sudding & Golstein 2008, Lavorel et al. 2011). Ecological strategies can be thought of as a trade-off between the functional traits of an individual plant and the environmental factors, generated by physical, physiological, or ontological constraints. Natural selection has an important role on the ecological strategies of a species, favouring certain combinations of attributes, that is, morphological, physiological, and phenological characteristics involving key aspects of life history and reflecting the interaction between the organism and the environment (Violle et al. 2007). Regardless of the environmental pressure, ecological strategies of terrestrial plants might ensure carbon gain and gene flow, allowing the endurance of a population (Westoby 1999, 2002).

The so-called "Plant Ecology Strategy Scheme" (Westoby 1998) groups species into categories along the spectrum of their functional traits. When two or more important functional traits are correlated between concurrent species, they define a strategic dimension in the range of traits (Westoby 1998). The position of a species along a certain strategic dimension is related to its optimum performance and competitive vigour (Westoby et al. 2002). Plant ecological strategies are generally related to three main factors: competitive ability and dominance, resource acquisition, and responsiveness to disturbances (Wilson et al. 1999). There are some relevant criteria for establishing the ecological relationships

between functional traits of plants and, to date, four main important dimensions of ecological strategies were identified: maximum plant height, size of branches and leaves, leaf structure and physiology, and seed production (Westoby et al. 2002, Wright et al. 2007). These dimensions can be used to differentiate species strategies consistently, even taking into account variations due to plasticity, acclimatisation, or ecotypes (Wright et al. 2007). Thus, although there may be disagreement about which functional traits better define plant ecological strategies, some of these traits have been commonly used in studies carried out in different vegetation types around the world: maximum plant height, wood density, leaf area, specific leaf area, fruit size, and seed size (Wright et al. 2007). Furthermore, these six traits include the four dimensions mentioned, allowing the assessment of the ecological strategies of plants in a given community.

Plant height represents the first dimension of plant strategy and can be considered as a strategy dimension on its own (Wright et al. 2007). This trait is associated with competition, plant fecundity, and interval for growth between disturbances (Cornelissen 2003). Wood density represents the second dimension and is an important trait used for estimating carbon storage and fluxes (Nelson et al. 1999). Leaf area and specific leaf area, in turn, describe the third dimension. Leaf area has important consequences for leaf energy and water. Interspecific variation in leaf area is related to environmental stress, climatic variation, geology, and altitude or latitude (Cornelissen 2003). Specific leaf area is related to potential relative growth and mass-based photosynthetic rates (Cornelissen 2003). Finally, fruit and seed sizes are related to seed production, the fourth dimension. Seed production is a key ecological attribute, because it influences dispersal and survival rates, contributing to natural regeneration (Leishman et al. 2000).

Although plant ecological strategies have been intensely studied in tropical forests (Wright et al. 2007), there are few studies in Neotropical savannas. The Brazilian cerrado covered originally about two million square kilometers, especially in the Central Plateau (Gottsberger & Silberbauer-Gottsberger 2006). The cerrado presents a wide physiognomic range, going from grassland to woodland, but most of its physiognomies lies within the definition of tropical savanna (Coutinho 1978). Given the peculiar environmental pressures that savannas, including the savanna physiognomies of the cerrado, are subjected to, such as fire regime, strong seasonality, nutrient-impoverished soils, and soil aluminium toxicity (Coutinho 1978, Gottsberger & Silberbauer-Gottsberger 2006), it is possible that the relationships among traits that have been found in forests do not exist in savannas and that the ecological strategies that are viable in forests are not similarly viable in savannas.

For tropical forests, Wright et al. (2007) found strong and weak correlations among the same six functional traits. The correlations are positive between height and fruit size, between height and seed size, between wood density and seed size, between leaf area and fruit size, and between fruit size and seed size. The correlations are negative between height and specific leaf area, between wood density and leaf area, between specific leaf area and seed size, and between specific leaf area and fruit size (Wright et al. 2007). Thus, we aimed to test whether the same correlations were valid for cerrado species or, in other words, to each extent the strategies of cerrado species corresponded to those of the tropical forest species. More specifically, we aimed to answer the following questions: Are there positive relationships between height and fruit size, between height and seed size, between wood density and seed size, between leaf area and fruit size, and between

fruit size and seed size? Are there negative relationships between height and specific leaf area, between wood density and leaf area, between specific leaf area and fruit size, and between specific leaf area and seed size? Are there causal relationships among these variables? How many ecological strategies can be identified for woody species in a cerrado site when accounting for these six important traits?

