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LUAN CARLOS DA SILVA OLIVEIRA

CHANGES IN SECONDARY XYLEM TRAITS PARALLELED THE EVOLUTION OF ALLOCATION TO BARK IN SAVANNA SPECIES

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Orientador: Prof. Dr. Vinícius de Lima Dantas

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Luan Carlos da Silva Oliveira

CHANGES IN SECONDARY XYLEM TRAITS PARALLELED THE EVOLUTION OF ALLOCATION TO BARK IN SAVANNA SPECIES

Dissertação apresentada como requisito parcial para a obtenção do título de Mestre no Programa de Pós-graduação em Ecologia e Conservação de Recursos Naturais em Ecologia da Universidade Federal de Uberlândia pela seguinte banca examinadora:

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Prof. Dr. Vinícius de Lima Dantas - presidente
Universidade Federal de Uberlândia – UFU

Prof.ª Dra. Amélia Guimarães Carvalho
Universidade Federal de Uberlândia – UFU

Prof. Dr. Rafael Silva Oliveira
Universidade Estadual de Campinas - Unicamp

Á Gaia...

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Sumário

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RESUMO[1]

- A evolução das espécies de savana com casca espessa a partir de linhagens ancestrais de floresta permanece pouco estudada. Nós compilamos traços funcionais morfológicos e anatômicos de 91 espécies do Cerrado, tanto de formações savânicas, como florestais, incluindo tecidos como casca, xilema e de toda a planta para testar a hipótese de que a alocação em casca envolveu a evolução paralela de outros traços a nível morfológico e anatômico.
- Nós usamos Análise de Componentes Principais (PCA) e correlações pareadas entre traços para entender padrões de covariação entre os traços, e contrastamos os traços individuais e os eixos de PCA, interpretados como eixos de estratégia, entre espécies com ocorrência em diferentes habitats. Para tal, as espécies foram classificadas em espécies de savana, floresta e generalistas. Nós também testamos o sinal filogenético dos traços e dos eixos funcionais.
- Nós encontramos três eixos principais refletindo a variação nas estratégias funcionais. O primeiro expressou um trade-off entre resistência ao fogo (alocação em espessura de casca e maior segmentação hidráulica) e competição por luz (alocação em alburno e cerne), e segregou espécies de savana, intolerantes à sombra, das demais espécies; esse eixo mostrou forte sinal filogenético. O segundo eixo indicou um trade-off entre segurança e eficiência hidráulica filogeneticamente conservado, mas que não segregou espécies segundo o habitat de ocorrência. O terceiro refletiu um trade-off entre sobrevivência e crescimento em altura, foi filogeneticamente lábil e segregou espécies de savana, generalistas e de florestas, sendo as primeiras as mais conservadoras no uso de recursos e as últimas as mais aquisitivas.
- Nossos resultados suportam a hipótese de que a evolução do fogo entre espécies de savana envolveu mudanças em múltiplos traços do caule, dos ramos e da planta inteira, que covariaram ao longo de eixos de estratégia e diferenciaram espécies de floresta e savana.

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[1] *O texto foi preparado para submissão na revista "New Phytologist" e obedece às normas de formatação do periódico.*

Palavras-chave: Anatomia da madeira, casca, cerrado, floresta, estratégias dos traços, savana, traços hidráulicos, trade-off funcional.

ABSTRACT

- The evolution of thick-barked tropical savanna woody species from ancient forest lineages remains poorly understood. We compiled trait data for 91 Neotropical savanna, forest and generalist species, including bark, size, and xylem traits to test the hypothesis that bark production involved parallel evolution of morphologic- and anatomic- level traits.
- We used a Principal Component Analysis and pairwise correlations to understand trait covariation, and contrasted individual traits and strategy axes among habitat groups. We also tested for phylogenetic conservatism in strategy axes and individual traits.
- We found three leading axes of trait strategies. The first expressed a trade-off between fire resistance (allocation to bark and higher hydraulic segmentation) and light competition (allocation to wood), segregated shade-intolerant savanna from the remaining shade-tolerant species, and showed strong phylogenetic signal. The second axis did not segregate habitat groups and reflected a phylogenetically conserved hydraulic safety-efficiency trade-off. The third reflected an evolutionarily labile survival-growth trade-off axis and separated resource conservative savanna and acquisitive forest species; generalist species showed intermediary traits in this axis and did not differ from forest and savanna species.
- Our results support the hypothesis that the evolution of fire resistance in savanna species involved changes in multiple stem, twig and whole-plant traits that co-vary along strategy axes and contrast between savanna and forest species.

Key-words: Bark, cerrado, forest, functional tradeoffs, hydraulic traits, savanna, trait strategies, wood anatomy.

INTRODUÇÃO

A savana é o segundo maior bioma tropical. Este bioma ocorre em paisagens caracterizadas por grande complexidade fisionômica, indo desde ecossistemas com campos abertos até fragmentos e faixas de floresta com dossel completamente fechado, principalmente em climas mésicos, formando mosaicos na paisagem (Ribeiro & Walter, 2008; Salazar *et al.*, 2012). Este padrão sugere que esses tipos de vegetação estão relacionados e evoluíram em proximidade, o que está de acordo com estudos que sugerem que espécies lenhosas das savanas mésicas diversificaram a menos de dez milhões de anos atrás a partir de ancestrais florestais, coincidindo com a ascensão e dominância das gramíneas C4 no mundo que, por serem altamente inflamáveis, aumentaram, drasticamente, a frequência de incêndios (Simon *et al.*, 2009; Maurin *et al.*, 2014). Este processo envolveu a evolução das adaptações para resistir à maior incidência de incêndios. Entre estas adaptações está o desenvolvimento de alocação precoce para produção de cascas espessas, sendo essa característica de fundamental importância, especialmente nas savanas Neotropicais (Dantas & Pausas, 2013).

O processo de evolução de uma casca espessa em relação à área transversal do caule e dos ramos ainda é pouco entendido. A alocação para uma casca espessa pode ser o resultado do espessamento de dois tecidos com diferentes funções. A casca interna a qual, definida pela perspectiva anatômica, é o floema secundário (Angyalossy *et al.*, 2016), o qual está ligado a funções fisiológicas, como o transporte e armazenamento de produtos da fotossíntese e água. Ela está correlacionada com o tamanho das folhas e da planta como um todo (Pausas, 2015; Rosell, 2016; Clair *et al.*, 2018). A casca externa, também definida como periderme ou ritidoma (Angyalossy *et al.*, 2016), protege o caule contra condições externas adversas, como o fogo, a seca, e temperaturas extremas (Rosell, 2016; Pausas, 2017; Rosell *et al.*, 2017). A extensão em que as cascas mais espessas de espécies de savana, em comparação com as espécies lenhosas da floresta, resultam principalmente dos padrões de alocação interna ou externa da casca, continua para ser totalmente elucidada.

Enquanto que investimentos em casca proporcionam benefícios relacionados ao isolamento térmico em ecossistemas com ocorrência frequente de fogo, eles também envolvem custos em termos de alocação de carbono (Lawes *et al.*, 2013). O fato de os solos tropicais serem geralmente pobres em nutrientes devido à lixiviação, sugere que mecanismos compensatórios e compromissos deveriam estar envolvidos na evolução deste traço, potencialmente afetando padrões de alocação para outros tecidos da planta. De fato, espécies que se diferenciam entre si em relação à alocação de casca, também diferenciam em outros traços, como altura da planta e crescimento em diâmetro (Lawes *et al.*, 2013; Dantas & Pausas, 2013) assim como atributos da folha e da copa (Dantas *et al.*, 2013b,a). Por exemplo, espécies de floresta com casca fina mantêm crescimento em diâmetro 68% maior do que espécies de savana (Rossatto *et al.*, 2009). No entanto, poucos estudos têm relacionado diretamente à variação na alocação para casca com traços da madeira entre espécies de floresta e savana, e ainda é pouco conhecido em que medida este atributo está correlacionado com outros ajustamentos morfológicos, fisiológicos e anatômicos de traços da madeira, formando síndromes.

A alocação de recursos na casca poderia, também, estar ligada a atributos hidráulicos da madeira. Por exemplo, falha hidráulica foi sugerida, recentemente, como mecanismo chave para mortalidade de plantas lenhosas causada pelo fogo nos ecossistemas em que os incêndios são superficiais e de baixa intensidade, como é o caso das savanas. Aumentos na indução de calor, déficit de pressão de vapor e deformação no xilema resultam em um aumento da vulnerabilidade à cavitação e perda de condução do xilema (West *et al.*, 2016; Bär *et al.*, 2018; Michaletz, 2018). Esta vulnerabilidade pode ser contornada, por exemplo, pela segmentação hidráulica que é caracterizada pela compartimentalização dos vasos hidráulicos de diferentes órgãos da planta, sendo assim, quando ela sofre danos em um órgão, a planta ainda consegue fazer com que esse dano não atinja a planta como um todo (Zanne *et al.*, 2006). Sendo assim, é possível aumentar as chances de sobrevivência do indivíduo, quando ocorre cavitações no xilema após incidência de fogo, através dos tecidos que se mantiveram sem danos. Tais atributos poderiam auxiliar na resistência ao fogo de espécies de savana e formar um único eixo de trade-off com traços relacionados à casca. Além disto, um estudo muito recente (Liu *et al.*, 2019) mostrou que atributos hidráulicos, como atributos relacionados à transporte de seiva em nível anatômico, estão fortemente relacionados com investimentos na altura da planta. Plantas altas têm xilemas com maior eficiência e menor segurança hidráulicas, isto é, vasos condutores maiores e mais largos, menor densidade de vasos e menor densidade da madeira. Além disto, espécies com vasos grandes geralmente têm o diâmetro das pontoações entre vasos maiores para melhor conexão entre os vasos, tal característica reduz a resistência dos vasos ao embolismo (Choat *et al.*, 2008). Isto resulta em um contrabalanço entre eficiência e segurança hidráulica (Choat *et al.*, 2008; Liu *et* *al.*, 2019). Já que a alocação precoce na espessura de casca potencialmente é contrabalanceada por investimentos em crescimento em diâmetro e altura do caule (Lawes *et al.*, 2013; Dantas & Pausas, 2013), a alocação para casca poderia ser parte de mesmo eixo de compromisso que atributos hidráulicos. Outro compromisso que pode estar potencialmente ligado com investimentos na casca é o bem estabelecido no contrabalanço entre sobrevivência e crescimento. Plantas que investem em crescimento tendem a investir menos recursos em estrutura mecânica e em tecidos de armazenamento, levando à uma menor taxa de sobrevivência (Negreiros *et al.*, 2016). Por outro lado, estudos têm sugerido que traços relacionados ao tamanho da planta são mais evolutivamente conservados comparado com traços relacionados à casca (Simon *et al.*, 2009; Stepanova *et al.*, 2013; Pace *et al.*, 2015; Román-Jordán *et al.*, 2017). Se isto está correto, traços relacionados à casca podem evoluir de forma independente em relação ao tamanho da planta e não estarem relacionados com atributos hidráulicos.

