

# The role of fire in structuring trait variability in Neotropical savannas

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**Abstract** Intraspecific trait variability plays a fundamental role in community structure and dynamics; however, few studies have evaluated its relative importance to the overall response of communities to environmental pressures. Since fire is considered a key factor in Neotropical savannas, we investigated to what extent the functional effects of fire in a Brazilian savanna occurs via intra- or interspecific trait variability. We sampled 12 traits in communities subjected to three fire regimes in the last 12 years: annual, biennial, and protected. To evaluate fire's relative effects, we fitted a general linear mixed models with species as random and fire as fixed factors, using: (1) all species in the communities (i.e., considering intra- and interspecific variabilities); (2) 18 species common to all fire regimes (i.e., intraspecific variability only); and (3) all species with their overall average trait values (i.e., interspecific variability only). We assessed the relative role of intra- or interspecific variability by comparing the significance of each trait in the three analyses. We also compared

the within and between fire variabilities with a variance component analysis. Five traits presented larger intraspecific than interspecific variability, and the main effect of fire occurred at the intraspecific level. These results confirm that it is important to consider intraspecific variability to fully understand fire-prone communities. Moreover, trait variability was larger within than among fire regimes. Thus, fire may act more as an external filter, preventing some of the species from the regional pool from colonizing the cerrado, than as an internal factor structuring the already filtered cerrado communities.

**Keywords** Cerrado · Fire regimes · Intraspecific variability · Plant traits · Variance components

## Introduction

Most studies on the effects of biotic interactions and abiotic drivers in plant communities have focused on interspecific trait variability, considering plant traits as species average values (e.g., Westoby et al. 2002; Wright et al. 2005; Pausas and Verdú 2008; Kraft and Ackerly 2010). Including intraspecific variability in community studies is a promising path to improve our ability for understanding assembly processes, habitat selection, and community functioning, regardless of whether this variability has a genetic basis or not (McGill et al. 2006; Albert et al. 2010; Bolnick et al. 2011). Intraspecific variability is associated with greater resource use efficiency, greater microsite occupancy, and higher resilience at the community level (Bolnick et al. 2011). Moreover, since intraspecific variability plays a fundamental role in species coexistence and interactions (Violle et al. 2012), the evaluation of the phenotypic community structure is significantly affected by its inclusion (Jung et al. 2010;

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Cianciaruso et al. 2012). Few studies have evaluated the relative importance of intraspecific variability to the response of communities to environmental gradients (Albert et al. 2010). However, the recent rise of variance-based statistics have provided a common ground for comparing and decomposing the effects of community processes into its intra- and interspecific components (de Bello et al. 2010; Messier et al. 2010; Violle et al. 2012). Plant communities are generally assembled by two main processes: habitat filtering and limiting similarity (Weiher and Keddy 1995; Wilson 1999). Since habitat filtering tends to reduce interspecific trait variability (Kraft and Ackerly 2010; Pausas and Verdú 2010), in strongly filtered communities, the intraspecific variability is expected to play an important relative role in community structure and resilience.

Fire exerts an important pressure in many biomes worldwide (Pausas and Keeley 2009), acting as an environmental filter in plant communities (Verdú and Pausas 2007) and as a driving force for species evolution (Keeley et al. 2011, 2012; He et al. 2012). Most studies on fire effects in plant traits at a community scale have focused on changes related to shifts in species composition (e.g., Pausas et al. 2004; Saura-Mas and Lloret 2007; Verdú and Pausas 2007; Pausas and Verdú 2008; Moretti and Legg 2009). Recent studies have emphasised the role of intraspecific trait variability in fire-prone ecosystems (Moreira et al. 2012; Pausas et al. 2012; Cianciaruso et al. 2012), but to what extent the effects of recurrent fire in plant communities are related to intraspecific variability remains poorly explored.

The origin of Neotropical savannas is associated with the spread of flammable  $C_4$  grasses in South America about 4–8 million years ago (Berling and Osborn 2006; Simon et al. 2009). The appearance of such grasses increased the frequency of fires, imposing a strong filtering as well as a selective pressure on the coexisting woody species. The resulting communities have an herbaceous layer of tall flammable grasses coexisting with woody species adapted to survive fires. Typical wildfires in the Brazilian savannas (known as “cerrado”) occur in the wet season (generating small fires) or during the transition from dry to wet (generating larger fires; Miranda et al. 2009). In this vegetation type, because grasses are often tall and trees relatively short, there is no clear fuel gap between grasses and woody plants, and fires often affect both the herbaceous layer and the coexisting shrubs and trees, generating regimes of frequent low intensity fires (crown and surface fires). Consequently, the long fire history has filtered cerrado communities by preventing the establishment of species not adapted to fire, and by driving the evolution of a fire-adapted flora (Simon et al. 2009), thus limiting interspecific phenotypic and functional variability.