Methods

We measured trait data for woody species at the Vaçununga State Park, a protected area managed by the São Paulo Forestry Institute, located in Santa Rita do Passa Quatro municipality, southeastern Brazil (21°36'-21°43'S and 47°35'-47°37'W; Colli et al. 2004). Climate is classified as Cwa according to Köppen (1931), with dry winter (May to September) and wet summer (October to April). Soils are mostly Neosols and Latosols, according to the Brazilian classification (Embrapa 2006), or Entisols and Oxisols, according to the USDA classification (Soil Survey Staff 2014). The park comprises 2,045.06 ha, divided into six fragments: Capão da Várzea, Capetinga Oeste, Praxedes, Maravilha, Capetinga Leste, and Pé-de-Gigante. The first five fragments comprise 832.14 ha and are predominantly covered by seasonal semideciduous forest. The last fragment comprises 1,212.02 ha and is predominantly covered by cerrado, from open to closed physiognomies (Ruggiero et al. 2002).

In the Pé-de-Gigante fragment, we placed 68 plots of 25 m² spread through patches available to researches, in which we sampled all woody individuals with stem diameter at soil level ≥ 3 cm (SMA 1997). We recorded 1,036 individuals and

identified them as belonging to 84 species. We used the list of individuals per species to sample 5-10 individuals of each species, from which we measured the following functional traits: maximum plant height, wood density, leaf area, and specific leaf area. We also measured fruit size and seed size, but not necessarily from the selected individuals, since the availability of fruits was a determinant factor. In this case, we collected fruits from at least five individuals per species from the plots or nearby.

To measure each trait, except fruit size, we used the available protocol for standardised measurements of plant functional traits (Pérez-Harguindeguy et al. 2013). To measure plant maximum height, we used a Hastings-M 50 telescopic ruler. To measure wood density, we cut one branch of approximately 10 cm length, and kept it in a plastic bag in an insulated box until measurement. At the laboratory, we removed the outer bark and any other attached material with a knife and measured the diameter of the branch with a digital caliper. We used the diameter and the length of the branch to calculate the volume of the cylinder. Then, we oven-dried the branch at 80°C for 48 h and weighed their dry mass in an analytical balance to 0.001 g. We divided the dry mass by the volume and obtained wood density, expressed in g cm^{-3} . To calculate leaf area and leaf specific area, we collected five leaves, those that were more exposed to the sun and without herbivory damage, of each selected individual and kept them in plastic bags in an insulated box until measurement. At the laboratory, we scanned the fresh leaves and calculated leaf area, expressed in cm^2 , by using the ImageJ software (Abramoff et al. 2004). Then, we oven-dried the leaves at 80°C for 72 h and weighed them in an analytical balance to 0.001 g. By dividing leaf area by leaf dry mass, we obtained specific leaf area, expressed in $\text{mm}^2 \text{mg}^{-1}$. We collected fruits and kept them in

plastic bags in an insulated box until measurement. At the laboratory, we measured their volume using the water-displacement method. We obtained fruit volume in ml and transformed it to mm^3 . Then, we removed the seeds from the fruits and, to measure seed size, we oven-dried them at 80°C for 48 h and weighed them by using an analytical balance to 0.001 g.

After having the measurements of each individual, we obtained the average values for each trait and each species, which we used in the subsequent analyses. We log-transformed leaf area, specific leaf area, fruit size, and seed size to achieve normality. To answer the first two questions, we used Pearson correlation analyses (Zar 2010). To answer the third question, we postulated a structural equation model (Figure 1), which considered expected causal relationships among traits (Wright et al. 2007). We conducted several tests to check whether our data followed the requirements of the model, that is, collinearity among the variables, multinormality, and presence of outliers. After that, we found the covariance matrix and assessed model fit (Shipley 2000). We removed non-significant paths of the original model and tested whether model fit was improved (Shipley 2000). To answer the fourth question, we used a non-hierarchical cluster analysis (K-means; Legendre and Legendre 2012), looking for the best partition from two to five groups, which were sufficient to divide the species, and 1,000 iterations. By using Principal Component Analysis (Jongman et al. 1995), we extracted axis scores from the first two components. We carried out our analyses in the R environment (R Core Team 2015), using the “lavaan” package (Rosseel 2012).

Results

Of the 84 species initially sampled, we collected data of all six functional traits for 28 of them (Table 1). The remaining species did not fruit during our fieldwork period. Fruit size and seed size were positively correlated ($R = 0.721$, $P < 0.001$), as well as fruit size and leaf area ($R = 0.494$, $P = 0.008$). The relationships between the other functional traits were not significant ($P > 0.05$) and, thus, considered independent (Figure 2).

The structural equation model we postulated to assess the causal relationships among the functional traits was statistically plausible ($P = 0.465$; Figure 3). However, the only two significant paths within the model were the same that were significantly correlated as independent pairs. The removal of non-significant paths, though, did not improve model fit ($P = 0.659$).

When looking for strategies among the species based on the six functional traits, we identified two groups and, therefore, two ecological strategies: (1) short species with high specific leaf area and small leaves, fruits, and seeds; and (2) tall species with low specific leaf area and large leaves, fruits, and seeds (Figure 4). The first axis of the principal component analysis was positively related with specific leaf area and negatively related with height, leaf area, fruit size, and seed size (Figure 4). The second axis of the principal component analyses was positively related with leaf area and negatively related with height, wood density, fruit size, and seed size (Figure 4).

