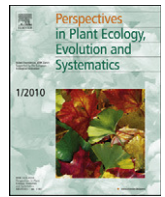




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## Research article

## Plant functional types in Brazilian savannas: The niche partitioning between herbaceous and woody species

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## ABSTRACT

An essential characteristic of savannas is the presence of two main plant functional types: grasses and trees. The tree–grass coexistence in savannas is expected to be stabilised either deterministically by water availability or by occurrences of fire and herbivory. However, under a neutral macroevolutionary perspective, functional types could arise purely as a consequence of branching processes in plant lineages. We sought plant functional types in cerrado by assessing 360 species and 11 functional traits that correspond to important dimensions of the niche of plants. Then, we tested whether random branching processes in plant lineages could generate the observed plant functional types. We sought functional types with the *k*-means partitioning analysis. We constructed a phylogenetic tree for all species sampled and tested whether the phylogeny could be generated by one of the branching processes that can randomly produce functional types: (1) pure birth, (2) rate-constant birth–death, and (3) rate-variable birth–death models. Then, we compared the functional types we observed with a multivariate analysis of variance in a phylogenetic context. Two major functional types characterised the cerrado plant community – one type dominated by grasses and herbaceous shrubs and other by woody shrubs and trees. These functional types were different from the functional types simulated under Brownian motion of evolution of traits. Thus, underlying adaptive processes rather than random evolutionary processes accounted for the plant functional types. The herbaceous and woody functional types seem to have appeared as a consequence of adaptive processes of plants to cope mainly with water availability, fire, and herbivory. However, the niche partition between herbaceous and woody species supports that the reduction in the competitive interactions may be also important to the stable coexistence between trees and grass in savannas.

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## Introduction

An essential characteristic of savannas is the presence of two main plant functional types (non-phylogenetical groups of species that have similarities in their resource uses and responses to biotic and abiotic factors; Wilson, 1998): grasses and trees (Bourlière and Hadley, 1970; Scholes and Archer, 1997; Sankaran et al., 2005; Gottsberger and Silberbauer-Gottsberger, 2006a). Although differences in the relative abundance of plants in these groups promote considerable variations in the physiognomy of savannas (Gottsberger and Silberbauer-Gottsberger, 2006a), the coexistence of grass and tree species maintains savannas clearly distinct from grasslands and forests (Higgins et al., 2000; Batalha and Martins, 2002; Bond et al., 2005). Most authors agree that the association

among several factors, such as species interactions (competition and facilitation), resource availability (nutrients and water), and disturbance regimes (fire and herbivory), determines the balance between herbaceous and woody plants (Scholes and Archer, 1997; Sankaran et al., 2004). However, the predominant mechanisms that allow the persistence of the these two groups in savannas – the tree–grass coexistence hypotheses – are still in intense debate by ecologists (Higgins et al., 2000; Baudena et al., 2010; February and Higgins, 2010).

The fossil evidence of savannas occurring globally for at least 8 million years (Bond et al., 2005; Beerling and Osborne, 2006) easily dispels that they are dynamic plant communities continuously moving towards either forest or grasslands. This long historical existence indicates therefore that savannas are stable systems and, as such, they are thought to support stable long-term interactions between trees and grasses (Baudena et al., 2010). A first attempt to explain this stable coexistence was with resource-based models, which invoke the partitioning of rooting niches of herbaceous and

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woody species (Walker and Noy-Meir, 1982; Scholes and Archer, 1997; Sankaran et al., 2004). Nevertheless, differences in root depth between trees and grasses are rarely observed in field (Scheiter and Higgins, 2007; February and Higgins, 2010), and disturbance-based models have been increasingly tested. According to these models, disturbances, such as fire, drought, and herbivory, sustain predominantly the tree–grass stability, because they prevent the recruitment of tree seedlings into adult classes and, consequently, savannas from becoming forests (Higgins et al., 2000). More recently, Sankaran et al. (2005) demonstrated that disturbances are major determinants only in humid savannas, where water availability would allow the tree dominance. In dry savannas, however, the trees are constrained by the low soil moisture availability, and tree–grass coexistence is deterministically stable (Sankaran et al., 2005). Thus, depending on prevailing environmental conditions, the tree–grass coexistence in savannas is expected to be stabilised either deterministically by resources (water availability) or by disturbances (fire and herbivory; Sankaran et al., 2005; Baudena et al., 2010).

