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CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE  
Programa de Pós-Graduação em Ecologia e Recursos Naturais

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Padrões de floração e suas relações com o clima,  
fotoperíodo, visitantes e filogenia em duas comunidades  
de cerrado

São Carlos – SP  
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# Padrões de floração e suas relações com o clima, visitantes e filogenia em duas comunidades de cerrado

Orientador: Dr. Marco Antônio Batalha

Dissertação apresentada ao Programa de Pós-graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de Mestre em Ecologia

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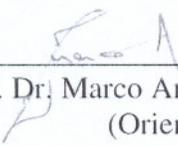
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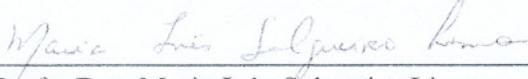
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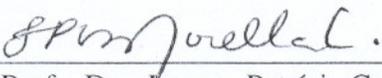
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## Resumo

Entender as relações entre a floração e o clima, o componente biótico e a filogenia das espécies vegetais é fundamental, já que a fenologia da floração exerce influência sobre a capacidade das espécies de encontrarem polinizadores, parceiros, dispersores e ambientes favoráveis para o estabelecimento de plântulas. Qualquer mudança no período habitual de floração, seja por mudanças climáticas, de regime de fogo ou pela invasão de espécies exóticas, pode ocasionar graves consequências para a manutenção dos processos ecológicos da comunidade, causando assincronia entre a reprodução das espécies vegetais a atividade de polinizadores e dispersores.

O cerrado geralmente está sujeito a um ritmo estacional, com alternância entre verão chuvoso e inverno seco. A floração do cerrado tem sido relacionada ao regime de chuvas, porém outros fatores ambientais, como o fotoperíodo e a atividade de polinizadores, também são estacionais e podem influenciar a floração dos componentes da flora do cerrado. Há três categorias de teorias que procuram explicar a influência de diversos fatores na fenologia da floração: *i*) teoria climática, segundo a qual a floração tende a seguir variações previsíveis de fatores climáticos, *ii*) teoria biótica, de acordo com a qual as espécies que compartilham polinizadores floresceriam em épocas distintas para evitar concorrência por esse recurso, ou floresceriam em épocas semelhantes, para atrair mais polinizadores, e *iii*) teoria filogenética, segundo a qual o período de floração seria determinado pela filogenia das espécies e, portanto, espécies aparentadas teriam padrões de floração semelhantes.

No primeiro capítulo, estudamos as relações das espécies do componente arbustivo-arbóreo do cerrado com o clima, visitantes e filogenia em uma área disjunta de cerrado. Relacionamos 16 espécies e 585 indivíduos que floresceram pelo menos três vezes com o comprimento do dia por meio de análise de regressão múltipla com funções circulares ( $R_{adj}^2$

= 0.88,  $F = 26.97$ ,  $P < 0.001$ ). Testamos as relações entre os polinizadores de 36 espécies e 766 indivíduos com a fenologia da floração por meio de análise de modelos nulos. Encontramos floração agrupada no grupo de espécies polinizadas por abelhas, corroborando o postulado da floração em massa da teoria biótica. Também utilizando modelos nulos, não encontramos restrição filogenética na época de floração das mesmas 36 espécies.

Já no segundo capítulo, relacionamos a floração de ambos componentes da flora do cerrado do Parque Nacional das Emas (GO) com variáveis ambientais estacionais. Encontramos relações entre a floração de 428 espécies do componente herbáceo-subarbustivo com a temperatura e a precipitação ( $R_{adj}^2 = 0.9628$ ,  $F = 72.1$ ,  $P < 0.001$ ). Para as 130 espécies do componente arbustivo-arbóreo encontradas com flores, o comprimento do dia e a temperatura média foram as variáveis ambientais presentes no melhor modelo de regressão ( $R_{adj}^2 = 0.9394$ ,  $F = 43.65$ ,  $P < 0.001$ ). Estes resultados estão de acordo com a previsão da teoria climática, uma vez que as raízes profundas do componente arbustivo-arbóreo consegue absorver água suficiente para sustentar a floração mesmo na estação seca, o que não ocorre para as espécies do componente herbáceo-subarbustivo que segue, portanto, a precipitação.