Discussion

Contrary to what was found in tropical forest, five strong correlations among the six functional traits (Wright et al. 2007), we found only two significant

correlations: fruit size was positively correlated to both leaf area and seed size. The correlation between fruit size and leaf area followed the leaf-twig size relationship, also known as the “Corner’s Rule” (Corner 1949), which postulates a correspondence between the size of axes (stem and branches) and their appendages (leaves, flowers, and fruits). This rule describes the tendency for species with thick twigs to have large appendages and wide branching, since, to support these appendages, plants should invest in vascular, meristematic, and biomechanical demands (Cornelissen 1998). The correlation between fruit and seed size is related to seed production, which can also determine the number of seeds per unit of reproductive effort. Small fruits necessarily have small seeds, but large fruits can have either small or large seeds (Wright et al. 2007). In the cerrado, species with large fruits seem to have large seeds, like *Hymenaea stigonocarpa*, and, thus, the positive correlation between fruit and seed size. Larger seeds have more advantages than smaller ones, because they have a higher probability of establishing a seedling (Moles & Westoby 2006), which may be a competitive advantage in the poor soil of the cerrado (Gottsberger & Silberbauer-Gottsberger 2006).

Height, wood density, and specific leaf area were not correlated with any other trait and, thus, were independent. Height, for instance, exerts multiple functions for the plant, and taller species have advantages over smaller ones, because they can intercept more light and avoid fire reaching green leaves and meristems in canopy (Cornelissen 2003), important adaptations for species survival and persistence in the cerrado (Hoffmann et al. 2003). Taller plants must also invest in stems to support the structure and the maintenance of the vascular tissue (Westoby et al. 2002). Hence, the multiple functions and trade-off associated to

height make it a plastic trait, so that plant maximum height can vary in four orders of magnitude, going from centimeters to meters (Wright et al. 2007). Similarly to height, wood density is a dimension on its own, independent of other traits (Westoby et al. 2002). Species with denser wood tend to be more resistant to pathogens and mechanical damage attacks (Turner 2001), to have lower stem diameter (Enquist et al. 1999), to store less water in the wood (Stratton et al. 2000), to be more resistant to xylem cavitation (Hacke et al. 2005), and to have leaves with larger daily fluctuations in water potential (Bucci et al. 2004).

Plants are positioned along a “leaf economic spectrum” that describes a single axis of leaf trait variation and the universal tendency for species to have a quick or slow return of nutrient and dry mass invested in leaves (Wright et al. 2004). One of the six functional traits that describe the leaf spectrum is specific leaf area. Specific leaf area was an important predictor of plant strategy among cerrado woody species, which may be divided into two groups: high or low specific leaf area. Species with high specific leaf area have high concentration of nitrogen and phosphorus in leaves and high photosynthetic rates, being extremely efficient in rapid growth (Fonseca et al. 2000). Hence, species with higher specific leaf area tend to prevail in resource-rich environments, where plants can be more productive (Wilson et al. 1999). Conversely, species with low specific leaf areas tend to have lower nutrient content and photosynthetic rates, prevailing in low-resource environments, where plants are constrained and leaves are more expensive (Fonseca et al. 2000). Specific leaf area and soil-nutrient status are tightly correlated (Ordoñez et al. 2009, Wright et al. 2001). This relationship holds true for our study site (Miatto et al. 2016). Thus, it seems that species with high or low specific leaf area had their strategy finely adjusted to soil nutrient availability.

The differences between cerrado and forest species regarding relationships among traits may be due to the fact that the former tend to be associated with nutrient-poor and acid soils, with high concentrations of aluminium, subjected to fire regime, and strong seasonality (Coutinho 1978, Gottsberger & Silberbauer-Gottsberger 2006). The environment can strongly influence plant ecological strategies, and each species can develop its way to optimise establishment, survival, growth, and reproduction. Our results allowed a better understanding of the adaptations of cerrado woody plants to the environmental restrictions they have to cope with, such as fire regime, drought, low-nutrient soils, and aluminium toxicity. Pairwise correlations and the structural equation model indicated that ecological dimensions in cerrado woody plants are not strongly related to those of tropical forest ones, but they do exist. Maximum plant height, size of branches and leaves, leaf structure and physiology were shown to be indeed different dimensions, independent among themselves in cerrado woody species. Apparently, specific leaf area is, per se, a good predictor of plant strategies in cerrado woody species. Adaptation to soil at a fine scale is likely determining species differentiation in the cerrado. Nevertheless, functional traits in cerrado woody species showed to be distinctly adjusted, with a consequence for plant strategies.