Neste estudo, nós investigamos traços de caule e ramo, assim como suas relações com atributos morfológicos e anatômicos da madeira em espécies de savana, floresta e generalistas do Cerrado na Região Sudeste do País. Nosso objetivo foi entender melhor os mecanismos envolvidos na evolução da alocação na espessura de casca em espécies lenhosas de savana. Nós compilamos e medimos traços morfológicos e anatômicos para responder às seguintes questões: (1) quais são os eixos de estratégias principais ao se correlacionar traços de caule e da planta inteira em espécies de savana, floresta e generalistas? (2) Casca, traços morfológicos relacionados ao tamanho e anatomia da madeira estão relacionados a esses eixos? (3) Quais eixos e traços contrastam mais entre espécies com diferentes grupos de habitat de ocorrência (savana, floresta e espécies generalistas)? (4) Alocação na espessura de casca está mais relacionada com investimentos na casca interna ou externa? (5) Há evidência de conservantismo filogenético nestes eixos e traços? Nossas hipóteses são de que a alocação de recursos na casca e anatomia da madeira podem estar parcialmente relacionadas e formar eixos de trade-off, de forma direta, através da segmentação hidráulica auxiliando na resistência ao fogo (West *et al.*, 2016), ou indiretamente, mediada pela altura da planta e densidade da madeira (Lawes *et al.*, 2013; Liu *et al.*, 2019). Alternativamente, atributos da casca e da anatomia da madeira poderiam não ser relacionadas, refletindo eixos com funções diferentes e descoordenadas potencialmente, sendo resultado de diferentes históricos evolutivos (Simon *et al.*, 2009; Stepanova *et al.*, 2013; Pace *et al.*, 2015; Román-Jordán *et al.*, 2017). Também acreditamos que traços e eixos relacionados com a casca irão contrastar mais entre espécies de floresta e savana, e que a casca mais espessa encontrada em espécies de savana se deve à casca externa, ressaltando o papel fundamental do fogo na evolução das savanas através de ancestrais florestais (Bond, 2008; Simon *et al.*, 2009; Dantas *et al.*, 2013b,a). Finalmente, nós acreditamos que traços relacionados com a casca são evolutivamente lábeis, enquanto atributos relacionados a recursos e tamanho da planta apresentam forte sinal filogenético (Simon *et al.*, 2009).

INTRODUCTION

The savanna is the second largest tropical biome. Savannas often occur in landscapes characterized by great physiognomic complexity, ranging from widespread open grassy ecosystems to forest patches and strips with a fully closed canopy, particularly in mesic climates, forming landscape mosaics (Ribeiro & Walter, 2008; Salazar *et al.*, 2012). This pattern suggests that these vegetation types could be related and evolved in close proximity. Accordingly, studies suggest that mesic savanna woody species diversified less than 10 Mya from forest ancestors coinciding with the rise to dominance of flammable C_4 grasses worldwide and increasing fire frequency (Simon *et al.*, 2009; Maurin *et al.*, 2014). This process involved the evolution of adaptations to resist fire, among which early allocation to bark (i.e. high bark to stem cross-sectional area biomass allocation) resulting in higher bark thickness to stem diameter ratios compared to forest species is of fundamental importance, especially in Neotropical savannas (Dantas & Pausas, 2013).

The evolution of thick bark in savanna ecosystems remains poorly understood. Bark allocation may result from the thickening of two sections with different main functions. The inner bark is the secondary phloem (from an anatomic perspective; Angyalossy *et al.*, 2016), which is linked to physiological functions, like the transport and storages of photosynthates and water and is correlated to leaf and whole plant sizes (Pausas, 2015; Rosell, 2016; Clair *et al.*, 2018). The outer bark, also called periderm or rhytidome (Angyalossy et al. 2016), protects the stem against external hazards, such as fire, drought and extreme temperatures (Rosell, 2016; Pausas, 2017; Rosell *et al.*, 2017). The extent to which the thicker barks of savanna compared to forest woody species results mostly from inner or outer bark allocation patterns remains to be fully addressed.

While investments to bark provide heat insulation benefits in fire ecosystems, it also involves costs in term of carbon allocation (Lawes *et al.*, 2013). Because tropical soils are often nutrient-poor due to the intensive leaching, tradeoffs were probably involved in the evolution of this trait, potentially affecting patterns of allocation to other plant tissues. In fact, species differing in bark allocation often also differ in other traits, such as stem height and diameter growth (Lawes *et al.*, 2013; Dantas & Pausas, 2013) as well as in leaf and canopy attributes (Dantas *et al.*, 2013). Moreover, thin-barked forest species keep stem diameter growth rates 68% higher than savanna species (Rossatto *et al.*, 2009). However, few studies have directly related variation and bark allocation to other woody traits across savanna and forest species, and the extent to which this trait is correlated to other morphological, physiological and anatomical adjustments in woody plants, forming syndromes, remains poorly known.

Bark allocation could be connected to hydraulic traits. For instance, hydraulic failure was recently suggested to be a key mechanism of fire-driven tree mortality in low-intensity fire ecosystems, such as savannas. Increased heat-induced, vapor pressure deficit, and xylem deformation result in increased vulnerability to cavitation and loss of xylem conductivity (West *et al.*, 2016; Bär *et al.*, 2018; Michaletz, 2018). Thus, fire resistance is likely to be increased by other traits, such as a high hydraulic segmentation (Zanne *et al.*, 2006), allowing more chances of survival to the plant in case of xylem cavitation after the fire. Such traits could aid for the fire resistance of savanna species, either forming a single tradeoff or a separate axis with bark-related traits. In addition, a very recent survey (Liu *et al.*, 2019) showed that hydraulic traits, such as wood anatomic-level sap transport traits, are closely related to plant height investment. Tall plants have greater xylem efficiency and lower hydraulic safety, that is, wider conduits, lower conduit density, and lower sapwood density. Species with large vessels often have larger pit membrane areas connecting vessels, which reduces hydraulic resistance to embolism (Choat *et al.*, 2008), and results in a hydraulic efficiency-safety tradeoff (Choat *et al.*, 2008; Liu *et al.*, 2019). Since early allocation to bark potentially involves trade-offs with investment in stem and height growth (Lawes *et al.*, 2013; Dantas & Pausas, 2013), variation in relative bark allocation could be coupled with this tradeoff axis. Another trade-off potentially connected with bark investments is related to plant survival and growth. Plants that invest in growth invest fewer resources in structure and storage tissues leading to less survival (Negreiros *et al.*, 2016). On the other hand, studies have suggested that size-related traits are more evolutionarily conserved compared to bark-related traits (Simon *et al.*, 2009; Stepanova *et al.*, 2013; Pace *et al.*, 2015; Román-Jordán *et al.*, 2017). If this is correct, bark traits could change somehow independently from size-related traits.

In this study, we investigated stem and twig bark traits, as well as their relationships with morphological and anatomical wood traits across savanna, forest and generalist species from a Brazilian savanna landscape (Cerrado) in Southeastern Brazil. We aimed at better understanding the mechanisms involved in the evolution of bark allocation in savanna woody species. We used measured and compiled morphological and anatomical traits to answer the following questions: (1) What are the leading axes of stem and whole plant trait strategies across savanna, forest and generalist species? (2) Are bark, woody and size-related morphological and anatomical traits connected in these axes? (3) What axes and traits contrast the most among species from different habitat-preference groups (savanna, forest and generalist species)? (4) Is bark allocation in savanna species best explained by investment in inner or outer bark? (5) Is there evidence for phylogenetic conservatism in these traits and axes? We hypothesize that bark and wood anatomy traits were partially related and varied across the same tradeoff axes. Specifically, we expected bark traits to be directly related to hydraulic segmentation (West *et al.*, 2016) and size-related traits, as well as wood density (Lawes *et al.*, 2013; Liu *et al.*, 2019). Alternatively, bark and wood anatomic traits could be unrelated, reflecting different and uncoordinated functions and axes, potentially resulting from different evolutionary histories (Simon *et al.*, 2009; Stepanova *et al.*, 2013; Pace *et al.*, 2015; Román-Jordán *et al.*, 2017). We also hypothesized that bark-related traits and axes would contrast the most between forest and savanna species, and that the thicker barks of savanna species would mainly reflect investments in outer bark, highlighting the key role of fire in the evolution of savannas species from forest ancestors (Bond, 2008; Simon *et al.*, 2009; Dantas *et al.*, 2013). Finally, we hypothesized that bark related traits should be evolutionarily labile, whereas resource- and size-related traits should present strong phylogenetic signals (Simon *et al.*, 2009).