As long as interspecific trait variability is reduced in strongly filtered communities, intraspecific variability

should have an important relative role in community response to disturbances. We predict that, in cerrado which has been strongly filtered by fire, intraspecific trait variability plays a fundamental role in the functional response to different fire regimes, and should account for an important fraction of the overall variability of the community. If so, the relative importance of changes in species composition observed in cerrado communities submitted to different fire regimes (Silva and Batalha 2008) should not explain most of the functional trait variability; instead, an important part of the variability should occur at the intraspecific level. To evaluate this, we studied 12 functional traits of woody plants occurring in different fire regimes in a cerrado reserve. The current management of cerrado reserves has generated a patchwork of fire regimes, from annual fires to fire-protected zones, suitable for studying trait variability generated by fire.

## Materials and methods

### Study area

We used data collected at Emas National Park (ENP; central Brazil: 17°49′–18°28′S, 52°39′–53°10′W), a World Natural Heritage site (Unesco 2001) located in the Brazilian Central Plateau. ENP is one of the most important cerrado reserves in Brazil (Conservation International 1999). The reserve has a tropical warm wet climate, with dry winters (Aw type following Köppen 1931); most soils are Oxisols. The topography is mostly flat and homogeneous. The cerrado includes a wide range of physiognomies, from open grassland to woodland with different tree densities (Coutinho 1990); most of these physiognomies occur inside ENP, but open formations dominate.

The ENP was burned annually by farmers in the dry season until 1984 to promote forage regrowth. In 1984, the reserve was fenced, cattle were removed, and a fire exclusion policy was established (Ramos-Neto and Pivello 2000). During the fire exclusion period (1984–1994), fires burned large areas every 3 years, due to dry biomass accumulation (França et al. 2007). Since 1994, annual and biennial prescribed burns within firebreaks have been applied in 10-km<sup>2</sup> strips to remove plant dry mass and prevent large fires (França et al. 2007). These management actions have driven the average fire return interval to about 6–7 years (França et al. 2007), but the outcome of this management is a patchwork of different fire regimes within the park.

### Sampling

Data were collected during a 3-month period of the 2006 rainy season, from areas with similar physiognomies (open

savannas) and topography (flat areas), but different fire history during the last 12 years (Silva and Batalha 2010): (1) an annually burned firebreak (18°18'50"S, 52°54'00"W; sampled 1 year after the last fire); (2) an area burned 5 times during the last 12 years, with a mean fire interval of 1.8 years (18°19'01"S, 52°54'10"W; sampled 3 years after the last fire); and (3) a site protected from fire for 12 years (18°17'28"S, 52°53'41"W). For simplicity, we refer to these fire regimes as 'annual', 'biennial' and 'protected'. In each fire regime, 250 points separated by 10-m intervals were sampled along a 2.5-km transect. At each point, four plants were sampled using the point–center–quarter method (Müller-Dombois and Ellenberg 1974). Thus, in each of the fire regimes, a total of 1,000 individual plants were sampled from 50 woody species. The distance between adjacent transects ranged from 0.5 to 2 km, and since the sites were all located in flat and homogeneous areas, no important environmental variability was expected among transects.

For each species, we randomly picked seven individuals per fire regime by sampling their identification code from the pool containing the code of all individuals of the target species. When seven individuals were not available, we made an extra effort within the fire regime to complete the dataset. In these seven selected individuals per species and fire regime, we measured the following 12 functional attributes: plant height, basal area, bark thickness, wood density, specific leaf area, leaf dry matter content, and the concentration of nitrogen, phosphorous, potassium, calcium, magnesium, and sulfur in leaves. All traits were measured according to Cornelissen et al. (2003), except for chemical leaf traits, which were measured following Allen (1989). Wood density and chemical leaf attributes were measured in five individuals per species and fire regime. For multi-stemmed plants, basal area and bark thickness were measured at the main (oldest) stem that was not killed by fire. To measure woody density, we collected a woody cylindrical sample of the plant's main stem (or as close to it as possible), removed all the bark, and, using a calliper, measured its diameter and length. We used these measures to estimate the volume of the sample. The woody density was obtained by dividing the dry mass of the sample (oven-dried at 80 °C for 72 h) by its fresh volume. Bark thicknesses were estimated by removing a bark sample from the main stem with a knife and measuring its thickness with a calliper.