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References

- Abramoff MD, Magalhães PJ & Ram SJ. 2004. Image processing with ImageJ. *Biophotonics International* 11:36-42.
- Bucci SJ, Goldstein G, Meinzer FC, Scholz FG, Franco AC & Bustamante M. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiology* 24:891-899.
- Colli AMT, Salino A, Souza SA, Lucca ALT & Silva RT. 2004. Pteridófitas do Parque Estadual do Vassununga, Santa Rita do Passa Quatro (SP), Brasil. Glebas Capetinga Leste e Capetinga Oeste. *Revista do Instituto Florestal* 16:25-30.
- Cornelissen JHC, Castro-Diez P, Carnelli AL. 1998. Variation in relative growth rate among woody species. In: Lambers H, Poorter H & Vuuren MMI. *Physiological mechanisms and ecological consequences*. Backhuys, Leiden, pp. 363-392.
- Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, Heijgen MGA, Pausas JG & Poorter H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335-80.
- Corner E. 1949. The Durian theory or the origin of the modern tree. *Annals of*

- Botany 13:368-414.
- Coutinho LM. 1978. O conceito de cerrado. *Revista Brasileira de Botânica* 1:17-23.
- Embrapa. 2006. Sistema brasileiro de classificação de solos. Embrapa, Rio de Janeiro.
- Enquist BJ, West GB, Charnov EL & Brown JH. 1999. Allometric scaling of production and life-history variation in vascular plants. *Nature* 401: 907-911.
- Fonseca CR, Overton JM, Collins B & Westoby M. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* 88: 964-77.
- Gottsberger G & Silberbauer-Gottsberger I. 2006. Life in the cerrado: a South American tropical seasonal vegetation. Vol. 1. Origin, structure, dynamics and plant use. Reta, Ulm.
- Hacke UG, Sperry JS & Pittermann J. 2005. Efficiency versus safety tradeoffs for water conduction in angiosperm vessels versus gymnosperm tracheids. In: Holbrook NM & Zwieniecki MA. *Vascular transport in plants*. Elsevier, Oxford, pp. 333-353.
- Hoffmann WA & Solbrig OT. 2003. The role of topkill in the differential response of savanna woody plants to fire. *Forest Ecology and Management* 180: 273-286.
- Jongman RHG, Braak CJF, Tongeren OFR (1995) *Data analysis in community and landscape ecology*. Cambridge University, Cambridge
- Köppen W. 1931. *Grundriss der Klimakunde*. Gruyter, Berlin.
- Lavorel S, Grigulis K, Lamarque P, Colace MP, Garden D, Girel J, Pellet G & Douzet R. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology* 99: 135-147.
- Legendre P & Legendre I. 1998. *Numerical Ecology*. Elsevier, New York.
- Leishman MR, Wright IJ, Moles AT & Westoby M. 2000. The evolutionary ecology of

- seed size. In: Fenner M. *Seeds: the ecology of regeneration in plant communities*. CAB International, Wallingford, pp. 31–57.
- Miatto RC, Wright IJ & Batalha MA. 2016. Relationships between soil nutrient status and nutrient-related leaf traits in Brazilian cerrado and seasonal forest communities. *Plant and Soil*: in press.
- Moles AT & Westoby M. 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113: 91–105.
- Nelson BW, Mesquita R, Pereira JLG, Souza SGA, Batista GA & Couto LB. 1999. Allometric regressions for improved estimate of secondary forest biomass in the Central Amazon. *Forest Ecology and Management* 117: 149-167.
- Ordoñez JC, Bodegom PM, Witte JPM, Wright IJ, Reich PB & Aerts R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography* 18: 137-149.
- Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, Vos AC, Buchmann N, Funes G, Quétier F, Hodgson CJG, Thompson K, Morgan HD, Steege H, Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S & Cornelissen JHC. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167-234.
- R Core Team. 2015. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL: <https://www.r-project.org>.
- Rosseel Y. 2012. Lavaan: an R package for structural equation modeling. *Journal of Statistical Software* 48: 1-36.
- Ruggiero PGC, Batalha MA, Pivello VR & Meirelles ST. 2002. Soil-vegetation

- relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeastern Brazil. *Plant Ecology* 160: 1-16.
- Soil Survey Staff. 2014. Keys to soil taxonomy. Department of Agriculture, Washington.
- Shipley B. 2000. Cause and correlation in biology: a user's guide to path analysis, structural equations, and causal inference. Cambridge University, Cambridge.
- SMA. Secretaria de Estado do Meio Ambiente. 1997. Cerrado: bases para conservação e uso sustentável das áreas de cerrado do estado de São Paulo. SMA, São Paulo.
- Stratton L, Goldstein G & Meinzer FC. 2000. Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant Cell and Environment* 23: 99-106.
- Sudding, KN & Goldstein, LJ. 2008. Testing the Holy Grail framework: using functional traits to predict ecosystem change. *New Phytologist* 180: 559-562.
- Turner IM. 2001. The ecology of trees in the tropical rain forest. Cambridge University, Cambridge.
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I & Garnier E. 2007. Let the concept of trait be functional! *Oikos* 116: 882-892.
- Weber WA. 1982. Mnemonic three-letter acronyms for the families of vascular plants: a device for more effective herbarium curation. *Taxon* 31: 74-88.
- Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199: 213-227.
- Westoby M. 1999. Generalization in functional plant ecology: the species sampling problem, plant ecology strategies schemes, and phylogeny. In: Pugnaire FI, & Valladares F. *Handbook of functional plant ecology*. Marcel Dekker, New York,

pp. 847-872.