Although the tree–grass persistence in savannas has been increasingly evaluated (Higgins et al., 2000; Baudena et al., 2010; February and Higgins, 2010), the phylogenetic history of the trees and grasses in savanna has not received much consideration. Under a neutral macroevolutionary perspective, functional types could arise purely as a consequence of branching processes in plant lineages (Raup and Gould, 1974; Bookstein, 1988; Pie and Wietz, 2005). Evolutionary radiations result in a certain distribution of trait values within a species assembly as lineages diversify, that is, in a certain morphospace (Ricklefs and Travis, 1980). However, when extinction occurs everywhere in the morphospace and speciation occurs next to an extant lineage, the species have similar functional trait values and the occupation of the morphospace is consequently restricted (Pausas and Verdú, 2008). In this case, the resulting functional group is a product of a random evolutionary process rather than an underlying adaptive process (Bookstein, 1988; Pie and Wietz, 2005; Pausas and Verdú, 2008). Moreover, when a species lineage expands into morphospace, it becomes less and less probable that a random morphological change will lead outside the volume of the morphospace already occupied by the lineage, probably due to genetic, developmental, and ecological constraints (Gavrilets, 1999; Pie and Wietz, 2005; Pausas and Verdú, 2008). Thus, plant functional types, which by definition are groups of plants with limited occupation of the morphospace (Wilson, 1998), should be tested against departures from functional types obtained under a neutral evolutionary mode.

Wherever drought, fire, and herbivory are important ecological factors, they act as environmental filters selecting species with similar niches (Díaz et al., 1998; Weiher et al., 1998; Pausas and Verdú, 2008). Plant species assembled by the same environmental filters exhibit frequently similar tolerances to abiotic conditions or responses to biotic injuries and, as a result, share similar morphological and physiological characteristics, that is, similar functional traits (Cornwell et al., 2006; Pausas and Verdú, 2008; Silva and Batalha, 2010). However, several functional types emerge generally from communities under environmental filters (Díaz et al., 1998; Pausas and Lavorel, 2003; Keith et al., 2007), simply because different ecological strategies solve the same ecological problems (Bond and Midgley, 2001; Winkler and Fischer, 2001; Wainwright, 2007). Even in communities where an environmental condition is predominant, such as in Australian dry woodlands with a pronounced annual drought (ca. 300 mm of annual rainfall), a number of functional types appear (Leishman and Westoby, 1992). Thus, plant functional types other than trees and grasses are also predicted to be important in savannas.

In this study, we sought plant functional types in cerrado, the largest savanna region in South America (Gottsberger and Silberbauer-Gottsberger, 2006a), by assessing 360 species and 11 functional traits. We chose traits that are considered vital for regeneration, reproduction and dispersal (Cornelissen et al., 2003) and, hence, that correspond to important dimensions of the niche of plants (Kraft et al., 2008). Then, we tested whether random branching processes in plant lineages could generate the observed plant functional types. In a nutshell, we tried to answer the following questions: (1) Are there important functional types in cerrado other than trees and grasses?; (2) Could the evolution of cerrado species be determined predominantly by random branching processes?; If so, (3) could the plant functional types in cerrado be generated by random evolution of traits?

## Methods

We surveyed a woodland cerrado site, in Itirapina Experimental Station, Itirapina municipality, southeastern Brazil, located approximately at 22°13'S, 47°51'W. Regional climate is warm temperate with rainy summers and dry winters (Köppen, 1948). Within a grid with 200 quadrats of 25 m<sup>2</sup> (5 m × 5 m), we randomly picked 50 quadrats, where we sampled all vascular plants in 12 monthly field trips from August 2005 to July 2006. We identified the species and characterised their niches classifying them in relation to 11 qualitative functional traits: (1) life-forms (phanerophyte, chamaephyte, hemicryptophyte, geophyte, and therophyte); (2) growth-forms (dwarf shrub, epiphyte, erect leafy, herbaceous and woody liana, palmoid, parasite, semi-basal, short basal, shrub, succulent, tree, and tussock); (3) height class (up to 0.25 m, 0.25–0.5 m, 0.5–1.0 m, 1.0–5.0 m, and higher than 5.0 m); (4) pollination mode (anemophily, cantherophily, chiropterophily, generalist pollination, melittophily, myiophily, ornithophily, phalenophily, psychophily, sphingophily, and by thrips); (5) flower odour (fruity, spicy, resinous, sweet, unpleasant, and no odour); (6) anthesis (diurnal, nocturnal, or both); (7) perianth colour (blue, brown, cream, green, orange, pink, red, violet, white, and yellow); (8) flower sexuality (hermaphrodite and unisexual); (9) propagule type (dry seed, fleshy seed, dry fruit, and fleshy fruit); (10) dispersal mode (active and passive autochory, anemochory of plumed seed and of winged seed, endozoochory, epizoochory, and synzoochory); and (11) presence of trichomes in the leaves. The life-forms and growth-forms were classified according to Cornelissen et al. (2003), the height classes, according to Skov (2000), and the reproductive and dispersal traits, according to Gottsberger and Silberbauer-Gottsberger (2006a,b). We obtained additional data on plant species and functional traits in cerrado from published studies (Gottsberger and Silberbauer-Gottsberger, 2006a,b; Martins and Batalha, 2006).