Leaf traits were measured in completely expanded, hardened, and mature sun leaves, with no symptoms of pathogen, herbivory, or senescence, and haphazardly selected from the outer canopy. To measure specific leaf area, we collected two leaves from each sampled individual, kept them in a cooler, and subsequently scanned them. We used these digitalized images to estimate leaf area with

Image J 1.33 software (Rasband 2004). We determined specific leaf area by dividing the area of the fresh leaves by their oven-dried (80 °C for 72 h) mass.

## Analyses

To evaluate the role of fire in trait variability, and the relative importance of intra- and interspecific variability, we performed three analyses: firstly, we fitted a general linear mixed model (GLMM) with fire regimes (protected, biennial, annual) as fixed factor and species as random factor using the actual trait values of all individuals in each fire regime (that is, considering intra- and interspecific variabilities). We used an equal number of individuals per species in each fire regime (seven) so that the effects of variability observed were not affected by differences in abundance but exclusively by the intra- and interspecific variabilities. Secondly, to assess whether this variability was mainly related to changes in species composition or to intraspecific trait variability, we excluded intraspecific variability by calculating an overall mean trait values for each species, regardless of the fire regime, and matched these mean trait values with species presence and absence per fire regime. We performed an analysis of variance with fire as fixed factor, which permitted to assess the trait variability explained by differences in species composition only. Finally, to test whether fire generated intraspecific variability, we fitted a GLMM using the 18 species common to all fire regimes (that is, excluding interspecific variability), using fire as fixed factor and species as random factor. Of the 50 species sampled, these 18 species (Supplementary material: Table A1) represented: 28 % of the woody species occurring across all sites, 46 % of the woody species in the protected (unburned) site, 50 % of the woody species in the biennially burned site, and 64 % of the woody species in the annually burned site (Silva and Batalha 2010). We assessed the relative role of intra- and interspecific variability generated by fire, by comparing the significance of each trait in the three analyses. We repeated all the analyses considering two fire regimes in order to perform the three pairwise comparison tests for each trait.

We also compared the variability generated by fire with the overall trait variability, to assess the importance of fire in generating trait variability. Hence, we performed a variance component analysis in a GLMM, including all species and fire regimes, with fire regimes nested in species as random factor. We performed the same analysis using only the 18 common species to partition the variability in intra- and interspecific variability, and investigated whether the variability within species was larger than the variability among species, as a measure of the importance of the intraspecific variability to the overall trait variability. When necessary, we log-transformed the trait values prior

to the analysis to approximate normality. All analyses were carried out with the “nlme” and “ape” libraries in the R environment (R Development Core Team 2009).

## Results

Fire regimes significantly affected most traits when both species composition and intraspecific variability were considered (Tables 1, 2). Removing the intraspecific variability resulted in the loss of most of the significant relationships, and only basal area and plant height (out of 12 traits) were significantly related to fire regimes. In contrast, removing the variability in species composition (when only the 18 species common to all fire regimes were considered) did not alter most of the relationship between fire regimes and traits observed in the whole community approach (Tables 1, 3). In both the first and the last cases, plant height was lowest in the annually burned site and highest in the protected site (Tables 2, 3). Specific leaf area was lowest at the annually burned site in comparison with the protected site. Leaf nitrogen, magnesium, and phosphorus were lowest and leaf calcium was highest in the annually burned site. For any trait, fire was the main factor explaining trait variability, since the within-fire variability was larger than the between-fire variability (Table 2). Nevertheless, the proportion of the variability explained by fire increased when the effect of species composition was excluded (Table 3).

