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Trait diversity on the phylogeny of cerrado woody species

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During the Neogene, the Brazilian cerrado became established as a large-scale vegetation type. Cerrado lineages started to diversify less than 10 million years ago, coinciding with the rise to dominance of flammable C_4 grasses and the expansion of the savanna biome. Cerrado lineages are strongly associated with adaptations to fire and have sister groups in fire-free nearby forests, implying that the cerrado formed in situ via adaptive shifts to resist fire. By including phylogeny into the analysis of biological traits, we investigated trait diversity of cerrado woody species in a phylogenetic context, sampling a cerrado site in central Brazil. Decomposing trait diversity along the nodes of a phylogenetic tree of cerrado woody species, we found that the rate of trait diversification was higher in the past, coinciding with the major species diversification of angiosperms in mid-Cretaceous, long before the cerrado originated. Some more recent adaptive shifts to resist fire, however, must have occurred during the origin and expansion of the cerrado woody flora. Analysing values of each trait separately at the tips of the phylogenetic tree, we found that most trait values were randomly distributed, probably because we analysed only species that had already been filtered by drought, fire, and soil. Analysing values of all traits simultaneously at the tips, we found close to root events and broad, macro-evolutionary patterns, called 'global structures', opposing some lineages, especially Fabaceae and Myrtaceae, with different ecological strategies. Fabaceae presented compound, large, tender leaves, with high nitrogen content due to symbiosis with nitrogen-fixing bacteria, and Myrtaceae presented simple, small, tough leaves, with low nitrogen and high potassium content. We also found relatively recent events that induced divergence of the evolutionary strategies close to the tips, called 'local structures', involving more recent changes in most lineages.

Phylogeny has long been recognised as a major source of biological variation (Jombart et al. 2010). Formerly, the effect of phylogeny was seen as a confounding factor that should be 'corrected', because species would not be independent data points and would violate one of the assumptions of most statistical tests (Felsenstein 1985, Harvey and Pagel 1991). Some authors questioned this view (Westoby et al. 1995), stating that "phylogenetic correction" was not in fact a correction, but a conceptual decision to give priority to one interpretation over another. Nevertheless, since many communities are likely to be phylogenetically structured, including phylogeny into ecological studies may shed light on community assembly processes (Webb et al. 2002). Phylogeny, hence, becomes not a bias, but a source of important biological information that may be used to identify historical and ecological strategies (Jombart et al. 2010).

Besides this phylogenetic approach, methods based on ecological similarities among co-occurring species using functional traits may provide information about community structure and assembly processes (Kraft et al. 2008, Kraft and Ackerly 2010). Both phylogenetic- and functional-based methods have been broadly applied to many communities, including tropical savannas, but few studies applied both approaches together (Kraft and Ackerly 2010, Silva and Batalha 2010). Combining them, however, may provide far more insights into the processes of community assembly than using either one or the other separately (Swenson and Enquist 2009, Kraft and Ackerly 2010). Some methods have been developed to include phylogeny into the analysis of biological traits (Jombart et al. 2010, Pavoine et al. 2010), which allow one to investigate trait diversity in a phylogenetic context.

During the Neogene, between 25–2 million years ago, the Brazilian cerrado became established as a large-scale vegetation type (Gottsberger and Silberbauer-Gottsberger 2006). Time-calibrated phylogenies suggest that cerrado lineages started to diversify less than 10 million years ago, with most of them diversifying 4 million years ago or less, coinciding with the rise to dominance of flammable C_4 grasses and the expansion of the savanna biome worldwide (Pennington et al. 2006, Simon et al. 2009). During the Quaternary, there were marked modifications and changes of climate with shifts toward more arid conditions (Brown Jr and Ab'Sáber 1979), which lead to an increase in fire frequency (Behling et al. 1998).

Nowadays, the cerrado presents a high richness, with about 2000 woody species (Castro et al. 1999), thought to be the outcome of complex evolutionary patterns, in which

paleoclimatic variations and exchange of floristic elements with surrounding vegetation types played a major role (Forni-Martins and Martins 2000). Among cerrado woody species, there are many taxa that appear to be phylogenetically isolated, because they have no non-savanna congeners (Sarmiento 1983). About half of the cerrado flora is endemic and represented by many congeners (Gottsberger and Silberbauer-Gottsberger 2006), suggesting that cerrado species evolved predominantly in situ (Pennington et al. 2006). Plant phylogenies show that cerrado lineages are strongly associated with adaptations to fire and have sister groups in fire-free nearby forests, implying that the cerrado indeed formed in situ via adaptive shifts to resist fire, rather than via dispersal of lineages already adapted to fire (Simon et al. 2009).

By including phylogeny into the analysis of biological traits, we investigated trait diversity of cerrado woody species in a phylogenetic context. We sampled a cerrado site in central Brazil, measured some functional traits, constructed a phylogenetic tree, and tried to answer the following questions: 1) are trait values of the species in the phylogeny organised so that only one node expresses the whole trait diversity? Skewness of trait diversity toward a single node is expected if the rate of evolution is drastically high in a single branch of the tree or if the rate of evolution was higher in the past leading to a high importance of trait diversity at the root node (Pavoine et al. 2010). 2) Are trait diversity values evenly distributed across nodes? If not, trait diversity would be skewed toward few nodes. Skewness of trait diversity toward few nodes is expected if only a few nodes have high contributions to trait diversity, whereas many have low or no contributions (Pavoine et al. 2010). 3) Are values of the species organised within the phylogeny so that trait diversity is clustered near the root or near the tips? If skewness is concentrated toward the root node, species have more different trait values if they are distantly related on the phylogeny; if skewness is concentrated toward the tips, species have more different trait values if they are closely related (Pavoine et al. 2010). 4) Considering each trait separately and analysing their values at the tips, are trait values phylogenetically autocorrelated? If closely related species tend to have more similar values of a given trait than expected at random, this trait is said to present a positive phylogenetic autocorrelation; if closely related species tend to have more dissimilar values of a given trait than expected at random, this trait is said to present a negative phylogenetic autocorrelation (Jombart et al. 2010). Positive phylogenetic autocorrelation most often results in global patterns of similarity in related taxa, whereas negative phylogenetic autocorrelation corresponds to dissimilarities among tips localised in specific parts of the tree, which are called local structures (Jombart et al. 2010). 5) Extracting few synthetic variables with global or local phylogenetic structures, how are traits related? We expected, when taking all traits into account together, to find both global phylogenetic structure opposing some lineages and local phylogenetic structure opposing closely related species (Jombart et al. 2010). In sum, our main objective was the characterisation of the cerrado woody flora in terms of how much traits diversified in the past and which lineages were concerned.