Most of the cerrado species present belowground organs, which allow them to sprout after fires that remove completely the aboveground parts of the plant (Gottsberger and Silberbauer-Gottsberger, 2006a,b). As a consequence, the traditional classification of cerrado species according to survival after fire (that is, sprouters, resisters, and seeders sensu; Bond and Van Wilgen, 1996) become impracticable. For that reason, we used the life forms of species as a proxy for regenerative strategies of cerrado plants.

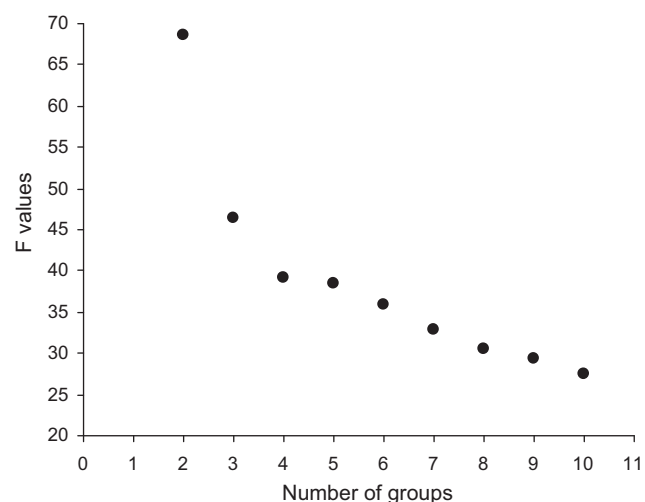
To answer our first question, we constructed a matrix with the species in rows and the functional traits as dummy variables in columns. Then, we sought functional types with the *k*-means partitioning analysis (Legendre and Legendre, 1998). The *k*-means partitioning consists in, given *n* objects in a *p*-dimensional space, determining the partition of the objects in *k* groups, so that objects

within a given group are more similar among themselves than among objects in other groups (Legendre and Legendre, 1998). We randomly assign the objects into 2–10 groups and, for each value of  $k$ , we calculated the pseudo-statistics  $F$  (Calinski and Harabasz, 1974), with the  $k$ -means software (Legendre, 2001). The best partition is that in which the number of groups showed the highest  $F$  value (Legendre and Legendre, 1998). In addition, we compared the number of groups by plotting the  $F$  values against  $k$ . An abrupt change between the highest and the second highest  $F$  values (i.e., the knee point detection) would confirm the number of groups in the data for the highest  $F$  value. To obtain the functional traits that were better associated with the functional types, we also ordered the data with a principal component analysis and constructed a biplot with both species and functional trait scores, distinguishing the functional types previously assigned by the partitioning analysis (Legendre and Legendre, 1998).

To answer our second and third questions, we constructed first a phylogenetic tree for all species using the phylomatic module (Webb and Donoghue, 2004) of the Phylocom software (Webb et al., 2008). The phylomatic is a phylogenetic toolkit for the assembly of phylogenetic trees based on several published phylogenies (Webb and Donoghue, 2004). The lengths of the branches were estimated from ages of the current phylomatic tree (tree R20080147). We fixed the root and all dated nodes, and we extrapolated branch lengths, placing the non-dated nodes evenly between dated nodes and between dated nodes and terminals, using the *bladj* algorithm in the Phylocom software (Webb et al., 2008). When a family node presented polytomies, we distributed the genera into their subfamilies following the last angiosperm phylogenetic relationship (Angiosperm Phylogeny Website, <http://www.mobot.org/MOBOT/research/APweb/> and several recent published papers). We assigned branch lengths of these genera by spacing undated nodes evenly above the family node.