## Discussion

Fire regimes in the cerrado were significantly related to trait variability at a landscape scale. Although the Brazilian cerrado has been subject to recurrent fires during the last few million years (Simon et al. 2009), current fire regimes still have a significant impact in generating trait variability (Silva and Batalha 2010; Cianciaruso et al. 2012), and especially intraspecific trait variability. In fact, removing all intraspecific variability resulted in the loss of most of the significant relationships, whereas removing the variability in species composition did not, even though the species composition was significantly different among fire regimes (see Silva and Batalha 2008). Thus, the intraspecific variability seems to represent an important fraction of the overall variability generated by fire and cannot be neglected in future studies in cerrado. These results, combined with others reporting the importance of fire in generating intraspecific variability (e.g., Moreira et al. 2012; Pausas et al. 2012), suggest that studies on the effects of fire in plant communities would benefit from a more detailed observation of trait variability beyond species average values. All these results support our hypothesis of the prominent importance of intraspecific variability in strongly fire-filtered communities.

Partitioning the overall trait variability of the 18 species common to all fire regimes resulted in all but five traits presenting a larger intra- than interspecific variability (Table 3). The combined effect of fire in filtering the

**Table 1** Results of the GLMM for the effects of fire regime (protected, biennial, and annual) on 12 functional traits considering (1) inter + intraspecific variability, which combines all species in the community and individual plant traits (see Table 2;  $df1 = 2$ ,  $df2$

ranges between 374 and 593); (2) interspecific variability only ( $df1 = 2$ ,  $df2$  ranges between 96 and 98); and (3) intraspecific variability among the 18 most common species (see Table 3;  $df1 = 2$ ,  $df2$  ranges between 246 and 352)

Trait	Inter + intraspecific (all; individual values)		Interspecific (all; mean species values)		Intraspecific (18 common species; individual values)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Basal area (cm <sup>2</sup> )	0.704	0.495	3.88	<b>0.024</b>	4.206	<b>0.041</b>
Plant height (cm)	32.934	<b>&lt;0.001</b>	6.625	<b>0.002</b>	86.541	<b>&lt;0.001</b>
Wood density (mg mm <sup>-3</sup> )	2.088	0.1252	2.105	0.127	0.968	0.326
Bark thickness (mm)	33.661	<b>&lt;0.001</b>	2.439	0.093	49.479	<b>&lt;0.001</b>
Specific leaf area (mm <sup>2</sup> mg <sup>-1</sup> )	7.891	<b>&lt;0.001</b>	0.225	0.799	8.694	<b>0.003</b>
Leaf dry matter content (mg g <sup>-1</sup> )	0.696	0.499	0.312	0.733	0.991	0.320
Leaf nitrogen (mg g <sup>-1</sup> )	4.531	<b>0.0113</b>	0.477	0.622	34.670	<b>&lt;0.001</b>
Leaf phosphorous (mg g <sup>-1</sup> )	14.936	<b>&lt;0.001</b>	0.187	0.83	58.185	<b>&lt;0.001</b>
Leaf calcium (mg g <sup>-1</sup> )	9.389	<b>&lt;0.001</b>	0.440	0.646	16.158	<b>&lt;0.001</b>
Leaf magnesium (mg g <sup>-1</sup> )	12.604	<b>&lt;0.001</b>	0.585	0.559	3.350	0.068
Leaf potassium (mg g <sup>-1</sup> )	2.487	0.0843	0.163	0.850	0.006	0.937
Leaf sulphur (mg g <sup>-1</sup> )	0.701	0.4967	0.501	0.608	0.674	0.412

The subset of the data used in each analysis: number of species and trait resolution is shown in parentheses

Significant values in bold ( $P < 0.05$ )

**Table 2** Trait values of all species within the three fire regimes and results of variance component analysis comparing fire type and species