Methods

We carried out this study in Emas National Park (ENP), located in the Brazilian Central Plateau, southwestern Goiás State (17°49'–18°28'S and 52°39'–53°10'W; Fig. 1). The ENP is one of the largest and most important savanna reserves in South America, covering ca 133 000 ha. Regional climate is tropical and humid, with a wet summer and dry winter, classified as Aw (Köppen 1931). The dry season is from June to August and the wet season from September to May. Annual rainfall and mean temperature lie around 1745 mm and 24.6°C, respectively. In the park, we find a gradient from open (68.1% of its area) to closed savannas (25.1%), as well as other vegetation types, such as wet grasslands (4.9%) and riparian and semideciduous forests (1.2%) (Ramos-Neto and Pivello 2000). ENP has been included by Unesco (2001) in the World Heritage List, as one of the sites containing fauna, flora and key habitats that characterise the cerrado.

Up to 1984, ENP was exploited by farmers for cattle ranching, and dry season burnings were used to promote forage regrowth every year. Afterwards, the reserve was totally fenced, cattle were no longer allowed inside, and a fire exclusion policy was established (Ramos-Neto and Pivello 2000). As a consequence, uncontrolled wildfires began to occur every 3–4 years, burning on average 80% of its total area (Ramos-Neto and Pivello 2000, França et al. 2007). Since 1994, when a catastrophic fire burned almost 95% of ENP's area, approximately 10 km² of preventive firebreaks are burned annually in the dry season, and a fire brigade stays in the park to prevent anthropogenic fires during this period (França et al. 2007). Despite these precautions, in August 2010, another anthropogenic fire burned 93% of ENP's area.

Figure 1. Location of Emas National Park (ENP) in South America and location of plots in ENP, central Brazil (17°49′–18°28′S, 52°39′–53°10′W).

We used a stratified random sampling (Sutherland 2006), in which we divided the study site into 10 strata according to time since last burning, using satellite images from 1973 to 2009. Then, we randomly placed 10 plots, each one with 5 × 5 m, in each stratum. So, we placed 100 plots in total (Fig. 1), which allowed us to capture key characteristics in the study site. In each plot, from September 2009 to January 2010, we sampled all woody individuals with stem diameter equal to or higher than 3 cm at soil level (SMA 1997). We identified all individuals to species level by comparing vouchers to ENP's reference collection (Batalha and Martins 2002). We used Plantminer (Carvalho et al. 2010) to search for families, authors and synonyms concerning our species list.

We constructed a phylogenetic tree for all sampled species with the Phylomatic software, a phylogenetic toolkit for the assembly of phylogenetic trees (Webb and Donoghue 2005). Phylogenetic distances among species from different families were estimated from the current Phylomatic tree (R20080147). We improved tree resolution by consulting recent phylogenies of some clades: Fabaceae (Simon et al. 2009), Malpighiales (Wurdack and Davis 2009), and Myrtaceae (Costa 2009). We placed undated nodes in the tree evenly between dated nodes with the Branch Length Adjustment algorithm in Phylocom (Webb et al. 2008).

We used 10 quantitative plant traits (Table 1) that are relatively easy to measure and represent functional characteristics related to environmental filters, such as drought, fire, and nutrient-poor soils (Cornelissen et al. 2003, Pausas and Paula 2005): basal area, height, bark thickness, wood density, leaf toughness, leaf size, specific leaf area, leaf nitrogen content, leaf phosphorus content and leaf potassium content. The importance of these traits and the way they were measured are described in detail by Cornelissen et al. (2003). We collected data about the functional traits for all individuals sampled in the plots. For each trait and each species with two or more individuals, we calculated average values. For singleton species, we used the measured value of each trait.

We log-transformed some traits with a skewed distribution (basal area, height, leaf size and leaf potassium content) to avoid extreme values. Using all 10 traits, we computed the functional distances among species, calculating Euclidean distances based on trait values standardised by the range (Pavoine et al. 2009). To answer the first three questions raised at the end of the introduction, we measured trait diversity by the quadratic entropy index, which can be decomposed among the nodes of a phylogenetic tree (Pavoine et al. 2010). The contribution to trait diversity of a particular node was equal to the trait diversity among the groups of species descending from it (Pavoine et al. 2010). Following Pavoine et al. (2010), we tested whether trait values of the species in the phylogeny were organised so that only one node expressed the whole trait diversity, whether trait diversity values were evenly distributed across nodes, and whether trait values were distributed within the phylogeny so that trait diversity was clustered either near the root or near the tips. We did all three tests with 999 permutations. To answer the fourth question, we tested whether each trait was phylogenetically autocorrelated using the test of Abouheif (1999), which performs well at detecting phylogenetic structures (Pavoine et al. 2008). To answer the fifth question, we did a phylogenetic principal component analysis (pPCA; Jombart et al. 2010), which is designed to summarise a set of traits into a few synthetic variable exhibiting positive phylogenetic autocorrelation (global structures) or negative phylogenetic autocorrelation (local structures). We conducted all analyses in R (R Development Core Team 2009), using the 'ape' (Paradis et al. 2004), 'ade4' (Dray and Dufour 2007), and 'adephylo' (Jombart and Dray 2008) packages. We also used the 'decdiv' function (Pavoine et al. 2010).

Results

We sampled 531 individuals, belonging to 55 species, for which we calculated average trait values (Appendix 1) and constructed the phylogenetic tree (Fig. 2). Observed value for the 'single-node skewness' test was not different from random ($p = 0.595$; Fig. 3, Appendix 2), but observed values for the 'few nodes skewness' and 'tips/root skewness' tests were greater than expected by chance ($p = 0.03$ and 0.005, respectively; Fig. 3, Appendix 2). We found positive phylogenetic autocorrelation for three traits (Appendix 3), leaf toughness ($p = 0.024$), leaf size ($p = 0.001$), and leaf nitrogen content ($p = 0.003$), indicating that trait values were more similar than expected by chance across closely related species. The other traits were not significantly phylogenetically autocorrelated ($p > 0.05$ in all cases).

We found both global and local phylogenetic structures in the pPCA (Fig. 4, 5, Appendix 3). The first global principal component opposed especially the Fabaceae, with the largest negative scores, to the Myrtaceae, with the largest positive scores (Fig. 4). There was a tradeoff between leaf size, specific leaf area, leaf nitrogen content, and leaf phosphorus content,

Table 1. Plant traits used to calculate trait diversity on the phylogeny and their functional relevance (see Cornelissen et al. 2003 for more details).