Then, we tested whether the phylogeny could be generated by one of the branching processes that can produce randomly functional types: (1) pure birth, (2) rate-constant birth–death, and (3) rate-variable birth–death models (Nee, 2001; Rabosky, 2006). We compared the fits of the three models of evolution by means of likelihood ratio tests, using the *laser* package for R (Rabosky, 2006). In likelihood methods, model selection is similar to hypothesis testing, by comparing a rate-constant model (models 1 and 2) to a model where diversification rates have varied over time (model 3). The Akaike Information Criterion (AIC; Akaike, 1973) has been widely used to select among different models of diversification (Rabosky, 2006; Rabosky and Lovette, 2008). AICs are calculated for a set of models, and the model with the lowest AIC is taken to be the model that best approximates the data (Rabosky, 2006). We also did this analysis considering only the phylogeny of Fabaceae (54 species in total, see Appendix 1 in Supplemental Material), because this family shows the best time-calibrated resolution of polytomies among genera when comparing to published phylogenies of other cerrado families (Simon et al., 2009). In addition, the Fabaceae assembles species with most of the functional traits studied here. The remaining polytomies within genera were solved by dichotomising randomly the phylogeny of congeners.

To answer our last question, considering all sampled species, we first summarised all trait information into three orthogonal ordination axis (Ricklefs and Travis, 1980), with a principal coordinate analysis (Legendre and Legendre, 1998). Then, we compared the functional types we observed with a multivariate analysis of variance in a phylogenetic context. We compared the observed value of the Wilk's statistic (i.e., the likelihood ratio statistic) of this multivariate analysis of variance to a distribution of values of the Wilk's statistic expected from simulated functional types. These simulated



**Fig. 1.** Distribution of  $F$  values from the pseudo-statistics proposed by Calinski and Harabasz (1974) against number of groups in the  $k$ -means partitioning analysis (Legendre and Legendre, 1998).

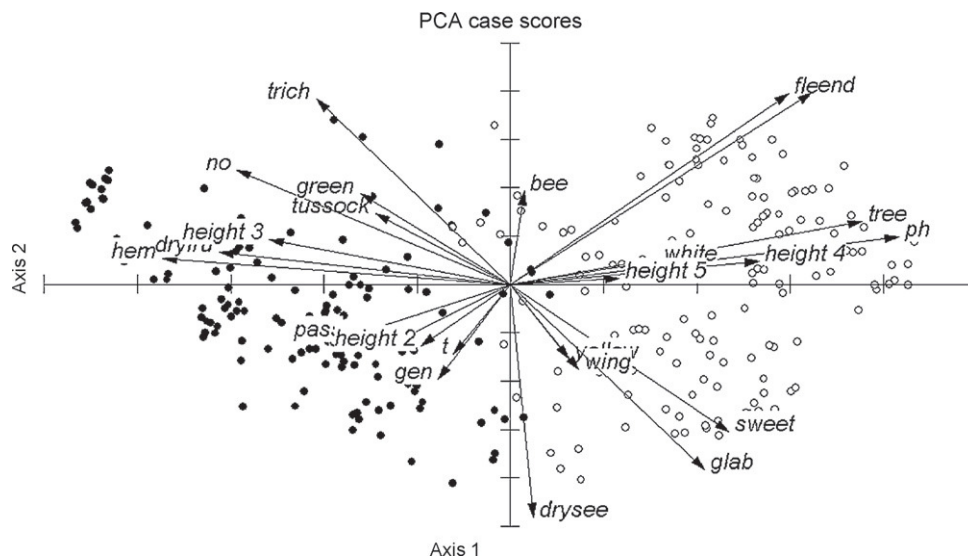
functional types were obtained from trait axes generated under a Brownian motion model of evolution of the species. We simulated the values of the trait axes using the phylogeny of all species and the observed independent contrasts between them (i.e., the evolutionary variance-covariance matrix, Revell et al., 2007). We compared the observed values of the Willis statistic to a distribution of 1000 simulated values with the *geiger* package for R (Harmon et al., 2008). If the value of the Willis statistic for the observed functional types was not different from the values expected from simulated functional types, then we could not reject the possibility that the observed functional types were generated by random branching processes during the evolution of cerrado plants (Pie and Wietz, 2005).

