

# Can antiherbivory resistance explain the abundance of woody species in a Neotropical savanna?

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**Abstract:** The disturbance resistance model states that, in nutrient-poor communities, species more resistant to herbivory should dominate over the more palatable ones. Here we postulated that the disturbance resistance model should explain the species abundances in a nutrient-poor Neotropical savanna community. If so, the highly resistant species should be the commonest, whereas the poorly resistant ones should be rare. In an area of 2500 m<sup>2</sup> of woodland cerrado, a type of savanna, we measured the abundance of all 61 species as the total basal area and 9 antiherbivore defence traits from 10 individuals of each species. We used multiple and simple linear regressions to test the relationships between abundance and each trait or total investment in defence. Abundance was negatively related to specific leaf area ( $R^2 = 0.18$ ,  $b = -0.87$ ,  $P < 0.001$ ), but not with the other traits nor with total defence. The relationship between specific leaf area and abundance showed that plant functional traits may influence species abundance and supported the idea that nonrandom and resource-mediated processes should prevail at a fine scale. Nevertheless, we did not find strong evidence that antiherbivory resistance can explain species abundance in resource-poor communities, in contrast to the prediction of the disturbance resistance model.

*Key words:* cerrado, defence traits, herbivory, palatable leaves, specific leaf area.

**Résumé :** Le modèle de résistance aux perturbations stipule que, dans les communautés pauvres en nutriments, les espèces plus résistantes à l'herbivorie devraient dominer sur les espèces plus savoureuses. L'auteur postule que le modèle de résistance aux perturbations devrait expliquer l'abondance des espèces dans une communauté de la savane néotropicale pauvre en nutriments. S'il en est ainsi, les espèces hautement résistantes devraient être les plus communes, alors que les faiblement résistantes devraient être rares. Sur une surface de 2500 m<sup>2</sup> de forêt fermée (woodland cerrado), un type de savane, l'auteur a mesuré l'abondance de l'ensemble des 61 espèces, en terme de surface basale totale et de 9 traits de défense antiherbivore, à partir de 10 individus pour chaque espèce. Il a utilisé des régressions linéaires simples et multiples pour tester les relations entre l'abondance et chaque trait ou encore l'investissement total dans la défense. On observe une relation négative entre l'abondance et la surface foliaire spécifique ( $R^2 = 0,18$ ,  $b = -0,87$ ,  $P < 0,001$ ), mais pas avec les autres traits ni avec la défense totale. La relation entre la surface foliaire spécifique et l'abondance montre que les traits fonctionnels de la plante peuvent influencer l'abondance des espèces et supporte l'idée que des processus aléatoires et exercés par les ressources devraient prévaloir à une fine échelle. Cependant, l'auteur n'a pas trouvé de preuves que la résistance antiherbivore puisse expliquer l'abondance des espèces dans des communautés limitées par la disponibilité des ressources, contrairement au modèle de prédiction de la résistance aux perturbations.

*Mots-clés :* cerrado, traits de défense, herbivorie, feuilles savoureuses, surface foliaire spécifique.

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## Introduction

There is an ongoing debate about the processes that determine abundance in plant communities. In some situations, stochastic events, limited dispersion, and ecological equivalence can explain species co-occurrence in a given community (Hubbel 2005); in others, abundance is mediated by niche-related processes (Cornwell and Ackerly 2010). In the first case, one should not find relationships between abundance and species traits within a given community, whereas in the second case one should find them (Cornwell and Ackerly 2010).

Herbivory is an ecological and evolutionary agent exerting a strong selective pressure in plant communities by increasing plant mortality, removing biomass that might be allocated to growth or reproduction (Coley et al. 1985), reducing plant competitive ability (Coley and Barone 1996), and, consequently, it may lead to a decrease in the abundances of certain plant species (Craine 2009). As a result, plants have evolved different chemical, mechanical, phenological, or physiological antiherbivore defences (Coley and Barone 1996; Strauss and Agrawal 1999), and the possession of such defences may determine whether a plant species will occur or not in a given location (Fine et al. 2006). Hence, spe-

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cies dominance and rarity in some plant communities are strongly influenced by the top-down effects of herbivory (Brown and Gange 1989; Carson and Root 1999).

There are two main plant strategies to deal with herbivory: tolerance and resistance (Núñez-Farfán et al. 2007). Tolerance is the ability of fast-growing species to maintain their fitness in the face of herbivory, whereas resistance is the strategy of decreasing leaf palatability to reduce the amount of consumption experienced by plants (Mauricio 2000). In nutrient-poor communities, resistance should prevail over tolerance as an antiherbivory strategy, since leaf loss would imply nutrient loss (Fine et al. 2006), and the disturbance resistance model postulates that, in such communities, the most resistant species should dominate, since herbivores would selectively feed on less resistant, nutrient-rich species (Herms and Mattson 1992; Burt-Smith et al. 2003; Craine 2009). Thus, the resistant species are expected to be the commonest in nutrient-poor communities, whereas the poorly resistant ones should be rare (Craine 2009).