Trait	Details	Functional relevance
Basal area	continuous measure, m^2	space occupation, resource uptake, total mass
Height	continuous measure, m	competitive vigor, fecundity, growth time between disturbances, positively correlated with above-ground biomass, root depth, and leaf area
Bark thickness	continuous measure, mm	bud and meristem protection
Wood density	continuous measure, mg mm^{-3}	resistance, lifespan, carbon storage
Leaf toughness	continuous measure, N	leaf tissue density, negatively correlated with growth rate, positively correlated with leaf lifespan
Leaf size	continuous measure, mm^2	energy and water balance, allometric factors, nutrient stress, and disturbance
Specific leaf area	continuous measure, mm^2 mg^{-1}	leaf lifespan, leaf defense, positively correlated with growth rate and maximum photosynthetic rate
Leaf nutrients (N, P, K)	continuous measure, mg g^{-1}	maximum photosynthetic rate, nutrient stress

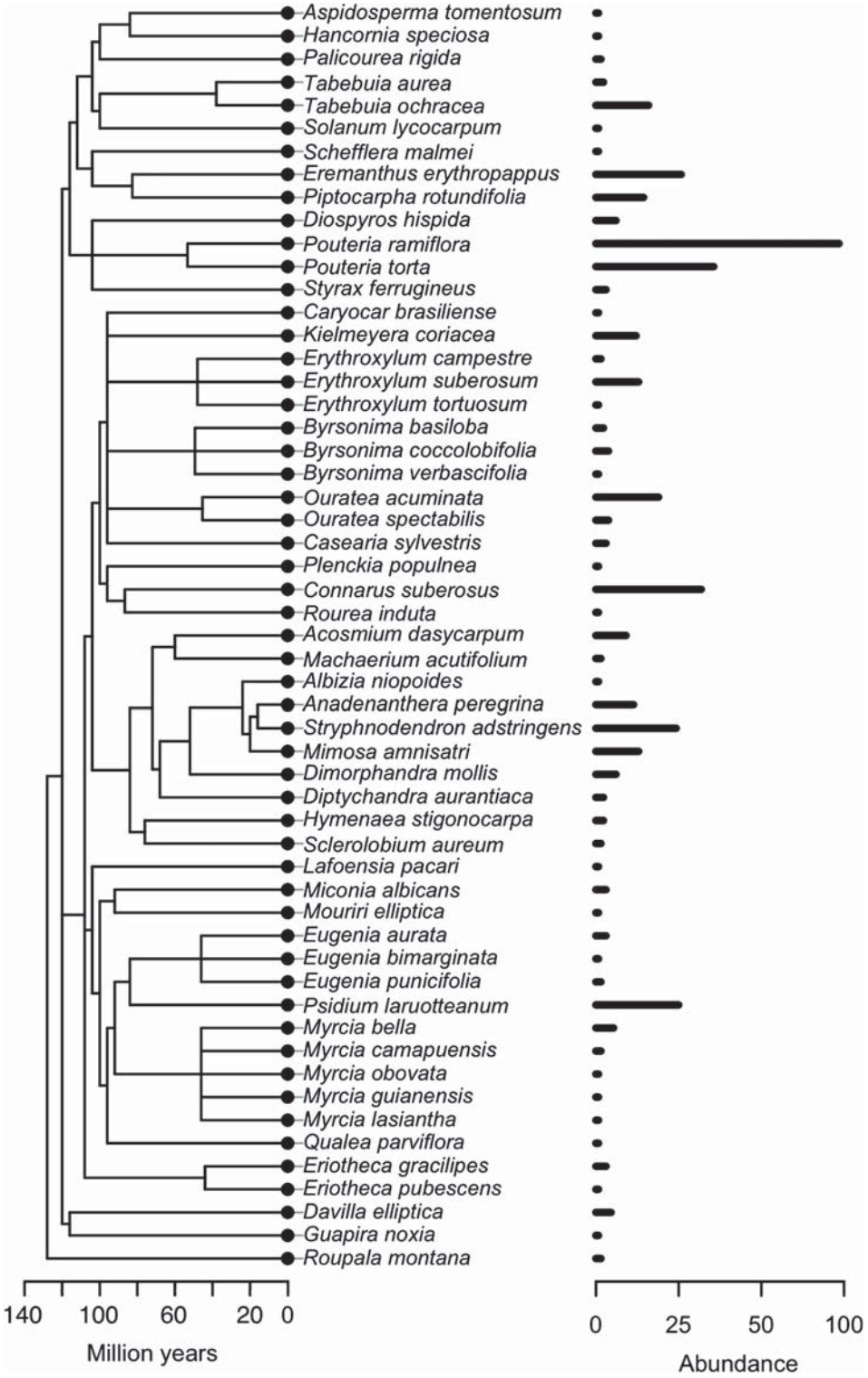

Figure 2. Phylogenetic tree assembled for the cerrado species sampled in Emas National Park, central Brazil, with abundances. The relationship among species was based on the current Phylomatic tree (tree R20080147; Webb and Donoghue, 2005).

with negative loadings in the first global principal component, and bark thickness, leaf toughness, and leaf potassium content, with positive loadings (Fig. 5). Conversely, the first local principal component showed a strong opposition among related species. Leaf size presented positive loadings in the first local principal component, whereas height, basal area, and wood density presented the most negative loadings (Fig. 5).

Discussion

Trait diversity decomposition was not skewed toward a single node, but it was skewed toward few nodes, and those few nodes were closer to the root. Skewness toward few nodes pointed out that the rate of evolution of cerrado woody species was drastically high in a few branches of the tree – for

example, in the node separating the Malvids from the Fabids – and skewness toward the root pointed out that the rate of evolution was higher in the past, about 120–80 million years ago, which coincides with the major species diversification of angiosperms in mid-Cretaceous (Crane et al. 1995). The cerrado appeared much later, about 25 million years ago (Gottsberger and Silberbauer-Gottsberger 2006), and most of its lineages started to diversify about 10 million years ago, when the dominance of flammable C_4 grasses rose and the savanna biome expanded (Pennington et al. 2006, Simon et al. 2009). So, we postulate that skewness of trait diversity toward few nodes and the root is related to the major species diversification of angiosperms in mid-Cretaceous, but some more recent adaptive shifts to resist fire must have occurred during the origin of the cerrado that would allow woody species to withstand the increase in fire frequency (Simon et al. 2009).