MATERIAL AND METHODS[2]

Data

Our primary database was collected by Sonsin *et al.* (2014) in the private Cerrado reserve of the "Palmeira da Serra" Ranch, in the municipality of Pratânia, São Paulo state, Brazil, covering an area of about 180 ha (22°49'1.31"S, 48°45'1.08"W). This area has an average temperature of 19.8 °C and an annual rainfall of 1317 mm (Sonsin-Oliveira, 2010). Its climate is classified as Cfa according to Köppen (Alvares *et al.*, 2013). The prevailing vegetation is Cerrado, characterized by tropical mosaics of grassland, savanna, and forest. The sampled areas within the reserve included areas of typical savanna (locally called cerrado *sensu stricto*) and adjacent gallery forest, distributed alongside small streams. Soils were very similar between the two habitats, but slightly sandier and with lower aluminum content in the forest (Sonsin *et al.*, 2014). In general, the area is composed of yellow-reddish Oxisols (Rossi, 2017).

Sampling

We firstly collected data from 48 species from 2002 to 2004 (Oliveira, 2006). We haphazardly selected 2 to 4 individuals of each species during random walks in the track network of the reserve. We used the most developed branches of the selected woody individuals and obtained discs of ca. 3 to 6 cm in thickness. Aiming to reach a richer database we selected other 43 species using the same method and area from 2006 to 2010

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[2] *Materiais e métodos foi escrito como se tivéssemos participado da coleta e processamento do material porque as coletoras dos dados vão entrar como autoras do artigo.*

(Sonsin-Oliveira, 2010). The final dataset included 91 species, 211 individuals from forest and savanna habitats, as well as generalist species (Sonsin *et al.*, 2014).

Anatomical traits

We obtained sections of approximately 15 to 20 µmm of thickness of the transverse and longitudinal sections - radial and tangential, which were double-stained with 1% aqueous safranin and 1% aqueous Astra blue (1:9) (Bukatsch, 1972). We permanently made the histological slices with synthetic resin (Entellan®). The dissociation of the cells followed the Franklin method (1945, modified by Kraus & Arduin, 1997) and the safranin 1% aqueous dye (Sass, 1958) was used for the staining of these cells. We made the semi-permanent slices on glycerin using a small amount of the dissociated material. We carried out the qualitative and quantitative microscopic analysis following the instructions of the IAWA Committee (1989) using the Zeiss Axioskop 40 light microscope, coupled to the Axio Cam MRC camera and a computer, with the aid of the Axivision and Axioviewer Image Analysis Systems (Sonsin-Oliveira, 2010).

We made 30 measures from each individual of the following wood anatomical traits: fiber length (FL), vessel element length (VEL), intervessel pit diameter (IPD), ray-vessel pit diameter (RPD), vessel element diameter (VDi), fiber wall thickness (FWT), ray per millimeter (R/mm) and vessel density (VDe). Fibers are related to plants woody structure, mostly mechanical support, while all vessels traits area related to hydraulic efficiency vs. safety (Chave *et al.*, 2009). VEL is linked to water vertical reach, the greater its value more efficient water transport vertically; IPD represents the size of pits that link the vessels horizontally, the greater its value, the greater is the exchange of fluids among vessels; RPD is the same as IPD but radially speaking; VDi is also linked to water transport efficiency, the greater its value more efficient the water transport; R/mm and VDe are the density of rays and vessels, respectively, the greater their value, more enhanced is hydraulic resistance (Choat *et al.*, 2008).

Morphological traits

We selected and photographed the transverse section of the most conserved and representative disc of each species to measure the areas of the total bark, periderm, secondary phloem, and secondary xylem (excluding the pith), using scaled images and the software ImageJ (Schneider *et al.*, 2012; Rueden *et al.*, 2017). We made four measures of each tissue per photo. We calculated relative bark (total), periderm, phloem, and xylem areas by dividing their cross-sectional area by that of the entire twig, based on diameter measurements progressively excluding the inner sections, and assuming a circular shape. The areas of the outer tissues were obtained as the differences between the areas considering or excluding the different bark components. We found the diameter values by using the average of two diameter measures of each image including the pith.

To complement our primary dataset, we searched for data on the components of relative stem bark thickness (bark thickness and stem diameter), wood density (WD) and maximum plant height (Hmax) for the collected species (see Table A1 in appendix for more details on the data source). Based on the compiled stem bark and diameter information we calculated relative bark area by first calculating the difference between stem diameter with and without summing the thickness of the bark multiplied by two. The areas were calculated assuming a circular shape. We subsequently divided the bark area by the stem cross-sectional area. This metric was used as an indication of the amounts of resources/carbon invested in these tissues (Lawes *et al.*, 2013). We found data on relative bark thickness from stem for 60 species (12 forest, 20 generalist and 28 savanna species), on maximum tree height for all 91 species (26 forest, 29 generalist and 36 savanna species) and wood density for 71 species (17 forest, 24 generalist and 30 savanna species). To facilitate symbols comprehension there's Table 1.

Table 1 *Traits abbreviations and units of measurement.*

Initials	Meaning
Hmax	Maximum tree height (m)
WD	Wood density (g/cm^3)
BA stem	Relative bark area from stem (cm^2/cm^2)
BA twig	Relative total bark area from twig (cm^2/cm^2)
Periderm	Relative periderm area from twig (cm^2/cm^2)
Phloem	Relative secondary phloem area from twig (cm^2/cm^2)
Xylem	Relative secondary xylem area from twig (cm^2/cm^2)

Initials	Meaning
VDe	Vessel density (vessel/mm^2)
FL	Fiber length (µm)
R/mm	Ray per millimeter
VEL	Vessel element length (µm)
FWT	Fiber wall thickness (µm)
IPD	Intervessel pit diameter (µm)
RPD	Ray-vessel pit diameter (µm)
VDi	Vessel element diameter (µm)

Species habitat classification

We classified species into savanna, forest, and generalist according to occurrence information from the literature (Mendonça *et al.*, 2008) comparing it's information to "Flora do Brasil"'s (http://floradobrasil.jbrj.gov.br). Species were considered savanna or forest species when recorded exclusively in either habitat or generalist when recorded in both. Occurrence in transitional forests, locally called "cerradão", was not considered for classification purposes, as this vegetation contain both typical savanna and forest species, and have only very few (if any), exclusive species. Indeed, none of our species occurred solely in this physiognomic type.

Phylogenetic Tree

We built a phylogenetic tree using the function S.PhyloMaker created by Qian & Jin (2016) for R (R Core Team, 2018) with the aid of the phytools package (Revell, 2012). The function uses an improved version of the angiosperm supertree created by Zanne *et al.* (2014). To build the tree we chose the Scenario 3 (Qian & Jin, 2016) that adds genera or species to their families or genera using the same approach implemented in Phylomatic and BLADJ (Webb *et al.*, 2008).

Statistical analysis

To evaluate which traits varied along the same axes of trait strategy, forming tradeoffs, and to understand whether and how these axes contributed to differentiating savanna, forest and generalist species, we first performed a Principal Component Analysis (PCA) including all traits. Since we did not find functional traits for all species in our literature search, these multivariate analyses (see below) were carried with 12 forest, 20 generalist and 28 savanna species (60 species; rather than the 91 species used for separate twig bark-related and wood anatomic-level trait analyses determined as Scenario 2 in Appendix). We selected the three leading axes of trait strategy, that is, those among the resulting principal component axes that explained more than 10% of trait variability. We compared and tested the significance of the pairwise associations between these three leading axes and each individual trait, as well as among each pair of traits using Pearson correlations. To evaluate whether and which of these axes and traits were important to segregate savanna, forest and generalist species, we tested for differences in species scores and individual traits among species from different habitats using a Kruskal-Wallis test and post-hoc comparisons. Except for the comparison among habitat groups (which used non-parametric statistics), we log-transformed the traits to improve normality (when relevant). We tested for phylogenetic signal in all traits and leading axes of trait strategy using the function “phylosignal” of the picante package (Kembel *et al.*, 2010). We corrected the P-values for multiple comparisons in the individual traits contrasts among habitat groups as well as in the phylogenetic signal test using the Benjamini and Hochberg method (Benjamini & Hochberg, 1995). All analyses were run in R (R Core Team, 2018) using the picante (Kembel *et al.*, 2010) and FactoMineR (Lê *et al.*, 2008) libraries.

RESULTS

We found three leading axes of trait strategy explaining 51% of the total trait variation (Fig. 1). The first explained 24.42% and was mainly related to a fire resistance-light competition tradeoff. This axis was significantly (and strongly) positively correlated to all bark-related traits (more strongly with twig bark traits), and negatively correlated to relative xylem area (Xylem), maximum stem height (Hmax), fiber length (FL), vessel element length (VEL) and intervessel pit diameter (IPD) (Table 2). The second axis explained 14.50% of the trait variability and was mainly correlated (positively) with anatomic wood traits, such as IPD, ray-vessel pit diameter (RPD) and vessel element diameter (VDi), although also showing significant (but weaker) positive correlation with Hmax, periderm, and total twig bark areas (BA_twig; Table 2). The third axis explained 11,91% of the variation and was mainly correlated to anatomic traits, showing positive and significant relationships with FL, VEL and fiber wall thickness (FWT). It also showed a moderate negative correlation with VDi and a weaker correlation with relative stem bark area (BA_stem, positive) and Hmax (negative; Table 2).