The Brazilian cerrado, with most of its physiognomies within the definition of tropical savanna, is characterized by acidic and nutrient-poor soils, with high amounts of aluminium (Ruggiero et al. 2002; Dantas and Batalha 2011). There is a large abundance of herbivore insects living in cerrado (Marquis et al. 2002; Morais et al. 2011), and preliminary estimations of the amounts of insect herbivory in Neotropical savannas suggested that leaf-chewing insects can consume from 6.8% to 17% of leaf biomass (Marquis et al. 2001; Costa et al. 2008). For instance, since these studies did not consider other types of herbivores such as galls and miners, the amount of herbivory is probably underestimated. Cerrado woody species generally possess sclerophyllous leaves with high trichome density and latescence substances (Goodland and Pollard 1973; Diniz et al. 1999; Silva and Batalha 2011). Whereas some of these plant features are suggested to be related to soil chemical properties within the cerrado (Goodland and Pollard 1973), the same features are considered important antiherbivore resistance mechanisms in communities worldwide (Agrawal and Fishbein 2006; Craine 2009). Since the cerrado occurs on nutrient-poor soils and possesses a large abundance of herbivores and resistant plants, the abundance and rarity of cerrado woody species should be highly influenced by the different investments in antiherbivory resistance among coexisting species.

Since a plant community generally shares the same herbivore assemblage and resistance against specific herbivores is more costly than general defences, plants in the same community are likely to have similar defensive strategies, even when they are not closely related (Agrawal and Fishbein 2006; Núñez-Farfán et al. 2007). Hence, if herbivores exert strong ecological pressure in a given community, species that invest more in basic resistance traits, such as less palatable leaves with low nutrient content and high chemical and mechanical defences, are expected to be the commonest. Based on these assumptions, we asked whether the disturbance resistance model explained species abundance in a nutrient-poor (Dantas and Batalha 2011) cerrado community. We expected that the more resistant the species, the more successful it should be. Consequently, more resistant species should be the commonest.

## Material and methods

We studied a woodland cerrado site at the Federal University of São Carlos in southeastern Brazil (approximately 21° 58'05.3"S, 47°52'10.1"W). A woodland cerrado is a savanna dominated by 3–8 m tall trees and shrubs, with more than 30% crown cover, but still with a fair amount of herbaceous vegetation (Oliveira-Filho and Ratter 2002). The study site is on dystrophic Oxisol, 850 m above sea level, under mesothermic, subtropical climate, with wet summers and dry winters (Cwa; Köppen 1931). The mean annual temperature and precipitation lie around 21.3 °C and 1315 mm, respectively. In an area of 2500 m<sup>2</sup>, divided into one hundred 5 m × 5 m contiguous plots, we sampled all individuals of the woody component, that is, individuals with a stem diameter at soil level equal to or greater than 3 cm (Secretaria de Estado do Meio Ambiente 1997). We identified them to the species level using identification keys based on vegetative characters (Mantovani et al. 1985; Batalha and Mantovani 1999) and compared the collected material to vouchers lodged at the Federal University of São Carlos and State University of Campinas herbaria. We used Plantminer (Carvalho et al. 2010) to check species names, to place all species in families according to the latest phylogenetic classification, and to find authority names of all the species.

### Measuring plant defences and abundances

For each species in the sample, we picked 10 individuals at random. When, for a given species, there were fewer than 10 individuals in the sample, we made an additional effort to look for more individuals near the plots. Thus, the sample size was 10 individuals per species (Cornelissen et al. 2003). From September 2008 to April 2009, for each individual in the sample, we haphazardly collected fully expanded and hardened green leaves without obvious symptoms of pathogen or herbivore attack from the upper reachable part of the canopy. In these leaves, we measured the following leaf defence traits: carbon to nitrogen ratio, specific leaf area, leaf water per area, latex content, number of trichomes, toughness, and presence of alkaloids, terpenoids, and tannins (Agrawal and Fishbein 2006).

We measured the total carbon (C) and nitrogen (N) concentrations to calculate the C:N ratio, as an indicator of leaf nutritional quality. For each species, carbon and nitrogen concentrations were determined in five replicates at the University of São Paulo. Nutritional quality is an important constitutive plant defence, since high C:N ratios make nitrogen acquisition by herbivores difficult (Agrawal and Fishbein 2006).