No terceiro capítulo, apresentamos uma aplicação para a grande rede que confere e sugere nomes aceitos de espécies vegetais, busca famílias, autores e sinónimas em três bancos de dados de informações taxonômicas disponíveis na rede mundial de computadores.

**Palavras-chave:** cerrado, componente herbáceo, componente arbóreo, fenologia, floração, filogenia, polinizadores, informações taxonômicas, informática para a biodiversidade.

## Abstract

Knowing how flowering relates with climatic, biotic, and phylogenetic factors is important, since flowering phenology affects the ability of species of finding pollinators, mates, dispersers, and optimal conditions for seedling development. Any changes in this well established flowering pattern, due to changes in fire frequency, alien species invasion, or climate change, may disrupt the synchrony between flowering phenology and pollinators and dispersers activity.

The cerrado is usually under a seasonal rhythm, with alternating rainy summers and dry winters. Flowering phenology of cerrado communities has been related to the rainfall seasonality. However, other environmental factors such as photoperiod and pollinator activity are also seasonal and may influence flowering phenology of cerrado flora. There are three categories of theories that try to explain the influence of several factors on flowering phenology: *i)* climatic theory, according to which flowering events are likely to follow predictable variations of climatic factors, *ii)* biotic theory, which states that species with shared pollinators are likely to either flower in similar times to attract more pollinators, or flower in distinct times to avoid competition for pollinators, and *iii)* *phylogenetic theory*, according to which flowering times are under phylogenetic constraint and, thus, related species are likely to have similar flowering patterns.

In the first chapter, we related the flowering phenology of the woody component of a disjunct cerrado area with climate, visitors, and phylogeny. We found relationships between day length and the 16 species and 585 individuals that we found flowering at least three times, using a multiple regression analysis with circular functions ( $R_{adj}^2 = 0.88$ ,  $F = 26.97$ ,  $P < 0.001$ ). By using null model analysis, we searched for pollinator constraints on flowering

times of species with shared pollinators. We found evidence of such constraints in the group of species pollinated by bees, which corroborates the predictions of the biotic theory.

In the second chapter, we focused on the climatic theory, trying to relate the environmental factors with the flowering patterns of both components of the cerrado flora at the Emas National Park (Central Brazil). We found evidence of relationships between the flowering patterns of 428 species of the ground layer we found flowering with temperature and rainfall ( $R_{adj}^2 = 0.9628$ ,  $F = 72.1$ ,  $P < 0.001$ ). For the 130 species of the woody component that we found flowering, day length and mean temperature were the best predictors of their flowering patterns ( $R_{adj}^2 = 0.9394$ ,  $F = 43.65$ ,  $P < 0.001$ ). These results also corroborate the predictions of the climatic theory, since the woody component can absorb water from deep soil layers in the dry season. So, woody species can follow more predictable variables, such as day length, whereas herbaceous species, with their shallow root system, follow rainfall seasonality.

Finally, in the third chapter, we present an Internet application that searches accepted names, families, authors, and synonyms of plant species in three taxonomic information databases freely available in the Internet.

**Key-words:** cerrado, herbaceous component, woody component, phenology, flowering, phylogeny, pollinators, taxonomic information, biodiversity informatics.

# **I - Introdução geral**

No atual contexto de mudanças climáticas, entender as relações entre a biologia reprodutiva das espécies vegetais e o clima, o componente biótico e a filogenia é fundamental (Inouye 2008). Segundo Lieth (1974), a fenologia é o estudo da ocorrência de eventos biológicos, a influência dos fatores bióticos ou abióticos nesses eventos e as relações entre as fenofases de espécies diferentes ou de uma única espécie. A fenologia da floração é uma etapa fundamental da biologia reprodutiva das angiospermas, já que exerce influência sobre a capacidade das espécies de encontrarem polinizadores, parceiros, dispersores e ambientes favoráveis para o estabelecimento de plântulas (Inouye 2008). Qualquer mudança no período habitual de floração das espécies de uma comunidade, seja por mudanças climáticas, de regime do fogo, ou ocasionadas pela presença de espécies não nativas, pode ocasionar graves consequências para a manutenção dos processos ecológicos dessa comunidade. A quebra dos padrões temporais de floração pode causar assincronia entre a fenologia reprodutiva das plantas e a de polinizadores e dispersores (Visser & Holleman 2001, Memmott et al. 2007 e Inouye 2008), além de fazer com que os diásporos encontrem condições impróprias no ambiente, como baixa disponibilidade de recursos para a germinação de sementes e estabelecimento e desenvolvimento de plântulas (Rathcke & Lacey 1985).