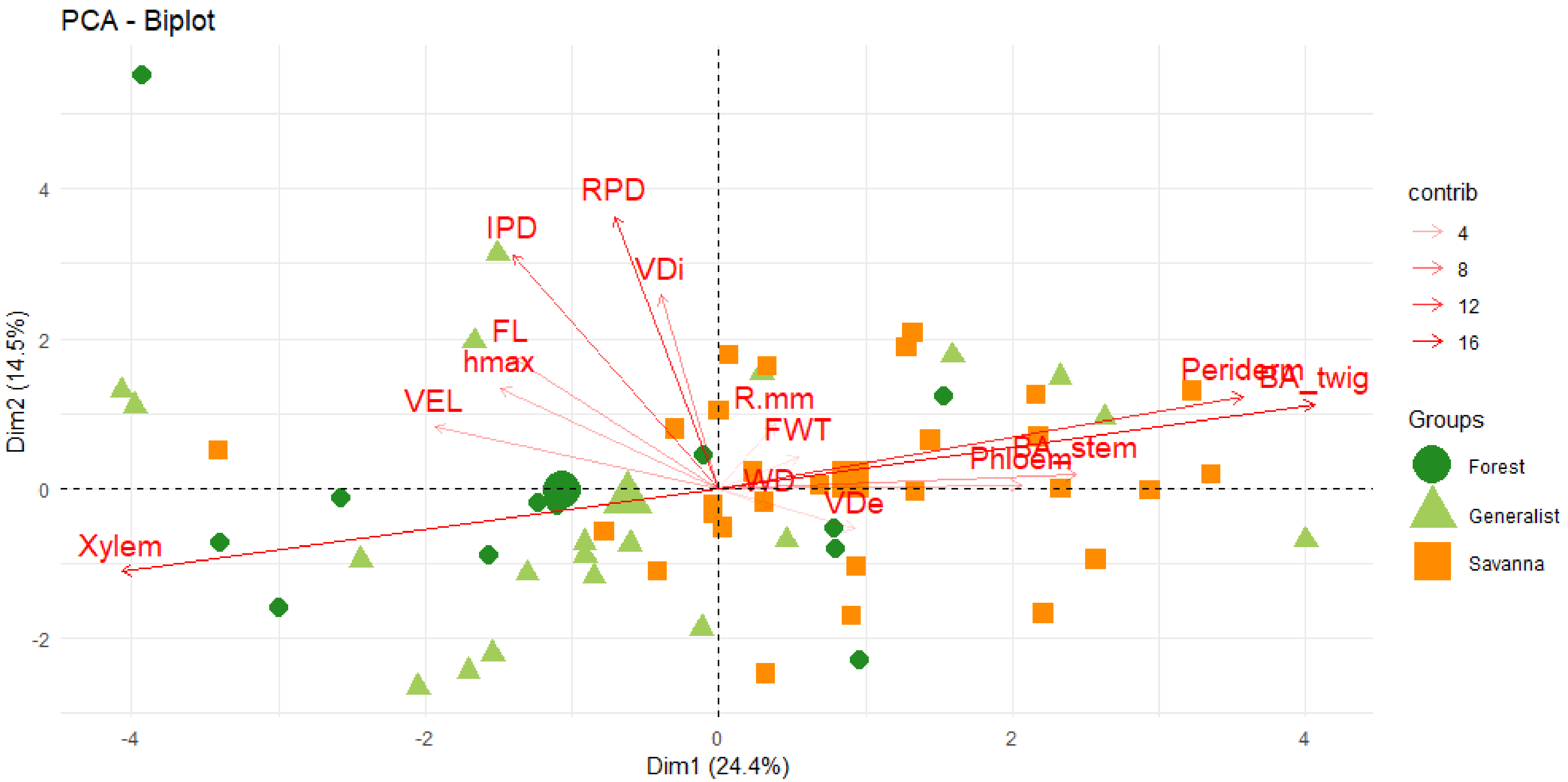

Figure 1 *First two principal component axes of wood anatomical and morphological traits of savanna, forest and generalist woody species. FL = fiber length, VEL = vessel element length, IPD = intervessel pit diameter, RPD = ray-vessel pit diameter, VDi = vessel element diameter, FWT = fiber wall thickness, R.mm = ray per millimeter, VDe = vessel density, hmax = maximum tree height, WD = wood density, BA_stem = stem relative bark area, BA_twig = twig relative bark area, Periderm = relative periderm area from twig, Phloem = relative secondary phloem area from twig, Xylem = relative secondary xylem area from twig.*

Table 2 *Pairwise Pearson correlations between individual traits, and between traits and the three selected PCA axes across savanna, forest and generalist species.*

Traits	**Hmax**	**WD**	**BA_stem**	**BA_twig**	**Periderm**	**Phloem**	**Xylem**	**VDe**	**FL**	**R.mm**	**VEL**	**FWT**	**IPD**	**RPD**	**VDi**	**PC1**	**PC2**	**PC3**
Hmax		0.31	-0.20	-0.21	-0.21	-0.10	0.22	-0.14	0.09	-0.05	-0.02	-0.07	0.22	0.20	0.34	-0.35	0.31	-0.40
WD	0.02		0.15	0.01	0.08	-0.08	0.00	-0.09	-0.06	0.34	-0.26	0.12	-0.02	-0.16	-0.11	0.08	-0.06	-0.18
BA_stem	0.12	0.26		0.43	0.46	0.12	-0.44	0.20	-0.06	0.14	-0.01	0.11	-0.19	0.00	-0.14	0.57	0.04	0.27
BA_twig	0.10	0.95	0.00		0.87	0.50	-1.00	0.10	-0.17	0.08	-0.33	0.14	-0.13	0.02	0.07	0.94	0.26	0.00
Periderm	0.11	0.54	0.00	0.00		0.03	-0.87	0.10	-0.15	0.14	-0.22	0.15	-0.07	0.07	0.00	0.83	0.29	0.10
Phloem	0.46	0.53	0.38	0.00	0.85		-0.50	0.03	-0.07	-0.08	-0.29	0.07	-0.16	-0.12	0.13	0.48	0.01	-0.15
Xylem	0.09	0.99	0.00	0.00	0.00	0.00		-0.15	0.18	-0.08	0.33	-0.15	0.13	-0.02	-0.06	-0.95	-0.26	-0.01
VDe	0.27	0.47	0.13	0.46	0.44	0.82	0.26		-0.13	-0.04	-0.03	0.05	-0.02	-0.03	-0.18	0.21	-0.12	0.19
FL	0.47	0.65	0.65	0.19	0.25	0.58	0.18	0.31		0.00	0.49	0.52	0.27	0.19	0.10	-0.33	0.41	0.65
R.mm	0.70	0.01	0.30	0.52	0.27	0.54	0.52	0.76	0.99		0.06	-0.16	0.15	0.17	-0.12	0.09	0.20	-0.03
VEL	0.86	0.05	0.91	0.01	0.09	0.02	0.01	0.84	0.00	0.66		0.12	0.19	0.17	-0.09	-0.45	0.19	0.61
FWT	0.59	0.36	0.41	0.27	0.26	0.62	0.25	0.68	0.00	0.22	0.37		-0.03	-0.08	-0.15	0.13	0.10	0.68
IPD	0.09	0.87	0.14	0.31	0.60	0.23	0.31	0.89	0.04	0.24	0.14	0.85		0.66	0.25	-0.33	0.72	-0.02
RPD	0.13	0.23	0.99	0.89	0.60	0.38	0.88	0.81	0.14	0.20	0.19	0.56	0.00		0.45	-0.17	0.84	-0.09
VDi	0.01	0.41	0.28	0.61	0.97	0.33	0.67	0.17	0.43	0.37	0.48	0.26	0.06	0.00		-0.09	0.60	-0.43
PC1	0.01	0.54	0.00	0.00	0.00	0.00	0.00	0.10	0.01	0.49	0.00	0.34	0.01	0.21	0.48		0.00	0.00
PC2	0.02	0.66	0.74	0.04	0.03	0.93	0.05	0.34	0.00	0.13	0.15	0.45	0.00	0.00	0.00	1.00		0.00
PC3	0.00	0.16	0.04	1.00	0.43	0.25	0.93	0.14	0.00	0.80	0.00	0.00	0.86	0.52	0.00	1.00	1.00	

Pearson statistics are shown above and P-vales below the diagonal. FL = fiber length, VEL = vessel element length, IPD = intervessel pit diameter, RPD = ray-vessel pit diameter, VDi = vessel element diameter, FWT = fiber wall thickness, R.mm = ray per millimeter, VDe = vessel density, Hmax = maximum tree height, WD = wood density, BA_stem = stem relative bark area, BA_twig = twig relative bark area, Periderm = relative periderm area from twig, Phloem = relative secondary phloem area from twig, Xylem = relative secondary xylem area from twig.

Species scores in the first and third axes significantly differed among habitat groups (Fig. 1 and 2; Table 3). The first axis significantly differed between savanna and the other two groups, that is, segregated shade tolerant forest and generalist species from shade-intolerant savanna species. The third axis differed only between forest and savanna species, with generalist species showing intermediate trait values that did not significantly differed from the former two (Fig. 2; Table 3). PCA results excluding relative stem bark area and wood density (that is, including 91 rather than 60 species) showed similar results and is shown in appendix Fig. A1 and A2 as Scenario 2.