Low values of specific leaf area tend to correspond to relatively high investments in leaf defences, particularly structural ones (Cornelissen et al. 2003). Specific leaf area also indicates rapid growth and high leaf palatability (Agrawal and Fishbein 2006). Similarly, leaf water content is related to increased leaf palatability, and therefore low levels of leaf water should help prevent herbivory (Schädler et al. 2003; Agrawal and Fishbein 2006). To measure specific leaf area and leaf water content, we collected two leaves from each individual, kept them in a cooler, and weighed them while still fresh. We scanned the leaves to determine the leaf area using Image J 1.33 software (National Institutes of Health, Rock-

ville Pike, Bethesda, Md., USA) (Rasband 2004) and oven-dried them at 80 °C for 72 h to obtain leaf dry mass. We obtained specific leaf areas by dividing leaf area by leaf dry mass (Cornelissen et al. 2003). We calculated leaf water per area. We first measured the difference between fresh mass and dry mass, and then standardized it by dividing it by its leaf area. Hereafter, we consider leaf water as a synonym for leaf water per area.

Trichomes are also important physical defences against herbivores. Using five replicates for each species, we counted the number of trichomes on both leaf surfaces in 28 mm<sup>2</sup> discs using a dissecting microscope. We also measured leaf toughness, which is related to nutritional and defence constituents and probably influences herbivore activity (Agrawal and Fishbein 2006). We used a force gauge penetrometer (Chatillon DFE 010; AMETEK, Berwyn, Pa., USA) with a cone tip, drilling the leaf at both sides of the mid-rib.

Latex is an important chemical strategy against herbivory (Agrawal and Fishbein 2006). We measured latex by cutting the tip of an intact leaf in the field and collected the exuding latex onto a filter paper disc. When latex ceased to flow, this disc was placed onto another dry filter paper disc, oven-dried at 60 °C for 72 h, and weighed (Agrawal and Fishbein 2006). We assigned the trait value for each trait by calculating the mean of the 10 individuals of each species.

We analysed compounds often present in Brazilian plants that could act as chemical defences against herbivores (Lima 2000): alkaloids, terpenoids, and tannins. We carried out tests following Falkenberg et al. (2003): a series of three assays — Mayer, Dragendorff, and Wagner reactions — to determine the alkaloid presence; Liebermann–Burchard and Salkowisk reactions to test the terpenoid presence; and the ferric chloride reaction to determine the presence of tannins.

Abundance can be measured as the number of individuals (density), the total biomass, or resource use (Morlon et al. 2009). When abundance is measured as density, it generates bias owing to the sessile and clonal nature of plants (Murray et al. 2005). Thus, one can wrongly consider two stems of the same individuals as two different individuals and so on (Cornwell and Ackerly 2010). Here, we calculated species abundance as biomass expressed as the total basal area, since cerrado plants present a high degree of clonality (Hoffmann 1998). Moreover, it is an appropriate measure for scaling from plant traits to community processes (Lavorel and Garnier 2002; Cortez et al. 2007; Cornwell and Ackerly 2010). We measured the stem diameter at soil level of all individuals sampled and calculated the total basal area of each species by summing up the individual basal areas.

### Statistical analysis

We log-transformed individual trait values and calculated trait mean value per species. We performed stepwise multiple linear regressions, using all quantitative traits as explanatory variables and abundance as response variable, selecting the best model with Akaike information criterion (AIC). Prior to the regression, we log-transformed all quantitative trait mean values per species and the abundances and standardized them to zero mean and unit variance. After the multiple regressions, we tested variance inflation for each quantitative varia-

ble, following Fox and Monette (1992), to detect multicollinearity among explanatory variables. We also applied a simple linear regression between abundance and each defence trait, using the Bonferroni correction (Legendre and Legendre 1998), to test for global significance and another simple linear regression to test the relationship between abundance and total defence, expressed as a defence index. To obtain the defence index, we followed Fine et al. (2006): (i) for each species and each quantitative defence trait, we calculated the trait mean value based on the 10 sample individuals of each species; (ii) we standardized all quantitative defence traits to zero mean and unit variance; (iii) we summed up all values of defence traits, obtaining a single value of total defence per species, which we used in the regression as the defence index. The problem of this approach is that the traits have equal weights, but this is preferable to assigning subjectively different weights (Fine et al. 2006). To calculate this index, we used the inverse of specific leaf area and water content, since higher values of these traits represent low defence. To test the relationship between qualitative chemical defences and abundance, we performed a  $\chi^2$  test. We used R to conduct all the analyses (R Development Core Team 2010).