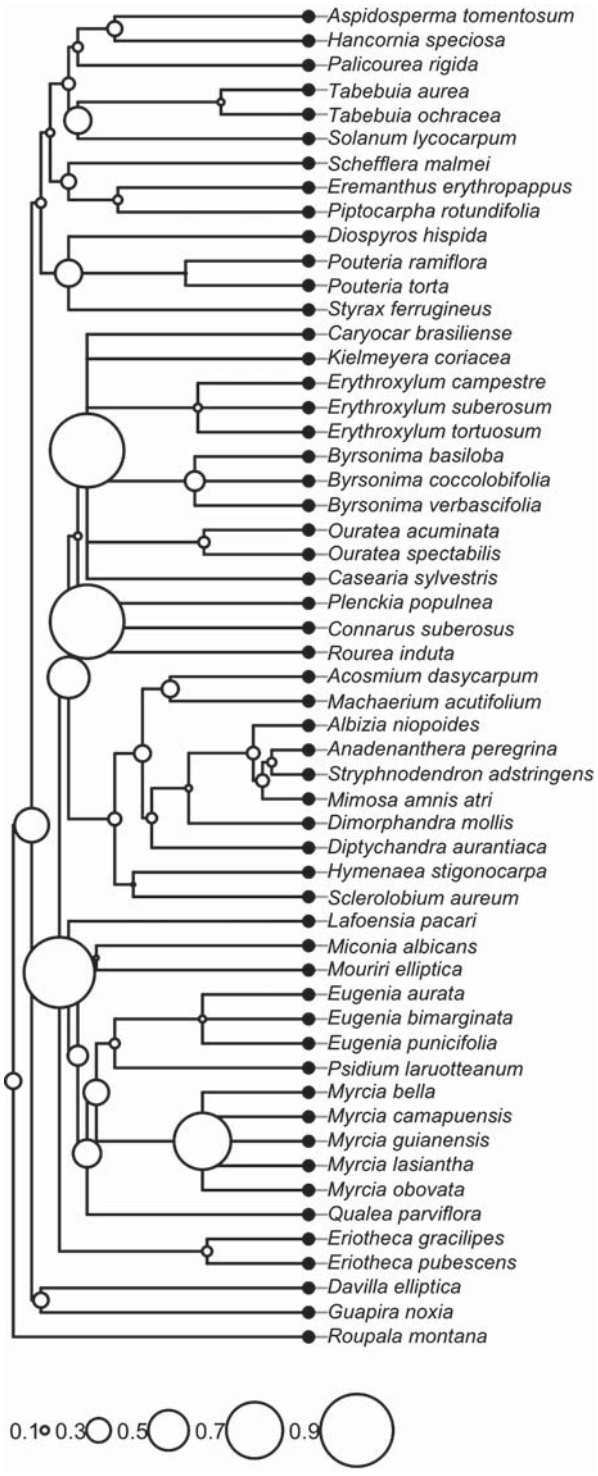

Figure 3. Decomposition of trait diversity among the nodes of the phylogenetic tree assembled for the cerrado species sampled in Emas National Park, central Brazil.

Besides looking at how trait diversity is distributed along the phylogenetic tree, one may also look at the tips only, testing whether closely related species are more similar or more different than expected by chance, that is, whether they present positive or negative phylogenetic autocorrelation. We measured functional traits related to environmental filters that occur in the cerrado, such as drought, fire, and nutrient-poor and aluminium-rich soils (Gottsberger and Silberbauer-Gottsberger 2006). Although positive phylogenetic autocorrelation is very common in lineages of plants (Prinzing et al. 2001, Ackerly 2003), most of the traits we tested were not phylogenetically autocorrelated. Since we analysed only cerrado species, we analysed only species that had already been filtered. In this case, trait values would define the within-habitat α-diversity, or the α niche, and would tend to be randomly distributed in the plant phylogeny (Silvertown et al. 2006). The high species-richness of cerrado communities (Castro et al. 1999) suggests that the traits that determine a plant's niche may be evolutionarily labile and evolve rapidly (Silvertown et al. 2006). If we had included species from the regional pool, such as forest species, or if we had tested phylogenetic autocorrelation according to fire frequency, we would have expected positive phylogenetic autocorrelation to be present in more traits (Pausas and Verdú 2008).

Nevertheless, we found positive phylogenetic autocorrelation for three traits, leaf toughness, leaf size, and leaf nitrogen content. Leaf toughness is a good indicator of the relative carbon investment in structural protection of photosynthetic tissues (Cornelissen et al. 2003) and significantly reduces herbivore attacks (Agrawal and Fishbein 2006). The cerrado contains a rich and abundant community of herbivorous insects (Marquis et al. 2002). In nutrient-poor communities, as the cerrado (Gottsberger and Silberbauer-Gottsberger 2006), plants tend to invest in defenses against herbivores, since they cannot replace damaged tissues rapidly (Fine et al. 2006). Closely related plants tend to share similar defense traits due to a high degree of evolutionary stasis and niche conservatism (Reich et al. 2003). Leaf size has consequences for the leaf energy and water balance and may be constrained by phylogenetic factors (Cornelissen et al. 2003). For instance, the two richest families in our sample, Fabaceae and Myrtaceae, presented leaves with very different sizes; the former with large, compound leaves and the latter with simple, small leaves. The positive phylogenetic autocorrelation in leaf nitrogen content is expected, since nitrogen tends to be the most limiting nutrient in cerrado soils (Gottsberger and Silberbauer-Gottsberger 2006) and the only nitrogen fixers in our sample were leguminous species (Cornelissen et al. 2003). Since nitrogen in soil is higher in frequently burned sites (Silva and Batalha 2008), we expect Fabaceae species to be more abundant in sites burned less frequently.