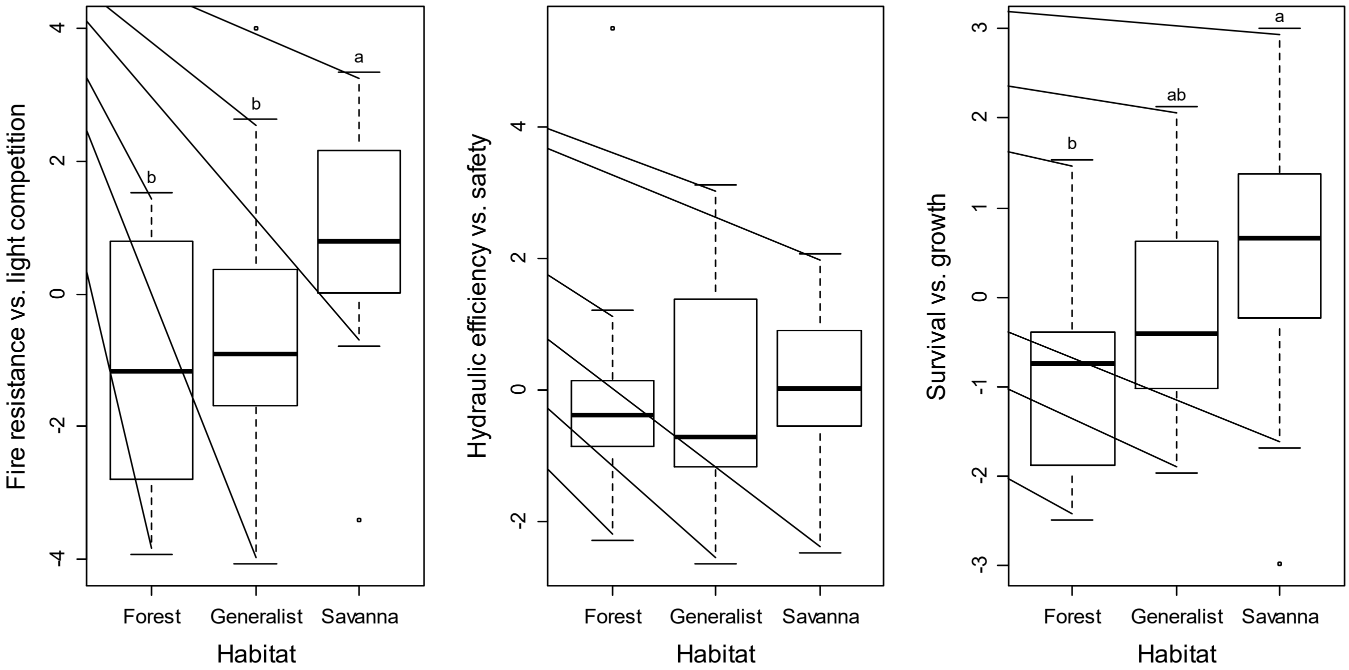

Figure 2 *Differences in principal component scores among savanna, forest and generalist species in the three-leading axis of trait strategies. See Table 2 for individual trait correlations with these axes.*

For individual traits, those that significantly differed among habitat types were Hmax, BA_stem, BA_twig, Periderm, and Xylem (Table 3). Forest and generalist species did not differ in any of the individual traits showing that generalist species are ecologically more related to forest than savanna species. Savanna species presented lower Hmax and Xylem, and higher BA_stem, BA_twig, and Periderm (Table 3). Regarding the pairwise trait correlations (Table 2), BA_stem was significantly correlated only to BA_twig and Periderm (positively), not with relative twig phloem area (Phloem), and negatively correlated to Xylem. BA_twig was also strongly negatively correlated to

Xylem, and with VEL, and was positively correlated to both relative Periderm and Phloem, although more strongly with the former. Accordingly, Xylem was related with the same traits as relative twig bark area, but in the opposite direction. Hmax was positively related to both wood density (WD) and VDi. WD was also positively related to ray per millimeter (R.mm) and negatively to VEL. VEL was also positively related to FL, which was also positively related to IPD and FWT. Finally, RPD was positively correlated to IPD and VDi. The first two leading axes of trait strategies, as well as most of the individual wood anatomy traits (except for VDe and RPD), presented a significant phylogenetic signal, indicating that they were highly conserved during species evolution (Table 4).

Table 3 *Traits and PCA axes mean and standard deviations for each habitat group and results for Kruskal-Wallis test and post-hoc pairwise comparison among groups.*

Traits	**Forest**	**Generalist**	**Savanna**	**K**	**P***
Maximum tree height (m)	14.04^{b} ± 6.93	13.26^{b} ± 8.44	8.57^{a} ± 6.74	12.9482	0.0058
Wood density (g/cm^3)	0.57 ± 0.16	0.59 ± 0.1	0.54 ± 0.12	2.5228	0.3541
Relative bark area stem (cm^2/cm^2)	0.01^{b} ± 0.01	0.02^{ab} ± 0.03	0.03^{a} ± 0.03	9.1518	0.0309
Relative bark area twig (cm^2/cm^2)	0.32^{b} ± 0.15	0.34^{b} ± 0.20	0.50^{a} ± 0.16	18.8000	0.0005
Relative periderm area twig (cm^2/cm^2)	0.12^{b} ± 0.13	0.15^{b} ± 0.16	0.27^{a} ± 0.15	18.5516	0.0005
Relative secondary phloem area twig (cm^2/cm^2)	0.20 ± 0.08	0.19 ± 0.08	0.23 ± 0.09	3.2725	0.2655
Relative secondary xylem area twig (cm^2/cm^2)	0.67^{b} ± 0.15	0.65^{b} ± 0.20	0.49^{a} ± 0.16	19.7388	0.0005
Vessel density	0.15 ± 0.23	0.12 ± 0.15	0.23 ± 0.32	5.5212	0.1581
Fiber length (µm)	820.91 ± 298.70	809.65 ± 300.68	754.21 ± 212.37	0.3765	0.8284
Ray per millimeter	5.30 ± 3.42	5.19 ± 2.95	4.53 ± 2.88	2.2067	0.3828
Vessel element length (µm)	462.95 ± 251.26	446.01 ± 215.73	359.2 ± 127.86	3.6830	0.2481
Fiber wall thickness (µm)	4.39 ± 1.22	4.68 ± 1.52	4.89 ± 1.46	3.5990	0.2481
Intervessel pit diameter (µm)	7.70 ± 8.92	4.13 ± 1.9	3.74 ± 2.05	4.4306	0.2338
Ray-vessel pit diameter (µm)	6.42 ± 5.34	5.09 ± 3.31	3.72 ± 2.23	3.6853	0.2481
Vessel element diameter (µm)	72.19 ± 23.13	70.33 ± 26.07	68.10 ± 19.28	0.4820	0.8284
PC1	-1.07^{b} ± 1.87	-0.62^{b} ± 2.06	0.90^{a} ± 1.44	7.1448	0.0017
PC2	-0.02 ± 1.96	-0.15 ± 1.66	0.11 ± 1.14	0.1740	0.8407
PC3	-0.79^{b} ± 1.28	-0.25^{ab} ± 1.03	0.52^{a} ± 1.40	5.1452	0.0088

*Different letters indicate significant differences in the post-hoc pairwise comparisons. *P-values were adjusted using Benjamini and Hochberg method (Benjamini & Hochberg, 1995) for all individual traits, but not for the PCA's axes.*

Table 4 *Test of phylogenetic signal in traits and PCA axes.*

Traits	K	PIC.variance.obs	PIC.variance.rnd.mean	PIC.variance.P	PIC.variance.Z
Hmax	0.334	1.389	2.143	0.069	-1.440
WD	0.159	0.001	0.000	0.960	1.939
BA stem	0.437	0.000	0.000	0.069	-1.255
BA twig	0.285	0.001	0.001	0.066	-1.673
Periderm	0.220	0.001	0.001	0.370	-0.425
Phloem	0.278	0.010	0.015	0.071	-1.428
Xylem	0.280	0.001	0.001	0.069	-1.579
VDe	0.278	0.065	0.093	0.069	-1.445
FL	0.766	0.003	0.007	0.003	-3.118
R/mm	0.460	0.013	0.026	0.003	-2.284
VEL	0.788	0.004	0.014	0.003	-3.273
FWT	0.500	0.036	0.073	0.012	-1.716
IPD	0.839	0.283	0.976	0.003	-1.270
RPD	0.340	0.026	0.038	0.066	-1.641
VDi	0.430	0.003	0.007	0.003	-2.476
PC1	0.657	0.029	0.064	0.001	-1.729
PC2	0.697	0.019	0.054	0.001	-2.498
PC3	0.319	0.036	0.045	0.240	-0.753

*K = K statistic, PIC.variance = Mean observed PIC variance, PIC.variance.P = P-value of observed vs. random variance of PICs PIC.variance.z = Z-score of observed vs. random variance of PICs. FL = fiber length, VEL = vessel element length, IPD = intervessel pit diameter, RPD = ray-vessel pit diameter, VDi = vessel element diameter, FWT = fiber wall thickness, R.mm = ray per millimeter, VDe = vessel density, Hmax = maximum tree height, WD = wood density, BA stem = stem relative bark area, BA twig = twig relative bark area, Periderm = relative periderm area from twig, Phloem = relative secondary phloem area from twig, Xylem = relative secondary xylem area from twig. *P-value adjusted using Benjamini and Hochberg method (Benjamini & Hochberg, 1995) for all traits except PCA's axes.*

DISCUSSION

We found three leading axes of trait strategies connecting bark, wood, and whole plant traits. All axes were related to both morphological and anatomical characteristics (Fig. 1; Table 2). However, morphological bark traits correlated much more strongly with the first axis, whereas anatomic traits correlated more strongly with the remaining two leading axes.