### Results

We sampled 2062 individuals belonging to 61 species and 27 families. Thus, the number of replicates was 61. Based on the selected individuals, we calculated defence traits and abundance for each species (see Table S1)<sup>1</sup>. Out of the 61 species, 26 species presented terpenoids and 57 tannins. Since only 1 species, *Tocoyena formosa* (Cham. & Schltdl.) K. Schum, presented alkaloids, and only 2, *Kielmeyera coriacea* Mart. & Zucc. and *Kielmeyera grandiflora* A. St.-Hil., presented latex, we did not consider these traits in further analyses. No multicollinearity or non-normality was detected in the data. Hence, we proceeded with stepwise selection, and the best model, according to the AIC, was the one containing specific leaf area and trichome density ( $\Delta\text{AIC} = 4.54$ ). The model was significant ( $R^2 = 0.21$ ,  $P = 0.001$ ), but the only trait that significantly explained the species abundance was specific leaf area, negatively related with it ( $b = -0.87$ ;  $P < 0.001$ ; Table 1). We found a similar result with the simple linear regressions using all traits and Bonferroni's correction (Table 1; Fig. 1): only the specific leaf area was related to abundance ( $b = -0.8$ ;  $R^2 = 0.18$ ,  $P < 0.001$ ). There was no significant relationship between species abundance and the defence index ( $b = 0.03$ ;  $R^2 = 0.015$ ,  $P = 0.338$ ) or other qualitative or quantitative defence traits (Table 1; Fig. S1<sup>1</sup>).

### Discussion

The specific leaf area was the only trait related to species abundance. Although other traits did not explain species abundance, this relationship indicated that environmental or biotic drivers influenced species abundance in the community, as expected. If stochastic events, limited dispersion, and ecological equivalence were the main factors explaining species abundance in the community (Hubbel 2005), one should

<sup>1</sup>Supplementary data are available with the article through the journal Web site (<http://nrcresearchpress.com/doi/suppl/10.1139/b11-087>).

**Table 1.** Summarized results for regression and  $\chi^2$  analysis, with species abundance as response variables and defence traits as explanatory variables, for data sampled in a cerrado site in São Carlos, Brazil (approximately 21°58'05.3"S, 47°52'10.1"W).

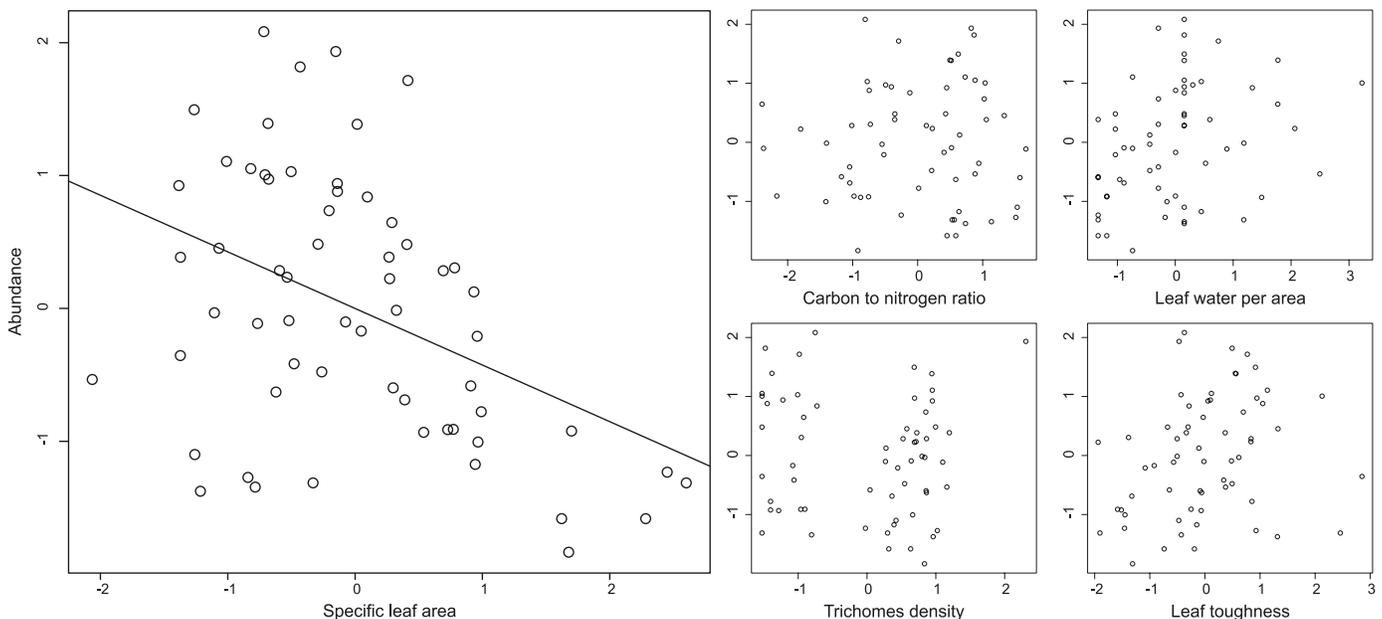
Type of analysis	Explanatory variables	Overall model $R^2$	Slope	$\chi^2$ <sup>a</sup>	$P$
Multiple regression	Specific leaf area	0.21	-0.87	—	<0.001
	Trichomes density	—	-0.33	—	0.145
Simple regression <sup>b</sup>	Specific leaf area	0.18	-0.8	—	<0.001
	Trichomes density	0.01	-0.05	—	~1
	Carbon:nitrogen ratio	0	0.03	—	~1
	Toughness	0.07	0.49	—	0.21
	Water content per area	0.1	0.59	—	0.068
	Defence index	0.02	0.03	—	0.27
$\chi^2$ test	Presence of terpenoids	—	—	33.7	0.99
	Presence of tannins	—	—	9.47	~1

**Note:** Traits used in the multiple regression model were selected using the Akaike information criterion ( $\Delta AIC = 4.54$ ).