Nos trópicos, sob estação seca bem definida e regular, encontram-se tipos vegetacionais (cerrado e florestas secas) sujeitos a um ritmo estacional (Rizzini 1997). O cerrado está sujeito a queimadas periódicas, possui lençol freático profundo, ocorre em solos inférteis e profundos, que, com poucas exceções, são latossolos, arenosos ou argilosos (Eiten 1977, Rizzini 1997). O cerrado apresenta grande variação fisionômica (Coutinho 1978), indo de uma fisionomia campestre (campo limpo) a uma florestal (cerradão), passando por fisionomias savânicas (campo sujo, campo cerrado e cerrado *sensu stricto*). No cerrado, há dois componentes, o arbustivo-arbóreo e o herbáceo-subarbustivo (Rizzini 1997), cujas importâncias variam de modo inverso. Enquanto que a importância do componente arbustivo-

arbóreo aumenta do campo limpo ao cerradão, a do componente herbáceo-subarbustivo diminui (Coutinho 1978). O cerrado normalmente está sob clima estacional, com verão chuvoso e inverno seco, sendo classificado como, Am, Aw ou Cwa seguindo Köppen (1948). Apesar do cerrado ser um dos pontos quentes para a conservação da biodiversidade no mundo (Myers *et al.* 2000), ele permanece “esquecido” e está desaparecendo rapidamente (Marris 2005).

A fenologia da floração do componente arbustivo-arbóreo do cerrado tem sido relacionada ao regime de chuvas e à estacionalidade à qual as áreas de cerrado estão submetidas (Batalha & Mantovani 2000, Oliveira & Gibbs 2000, Batalha & Martins 2004 e Lenza & Klink 2006). Neste trabalho, entretanto, procuramos usar técnicas (Pleasants 1980, Anderson *et al.* 2005 e Boulter *et al.* 2006) e variáveis diferentes das aplicadas até hoje em estudos no cerrado. Dessa forma, poderíamos identificar relações entre o clima, visitantes e filogenia que não foram observadas anteriormente. Procuramos seguir os postulados das três categorias de teorias que se propõem a explicar a influência de fatores bióticos e abióticos nos padrões de floração compiladas por Boulter *et al.* (2006): *i*) teoria climática, segundo a qual os padrões de floração seguem variações previsíveis de fatores ambientais, como precipitação, temperatura e comprimento do dia. Um dos postulados dessa categoria de teorias diz que, em áreas onde há estação seca, os regimes de chuvas ou de disponibilidade de água no solo tendem a serem as variáveis climáticas mais importantes na determinação dos padrões de floração (Wright & van Shaik 1994). Entretanto, onde há disponibilidade de água suficiente para a reprodução durante todo o ano, outros fatores mais previsíveis tendem a serem usados como estímulos para a sincronização da floração na comunidade. Dentre tais fatores, estão o comprimento do dia, o horário do pôr e nascer do sol e a quantidade de radiação solar disponível para as plantas (Borchert *et al.* 2004); *ii*) teoria biótica, que prevê que a atividade dos polinizadores, quando são considerados recursos limitantes, influenciaria nos padrões fenológicos da

floração (Bolmgren et al. 2003). Ainda de acordo com a teoria biótica, as espécies de uma comunidade poderiam tanto florescer em massa em determinada época do ano, o que atrairia mais polinizadores devido a maior disponibilidade de recursos (Thomson 1978), quanto florescer em épocas distintas dentro das guildas de polinização, o que evitaria a competição por polinizadores compartilhados (Pleasant 1980); finalmente, *iii*) teoria filogenética, segundo a qual a época de floração das espécies seria determinada pela filogenia e conservada em espécies aparentadas (Ollerton & Lack 1992 e Wright & Calderon 1995). Evidências da teoria filogenética foram observadas com maior intensidade entre espécies que compartilham gêneros ou famílias (Wright & Calderon 1995 e Boulter et al. 2006).