## Results

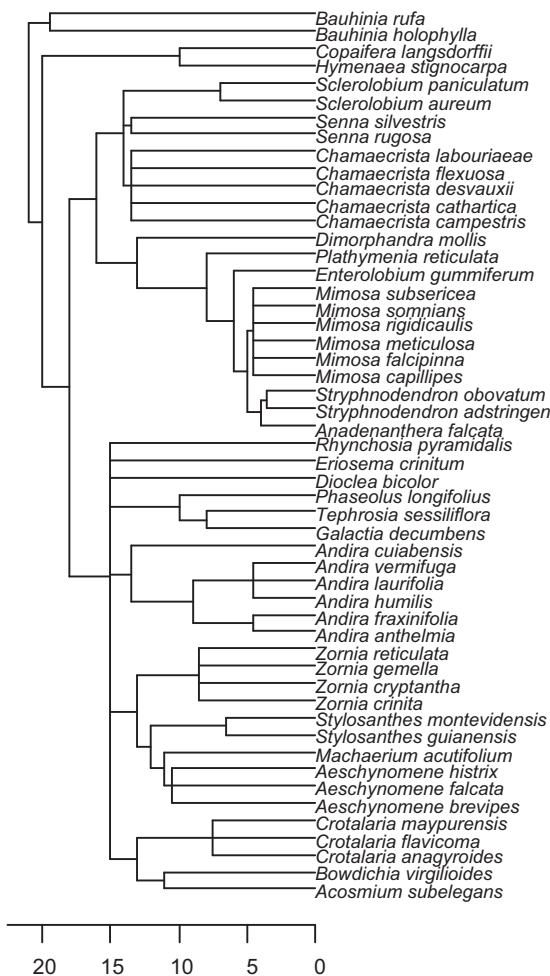
We obtained the functional traits of 360 plant species belonging to 67 families – 93 species sampled in Itrapina and the others, from literature (Appendix 1 in Supplemental Material). The highest value of  $F$  which represented the best partition of species in the  $k$ -means analysis was 68.630 for two groups (Fig. 1). For the other numbers of groups, the values of  $F$  decreased successively from three (46.413) to 10 groups (27.367) (Fig. 1). We found hence two main functional types in cerrado: one represented by herbaceous and small shrubby species (herbaceous type) and other represented by large shrubby and tree species (woody type) (Appendix 1 in Supplemental Material, Fig. 2). The herbaceous type was characterised mainly by the hemicryptophytic life-form, tussock habit, green flowers with no odour, dry fruits passively dispersed, and hairy leaves. The woody type was characterised mainly by phanerophytic life-form, tree habit, coloured flowers with sweet odour, fleshy fruit dispersed by animals, and glabrous leaves (Fig. 2).

The phylogeny of all species did not fitted well any evolution mode (AIC=92.658 for the pure birth and rate-constant birth–death model, and AIC=262.943 for the rate-variable birth–death model), mainly because of the lack of resolution of the phylogenetic tree. However, the branching pattern of the Fabaceae phylogeny (Fig. 3) fitted a rate-variable birth–death model (AIC=5.136, LH=0.432,  $r_1=0.146$ ,  $r_2=0.008$ ) better than the pure birth model (AIC=39.128, LH=−18.564,  $r=0.089$ ) and the rate-constant birth–death model (AIC=41.128, LH=−18.564,  $r=0.089$ ).





**Fig. 2.** Biplot of plant species belonging to the woody functional type (white circles) and to the herbaceous functional type (black circles) and main functional traits (vectors) in cerrado. The main functional traits were related to life-forms (ph = phanerophyte, hem = hemicryptophyte, t = therophyte), growth-forms (trees and tussocks), plant height (height 2 = 0.25–0.5 m, height 3 = 0.5–1.0 m, height 4 = 1.0–5.0 m, height 5 = higher than 5.0 m), pollination modes (generalist = gen, melittophily = bee), flower odour (sweet and no odour), flower color (green, yellow, and white), propagule type (dry fruit = dryfru, dry seed = drysee, flesh fruit = flesfr), dispersal mode (endozoochorous = end, passive autochourous = pass, anemochory of winged seed = wing) and presence (trich) or absence (glab) of trichomes. Short vectors were omitted.



**Fig. 3.** Phylogenetic tree of the Fabaceae species in cerrado. The relationship among genera was based on Phylomatic's reference tree (R20080147; Webb & Donoghue, 2004) and Simon et al. (2009). The scale is in million years.

The herbaceous and woody functional types were also different according to the multivariate analysis of variance (Wilks = 0.198,  $F = 472$ ,  $P < 0.001$ ). These functional types were different from the functional types simulated under random evolution of traits ( $P < 0.001$ ). Thus, underlying adaptive processes rather than random evolutionary processes accounted for the ecological strategies associated with herbaceous and woody functional types in cerrado.

### Discussion

Two major functional types emerged from cerrado plants: one type dominated by grasses and herbaceous shrubs and other by woody shrubs and trees. Grasses and trees are the growth-forms that characterise the savanna physiognomy (Scholes and Archer, 1997) and, as such, they are considered undeniably important functional types (Sankaran et al., 2004; Baudena et al., 2010). However, other important types could also appear in savannas because of the several ecological responses of plants to the same environmental problems (Bond and Midgley, 2001; Wainwright, 2007). This seems to be the case in cerrado, where two larger functional types – a herbaceous and a woody type – which encompass grasses and trees, seem to encapsulate the predominant ecological strategies of plants to cope with environmental constraints.