<sup>a</sup>Pearson's  $\chi^2$ .

<sup>b</sup> $P$  values were corrected using Bonferroni's method.

**Fig. 1.** Relationships between abundance and defence traits (standardized to zero mean and unit variance) in a cerrado site in São Carlos, Brazil. Specific leaf area was the only trait that presented a significant relationship with abundance ( $b = -0.8$ ;  $R^2 = 0.18$ ,  $P < 0.001$ ).



find no correlation between traits and abundance (Cornwell and Ackerly 2010). Our results supported the general idea that, at a fine scale, neutral processes are unlikely to determine species distribution (Cornwell and Ackerly 2010).

The commonest species presented the lowest values of specific leaf area. The same pattern was found in Californian plant communities (Cornwell and Ackerly 2010). Species with low specific leaf areas have thicker laminae, veins that protrude more, higher tissue density, or combinations of these (Westoby et al. 2002). Low values of specific leaf area are related mainly to slow growth rates, but also with a high defence allocation (Chapin et al. 1993), low leaf palatability (Neves et al. 2010; Schädler et al. 2003), low maximum photosynthetic capacity (Cornelissen et al. 2003), and long leaf life span (Westoby et al. 2002), most of which are related to nutrient stress (Craine 2009). The negative relationship be-

tween abundance and specific leaf area indicated that species with slow growth rates were dominating the community. Thus, the community seems to offer a greater availability of niches to slow-growing species, which demand fewer resources, than to fast-growing species, which demand more resources. Nevertheless, since other antiherbivory resistance traits were not related to abundance, one cannot unambiguously relate the negative relationship between the abundance and specific leaf area to the effects of herbivory in selecting species with high investments in antiherbivory resistance.

Total defence and other defence traits did not explain species abundance. Although studies have provided evidence that highly resistant species should dominate in resource-poor, unproductive communities (Fine et al. 2006; Hanley et al. 2007; Moles et al. 2011), none have tested this postulate in a community-wide approach. Up to now, the main evi-

dence of the model's predictions is based on a controlled laboratory experiment (Burt-Smith et al. 2003) and studies that have compared resistance, or the costs of resistance, in few species growing in resource-rich and resource-poor environments (Koricheva 2002; Fine et al. 2006; Hanley et al. 2007). Our study, which explicitly tested this idea in a community, did not corroborate the postulate of the disturbance resistance model, since more resistant species did not dominate our resource-poor community.

Investments in resistance against herbivory vary with nutrient availability at large scales, among different vegetation types (Fine et al. 2006). However, it is unclear whether heterogeneity in nutrient availability at fine scales could result in local interspecific or intraspecific differences in leaf structure and chemical features. Schädler et al. (2003), who also did not find any effects of leaf palatability on species abundance, suggested that the regulation that herbivory exerts on plant communities could be nonlinear, resulting from interacting effects of herbivore preferences, resource availability, and competition. For example, a selective pressure of herbivores on plants whose leaves have lower nutritional quality could have indirect effects on plant abundance by interfering in nutrient cycling (Belovsky and Slade 2000). Herbivores that preferentially feed on plants whose leaves are nutrient poor would favour species with leaves of high nutritional quality. Since leaves of high nutritional quality decompose faster, fast-growing plant species, which generally have different defence attributes (Craine 2009), would be favoured (Belovsky and Slade 2000). If this effect is strong enough, it could mask the consequences of direct top-down effects (Belovsky and Slade 2000). As long as leaf traits are very plastic in cerrado species (Hoffmann and Franco 2003), and because soil can vary at small distances (Souza and Martins 2004), resource availability could influence plant investments in resistance. Measuring local resource availability and competition could help to explain whether and how herbivory influences species abundance.

Moreover, if herbivores in cerrado are specialists instead of generalists, species-specific antiherbivory resistance should better explain species abundance than the general resistance traits used here. Finally, a weak selective pressure exerted by herbivory could also be the cause of the results we found here. This absence of selectivity could be a consequence of either predator control exerting top-down effects on herbivore populations (Hairston et al. 1960) or the widespread occurrence of sclerophyllous leaves among cerrado species, which could be exerting bottom-up effects on herbivores, maintaining herbivore populations at low densities (Polis 1999; Neves et al. 2010). The fact that we did not find a correlation between carbon:nitrogen ratio and species abundance seems to support this idea, since the consumption of leaves by leaf-cutting ants in cerrado is positively related to the amount of nitrogen in leaves (Mundim et al. 2009).