Fizemos este estudo com dados coletados em duas áreas. Uma delas foi a Estação Experimental de Itirapina (EEI; 22°13'S e 47°51'W), localizada na cidade de Itirapina, no interior do estado de São Paulo (Fig. 1). Testamos, entre maio de 2004 e abril de 2005, se cada um dos indivíduos do componente arbustivo-arbóreo dessa área estavam com flores. Fizemos as coletas em 50 parcelas sorteadas em um fragmento disjunto de cerrado *sensu stricto*, conhecido como Valério (Fig. 2). A outra área que utilizamos no nosso estudo foi o Parque Nacional das Emas (PNE; 17°49'-18°28'S e 52°39'-53°10'W; Fig. 3), localizado na cidade de Mineiros, estado de Goiás, na área nuclear do cerrado. O PNE é uma das maiores e mais importantes reservas em que ocorre o cerrado, com cerca de 133.000 ha. Utilizamos dados coletados entre novembro de 1998 e outubro de 1999, como parte de outro estudo já publicado (Batalha & Martins 2004). Esses dados foram coletados de maneira qualitativa, ou seja, bastava que um único indivíduo de uma espécie fosse encontrado com flores para que toda aquela espécie fosse considerada em floração naquele mês. No PNE, há áreas que vão desde o campo limpo até o cerrado *sensu stricto*, e os dados foram coletados em todas essas fisionomias.

No primeiro capítulo, procuramos relacionar a fenologia da floração do componente arbustivo-arbóreo de uma área disjunta de cerrado *sensu stricto* na EEI com fatores climáticos, bióticos e filogenéticos, de acordo com as três categorias de teorias citadas anteriormente. Para isso, procuramos responder às seguintes perguntas: *i)* o número de espécies florescendo está relacionado à temperatura, à precipitação ou ao comprimento do dia?; *ii)* os padrões de floração de espécies que compartilham polinizadores são agrupados ou divergentes?; *iii)* há sinal filogenético na concentração, duração e intensidade da floração? Este capítulo foi formatado segundo as normas do periódico *Plant Ecology*, para onde pretendemos submetê-lo.

No segundo capítulo, estávamos interessados em identificar quais fatores ambientais melhor explicaram a variação do número de espécies florescendo em cada mês, tanto para o componente herbáceo-subarbustivo, quanto para o componente arbustivo-arbóreo. Nesse capítulo, procuramos responder às seguintes perguntas: *i)* a floração do componente herbáceo-subarbustivo está relacionada à temperatura, à precipitação ou ao comprimento do dia?; *ii)* a floração do componente arbustivo-arbóreo está relacionada à temperatura, à precipitação ou ao comprimento do dia?; *iii)* os picos de floração são anuais? Submetemos o artigo correspondente a esse capítulo ao periódico *Biotropica*, portanto formatamo-lo seguindo as normas desse periódico.

Nos dois primeiros capítulos, trabalhamos com dados de centenas de espécies. Para cada uma dessas espécies, precisaríamos verificar a grafia dos nomes e buscar informações taxonômicas como família seguindo a última classificação da APG (Stevens 2008), autores e sinônimas. Como não havia ferramenta disponível que facilitasse esse trabalho, desenvolvemos uma aplicação chamada “Plantminer”. O Plantminer busca as informações taxonômicas de todas as entradas de uma lista de espécies vegetais em três bancos de dados disponíveis na Internet: World Checklist of Selected Plant Families