Plant traits	Fire regime			Variability		
	Protected	Biennial	Annual	Among fires	Within fires	Among species
Basal area (cm <sup>2</sup> )	51.47 ± 66.67 a	53.68 ± 87.11 a	40.10 ± 42.33 a	0.00	0.76	0.24
Plant height (cm)	1.78 ± 0.96 a	1.49 ± 1.00 b	0.78 ± 0.58 c	0.08	0.46	0.45
Bark thickness (mm)	6.72 ± 4.67 a	5.33 ± 3.77 b	3.13 ± 3.61 c	0.19	0.56	0.25
Wood density (mg mm <sup>-3</sup> )	0.44 ± 0.23 a	0.37 ± 0.11 a	0.44 ± 0.21 a	0.12	0.56	0.32
Specific leaf area (mm <sup>2</sup> mg <sup>-1</sup> )	5.99 ± 2.31 a	5.93 ± 1.70 a	5.74 ± 1.41 b	0.09	0.45	0.46
Leaf dry matter content (mg g <sup>-1</sup> )	468.92 ± 141.80 a	462.26 ± 134.93 a	459.82 ± 80.62 a	0.04	0.68	0.28
Leaf nitrogen (mg g <sup>-1</sup> )	16.26 ± 5.86 a	15.01 ± 4.65 b	16.37 ± 4.54 b	0.16	0.21	0.63
Leaf phosphorous (mg g <sup>-1</sup> )	0.87 ± 0.24 a	0.89 ± 0.18 b	0.93 ± 0.19 c	0.17	0.31	0.53
Leaf potassium (mg g <sup>-1</sup> )	4.70 ± 3.06 a	5.26 ± 2.89 a	4.85 ± 2.40 a	0.05	0.33	0.62
Leaf calcium (mg g <sup>-1</sup> )	3.14 ± 1.95 a	3.08 ± 1.73 a	3.09 ± 1.67 b	0.10	0.31	0.59
Leaf magnesium (mg g <sup>-1</sup> )	1.24 ± 0.78 a	1.35 ± 0.78 <sup>b</sup>	1.54 ± 1.00 b	0.12	0.36	0.52
Leaf sulphur (mg g <sup>-1</sup> )	0.70 ± 0.18 a	0.67 ± 0.16 a	0.67 ± 0.18 a	0.20	0.52	0.28

Protected sites with 12 years of the fire exclusion; *Biennial* and *Annual* fire frequency during this period. Trait values are mean ± SD (see text for sample size). In each row, values with different letters indicates significant differences in trait values among pairs of fire regimes determined by a general linear mixed model with species as random and fire as fixed factors

**Table 3** Trait values of the 18 species common in the three fire regimes

Plant traits	Fire regime			Intraspecific		Among species
	Protected	Biennial	Annual	Among fires	Within fires	
Basal area (cm <sup>2</sup> )	37.43 ± 45.60 a	35.44 ± 33.71 a	49.85 ± 68.26 b	0.055	0.679	0.266
Plant height (cm)	142.18 ± 65.68 a	120.36 ± 75.00 b	76.02 ± 55.76 c	0.385	0.503	0.112
Bark thickness (mm)	6.30 ± 4.24 a	5.06 ± 4.54 b	5.08 ± 4.77 c	0.287	0.479	0.234
Wood density (mg mm <sup>-3</sup> )	0.39 ± 0.11 a	0.38 ± 0.12 a	0.40 ± 0.17 a	0.006	0.553	0.442
Specific leaf area (mm <sup>2</sup> mg <sup>-1</sup> )	6.21 ± 1.85 a	6.05 ± 1.61 ab	5.75 ± 1.23 b	0.078	0.424	0.498
Leaf dry matter content (mg g <sup>-1</sup> )	440.36 ± 83.39 a	477.75 ± 171.89 b	453.62 ± 73.07 ab	0.068	0.573	0.360
Leaf nitrogen (mg g <sup>-1</sup> )	16.44 ± 5.35 a	15.11 ± 5.33 b	14.23 ± 5.21 c	0.100	0.209	0.681
Leaf phosphorous (mg g <sup>-1</sup> )	0.91 ± 0.18 a	0.85 ± 0.18 b	0.78 ± 0.17 c	0.235	0.335	0.431
Leaf potassium (mg g <sup>-1</sup> )	2.86 ± 1.95 a	2.74 ± 1.74 a	2.45 ± 2.00 b	0.053	0.337	0.611
Leaf calcium (mg g <sup>-1</sup> )	1.40 ± 1.18 b	1.13 ± 0.59 a	1.21 ± 0.73 a	0.074	0.261	0.666
Leaf magnesium (mg g <sup>-1</sup> )	4.68 ± 2.25 a	4.90 ± 3.20 a	4.63 ± 3.28 a	0.104	0.317	0.579
Leaf sulphur (mg g <sup>-1</sup> )	0.69 ± 0.16 a	0.72 ± 0.17 a	0.70 ± 0.18 a	0.130	0.745	0.125

Values are mean (±SD) of each trait in fire regime, and their variance components (scaled; among and within three fire regimes and among species). Protected sites with 12 years of the fire exclusion; *Biennial* and *Annual* fire frequency during this period. In each row, values with different letters represent significant differences in trait values among fire regimes determined by a general linear mixed model with species as random and fire as fixed factors

species of the regional pool for thousands of years, reducing the overall interspecific variability, and recent fire regimes in generating intraspecific variability may result in this relatively large importance of intraspecific variability. To what extent this pattern may also occur in other strongly filtered communities worldwide remains to be explored.