The fire resistance-light competition tradeoff axis

The axis that explained most of the trait variability was consistent with a tradeoff between fire resistance (especially outer bark) and light competition. Specifically, this axis correlated strongly with bark allocation (positively), especially outer bark, and xylem allocation (negatively), and opposed forest and generalist species from savanna species (Fig. 2). These results were expected, since the outer bark is the main responsible for the protection against environmental adverse conditions, such as fire (Pausas, 2015; Schafer *et al.*, 2015), a key driver of the distribution (Dantas *et al.*, 2016) and origin (Simon *et al.*, 2009; Maurin *et al.*, 2014) of tropical savanna. In addition, the axis was negatively correlated to IPD. The degree to which conduits are mutually connected can influence the rates of water transport as well as the ability to deal with xylem dysfunction or embolism (Choat *et al.*, 2008; Chave *et al.*, 2009; Liu *et al.*, 2019). Fire heating of xylem can air drive hydraulic failure and xylem deformation, which can result in the loss of vessel conductivity (West *et al.*, 2016; Bär *et al.*, 2018; Michaletz, 2018). Thus, since having low IPD increases hydraulic segmentation (Zanne *et al.*, 2006), hence, it increases the fire resistance of savanna species. In the other extreme, a large total xylem area is critical for providing mechanical support in stems and twigs of forest species that usually grow fast and tall to compete for light (Dantas *et al.*, 2013b,a; Wright *et al.*, 2019). These functions are probably aided by the longer vessels and fibers (Chave *et al.*, 2009) that were associated with these species (Fig. 1). Vessel length is positively associated to sapwood specific conductivity and shade tolerance (Bews, 1927; Markesteijn *et al.*, 2011b,a), whereas fiber length is associated with mechanical stability (Chave *et al.*, 2009). Overall, these results point to the key role of fire in the coordinated evolution of bark thickness, plant size, and xylem anatomy to adapt to savanna environments. Moreover, these results suggest that fire resistance forms a key tradeoff axis that is of fundamental importance to segregate species from different physiognomies in Cerrado.

The first PCA axis also showed a strong phylogenetic signal. This occurred despite that its main constituent traits (bark and xylem areas) did not show such a signal. These results support the idea that the coordination of xylem, whole plant and bark traits is evolutionarily conserved, even though allocation to a particular tissue is not. An implication is that clades containing shade-tolerant species are not all equally likely to adapt to savannas. Instead, only those taxa that showed pre-adaptations allowing the evolution of fire-resistance, including a certain degree of hydraulic safety, were likely to diversify and colonize this environment.

The hydraulic efficiency-safety tradeoff axis

The second axis was positively related to IPD, RPD, VDi, and Hmax. Taller plants need wider vessels to maintain sapwood area conductivity, but the associated larger intervessel pit diameter increases the vulnerability to embolism. This axis represents the well-known trade-off between hydraulic efficiency and safety (Choat *et al.*, 2008; Liu *et al.*, 2019). It did not help to differentiate species of different habitat preferences (Fig. 2) which is consistent with previous evidence that both savanna and forest species show a high diversity of water use strategies (Hao *et al.*, 2008). This axis also showed strong phylogenetic signal (Table 4), despite being orthogonal to the first axis. Combined, these results suggest that these resource use strategies also evolved in the deep evolutionary past, long before the Cerrado assembly. Despite that both the first and second axes were related to anatomic level xylem traits and were phylogenetically conserved, they were orthogonal and the latter did not differentiate species according to their habitat preferences. Thus, each axis was associated with different clades and those associated with the later occur in both habitats.

The growth-survival tradeoff axis

The third axis was positively and strongly related to FL, FWT, and VEL, and negatively related to Hmax and VDi (more weakly). Fibers protect vessels from implosion under drought and confer mechanical stability to woody plants (Chave *et al.*, 2009). Vessel length is positively related to sapwood conductivity and cavitation resistance (Bews, 1927; Markesteijn *et al.*, 2011b,a). This axis differentiated forest and savanna species but varied more subtly between savanna and generalist species compared to the first axis. It probably represents the growth-survival tradeoff in which species that grow fast have low mechanical strength, incurring in a higher risk of mortality (Wright *et al.*, 2010; Negreiros *et al.*, 2016). Low potential height, suggesting low height growth, and high mechanical strength, suggesting high survival, were associated with resource conservative savanna species, whereas resource acquisitive forest species were associated to the opposite traits (Reich, 2014). This tradeoff axis did not involve changes in xylem area which probably helps to explain the increase in the mechanical vulnerability of taller plants. We suggest that this tradeoff axis is related to the ability of forest species taking advantage of heterogeneous and pulse resource availability to invest in height growth at the expense of resource conservation. The ability of generalist species to grow slower and somehow conserve resources for resprouting after a fire may be a key trait allowing them to colonize savanna habitats. However, since these species do not have much hydraulic segmentation and a thick twig bark, they are probably more likely to experience top kill after fire damage, and resprouting from the ground, rather than epicormically (West *et al.*, 2016). This may explain why these species did not complete the transition to the savanna environment. The fact that this axis was evolutionarily labile suggests that a conservative resource strategy is an ease to evolve and is not associated with a particular clade.

The importance of inner vs outer bark allocation

Allocations to inner and to outer bark were not correlated and the inner bark did not differ among any of the habitat-preference groups. Thus, variation in this trait must have little adaptive value for the assembly of savanna under climates also suitable for forest. This result is consistent with previous evidence that the inner bark is tightly controlled by stem diameter across the angiosperms (Rosell, 2016). In contrast, total bark allocation correlated strongly with periderm area, suggesting very strong adaptations to resist fire and external hazards (Rosell, 2016; Pausas, 2017; Rosell *et al.*, 2017), and both differed between savanna and forest species.

Determinants of Stem Maximum Height

Even though maximum plant height was higher in forest species, it did not tradeoff exclusively with stem and twig fire resistances (Table 2). Instead, maximum tree height showed a similar correlation to all three axes. We suggest that, in the first axis, the lower tree height of savanna species, as well as the lower lengths of fibers and vessel elements may be partially an allometric consequence of the lower xylem allocation, instead of a tight constraint imposed by bark allocation. Xylem area was strongly negatively correlated to bark investments, suggesting that these traits trade-off more directly. In contrast, the variation of maximum height associated with the second axis probably results from constraints resulting from different hydraulic strategies and do not explain the differences in potential height between forest and savanna species. Finally, the variation associated with the third axis probably results from the different responsiveness of savanna and forest species to resource availability. Thus, maximum height seems to be modulated by multiple dimensions of plant strategy involving both resource and disturbance.

Stem height was also significantly correlated with wood density (WD), which scored low in the three axes and did not seem to contribute much to trait tradeoff and coordination, or to differences in habitat preferences among species at this scale. Previous studies, including forest species only, showed a weak correlation between WD and the growth-survival tradeoff (Wright *et al.*, 2010). Among savanna species, WD is highly influenced by soil nutrient status (Bucci *et al.*, 2006). Because, fire regime differences produce soils of contrasting fertilities (Pellegrini *et al.*, 2014, 2015), and forest and savanna species are favored by soils of different intrinsic fertility (e.g. Hoffmann *et al.*, 2012) soil chemistry and wood density often, but not always, differ between savanna and forest species (Hao *et al.*, 2008; Dantas *et al.*, 2013b,a; Maracahipes *et al.*, 2018). Since our data was compiled from different sources, it mainly reflects the intrinsic interspecific differences among species, rather than local features. Despite that WD was not correlated to any of the axes, nor to hydraulic traits demonstrating that WD and conductivity can be decoupled (Martínez-Cabrera *et al.*, 2009; Zanne *et al.*, 2010). Overall, high WD species were taller and have high ray density (R.mm) which can be explained by the fact that rays confer mechanical stability and flexibility, both attributes associated with wood density (Dória *et al.*, 2019).

Patterns of Trait Evolution

All wood anatomy traits, except VDe and RPD, presented a phylogenetic signal. In contrast, none of the bark and morphological traits did. This result agrees with previous studies showing that anatomic wood traits tend to be phylogenetically conserved (Stepanova *et al.*, 2013; Pace *et al.*, 2015; Román-Jordán *et al.*, 2017), whereas bark investments are more labile (Simon *et al.*, 2009). Plants developed their anatomical wood traits to deal with water availability long before they developed bark thickness for fire resistance purposes in the late Miocene-Pliocene (Simon *et al.*, 2009; Stepanova *et al.*, 2013; Pace *et al.*, 2015; Román-Jordán *et al.*, 2017). However, the tradeoff axis relating bark and wood allocation showed a strong phylogenetic signal, suggesting that this constraint is also ancient. Overall, these results highlight the importance of studying trait evolution from a trait strategy perspective, rather than focusing on individual traits only.

Concluding Remarks

We showed that differences in the rate of bark production relative to xylem are correlated with morphologic- and anatomic- level trait differences, as well as with differences in competition for light. Savanna species invest more in bark allocation and hydraulic segmentation providing them higher resistance to fire. On the other hand, forest species invest more in stem growth and mechanical stability, which are important in light-limited environments. Such tradeoff is strongly evolutionarily conserved, suggesting that only a few forest clades were able to evolve such traits and colonize savannas. We also showed that other aspects related to hydraulic efficiency-safety, such as those correlated with the second axis, are better explained by evolutionary history than habitat preferences since they are common among species regardless of habitat. We also found evidence for a growth-survival tradeoff axis contrasting resource acquisitive forest and conservatism savanna species. This axis, in contrast, was evolutionary labile. We suggest that this axis contributed to the early colonization of savannas due to its importance to resprouting ability. Among these early colonists, only a few clades developed the extreme fire-resistant traits associated with the first axis. Finally, we showed that the bark allocation of savanna species is mostly related to the outer, rather than the inner bark, reflecting the key role of fire in driving the evolution of this trait. Overall, these results shed light into the processes and mechanism that allowed the diversification of ancient forest lineages to successful colonize and originate the savanna biome.