(<http://apps.kew.org/wcsp/>), Tropicos (<http://www.tropicos.org>) e International Plant Names Index (<http://www.ipni.org>). Além das funções já citadas, o Plantminer também sugere os nomes aceitos mais prováveis de uma espécie que esteja com a grafia incorreta. Escolhemos disponibilizar essa aplicação por meio de um sítio na internet (<http://www.plantminer.com>). Esse meio de distribuição se justifica, já que torna a distribuição do aplicativo mais ampla e dependente apenas de um navegador de conteúdo da Internet. Dessa forma, o terceiro capítulo é um artigo que submeteremos à seção *Biodiversity letters* do periódico *Diversity and Distributions*. Nesse artigo, apresentamos e explicamos o funcionamento do Plantminer à comunidade de pesquisadores à qual ele é voltado, que são aqueles que trabalham com extensas listas de espécies vegetais, em áreas como a macroecologia e a ecologia de comunidades vegetais.

Escolhemos apresentar a dissertação em forma de capítulos, já que isto torna a publicação dos artigos científicos menos trabalhosa. Como as revistas que escolhemos exigem que o idioma usado seja o inglês, nossos capítulos foram escritos nesse idioma. Além disso, como os capítulos são independentes, alguma repetição torna-se inevitável.

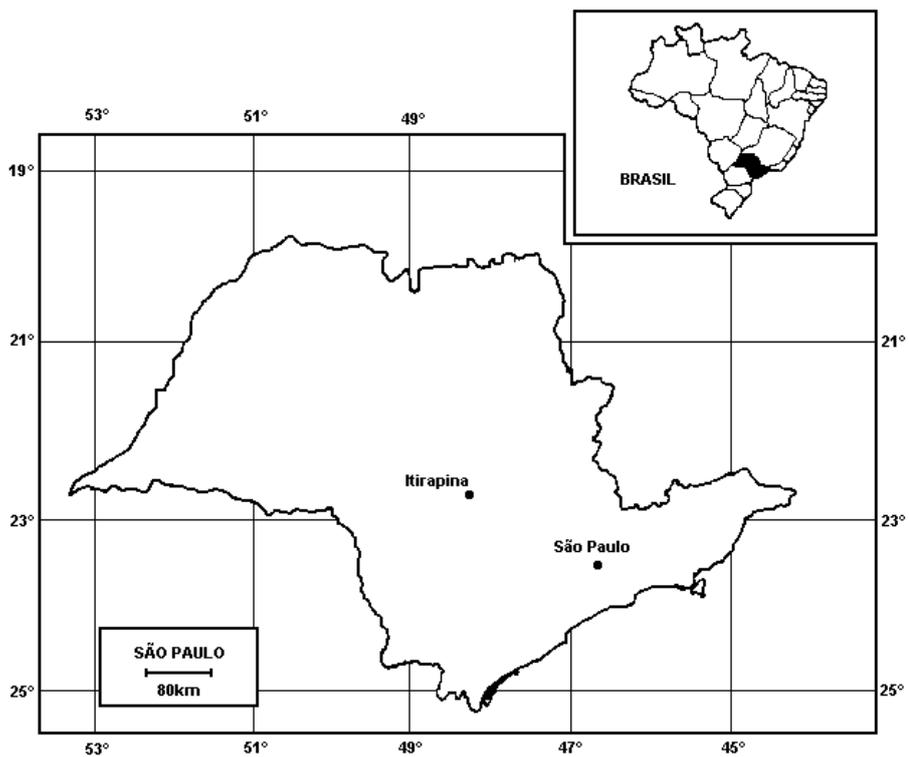


Figura 1 – Localização do município de Itirapina no estado de São Paulo (modificado de Salis *et al.* 1995).