There is much controversy in the field of community ecology about the drivers of species abundance worldwide. However, integrating species abundance into a wider context, considering biotic and abiotic interactions, is one promising path to obtain advances in this field (McGill et al. 2007). Here, we showed evidence that plant functional traits influence species abundance and that specific leaf area may develop an important role in this context, not only in cerrado but also in

other vegetation types (Cornwell and Ackerly 2010). Nevertheless, we did not find evidences that antiherbivory resistance can explain species abundance in resource-poor communities, in contrast to the prediction of the disturbance resistance model.

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## References

- Agrawal, A.A., and Fishbein, M. 2006. Plant defence syndromes. *Ecology*, **87**(7): 132–149. doi:10.1890/0012-9658(2006)87[132:PDS]2.0.CO;2.
- Batalha, M.A., and Mantovani, W. 1999. Chaves de identificação das espécies vegetais vasculares baseadas em caracteres vegetativos para a ARIE Cerrado Pé-de-Gigante (Santa Rita do Passa Quatro, SP). *Rev. Inst. Florest.* **11**: 137–158. [In Portuguese.]
- Belovsky, G.E., and Slade, J.B. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proc. Natl. Acad. Sci. U.S.A.* **97**(26): 14412–14417. doi:10.1073/pnas.250483797. PMID:11106378.
- Brown, V.K., and Gange, A.C. 1989. Differential effects of above- and below-ground insect herbivory during early plant succession. *Oikos*, **54**(1): 67–76. doi:10.2307/3565898.
- Burt-Smith, G.S., Grime, J.P., and Tilman, D. 2003. Seedling resistance to herbivory as a predictor of relative abundance in a synthesised prairie community. *Oikos*, **101**(2): 345–353.
- Carson, W.P., and Root, R.B. 1999. Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. *Oecologia (Berl.)*, **121**(2): 260–272. doi:10.1007/s004420050928.
- Carvalho, G.H., Cianciaruso, M.V., and Batalha, M.A. 2010. Plantminer: a web tool for checking and gathering plant species taxonomic information. *Environ. Model. Softw.* **25**(6): 815–816. doi:10.1016/j.envsoft.2009.11.014.
- Chapin, F.S., III, Autumn, K., and Pugnaire, F. 1993. Evolution of suites of traits in response to environmental stress. *Am. Nat.* **142**(s1): S78–S92. doi:10.1086/285524.
- Coley, P.D., and Barone, J.A. 1996. Herbivory and plant defences in tropical forests. *Annu. Rev. Ecol. Syst.* **27**(1): 305–335. doi:10.1146/annurev.ecolsys.27.1.305.
- Coley, P.D., Bryant, J.P., and Chapin, F.S., III. 1985. Resource availability and plant antiherbivore defence. *Science (Washington, D.C.)*, **230**(4728): 895–899. doi:10.1126/science.230.4728.895. PMID:17739203.
- Cornelissen, J.H.C., Lavorel, S., Garnier, 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., and Poorter, H. 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* **51**(4): 335–380. doi:10.1071/BT02124.
- Cornwell, W.K., and Ackerly, D.D. 2010. A link between plant traits and abundance: evidence from coastal California Woody Plants. *J. Ecol.* **98**(4): 814–821. doi:10.1111/j.1365-2745.2010.01662.x.
- Cortez, J., Garnier, E., Perez-Harguindeguy, N., Debussche, M., and Gillon, D. 2007. Plant traits, litter quality and decomposition in a