Westoby M, Falster DS, Moles AT, Vesk PA & Wright IJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology, Evolution and Systematics* 33: 125-159.

Wilson PJ, Thompson K & Hodgson JG. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* 143: 155-162.

Wright IJ, Reich PB & Westoby M. 2001. Strategy-shifts in leaf physiology, structure and nutrient content between species of high and low rainfall, and high and low nutrient habitats. *Functional Ecology* 15: 423-434.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ & Villar R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821-827.

Wright IJ, Ackerly DD, Bongers F, Harms KE, Ibarra-Manriquez G, Martínez-Ramos M, Mazer SJ, Müller-Landau HC, Paz H, Pitman NCA, Poorter L, Silman MR, Vriesendorp CF, Webb CO, Westoby M & Wright SJ. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99: 1003-1015.

Zar JH. 2010. *Biostatistical analysis*. Pearson Prentice-Hall, Upper Saddle River.

Table 1 – Average values of six functional traits measured in woody species sampled at the cerrado vegetation in the Pé-de-Gigante Reserve, Vaçununga State Park, Santa Rita do Passa Quatro, southeastern Brazil (mean). Legend: HEI = plant maximum height (m), WDN = wood density (g cm^{-3}), LAR = leaf area (cm^2), SLA = specific leaf area ($\text{mm}^2 \text{mg}^{-1}$), FSZ = fruit size (mm^2), and SSZ = seed size (g). Family names abbreviated according to Weber (1982).

| Species | Family | HEI | WDN | LAR | SLA | FSZ | SSZ |
|--|--------|-----|-----|-----|------|--------|------|
| <i>Anadenanthera peregrina</i> (Benth.) Speg. | FAB | 7.3 | 0.5 | 116 | 7.0 | 6370 | 0.01 |
| <i>Bowdichia virgilioides</i> Kunth | FAB | 5.4 | 0.6 | 84 | 8.9 | 778 | 0.02 |
| <i>Byrsonima coccolobifolia</i> Kunth | MLP | 3.8 | 0.5 | 65 | 16.0 | 250 | 0.06 |
| <i>Caryocar brasiliense</i> A.St.-Hil. | CCR | 5.7 | 0.4 | 297 | 8.1 | 50290 | 0.50 |
| <i>Cordeira sessilis</i> K. Schum. | RUB | 1.9 | 0.6 | 38 | 15.7 | 6650 | 0.20 |
| <i>Couepia grandiflora</i> (Mart. & Zucc.) Hook.f. | CHB | 4.2 | 0.4 | 42 | 7.5 | 667 | 0.01 |
| <i>Diptychandra aurantiaca</i> Tul. | FAB | 4.1 | 0.5 | 58 | 13.3 | 2139 | 0.10 |
| <i>Duguetia furfuracea</i> (A.St.-Hil.) Saff. | ANN | 1.9 | 0.5 | 29 | 6.9 | 22500 | 0.07 |
| <i>Eugenia puniceifolia</i> (Kunth) DC. | MRT | 3.4 | 0.5 | 9 | 15.4 | 273 | 0.04 |
| <i>Hymenaea stigonocarpa</i> Hayne | FAB | 4.9 | 0.4 | 113 | 8.3 | 123560 | 2.30 |
| <i>Miconia albicans</i> (Sw.) Steud. | MLS | 2.1 | 0.6 | 34 | 8.0 | 176 | 0.02 |
| <i>Miconia rubiginosa</i> (Bonpl.) DC. | MLS | 2.3 | 0.6 | 30 | 7.9 | 224 | 0.02 |
| <i>Myrcia guianensis</i> (Aubl.) DC. | MRT | 2.5 | 0.7 | 12 | 9.3 | 208 | 0.02 |
| <i>Neea theifera</i> Oerst. | NYC | 2.8 | 0.3 | 40 | 18.4 | 380 | 0.07 |
| <i>Ocotea corymbosa</i> (Meisn.) Mez | LAU | 8.5 | 0.4 | 19 | 12.6 | 190 | 0.04 |
| <i>Ouratea spectabilis</i> (Mart. ex Engl.) Engl. | OCH | 4.9 | 0.4 | 34 | 6.8 | 698 | 0.08 |
| <i>Palicourea rigida</i> Kunth | RUB | 1.5 | 0.2 | 143 | 14.0 | 203 | 0.02 |
| <i>Pouteria ramiflora</i> (Mart.) Radlk. | SPT | 5.7 | 0.6 | 82 | 9.1 | 13600 | 0.70 |
| <i>Pouteria torta</i> (Mart.) Radlk. | SPT | 4.9 | 0.4 | 75 | 9.4 | 10945 | 0.40 |
| <i>Qualea dichotoma</i> (Mart.) Warm. ex Wille | VOC | 2.5 | 0.4 | 37 | 14.0 | 2154 | 0.01 |
| <i>Qualea grandiflora</i> Mart. | VOC | 6.4 | 0.5 | 58 | 9.7 | 6000 | 0.10 |
| <i>Qualea parviflora</i> Mart. | VOC | 3.6 | 0.6 | 29 | 14.1 | 2560 | 0.40 |
| <i>Schefflera vinosa</i> (Schltdl.) Frodin & Fiaschi | ARL | 2.1 | 0.4 | 111 | 7.6 | 234 | 0.01 |
| <i>Siparuna guianensis</i> Aubl. | SIP | 4.2 | 0.6 | 67 | 15.1 | 830 | 0.01 |
| <i>Vatairea macrocarpa</i> (Benth.) Ducke | FAB | 3.0 | 0.5 | 266 | 8.1 | 5560 | 0.40 |