The resource-based model of tree–grass coexistence in savannas predicts niche partitioning between grasses and trees (Scholes and Archer, 1997). This model is frequently refuted in experiments focusing on the partition of rooting niches (Scheiter and Higgins, 2007; February and Higgins, 2010). Nevertheless, differences between herbaceous and woody species arise when other dimensions of the niche are considered (Fig. 1). In relation to the regenerative niche of plants, most of the herbaceous species were characterised by the hemicryptophytic and therophytic life-form, whereas the woody species, by the phanerophytic life-form. So, herbaceous species seem to have two main ecological strategies to deal with fire and drought, which are different from that of the woody species – the hemicryptophytes are able to resprout promptly after the disturbance and the therophytes to avoid the disturbances, whereas the phanerophytes are able to resist the disturbances (Bond and Midgley, 2001; Cornelissen et al., 2003).

The hemicryptophytes and phanerophytes are always well represented in cerrado sites, and these overrepresentations distinguish the cerrado from other vegetation types (Batalha and Martins, 2002). In regard to the aspects of niche associated with dispersal, for example, most of the herbaceous species disperse predominantly dry fruits without assistance of animals, whereas most of the woody species disperse predominantly fleshy fruits that are eaten by animals (Fig. 1). These findings are in accordance with the generalisation made by various authors that the biotic dispersal is associated with woody plants and the abiotic dispersal modes, with herb plants (Hughes et al., 1994; Ozinga et al., 2004). The distinct phenological periods between herbaceous and woody species are also an evidence of niche partitioning in cerrado (Batalha and Martins, 2004). Thus, the differences in several dimensions of the niche of herbaceous and woody species support the resource-based model of tree–grass coexistence in savannas.

However, some functional traits seem to be common in both herbaceous and woody species, such as the dispersal of dry seeds (Fig. 1). In this case, overall environmental filters may account for the similar responses of the plants (Díaz et al., 1998; Weiher et al., 1998). The dispersion of dry seeds tend to be common in communities with frequent disturbances, where a selective advantage is gained by those species that succeed in spreading high propagule densities across large parts of the landscape (Ozinga et al., 2004). Thus, the dispersal of dry seeds, mainly those winged ones, seems to be an overall ecological strategy favoured by the pronounced dry season and frequent fires in cerrado.

Our results also supported that random branching processes alone, which could potentially generate functional types (Bookstein, 1988; Pie and Wietz, 2005), do not explain the origin of herbaceous and woody species in cerrado. The phylogeny of Fabaceae was better described by the rate-variable birth–death model, in which both speciation and extinction have occurred at different times during the evolutionary process. Considering that the radiation of most of the plant species in cerrado was *in situ* via frequent recent adaptive shifts to resist fire stands (Simon et al., 2009), it is reasonable to suppose that other families also had similar variable rates of speciation and extinction. Under a neutral evolutionary scenario, these variable patterns of speciation and extinction could produce functional types (Pie and Wietz, 2005). Nevertheless, the simulated functional types evolving according to a stochastic model did not reproduce the discrete morphospace occupation of the observed functional types. Thus, adaptive processes explain the evolution of the distinct functional responses of herbaceous and woody species in cerrado.

We sought functional types considering traits that are considered vital for regeneration, reproduction and dispersion of plants (Cornelissen et al., 2003). However, we could not include two other important plant functional traits associated with the responsiveness to opportunities for rapid growth and the ability to cope with disturbances – the specific leaf area and the seed mass (Westoby, 1998). These traits are expected to vary largely among woody species in savannas (Hoffmann and Franco, 2003; Hoffmann et al., 2005). Nonetheless, between herbaceous and woody species, the variation of these traits is still not understood. As long as herbaceous and woody species exhibit distinct ecological strategies associated with the traits assessed here, differences are expected to arise when specific leaf area and seed mass are also evaluated. Further studies should seek differences in these traits to validate the generalisations concerning the herbaceous and woody functional types.