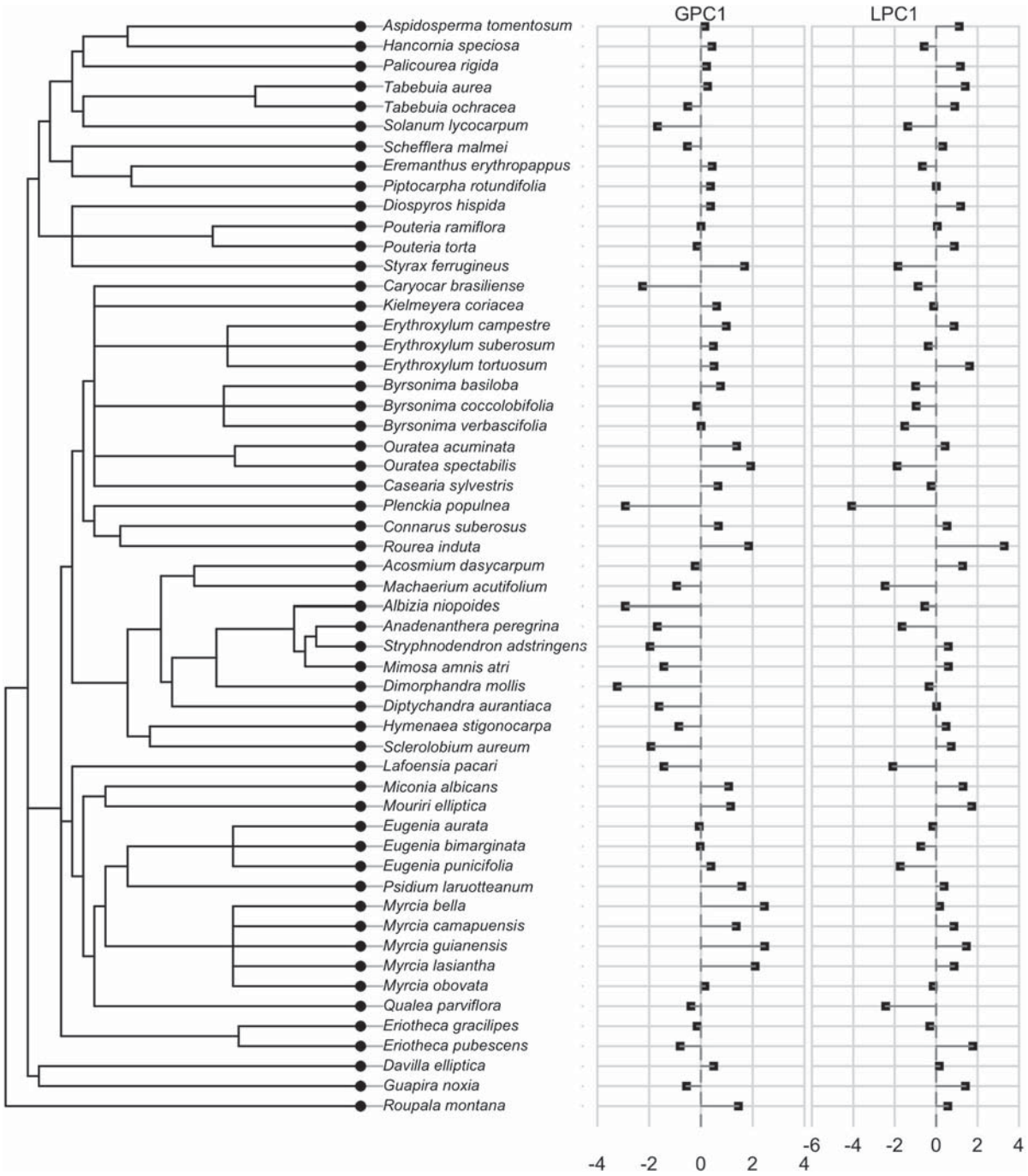

Figure 4. Positive and negative scores identified by phylogenetic principal component analysis of the species sampled in Emas National Park, central Brazil. GPC1 = first global principal component, LPC1 = first local principal component.

When we took all traits into account simultaneously, looking at the tips only, trait diversity was structured in relation to the phylogeny, and we found both global and local phylogenetic structures in the ordination. Global patterns reflect the general idea of phylogenetic signal or positive phylogenetic autocorrelation, whereas local patterns reflect the idea of negative phylogenetic autocorrelation (Jombart et al. 2010). Global patterns correspond to close to root events and broad, macro-evolutionary patterns, whereas local structures correspond to relatively recent events that induced divergence of the evolutionary strategies close to the tips, such as convergence and character displacement (Jombart et al. 2010). These local structures, which may be due to competitive exclusion (Webb et al. 2002), seem to be more subtle in the cerrado woody species phylogeny, because we were able to detect them only when analysing all traits together.

Our results suggested that the tradeoff between leaf size, specific leaf area, leaf nitrogen content and leaf phosphorus content, with negative loadings in the first global principal component, and bark thickness, leaf toughness and leaf potassium content, with positive loadings, may be due to ancient divergence of evolutionary strategies. For instance, Fabaceae and Myrtaceae, the two most important families among cerrado woody species (Castro et al. 1999), presented opposing