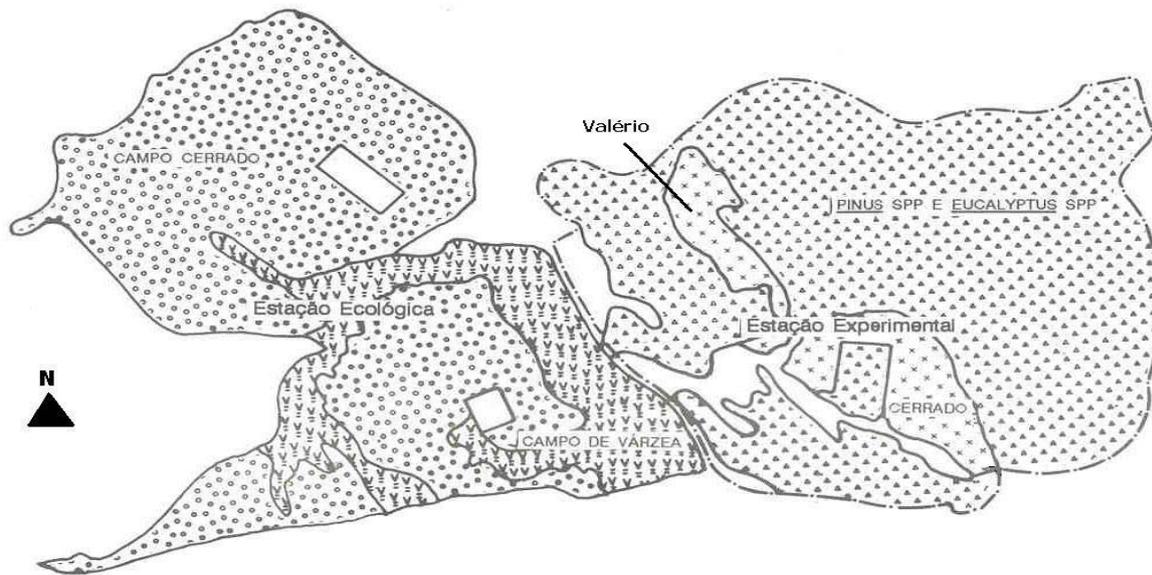


Figura 2 – Representação da Estação Ecológica e Experimental de Itirapina (SP), mostrando a localização do fragmento do Valério.