The functional types we found here should be seen as an starting point for the construction of more elaborate functional classifications for savanna species. The two groups we identified with *k*-means partitioning analysis were those in which species

were more similar among themselves than among species in other groups (Legendre and Legendre, 1998). However, these two large functional types contain smaller types into which species share a number of functional similarities. The purpose of clustering analyses, such as the *k*-means partitioning, is to identify various objects types that may be used to describe the structure of the continuum; it is thus immaterial to wonder whether these clusters are natural or unique (Legendre and Legendre, 1998; Anderson and Clements, 2000). Notwithstanding, functional types are still more useful than taxonomic groups when one is interested in explaining plant responses to environmental changes (Wilson, 1998; Díaz et al., 1998).

In conclusion, two major functional types characterised the cerrado plant community – the herbaceous and the woody functional types. These functional types seem to have appeared as a consequence of adaptive processes of plants to cope mainly with water availability and fire rather than as a consequence of stochastic branching processes during the evolution of plant lineages. However, the niche partition between herbaceous and woody species supports that the reduction in the competitive interactions may be also important to the stable coexistence between trees and grass in savannas.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ppees.2011.05.006.

#### References

- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, F. (Eds.), Proceedings of the Second International Symposium on Information Theory. Akademiai Kiado, Budapest, pp. 267–281.
- Anderson, M.J., Clements, A., 2000. Resolving environmental disputes: a statistical method for choosing among competing cluster models. *Ecol. Appl.* 10, 1341–1355.
- Batalha, M.A., Martins, F.R., 2004. Reproductive phenology of the cerrado community in Emas National Park (central Brazil). *Aust. J. Bot.* 52, 149–161.
- Batalha, M.A., Martins, F.R., 2002. Life-form spectra of Brazilian cerrado sites. *Flora* 197, 452–460.
- Baudena, M., D'Andrea, F., Provenzale, A., 2010. An idealized model for tree–grass coexistence in savannas: the role of life stage structure and fire disturbances. *J. Ecol.* 98, 74–80.
- Beerling, D.J., Osborne, C.P., 2006. The origin of the savanna biome. *Global Change Biol.* 12, 2023–2031.
- Bond, W.J., Van Wilgen, B.W., 1996. Fire and plants. Chapman & Hall, London.
- Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. *New Phytol.* 165, 525–538.
- Bond, W.J., Midgley, J.J., 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* 16, 45–51.
- Bookstein, F., 1988. Random walks and the biometrics of morphological characters. *Evol. Biol.* 23, 369–398.
- Bourlière, F., Hadley, M., 1970. The ecology of tropical savannas. *Ann. Rev. Ecol. Syst.* 1, 125–152.
- Calinski, T., Harabasz, J., 1974. A dendrite method for cluster analysis. *Commun. Stat.* 3, 1–27.
- Cornelissen, J.H.C., Lavorel, S., Garniel, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335–380.
- Cornwell, W.K., Schwillk, D.W., Ackerly, D.D., 2006. A trait based test for habitat filtering: convex hull volume. *Ecology* 86, 1465–1471.