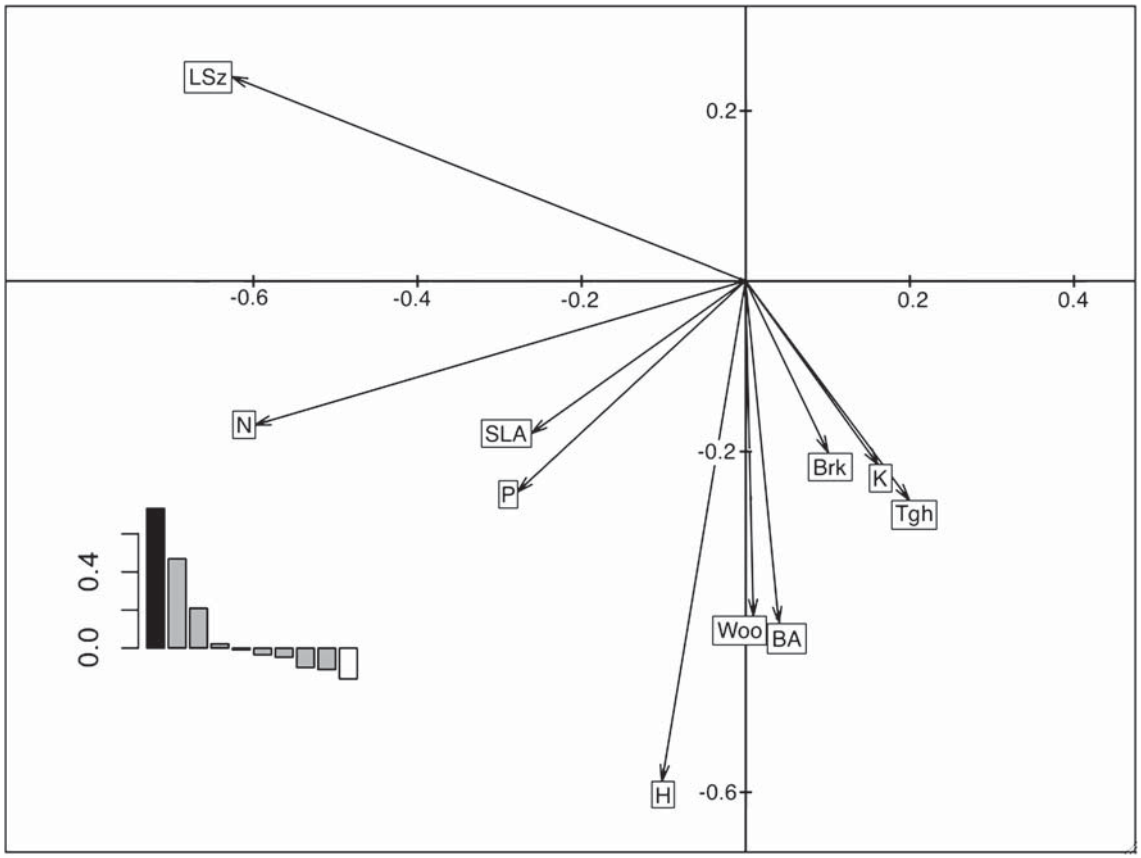

Figure 5. Loadings of the traits for first global (horizontal) and first local (vertical) principal components of the phylogenetic principal component analysis of the species sampled in Emas National Park, central Brazil. BA = basal area, H = height, Brk = bark thickness, Woo = wood density, Tgh = leaf toughness, LSz = leaf size, SLA = specific leaf area, N = leaf nitrogen content, P = leaf phosphorus content, K = leaf potassium content. In the barplot, eigenvalues of the first 10 principal components; first global principal component in black and first local principal component in white.

functional traits, pointing out different ecological strategies. On the one hand, Fabaceae presented compound, large, tender leaves, with high nitrogen content due to symbiosis with nitrogen-fixing bacteria. On the other hand, Myrtaceae presented simple, small, tough leaves, with low nitrogen and high potassium content. In contrast, the tradeoff between leaf size with positive loadings in the first local principal component, and height, basal area and wood density with the most negative loadings seems to be more labile, involving more recent character changes in most of the lineages (Jombart et al. 2010).

The single-node, few nodes, and tips/root skewness tests are adequate if the aim is to test whether trait diversity is reflected in phylogenetic diversity and to discuss how trait diversity is organised given the level of phylogenetic relatedness among species (Pavoine et al. 2010). The tests are neither too liberal nor too conservative; their type I errors are not affected by the number of species, the number of traits, or the model of evolution; and the power is usually high (Pavoine et al. 2010). The pPCA also uncovers efficiently phylogenetic structures, but its main drawback is that the eigenvectors of the phylogenetic proximity matrices are not directly related to a model of evolution, such as the Brownian motion or the Ornstein-Uhlenbeck models (Jombart et al. 2010). Moreover, since we analysed a community phylogenetic dataset, the long time scale increases the chances of multiple and independent evolution of traits that may bias our interpretation. Notwithstanding these limitations, phylogeny is indeed not a nuisance, but a source of relevant ecological information (Jombart et al. 2010). For instance, decomposing trait diversity along the nodes of a phylogenetic tree of cerrado woody species, we found that the rate of trait diversification was higher in the past. Analysing values of each trait separately at the tips of the phylogenetic tree, we found that most trait values were randomly distributed, probably because we analysed only species that had already been filtered by drought, fire, and soil. Analysing values of all traits simultaneously at the tips, we found (1) global structures, opposing some lineages, especially Fabaceae and Myrtaceae, with different ecological strategies, and (2) local structures, more subtle on the phylogeny of cerrado woody species, involving more recent changes in most lineages. Future studies should attempt to analyse more cerrado species, including herbaceous ones, and species from other vegetation types, such as riparian or seasonal forest, that make up the regional pool. It would also be interesting to relate trait diversity on the phylogeny of cerrado species with environmental factors as explanatory variables.

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Appendix 1

Species sampled in Emas National Park, central Brazil (17°49′–18°28′S, 52°39′-53°10′ W) with average trait values. BA = basal area (m^2), H = height (m), Brk = bark thickness (mm), Woo = wood density (mg mm^{-3}), Tgh = leaf toughness (N), LSz = leaf size (mm^2), SLA = specific leaf area (mm^2 mg^{-1}), N = leaf nitrogen content (mg g^{-1}), P = leaf phosphorus content (mg g^{-1}), K = leaf potassium content (mg g^{-1}).