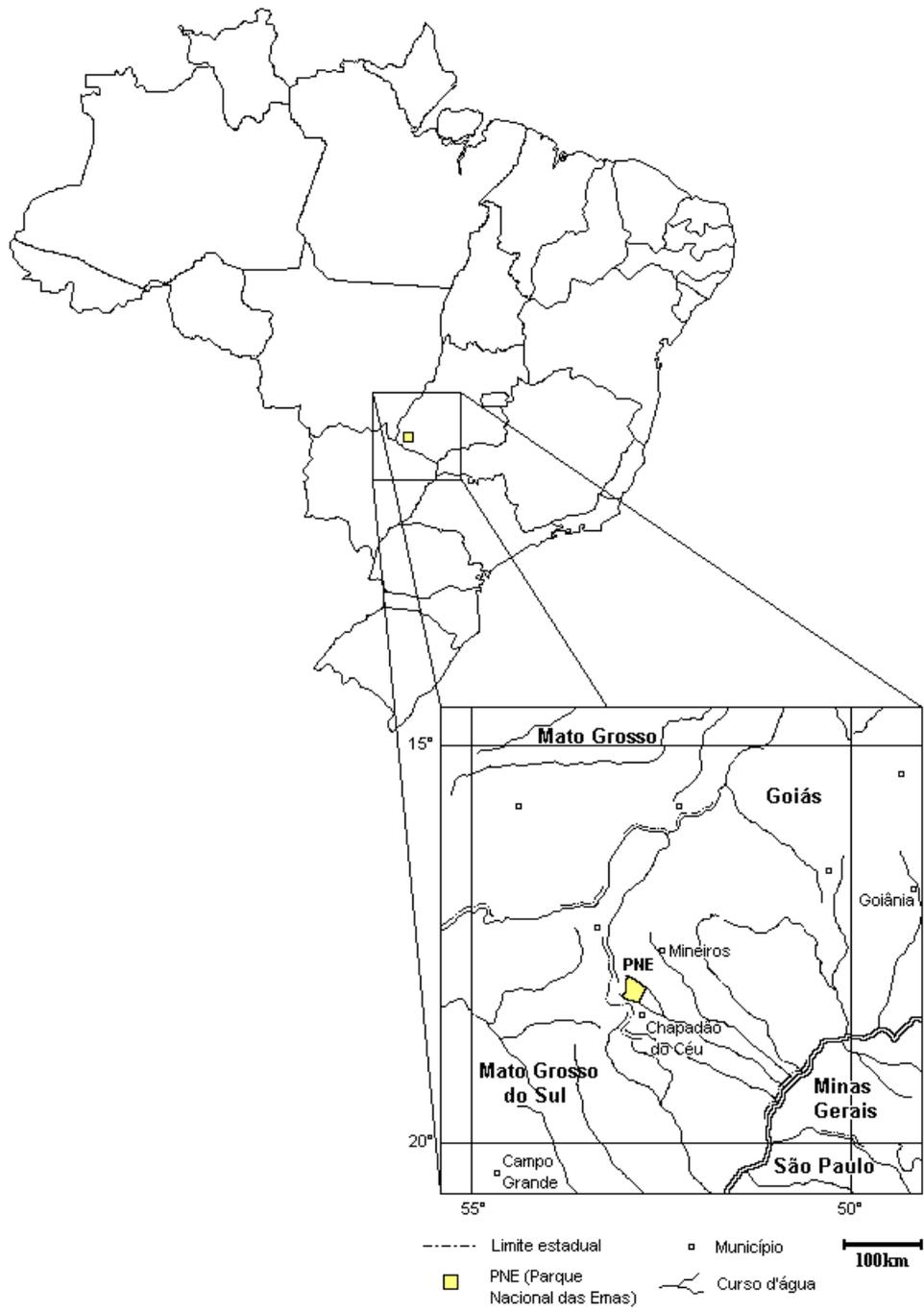


Figura 3 – Localização do Parque Nacional das Emas (PNE; GO).

## Referências bibliográficas

- Anderson, D. P., Nordheim, E. V., Moermond, T. C., Bi, Z. B. G., e Boesch, C. 2005. Factors influencing tree phenology in Taï National Park, Cote d'Ivoire. *Biotropica* 37: 631-640.
- Batalha, M. A., e Mantovani, W. 2000. Reproductive phenological patterns of cerrado plant species at the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and the woody floras. *Revista Brasileira de Biologia* 60: 129-145.
- Batalha, M. A., e Martins, F. R. 2004. Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). *Australian Journal of Botany* 52: 149-161.
- Bolmgren, K., Eriksoon, O., e Peter Linder, H. 2003. Contrasting flowering phenology and species richness in abiotically and biotically pollinated angiosperms.
- Borchert, R., Meyer, S. A., Felger, R. S., e Porter-bolland, L. 2004. Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography* 13: 409-425.
- Boulter, S. L., Kitching, R. L., e Howlett, B. G. 2006. Family, visitors and the weather: patterns of flowering in tropical rain forests of northern Australia. *Journal of Ecology* 94: 369-382.
- Coutinho, L. M. 1978. O conceito do cerrado. *Revista Brasileira de Botânica* 1: 17-23.
- Eiten, G. 1977. Delimitação do conceito de cerrado. *Arquivos do Jardim Botânico* 21: 125-134.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89: 353-362.

- Johnson, S. D. 1992. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. *The Journal of Ecology* 81: 567-572.
- Köppen, W. 1948. *Climatología*. Fondo de Cultura Económica, México.
- Lenza, E., e Klink, C. A. 2006. Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF. *Revista Brasileira de Botânica* 29: 627-638.
- Lieth, H. 1974. *Introduction to phenology and the modeling of seasonality*. Springer, Berlin.
- Marris, E. 2005. The forgotten ecosystem. *Nature* 437: 944-945.
- Memmott, J., Craze, P. J., Nickolas, M. W., e Price, M. V. 2007. Global warming and the disruption of plant-pollinator interactions. *Ecology Letters* 10: 710-717.
- Myers N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., e Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- Oliveira, P. E., e Gibbs, P. E. 2000. Reproductive biology of woody plants in a cerrado community of Central Brazil. *Flora* 195: 311-329.
- Ollerton, J., e Lack, A. J. 1992. Flowering phenology: An example of relaxation of natural selection? *Trends in Ecology & Evolution* 7: 274-276.
- Pleasants, J. M. 1980. Competition for bumblebee pollinators in Rocky Mountain plant communities. *Ecology* 61: 1446-1459.
- Ramirez, N. 2002. Reproductive phenology, life-forms, and habitats of the Venezuelan Central Plain. *American Journal of Botany* 89: 836-842.
- Rathcke, B., e Lacey, E. P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16: 179-214.
- Rizzini, C. T. 1997. *Tratado de Fitogeografia do Brasil: aspectos ecológicos, sociológicos e florísticos*. Âmbito Cultural Edições LTDA, Rio de Janeiro.
- Salis SM, Shepherd, G. J., e Joly, C. A. 1995. Floristic comparison of mesophytic semideciduous forests of the interior of the State of São Paulo, Southeast Brazil. *Vegetatio*