- Mediterranean old field succession. *Plant Soil*, **296**(1-2): 19–34. doi:10.1007/s11104-007-9285-6.
- Costa, A.N., Vasconcelos, H.L., Vieira-Neto, E.H.M., and Bruna, E.M. 2008. Do herbivores exert top-down effects in Neotropical savannas? Estimates of biomass consumption by leaf-cutter ants. *J. Veg. Sci.* **19**(6): 849–854. doi:10.3170/2008-8-18461.
- Craine, J.M. 2009. *Resource strategies of wild plants*. Princeton University Press, Princeton, N.J.
- Dantas, V.L., and Batalha, M.A. 2011. Vegetation structure: fine scale relationships with soil in a cerrado site. *Flora*, **206**(4): 341–346. doi:10.1016/j.flora.2010.11.003.
- Diniz, I.R., Morais, H.C., Botelho, A.M.F., Venturoli, F., and Cabral, B.C. 1999. Lepidopteran caterpillar fauna on lactiferous host plants in the central Brazilian cerrado. *Rev. Bras. Biol.* **59**(4): 627–635.
- Falkenberg, M.B., Santos, R.I., and Simões, C.M.O. 2003. Introdução à análise fitoquímica. *In Farmacognosia: da planta ao medicamento*. Edited by C.M.O. Simões, G. Schenkel, G. Gomann, J.C.P. Mello, L. Mentz, and P. Petrovick. Universidade Federal do Rio Grande do Sul, Porto Alegre. pp. 229–245. [In Portuguese.]
- Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., Sääksjärvi, I., Shultz, J.C., and Coley, P.D. 2006. The growth–defence trade-off and habitat specialization by plants in amazonian forests. *Ecology*, **87**(sp7): 150–162. doi:10.1890/0012-9658(2006)87[150:TGTAHS]2.0.CO;2.
- Fox, J., and Monette, G. 1992. Generalized collinearity diagnostics. *J. Am. Stat. Assoc.* **87**(417): 178–183. doi:10.2307/2290467.
- Goodland, R., and Pollard, R. 1973. The Brazilian cerrado vegetation: a fertility gradient. *J. Ecol.* **61**(1): 219–224. doi:10.2307/2258929.
- Hairston, N.G., Smith, F.E., and Slobodkin, L.B. 1960. Community structure, population control, and competition. *Am. Nat.* **94**(879): 421–425. doi:10.1086/282146.
- Hanley, M.E., Lamont, B.B., Fairbanks, M.M., and Rafferty, C.M. 2007. Plant structural traits and their role in anti-herbivore defence. *Perspect. Plant Ecol. Evol. Syst.* **8**(4): 157–178. doi:10.1016/j.ppees.2007.01.001.
- Herms, D.A., and Mattson, W.J. 1992. The dilemma of plants: to grow or defend. *Q. Rev. Biol.* **67**(3): 283–335. doi:10.1086/417659.
- Hoffmann, W.A. 1998. Post-burn reproduction of woody plants in a neotropical savanna: The relative importance of sexual and vegetative reproduction. *J. Appl. Ecol.* **35**(3): 422–433. doi:10.1046/j.1365-2664.1998.00321.x.
- Hoffmann, W.A., and Franco, A.C. 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically-independent contrasts. *J. Ecol.* **91**(3): 475–484. doi:10.1046/j.1365-2745.2003.00777.x.
- Hubbel, S.P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* **19**(1): 166–172. doi:10.1111/j.0269-8463.2005.00965.x.
- Köppen, W. 1931. *Grundriss der Klimakunde*. Gruyter, Berlin. [In German.]
- Koricheva, J. 2002. Meta-analysis of sources of variation in fitness costs of plant antiherbivore defences. *Ecology*, **83**(1): 176–190. doi:10.1890/0012-9658(2002)083[0176:MAOSOV]2.0.CO;2.
- Lavorel, S., and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* **16**(5): 545–556. doi:10.1046/j.1365-2435.2002.00664.x.
- Legendre, P., and Legendre, L. 1998. *Numerical ecology*. Elsevier, Amsterdam.
- Lima, M.I.S. 2000. Substâncias do metabolismo secundário de algumas espécies nativas e introduzidas no Brasil. *In Ecofisiologia vegetal*. Edited by W. Larcher. Rima, São Carlos. pp. 33–68. [In Portuguese.]
- Mantovani, W., Leitão Filho, H.F., and Martins, F.R. 1985. Chave baseada em caracteres vegetativos para identificação de espécies lenhosas da Reserva Biológica de Moji Guaçu, SP. *Hoehnea*, **12**: 35–66. [In Portuguese.]
- Marquis, R.J., Diniz, I.R., and Morais, H.C. 2001. Patterns and correlates of interspecific variation in foliar insect herbivory and pathogen attack in Brazilian cerrado. *J. Trop. Ecol.* **17**(1): 127–148. doi:10.1017/S0266467401001080.
- Marquis, R.J., Morais, H.C., and Diniz, I.R. 2002. Interactions among cerrado plants and their herbivores: unique or typical? *In The cerrados of Brazil*. Edited by P.S. Oliveira and R.J. Marquis. Columbia University, New York.
- Mauricio, R. 2000. Natural selection and the joint evolution of tolerance and resistance as plant defenses. *Evol. Ecol.* **14**(4/6): 491–507. doi:10.1023/A:1010909829269.
- McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I., and White, E.P. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.* **10**(10): 995–1015. doi:10.1111/j.1461-0248.2007.01094.x. PMID:17845298.
- Moles, A.T., Wallis, I.R., Foley, W.J., Warton, D.I., Stegen, J.C., Bisigato, A.J., Cella-Pizarro, L., Clark, C.J., Cohen, P.S., Cornwell, W.K., Edwards, W., Ejrnaes, R., Gonzales-Ojeda, T., Graae, B.J., Hay, G., Lumbwe, F.C., Magaña-Rodríguez, B., Moore, B.D., Peri, P.L., Poulsen, J.R., Veldtman, R., von Zeipel, H., Andrew, N.R., Boulter, S.L., Borer, E.T., Campón, F.F., Coll, M., Farji-Brener, A.G., De Gabriel, J., Jurado, E., Kyhn, L.A., Low, B., Mulder, C.P.H., Reardon-Smith, K., Rodríguez-Velázquez, J., Seabloom, E.W., Vesk, P.A., van Cauter, A., Waldram, M.S., Zheng, Z., Blendinger, P.G., Enquist, B.J., Facelli, J.M., Knight, T., Majer, J.D., Martínez-Ramos, M., McQuillan, P., and Prior, L.D. 2011. Putting plant resistance traits on the map: a test of the idea that plants are better defended at lower latitudes. *New Phytol.* **191**(3): 777–788. doi:10.1111/j.1469-8137.2011.03732.x. PMID:21539574.
- Morais, H.C., Sujii, E.R., Almeida-Neto, M., De-Carvalho, P.S., Hay, J.D., and Diniz, I.R. 2011. Host plant specialization and species turnover of caterpillars among hosts in the Brazilian cerrado. *Biotropica*, **43**(4): 467–472. doi:10.1111/j.1744-7429.2010.00736.x.
- Morlon, H., White, E.P., Etienne, R.S., Green, J.L., Ostling, A., Alonso, D., Enquist, B.J., He, F., Hurlbert, A., Magurran, A.E., Maurer, B.A., McGill, B.J., Olf, H., Storch, D., and Zillio, T. 2009. Taking species abundance distributions beyond individuals. *Ecol. Lett.* **12**(6): 488–501. doi:10.1111/j.1461-0248.2009.01318.x. PMID:19490012.
- Mundim, F.M., Costa, A.N., and Vasconcelos, H.L. 2009. Leaf nutrient content and host plant selection by leaf-cutter ants, *Atta laevigata*, in a Neotropical savanna. *Entomol. Exp. Appl.* **130**(1): 47–54. doi:10.1111/j.1570-7458.2008.00789.x.
- Murray, B.R., Kelaher, B.P., Hose, G.C., and Figueira, W.F. 2005. A meta-analysis of the interspecific relationship between seed size and plant abundance within local communities. *Oikos*, **110**(1): 191–194. doi:10.1111/j.0030-1299.2005.13943.x.
- Neves, F.S., Araújo, L.S., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Sanchez-Azofeifa, G.A., and Quesada, M. 2010. Canopy herbivory and insect herbivore diversity in a dry forest–savanna transition in Brazil. *Biotropica*, **42**(1): 112–118. doi:10.1111/j.1744-7429.2009.00541.x.
- Núñez-Farfán, J., Fornoni, J., and Valverde, P.L. 2007. The evolution of resistance and tolerance to herbivores. *Annu. Rev. Ecol. Evol.*