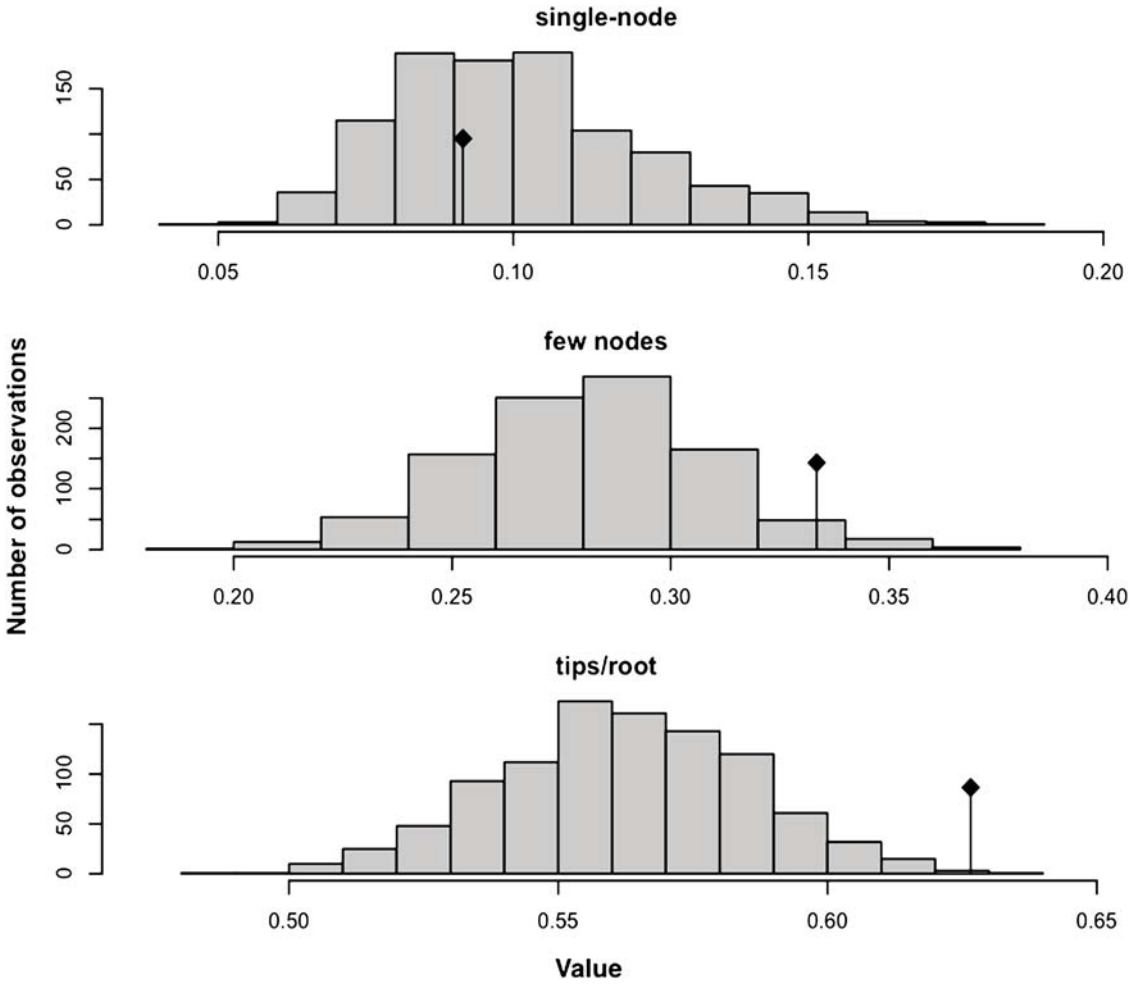
Species	BA	H	Brk	Woo	Tgh	LSz	SLA	N	P	K
Acosmium dasycarpum	0.002	0.821	8.871	0.436	1.808	10697.083	6.983	21.121	1.032	4.995
Albizia niopoides	0.001	1.790	6.470	0.553	0.740	11511.000	13.330	32.100	1.610	7.140
Anadenanthera peregrina	0.010	2.603	16.021	0.579	0.274	16813.000	7.390	26.602	1.327	5.193
Aspidosperma tomentosum	0.002	0.830	11.170	0.413	0.880	5681.000	7.228	19.980	1.130	7.650
Byrsonima basiloba	0.050	2.083	4.923	0.551	1.343	8648.000	5.066	13.843	0.807	4.677
Byrsonima coccolobifolia	0.008	2.768	9.304	0.441	0.832	7494.400	8.802	17.814	1.100	7.602
Byrsonima verbascifolia	0.008	3.210	14.660	0.463	0.530	10873.000	7.615	15.830	1.250	11.220
Caryocar brasiliense	0.007	2.900	11.930	0.401	0.550	51227.000	9.081	21.590	1.630	6.630
Casearia sylvestris	0.002	1.725	7.365	0.482	0.798	1200.750	8.667	20.403	1.118	8.033
Connarus suberosus	0.004	1.390	12.059	0.429	1.995	13160.595	5.972	14.422	0.838	4.954
Davilla elliptica	0.002	1.185	7.218	0.560	1.192	3663.833	7.734	17.645	1.190	8.078
Dimorphandra mollis	0.007	1.949	10.700	0.438	0.126	33899.000	8.504	33.929	1.359	4.530
Diospyros hispida	0.003	1.430	6.529	0.348	1.210	19711.375	4.683	13.450	1.054	10.585
Diptychandra aurantiaca	0.002	1.560	11.420	0.563	0.503	12617.667	14.715	20.730	1.097	3.487
Eremanthus erythropappus	0.004	1.209	12.527	0.466	0.726	3012.500	9.048	18.676	1.444	14.140
Eriotheca gracilipes	0.006	2.313	10.820	0.359	2.838	30491.500	4.508	19.703	0.935	6.188
Eriotheca pubescens	0.001	1.050	6.340	0.257	2.890	59792.000	4.943	19.010	1.390	9.180
Erythroxylum campestre	0.001	1.135	12.365	0.493	1.255	2555.000	6.919	16.855	0.990	4.850
Erythroxylum suberosum	0.003	1.398	11.524	0.525	1.053	2864.882	8.164	18.545	1.226	6.797
Erythroxylum tortuosum	0.002	0.890	7.670	0.487	1.220	5180.000	6.199	15.950	0.960	3.060
Eugenia aurata	0.002	1.130	11.030	0.435	1.060	2087.500	10.200	23.525	1.370	8.673
Eugenia bimarginata	0.005	1.560	11.630	0.445	1.540	4026.000	8.492	22.670	1.210	7.140
Eugenia punicifolia	0.003	1.880	14.105	0.545	0.850	874.500	10.183	22.460	1.525	8.290
Guapira noxia	0.007	0.680	5.700	0.205	0.730	12436.000	10.518	21.740	1.030	16.830
Hancornia speciosa	0.011	2.760	2.600	0.361	1.070	3150.000	10.468	15.750	0.890	6.890
Hymenaea stigonocarpa	0.003	1.603	2.423	0.523	1.500	22160.667	7.937	17.357	1.207	5.527
Kielmeyera coriacea	0.006	1.785	15.136	0.283	2.025	8908.438	5.898	16.818	1.089	6.378
Lafoensia pacari	0.006	2.200	6.370	0.551	0.390	2718.000	13.230	26.210	1.790	11.480
Machaerium acutifolium	0.010	4.080	17.110	0.563	1.975	16743.500	7.280	24.075	1.140	4.335
Miconia albicans	0.001	1.743	5.870	0.607	0.758	4985.750	4.922	12.403	0.600	3.955
Mimosa amnis-atri	0.002	1.074	4.315	0.583	0.166	7690.353	10.623	23.556	1.324	5.748
Mouriri elliptica	0.002	0.970	9.870	0.543	1.030	5567.000	6.504	15.550	0.210	3.570
Myrcia bella	0.004	1.301	12.701	0.498	1.171	908.714	7.330	11.470	0.624	4.666
Myrcia camapuensis	0.002	0.980	6.610	0.704	2.035	6382.500	4.072	12.510	0.760	3.700
Myrcia guianensis	0.001	0.710	7.910	0.743	2.450	4691.000	3.874	8.220	0.490	4.080
Myrcia lasiantha	0.005	1.540	15.230	0.261	0.950	936.000	6.375	11.970	0.770	2.550
Myrcia obovata	0.004	1.130	6.610	0.560	0.910	4087.000	9.135	17.850	1.280	8.160
Ouratea acuminata	0.003	1.513	11.622	0.462	1.509	3232.800	6.388	13.854	0.766	4.317
Ouratea spectabilis	0.007	2.616	12.120	0.495	3.662	5070.800	5.018	13.108	1.016	9.336
Palicourea rigida	0.004	1.380	9.465	0.229	2.310	16986.500	5.201	18.795	0.820	6.125
Piptocarpha rotundifolia	0.004	1.574	7.099	0.508	1.794	9672.211	5.889	16.956	1.020	7.049
Plenckia populnea	0.011	5.370	11.210	0.449	0.380	4079.000	15.755	33.310	2.170	14.540
Pouteria ramiflora	0.004	1.950	11.138	0.435	0.871	9964.381	7.308	16.035	1.095	5.870
Pouteria torta	0.003	1.343	7.497	0.449	0.795	8709.128	6.798	17.430	1.113	4.972

(Continued)

Apendix 1. *(Continued)*.