| | | | | | | | |
|---------------------------------------|-----|-----|-----|----|------|------|------|
| <i>Vochysia cinnamomea</i> Pohl | VOC | 4.0 | 0.4 | 66 | 6.3 | 3304 | 0.05 |
| <i>Vochysia tucanorum</i> Mart. | VOC | 2.0 | 0.4 | 26 | 12.0 | 400 | 0.01 |
| <i>Xylopia aromatica</i> (Lam.) Mart. | ANN | 5.4 | 0.5 | 23 | 10.3 | 823 | 0.01 |

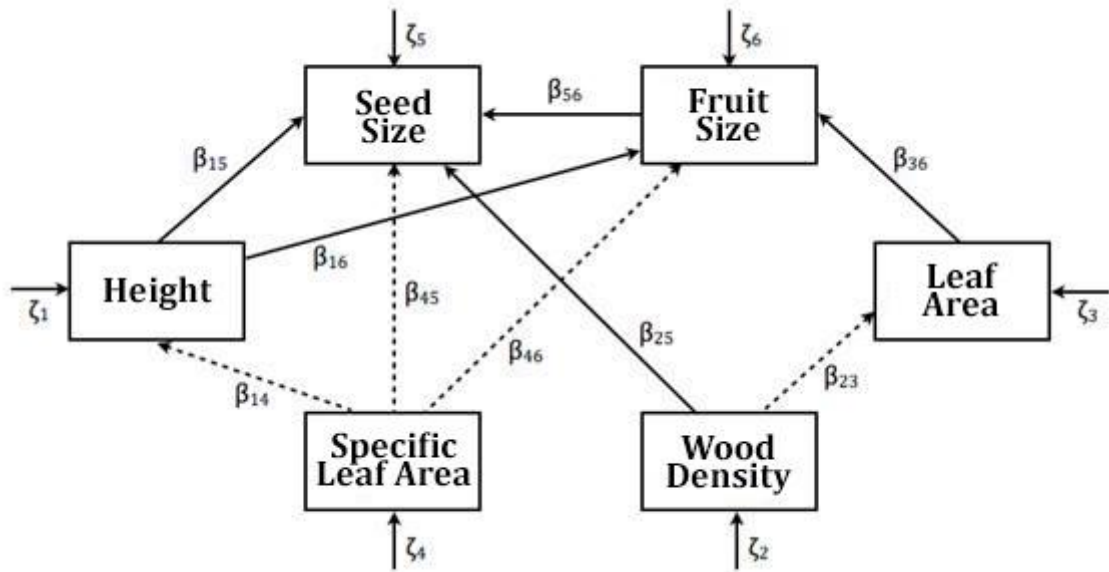


Figure 1. Postulated structural equation model of the relationships among the six functional traits. The direction of the relationship between any pair of traits is indicated by the type of the line connecting them: continuous lines indicate positive relationships and dotted lines, negative relationships. The symbol ζ indicates errors associated with each variable and the symbol β indicates the parameters that relate the variables.