CONCLUSÃO

Nesse trabalho, nós mostramos que as diferenças na proporção de casca nos ramos e no caule em relação a sua área transversal total, estão correlacionadas com as diferenças de características morfológicas e anatômicas, bem como com diferenças na competição por luz. Espécies de savana investiram mais recursos em atributos da casca e em segmentação hidráulica proporcionando a elas uma maior resistência ao fogo. Já, as espécies de floresta investem mais no crescimento do caule e na sua estabilidade mecânica, atributos importantes em ambientes com pouca luz. Tal compromisso parece ser fortemente conservado durante a evolução, sugerindo que apenas alguns clados, proximamente aparentados de espécies de floresta, foram capazes de desenvolver tais características. Mostramos também que outros aspectos relacionados à eficiência e segurança hidráulicas, como os correlacionados com o segundo eixo, são melhor explicados pela história evolutiva, uma vez que são comuns entre as espécies de ambos os habitats. Nós também evidenciamos um eixo de contrabalanço entre crescimento e sobrevivência que contrasta espécies de floresta, que são aquisitivas, e espécies de savana, que são armazenadoras de recursos. Este eixo, em contraste, era evolutivamente lábil. Sugerimos que este eixo tenha contribuído para a colonização inicial das savanas devido à sua contribuição para a capacidade de rebrota. Entre estas poucas espécies colonizadoras, apenas alguns clados proximamente aparentados desenvolveram as características para resistência a incêndios intensos, associadas ao primeiro eixo. Por fim, mostramos que a alocação em espessura de casca, característica das espécies de savana, está principalmente relacionada à alocação a casca externa, e não a interna, refletindo o papel fundamental do fogo na condução da evolução desta característica. No geral, esses resultados lançam luz sobre os processos e mecanismos que permitiram a diversificação de espécies ancestrais de floresta e o sucesso na colonização das savanas por seus descendentes.

APPENDIX

Table A1 *Data information sources for each species for the functional traits compiled from the literature.*

Specie	**Family**	**Wood Density**	**Height**	**Stem relative bark area**
Aegiphila verticillata Vell.	Lamiaceae		28	
Anadenanthera peregrina var. falcata (Benth.) Altschul	Fabaceae	1, 3, 24, 23	29	1
Annona coriacea Mart.	Annonaceae	21	28	33
Annona crassiflora Mart.	Annonaceae	23,	28	27, 33
Aspidosperma tomentosum Mart. & Zucc.	Apocynaceae	1, 15, 19, 22, 24, 23	28	31
Baccharis crispa Spreng.	Asteraceae		29	
Baccharis dracunculifolia DC.	Asteraceae		28	
Bauhinia rufa (Bong.) Steud.	Fabaceae	25	28	27, 33
Bowdichia virgilioides Kunth	Fabaceae	2, 3, 9, 12, 14, 20, 23	28	25
Byrsonima basiloba A.Juss.	Malpighiaceae	1, 24	29	1
Byrsonima coccolobifolia Kunth	Malpighiaceae	1, 3, 10, 12, 14, 22, 24	28	31, 27, 33, 1
Byrsonima verbascifolia (L.) DC.	Malpighiaceae	1, 14, 22, 24, 23	28	33, 1
Campomanesia pubescens (Mart. ex DC.) O.Berg	Myrtaceae	27	29	27
Caryocar brasiliense Cambess.	Caryocaraceae	1, 3, 4, 5, 22, 24, 23	28	1
Casearia sylvestris Sw.	Salicaceae	1, 7, 24, 23	28	27, 33, 1
Cecropia pachystachya Trécul	Urticaceae	6, 9, 23	28	25
Clusia criuva Cambess.	Clusiaceae	16	28	
Connarus suberosus Planch.	Connaraceae	1, 2, 20, 22, 24, 23	28	1
Copaifera langsdorffii Desf.	Fabaceae	9, 23	28	25
Cordia sellowiana Cham.	Boraginaceae	1	28	1
Cordiera concolor (Cham.) Kuntze	Rubiaceae		28	

Specie	**Family**	**Wood Density**	**Height**	**Stem relative bark area**
Couepia grandiflora (Mart. & Zucc.) Benth.	Chrysobalanaceae	3,	28	25
Dalbergia miscolobium Benth.	Fabaceae	20, 22	28	33
Dendropanax cuneatus (DC.) Decne. & Planch.	Araliaceae		28	
Dimorphandra mollis Benth.	Fabaceae	1, 22, 24	28	27, 33, 1
Diospyros lasiocalyx (Mart.) B.Walln.	Ebenaceae	1, 9, 24, 23	28	27, 33, 1
Eriotheca gracilipes (K.Schum.) A.Robyns	Malvaceae	1, 9, 10, 22, 24	28	1
Erythroxylum deciduum A.St.-Hil.	Erythroxylaceae	22, 23	28	
Erythroxylum pelleterianum A.St.-Hil.	Erythroxylaceae		28	
Erythroxylum suberosum A.St.-Hil.	Erythroxylaceae	1, 10, 22, 24	28	31, 33, 1
Erythroxylum tortuosum Mart.	Erythroxylaceae	1, 22, 24	28	33, 1
Eugenia bimarginata DC.	Myrtaceae	1, 24	29	1
Eugenia rigida DC.	Myrtaceae		28	
Ficus guaranitica Chodat	Moraceae	4	29	
Guapira noxia (Netto) Lundell	Nyctaginaceae	1, 22, 24	28	32, 33, 1
Guettarda viburnoides Cham. & Schltdl.	Rubiaceae	9	28	
Ilex theezans Mart. ex Reissek	Aquifoliaceae	16	28	
Kielmeyera rubriflora Cambess.	Calophyllaceae	23	28	31
Lacistema hasslerianum Chodat	Lacistemataceae		28	
Lafoensia pacari A.St.-Hil.	Lythraceae	1, 10, 22, 24, 23	28	31, 27, 1
Lamanonia ternata Vell.	Cunoniaceae	13	28	
Leptolobium elegans Vogel	Fabaceae	25	28	25
Licania tomentosa (Benth.) Fritsch	Chrysobalanaceae	23	28	
Lithraea molleoides (Vell.) Engl.	Anacardiaceae	23	29	
Luehea grandiflora Mart. & Zucc.	Malvaceae	13	28	25
Machaerium acutifolium Vogel	Fabaceae	1, 15, 19, 24, 23	28	33, 1
Magnolia ovata (A.St.-Hil.) Spreng.	Magnoliaceae	23	28	25
Miconia albicans (Sw.) Triana	Melastomataceae	1, 2, 3, 20, 24	28	27, 33, 1

Specie	**Family**	**Wood Density**	**Height**	**Stem relative bark area**
Miconia chamissois Naudin	Melastomataceae		28	
Miconia fallax DC.	Melastomataceae		29	
Miconia ligustroides (DC.) Naudin	Melastomataceae	26	28	33
Miconia theaezans (Bonpl.) Cogn.	Melastomataceae		29	
Moquiniastrum barrosoae (Cabrera) G. Sancho	Asteraceae		29	
Moquiniastrum polymorphum (Less.) G. Sancho	Asteraceae	25	28	25
Myrcia bella Cambess.	Myrtaceae	1, 24	28	33, 1
Myrcia guianensis (Aubl.) DC.	Myrtaceae	1, 3, 8, 11, 24	28	33, 1
Myrsine umbellata Mart.	Primulaceae	8	28	30
Ocotea corymbosa (Meisn.) Mez	Lauraceae	13	28	25
Ocotea pulchella (Nees & Mart.) Mez	Lauraceae	8, 16, 23	28	33
Ouratea spectabilis (Mart.) Engl.	Ochnaceae	1, 3, 24, 23	28	31, 27, 33, 1
Pera glabrata (Schott) Baill.	Peraceae	1, 9, 16, 23	28	33, 1
Persea venosa Nees & Mart.	Lauraceae		28	
Piptocarpha rotundifolia (Less.) Baker	Asteraceae	1, 22, 24, 23	28	33, 1
Platypodium elegans Vogel	Fabaceae	13, 23	28	25,
Plenckia populnea Reissek	Celastraceae	1, 24	28	33, 1
Pleroma oleifolia R. Romero & Versiane	Melastomataceae		29	
Pleroma stenocarpum (Schrank & Mart. ex DC.) Triana	Melastomataceae		29	
Pouteria torta (Mart.) Radlk.	Sapotaceae	1, 10, 13, 24, 23	28	27, 1
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	2, 9, 13, 20, 23	28	
Qualea dichotoma (Mart.) Warm.	Vochysiaceae	3, 9	28	32
Qualea grandiflora Mart.	Vochysiaceae	3, 10, 17, 22	28	31, 27
Qualea multiflora Mart.	Vochysiaceae	22, 23	28	31
Roupala montana Aubl.	Proteaceae	1, 9, 12, 24, 23	28	31, 27, 1
Schefflera vinosa (Cham. & Schltdl.) Frodin & Fiaschi	Araliaceae	3	28	33
Siparuna brasiliensis (Spreng.) A.DC.	Siparunaceae		28	

Specie	**Family**	**Wood Density**	**Height**	**Stem relative bark area**
Strychnos pseudoquina A.St.-Hil.	Loganiaceae	10, 22	28	25
Stryphnodendron polyphyllum Mart.	Fabaceae		28	
Styrax camporum Pohl	Styracaceae	26	28	32
Styrax ferrugineus Nees & Mart.	Styracaceae	1, 11, 22, 24	28	32, 33, 1
Styrax martii Seub.	Styracaceae		28	
Symplocos pubescens Klotzsch ex Benth.	Symplocaceae		28	
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	Bignoniaceae	1, 6, 24, 23	28	27, 1
Tabernaemontana catharinensis A.DC.	Apocynaceae		28	
Tapirira guianensis Aubl.	Anacardiaceae	1, 2, 9, 18, 20, 23	28	33, 1
Terminalia glabrescens Mart.	Combretaceae	9, 13	28	
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	Rubiaceae	6	28	31, 33
Vochysia cinnamomea Pohl	Vochysiaceae	3, 23	28	25
Vochysia rufa Mart.	Vochysiaceae	22	28	25
Vochysia tucanorum Mart.	Vochysiaceae	3	28	30, 32, 33
Zanthoxylum rhoifolium Lam.	Rutaceae	8, 23	28	33
Zeyheria montana Mart.	Bignoniaceae	25	28	