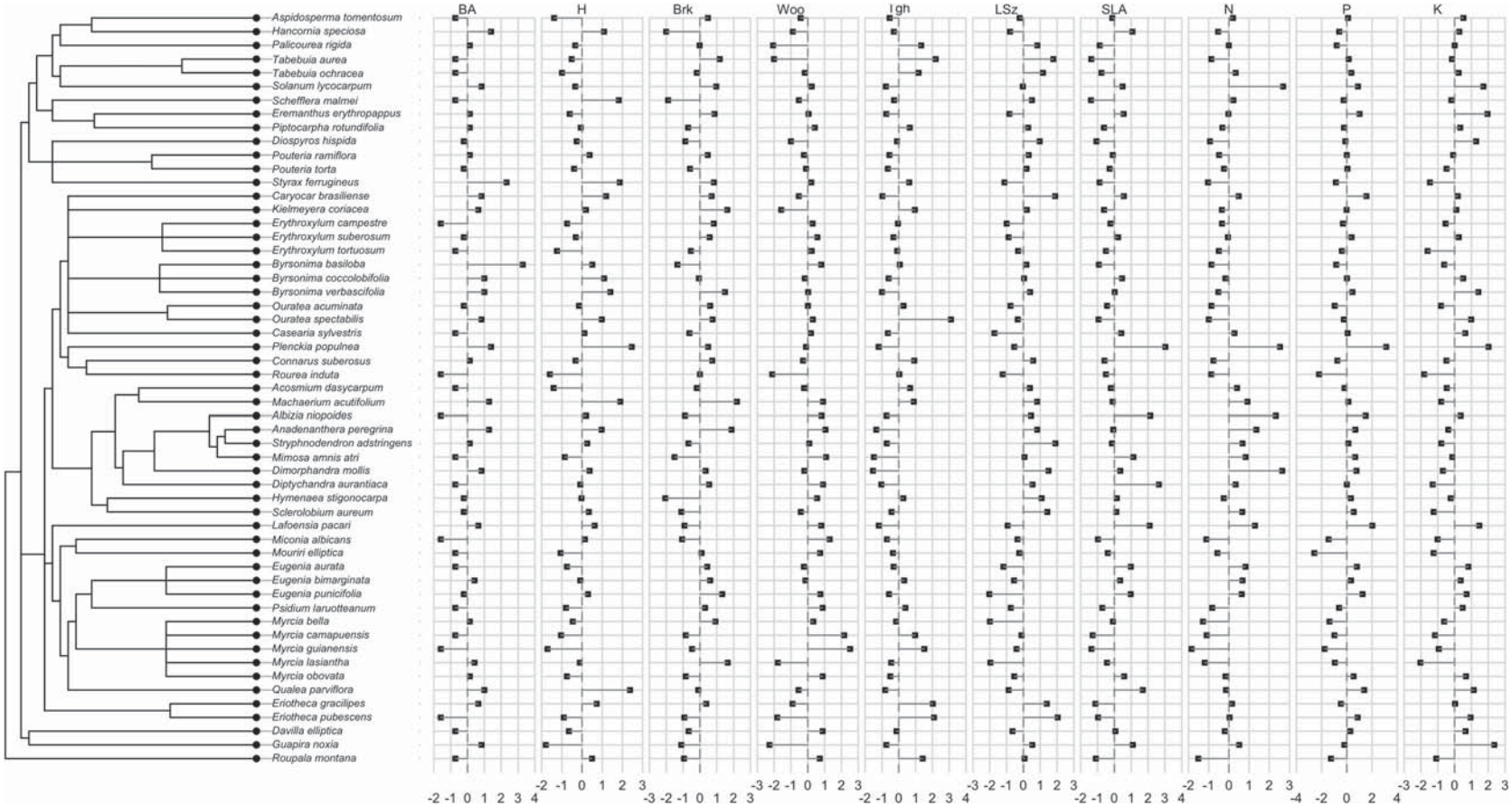
Species	BA	H	Brk	Woo	Tgh	LSz	SLA	N	P	K
Psidium laruotteanum	0.002	1.105	10.586	0.560	1.596	3290.758	5.621	14.096	0.887	7.498
Qualea parviflora	0.008	5.150	9.190	0.399	0.680	2888.000	12.127	17.980	1.570	9.950
Roupala montana	0.002	2.065	6.270	0.541	2.380	7738.500	4.577	10.145	0.665	3.825
Rourea induta	0.001	0.750	9.520	0.223	1.320	1997.000	6.200	13.800	0.340	2.810
Schefflera malmei	0.002	3.930	3.010	0.401	1.080	12199.000	3.809	20.090	1.010	5.610
Sclerolobium aureum	0.003	1.915	5.710	0.414	0.965	31410.500	7.874	22.605	1.285	3.575
Solanum lycocarpum	0.007	1.380	12.880	0.487	0.710	6925.000	8.875	34.190	1.400	12.750
Stryphnodendron adstringens	0.004	1.842	7.170	0.471	0.749	51890.161	7.169	22.678	1.140	4.345
Styrax ferrugineus	0.023	4.025	12.390	0.484	1.768	2229.250	5.186	12.890	0.798	3.253
Tabebuia aurea	0.002	1.267	13.600	0.235	2.967	45682.000	3.851	13.827	1.147	5.697
Tabebuia ochracea	0.002	1.003	8.873	0.441	2.193	24108.000	5.486	20.744	1.219	6.766

Appendix 2



Observed and randomised values for the single-node skewness test, few nodes skewness test, and tips/root skewness test. Observed value for the "single-node skewness" test was not different from random ($p = 0.595$), but observed values for the "few nodes skewness" and "tips/root skewness" tests were greater than expected by chance ($p = 0.03$ and 0.005, respectively).

Appendix 3



Positive and negative scores identified by phylogenetic principal component analysis of the species sampled in Emas National Park, central Brazil (17°49′–18°28′S, 52°39′-53°10′ W). BA = basal area, H = height, Brk = bark thickness, Woo = wood density, Tgh = leaf toughness, LSz = leaf size, SLA = specific leaf area, N = leaf nitrogen content, P = leaf phosphorus content, K = leaf potassium content. Leaf toughness, leaf size, and leaf nitrogen content presented positive phylogenetic autocorrelation according to Abouheif's test.