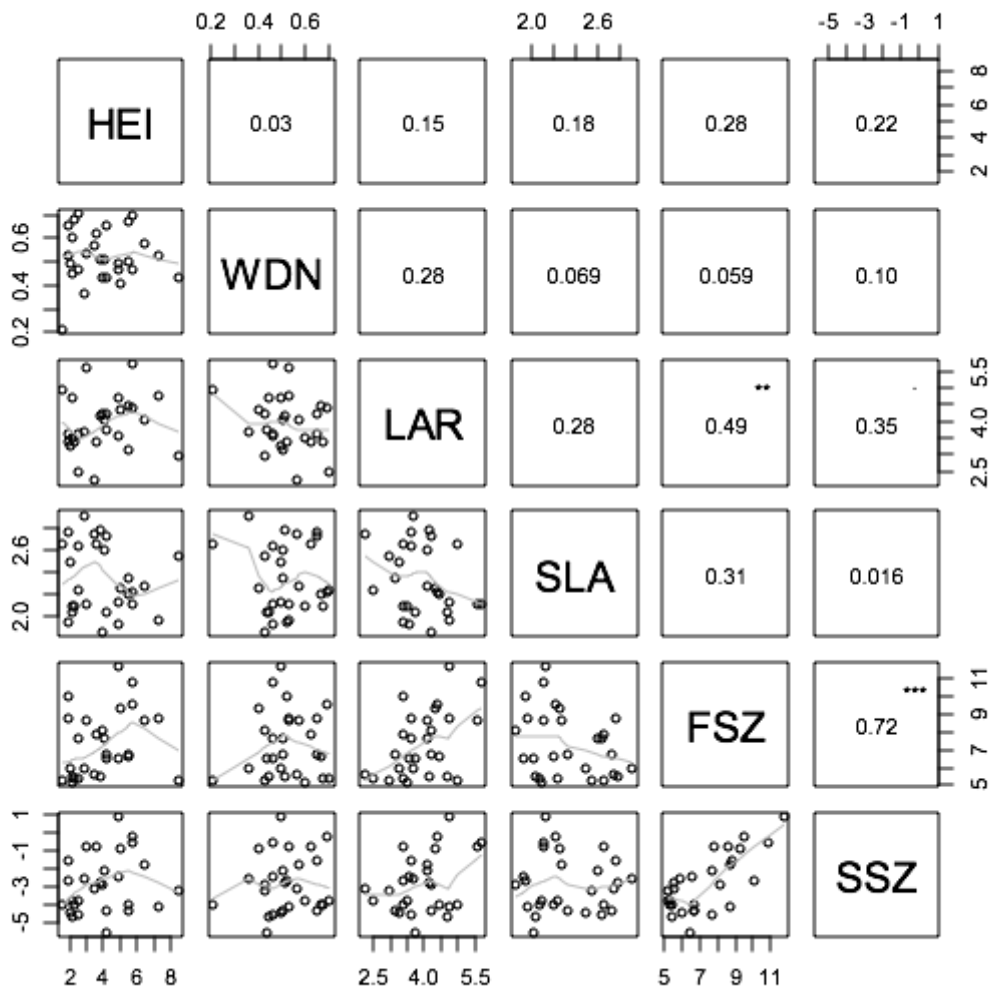


Figure 2. Pearson correlation coefficients among traits measured in 28 woody species sampled at the cerrado vegetation in the Pé-de-Gigante Reserve, Vaçununga State Park, Santa Rita do Passa Quatro, southeastern Brazil. Legend: HEI = plant maximum height, WDN = wood density, LAR = leaf area, SLA = specific leaf area, FSZ = fruit size, and SSZ = seed size. Tukey's running median smoothing line in grey. ** $P < 0.01$, *** $P < 0.001$. Leaf area, specific leaf area, fruit size, and seed size were log-transformed to achieve normality.

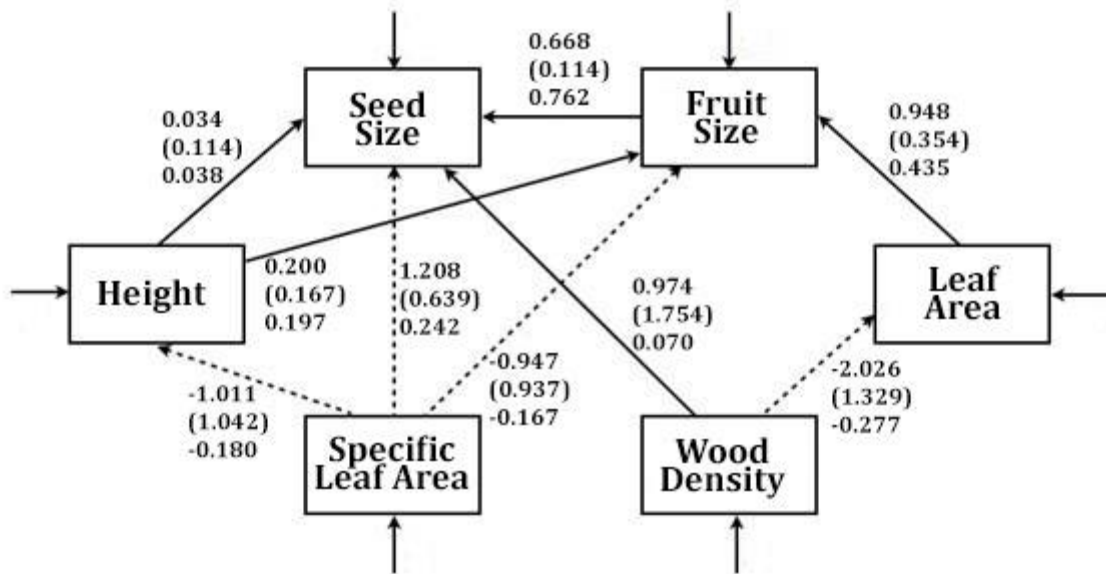


Figure 3. Structural equation model of the relationships among the six plant traits in 28 woody species sampled at the cerrado vegetation in the Pé-de-Gigante Reserve, Vaçununga State Park, Santa Rita do Passa Quatro, southeastern Brazil. The direction of the relationship between any pair of traits is indicated by the type of the line connecting them: continuous lines indicate positive relationships and dotted lines, negative relationships. Values are estimate, standard error, and total standard (completely standardised solution).