Plants burned annually were shorter and had higher basal areas than plants protected from fire. This is likely to be a consequence of the recurrent top-killing by fire under annual fire frequencies, that is, fire interfering with plant development causing a “bonsai effect” (or Oskar

syndrome; Higgins et al. 2007). Thus, these results confirm that fire acts by opening savanna physiognomies. Also, bark was thinner under annual fires. Although frequent surface fires in savanna environments lead to an expectation of greater investment in bark (Keeley and Zedler 1998; Jackson et al. 1999; He et al. 2012), annual crown-fires may have partially destroyed the bark of adults and limited the building of a thick protective bark. This suggests that the bark thickness observed in cerrado plants may be more than enough to protect them from frequent, but low intensity, cerrado fires. Also, we found plants in the



protected area to have higher specific leaf area than plants in the frequently burned sites; more frequent burning promoted smaller, thicker and tougher leaves. Since all the sites studied consisted of open physiognomies, it is unlikely that the differences in leaf trait result from different light incidence among fire regimes. Specific leaf area is considered a key trait that summarizes the allocation trade-off between growth and defense or reserves (Chapin et al. 1993; Gurvich et al. 2005). Therefore, lower specific leaf area values observed in the annually burned plants may be a consequence of slower growth rates, due to a higher allocation to reserves for annual resprouting (Moreira et al. 2012). Also, they may represent a great investment in leaf anti-herbivory resistance to protect the leaves from the increment in herbivory that usually takes place after fires (Lopes and Vasconcelos 2011; Kersch-Becker and Lewinsohn 2012).

The fact that frequently burned plants had the lowest foliar nutrients (N, P, Mg), thicker and tougher leaves (lower specific leaf areas), and higher Ca concentration, as opposed to the protected plants, suggest the existence of a nutrient stress (Coley et al. 1985; Ward et al. 1997; McLaughlin and Wimmer 1999; Craine 2009). In the cerrado, there is evidence of fires occurring with less than 3-year intervals, resulting in nutrient loss from the system (Pivello and Coutinho 1992). Since cerrado soils are nutrient-poor (Ruggiero et al. 2002; Dantas and Batalha 2011), individuals under high fire frequency could be facing a significant nutrient limitation. Although this reduction in the nutrient availability may be the consequence of the direct biomass consumption by fire, nutrient stress may also be a consequence of the indirect effects of increased herbivory after fire (Lopes and Vasconcelos 2011; Kersch-Becker and Lewinsohn 2012). Leaf traits are believed to be labile and present high plasticity (see Hoffmann and Franco 2003 for an example in the cerrado). However, the chemical leaf traits presented a low proportion of its variability explained by intraspecific variability in comparison with other traits. Recent studies have reported chemical leaf traits to be more evolutionarily conserved than other leaf traits (Cianciaruso et al. 2012), suggesting an association between phylogenetic conservatism and intraspecific variability, which could be a subject for further investigation.

When partitioning the variance into its intra- and inter-specific components, we observed that the variability within fire was greater than among fire regimes. Thus, although fire exerted a significant effect in trait variability at the intraspecific level, there was still a large variability not explained by fire regimes, suggesting that, although fire in cerrado acts as an important external filter (sensu Violle et al. 2012), preventing plants from the regional pool, without the appropriated traits, from colonizing open savannas (Simon

et al. 2009), other internal factors may be responsible for most of the trait variability observed at the landscape scale. Nevertheless, previous studies also found larger within (local) than among communities (regional) intraspecific variability (see Supplementary material in Albert et al. 2010; Moreira et al. 2012), suggesting that this could be a general pattern in many plant communities worldwide.

In recent years, investigating the role of intraspecific variability has been regarded as a fundamental issue in community ecology, allowing a more precise prediction of community responses to environmental changes, and a greater understanding of community functioning (Albert et al. 2010; Messier et al. 2010; Bolnick et al. 2011; Violle et al. 2012). Indeed, there is increasing evidence suggesting that intraspecific variability may be as large as or even larger than interspecific variability (de Bello et al. 2010; Messier et al. 2010; our results). Thus, to fully understand the effects of fire in cerrado, and possibly in other strongly filtered communities, intraspecific trait variability needs to be considered.

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