- Díaz, S., Cabido, M., Casanoves, F., 1998. Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.* 9, 113–122.
- February, E.C., Higgins, S.I., 2010. The distribution of tree and grass roots in savannas in relation to soil nitrogen and water. *S. Afr. J. Bot.* 76, 517–523.
- Gavrilets, S., 1999. Dynamics of clade diversification on the morphological hypercube. *Proc. R. Soc. Lond.* 266, 817–824.
- Gottsberger, G., Silberbauer-Gottsberger, I., 2006a. Life in the Cerrado: A South American Tropical Seasonal Vegetation Pollination and Seed Dispersion, vol. 2. Reta Verlag, Ulm.
- Gottsberger, G., Silberbauer-Gottsberger, I., 2006b. Life in the Cerrado: A South American Tropical Seasonal Vegetation. Vol. 1 Origin, Structure, Dynamics and Plant Use. Reta Verlag, Ulm.
- Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E., 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24, 129–131.
- Higgins, S.I., Bond, W.J., Trollope, W.S.W., 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *J. Ecol.* 88, 213–229.
- Hoffmann, W.A., Franco, A.C., 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. *J. Ecol.* 91, 475–484.
- Hoffmann, W.A., Franco, A.C., Moreira, M.Z., Haridasan, M., 2005. Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. *Funct. Ecol.* 19, 932–940.
- Hughes, L., Dunlop, M., French, K., Leishman, M., Rice, B., Rodgerson, L., Westoby, M., 1994. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *J. Ecol.* 82, 933–950.
- Keith, D.A., Holman, L., Rodoreda, S., Bedward, M., 2007. Plant functional types can predict decade-scale changes in fire-prone vegetation. *J. Ecol.* 95, 1324–1337.
- Köppen, W., 1948. *Climatología*. Fondo de Cultura Económica, Ciudad del Mexico.
- Kraft, N.J.B., Valencia, R., Ackerly, D.D., 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322, 580–582.
- Legendre, P., 2001. *Program K-means User's Guide*. Université de Montréal, Montréal.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Developments in Environmental Modelling. Elsevier, New York.
- Leishman, M.R., Westoby, M., 1992. Classifying plants into groups on the basis of associations of individual traits—evidence from Australian semi-arid woodlands. *J. Ecol.* 80, 417–424.
- Martins, F.Q., Batalha, M.A., 2006. Pollination systems and floral traits in cerrado woody species of the Upper Taquari region (central Brazil). *Braz. J. Biol.* 66, 543–552.
- Nee, S., 2001. Inferring speciation rates from phylogenies. *Evolution* 55, 661–668.
- Ozinga, W.A., Bekker, R.M., Schaminée, J.H.J., Van Groenendael, J.M., 2004. Dispersal potential in plant communities depends on environmental conditions. *J. Ecol.* 92, 767–777.
- Pausas, J.G., Verdú, M., 2008. Fire reduces morphospace occupation in plant communities. *Ecology* 89, 2181–2186.
- Pausas, J.G., Lavorel, S., 2003. A hierarchical deductive approach for functional types in disturbed ecosystems. *J. Veg. Sci.* 14, 409–416.
- Pie, M.R., Wietz, J.S., 2005. A null model of morphospace occupation. *Am. Nat.* 166, E1–E13.
- Rabosky, D.L., 2006. Likelihood methods for detecting temporal shifts in diversification rates. *Evolution* 20, 1152–1164.
- Rabosky, D.L., Lovette, I.J., 2008. Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution* 62, 1866–1875.
- Raup, D., Gould, S.J., 1974. Stochastic simulation and evolution of morphology: towards a nomothetic paleontology. *Syst. Zool.* 23, 305–322.
- Revell, L.J., Harmon, L.J., Langerhans, R.B., Kolbe, J.J., 2007. A phylogenetic approach to determining the importance of constraint on phenotypic evolution in the neotropical lizard *Anolis cristatellus*. *Evol. Ecol. Res.* 9, 261–282.
- Ricklefs, R.E., Travis, J., 1980. A morphological approach to the study of avian community organization. *Auk* 97, 321–338.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J., Zambatis, N., 2005. Determinants of woody cover in African savannas. *Nature* 438, 846–849.
- Sankaran, M., Ratnam, J., Hanan, N.P., 2004. Tree–grass coexistence in savannas revisited—insights from an examination of assumptions and mechanisms invoked in existing models. *Ecol. Lett.* 7, 480–490.
- Scheiter, S., Higgins, S.I., 2007. Partitioning of root and shoot competition and the stability of savannas. *Am. Nat.* 170, 587–601.
- Scholes, R.J., Archer, S.R., 1997. Tree–grass interactions in savannas. *Ann. Rev. Ecol. Syst.* 28, 517–544.
- Skov, F., 2000. Distribution of plant functional attributes in a managed forest in relation to neighbourhood structure. *Plant Ecol.* 146, 121–130.
- Silva, I.A., Batalha, M.A., 2010. Woody plant species co-occurrence in Brazilian savannas under different fire frequencies. *Acta Oecol.* 36, 85–91.
- Simon, M.F., Grether, R., Queiroz, L.P., Skemae, C., Pennington, R.T., Hughes, C.E., 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proc. Natl. Acad. Sci. U.S.A.* 106, 20359–20364.
- Wainwright, P.C., 2007. Functional versus morphological diversity in macroevolution. *Annu. Rev. Ecol. Syst.* 38, 381–401.
- Walker, B.H., Noy-Meir, I., 1982. Aspects of the stability and resilience of savanna ecosystems. In: Huntley, B.J., Walker, B.H. (Eds.), *Ecology of Tropical Savannas*. Springer-Verlag, Berlin, pp. 556–590.
- Webb, C.O., Ackerly, D.D., Kembel, S.W., 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24, 2098–2100.
- Webb, C.O., Donoghue, M.J., 2004. Phylomatic: tree assembly for applied phylogenetics. *Mol. Ecol. Notes* 5, 181–183.
- Weiher, E., Clarke, G.D.P., Keddy, P.A., 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81, 309–322.
- Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199, 213–227.
- Wilson, J.B., 1998. Guilds, functional types and ecological groups. *Oikos* 86, 507–522.
- Winkler, E., Fischer, M., 2001. The role of vegetative spread and seed dispersal for optimal life histories of clonal plants: a simulation study. *Evol. Ecol.* 15, 281–301.