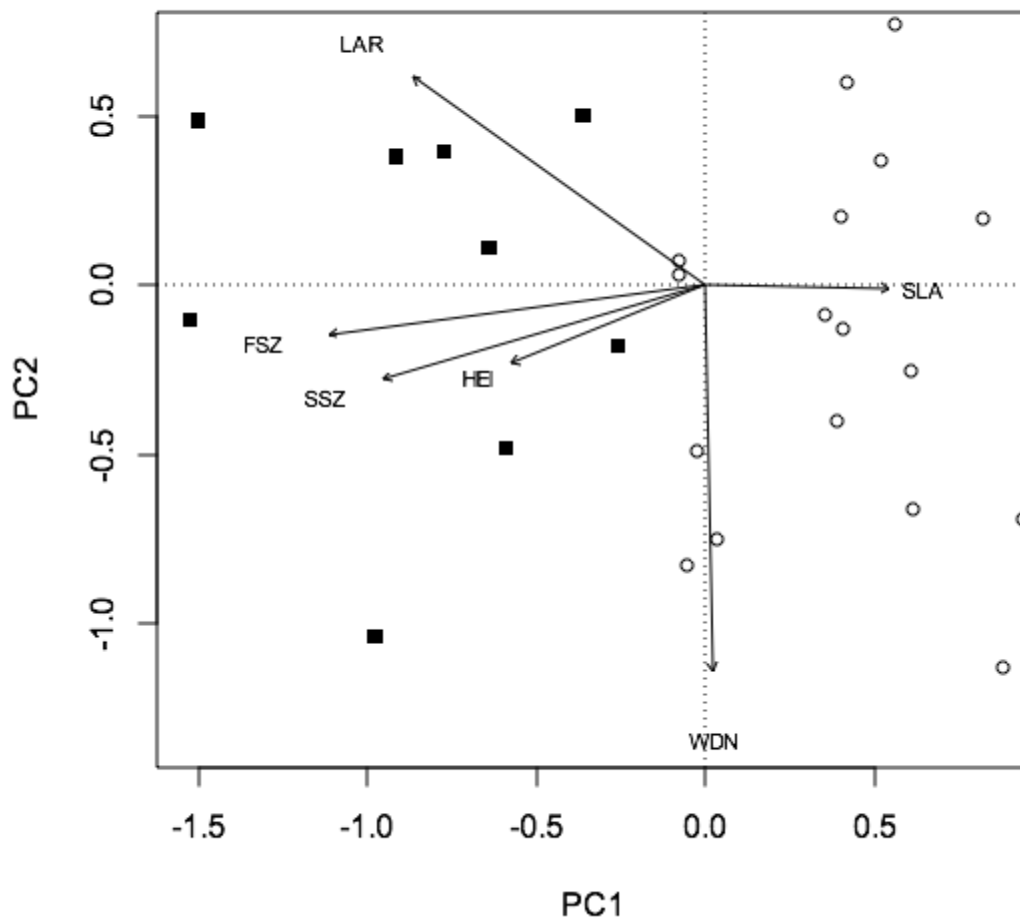


Figure 4. Biplot based on the non-hierarchical cluster analysis of 28 woody species sampled at the cerrado vegetation in the Pé-de-Gigante Reserve, Vaçununga State Park, Santa Rita do Passa Quatro, southeastern Brazil. The black squares and the white circle indicate the two ecological strategies. Legend: HEI = plant maximum height; LAR = leaf area; SLA = specific leaf area, FSZ = fruit size; SSZ = seed size; and WDN = wood density. The first axis of the principal component analysis (PC1) explained 37% of the variation in the traits and the second axis (PC2) explained 20%.

Considerações Finais

Propusemos quatro perguntas para o desenvolvimento deste trabalho, baseadas nos resultados encontrados para floresta tropical. Para as duas primeiras, encontramos apenas duas correlações estatisticamente significativas, que foram reforçadas com o modelo de equações estruturais.

Para a última questão, encontramos duas estratégias ecológicas, relacionadas principalmente com um traço funcional, a área foliar específica. As espécies foram divididas em dois grupos: espécies que possuem estratégias relacionadas com altas áreas foliares específicas e espécies que possuem estratégias com baixas áreas foliares específicas. Deste modo, nossos resultados foram diferentes dos encontrados para florestas tropicais e são justificados por meio das características peculiares que o cerrado apresenta. Três dimensões ecológicas foram consideradas independentes para as espécies de cerrado.

Frente ao histórico de classificação da vegetação, nosso trabalho contribui com informações que ainda não existiam na literatura e nos mostra que o modelo de estratégias de florestas tropicais não necessariamente podem ser aplicados para outros tipos vegetacionais, sobretudo, para os que apresentam estacionalidade ou algum outro efeito abiótico intenso, como é o caso do cerrado.