Citation codes: 1 = (Dantas et al., 2013a); 2 = (Silva et al., 2015); 3 = (Abe et al., 2018); 4 = (Balbinot et al., 2017); 5 = (Bucci et al., 2006); 6 = (Wittmann et al., 2008); 7 = (Costa et al., 2014) ; 8 = (Missio et al., 2017) ; 9 = (Imaña-Encinas et al., 2016); 10 = (Ribeiro et al., 2011); 11 = (Hao et al., 2008); 12 = (Jati et al., 2014); 13 = (Ferreira, 2015); 14 = (Barbosa & Fearnside, 2004); 15 = (Markesteijn & Poorter, 2009); 16 = (Melo Júnior & Boeger, 2017); 17 = (Machado Neto et al., 2015); 18 = (Santiago et al., 2004); 19 = (Markesteijn *et al.*, 2011a)*; 20 = (Vale et al., 2010); 21 = (Neves et al., 2017); 22 = (Vale et al., 2002); 23 = (Chave et al., 2009); 24 = (Batalha et al., 2011); 25 = (Maracahipes et al., 2018); 26 = (Miatto et al., 2016); 27 = (Dantas et al., 2013b); 28 = (Oliveira-Filho, 2017); 29 = (Lorenzi, 2002, 2009, 2016); 30 = (Hoffmann et al., 2003); 31 = (Souchie, 2015); 32 = (Diniz, 2009); 33 = (Miatto, 2011).*

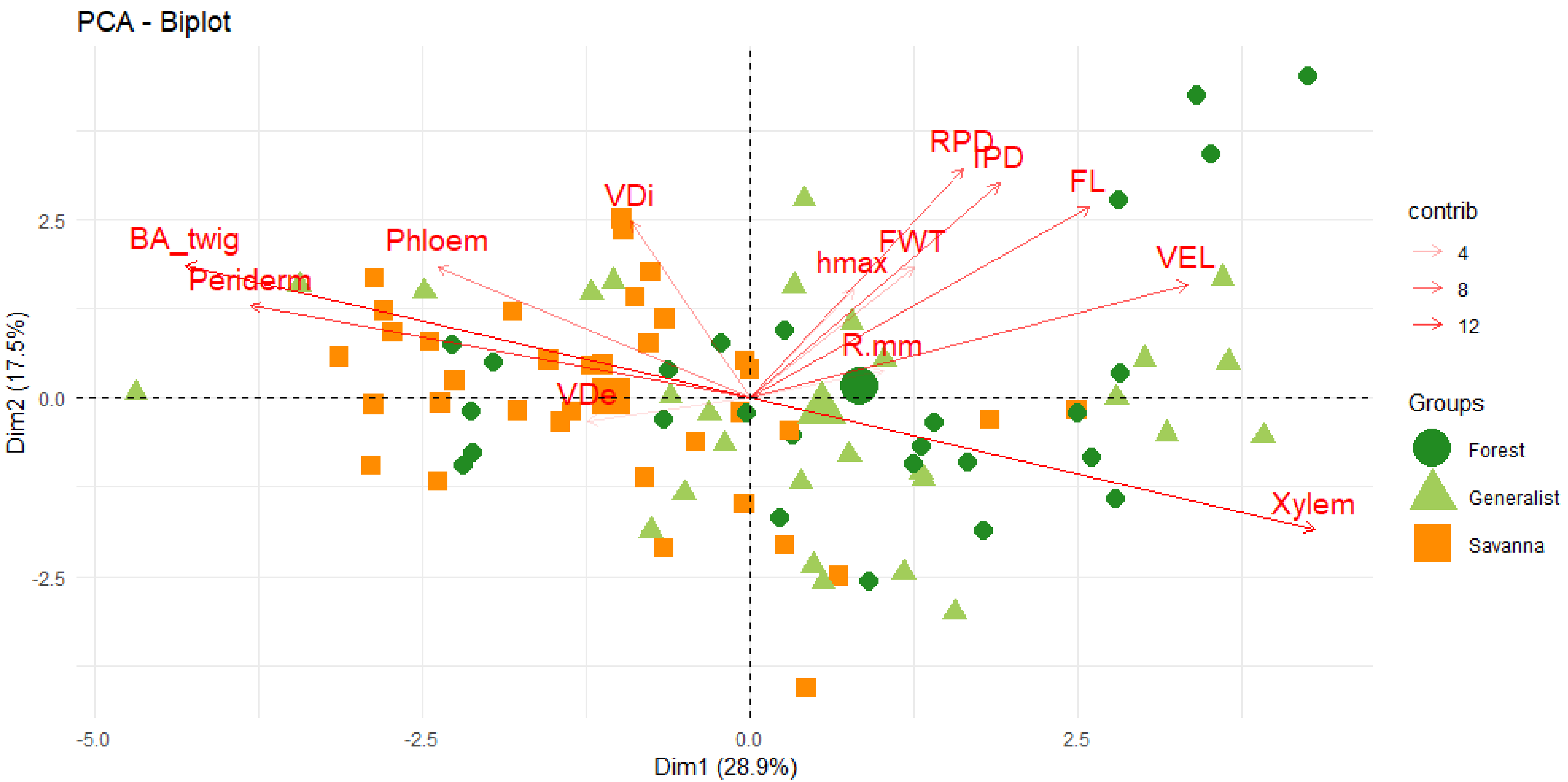

Figure A1 *First two principal component axes of wood anatomical and morphological traits of savanna, forest and generalist woody species for Scenario 2. FL = fiber length, VEL = vessel element length, IPD = intervessel pit diameter, RPD = ray-vessel pit diameter, VDi = vessel element diameter, FWT = fiber wall thickness, R.mm = ray per millimeter, VDe = vessel density, Hmax = maximum tree height, BA_twig = twig relative bark area, Periderm = relative periderm area from twig, Phloem = relative phloem area from twig, Xylem = relative xylem area from twig. PC1 explained 28.92%, PC2 17.54% and PC3 12.86%.*

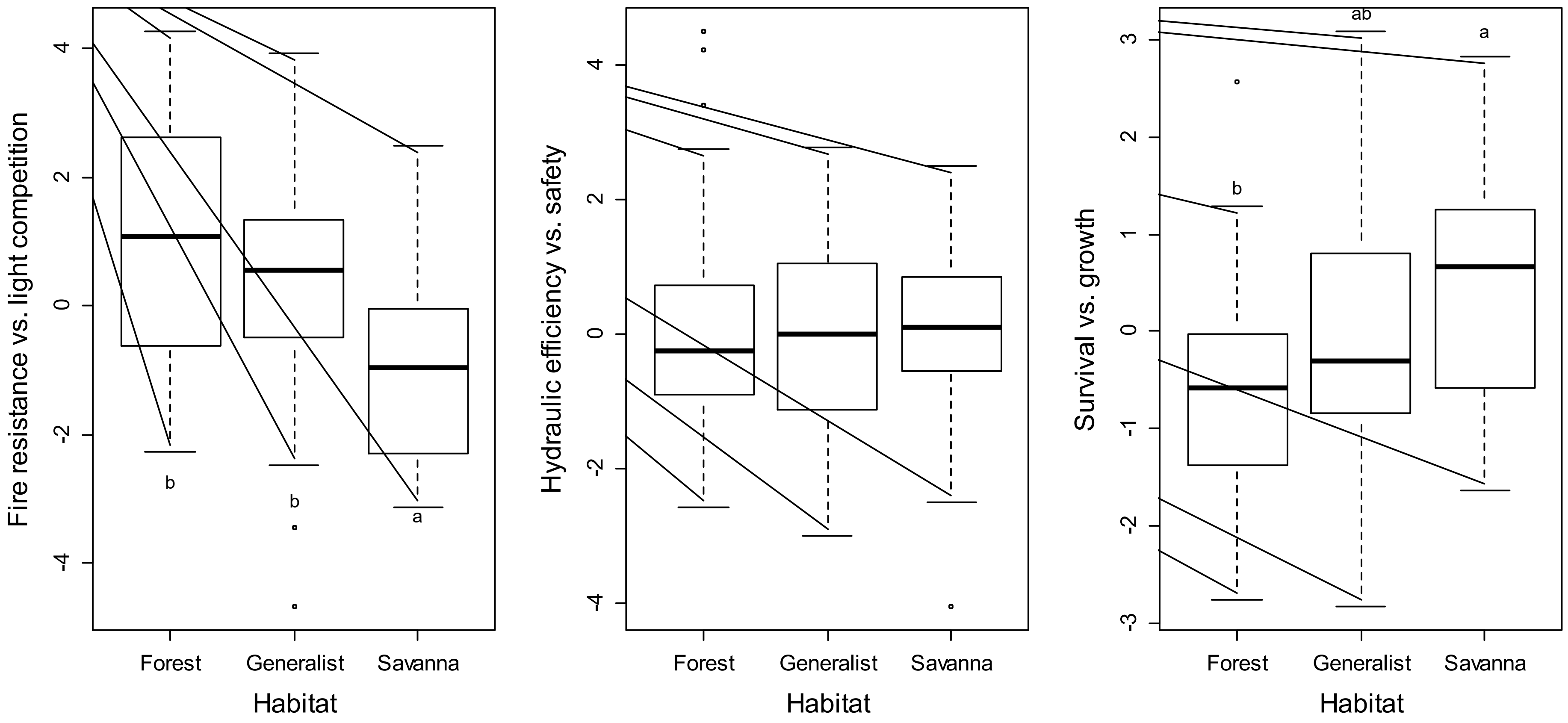

Figure A2 *Differences in principal component scores among savanna, forest and generalist species in the three-leading axis of trait strategies for Scenario 2.*

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