- Syst. **38**(1): 541–566. doi:10.1146/annurev.ecolsys.38.091206.095822.
- Oliveira-Filho, A.T., and Ratter, J.A. 2002. Vegetation physiognomies and woody flora of the cerrado biome. *In* The cerrados of Brazil: ecology and natural history of neotropical savannas. *Edited by* P.S. Oliveira and R.J. Marquis. Columbia University, New York. pp. 13–32.
- Polis, G.A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, **86**(1): 3–15. doi:10.2307/3546565.
- R Development Core Team. 2010. R: a language and environment for statistical computing. Wien, R Foundation for Statistical Computing. Available from <http://www.r-project.org> [accessed 5 Jul 2010].
- Rasband, W. 2004. ImageJ: image process and analysis in Java. National Institutes of Health, Bethesda, Md.
- Ruggiero, P.G.C., Batalha, M.A., Pivello, V.P., and Meirelles, S.T. 2002. Soil–vegetation relationships in cerrado (Brazilian savana) and semideciduous forest, southeastern Brazil. *Plant Ecol.* **160**(1): 1–16. doi:10.1023/A:1015819219386.
- Schädler, M., Jung, G., Auge, H., and Brandl, R. 2003. Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. *Oikos*, **103**(1): 121–132. doi:10.1034/j.1600-0706.2003.12659.x.
- Silva, D.M., and Batalha, M.A. 2011. Defense syndromes against herbivory in a cerrado plant community. *Plant Ecol.* **212**(2): 181–193. doi:10.1007/s11258-010-9813-y.
- Secretaria de Estado do Meio Ambiente. 1997. Cerrado: bases para conservação e uso sustentável das áreas de cerrado do estado de São Paulo. SMA, São Paulo.
- Souza, A.F., and Martins, F.R. 2004. Microsite specialization and spatial distribution of *Geonoma brevispatha*, a clonal palm in south-eastern Brazil. *Ecol. Res.* **19**(5): 521–532. doi:10.1111/j.1440-1703.2004.00670.x.
- Strauss, S.Y., and Agrawal, A.A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.* **14**(5): 179–185. doi:10.1016/S0169-5347(98)01576-6. PMID:10322530.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., and Wright, I.J. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* **33**(1): 125–159. doi:10.1146/annurev.ecolsys.33.010802.150452.