119: 155-164.

Stevens, P. F. (2001 onwards). Angiosperm Phylogeny Website. Version 9, June 2008.

<http://www.mobot.org/MOBOT/research/APweb/>.

Thomson, J. D. 1978. Effect of stand composition on insect visitation in two species mixtures of *Hireracium*. The American Midland Naturalist 100: 431-440.

Visser, M. E., e Holleman, L. J. M. 2001. Warmer springs disrupt oak and moth phenology.

Proceedings of the Royal Society of London 268: 289-294.

Wright, S. J., e Calderon, O. 1995. Phylogenetic patterns among tropical flowering phenologies. The Journal of Ecology 83: 937-948.

Wright, S. J, e van Schaik, C. P. 1994. Light and the phenology of tropical trees. The American Naturalist 143: 192-199.

# **II - Capítulo 1**

Padrões de floração de espécies arbustivo-arbóreas em  
área de cerrado *sensu stricto* na Estação Experimental  
de Itirapina (SP): relações com clima, fotoperíodo,  
visitantes e filogenia<sup>1</sup>

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<sup>1</sup> Trabalho formatado segundo as normas do periódico *Plant Ecology*.

**Flowering patterns of cerrado woody species in southeastern Brazil: relationships with climate, day length, pollinators, and phylogeny**

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## **Abstract**

The theories about the influence of different factors on flowering phenology fall into three categories: climatic, biotic, and phylogenetic theories. We tested these theories against data collected in a cerrado site in southeastern Brazil. To test if the peak of flowering activity coincided with a particular climatic variable or day length, we used multiple regression analysis with circular functions. We searched for evidence of relationships between flowering times and pollinator activity with null model analysis by randomizing and overlapping the flowering distributions of species with shared pollinators. Finally, we made a phylogenetic restriction analysis to test whether phylogenetically related groups had similar flowering times. We found evidence for both climatic and biotic theories, but not for the phylogenetic one. The best environmental predictor was day length, which species may use as cue due to its high previsibility. The clumped flowering of species pollinated by bees may attract more pollinators because of the high resource availability for them.

**Keywords:** flowering distribution comparison, phenology, phylogenetic restriction analysis, savanna

## **Introduction**

Flowering phenology has fundamental importance on plant species fitness, as it may be determinant for species to find pollinators, find mates, and minimize predators damage (Inouye 2008). Flowering times may also affect subsequent steps in the reproductive process, like seed dispersal and seed germination (Frankie et al. 1974; Mduma et al. 2007; Wright and Calderon 1995). The obvious importance of regular flowering times for some species (Ollerton and Lack 1992) may have lead plant species to achieve synchronization of flowering by linking it to predictable and seasonal environmental factors like rainfall, temperature, day length, and insolation (Ashton et al. 1998; Borchert et al. 2002). In the current context of climate change, knowing how flowering phenology is affected by environmental, biotic, and phylogenetic factors is vital. Deviations in well established start time, duration, and intensity of flowering may break interactions between flowers and pollinators activities, since they respond in different ways to new climate conditions (Inouye 2008; Memmott et al. 2007; Visser and Holleman 2001), which may also lead towards an increase in competition for pollinators and dispersers.

There are three types of theories that try to explain the influence of different factors on flowering phenology (Boulter et al. 2006): (1) climatic theory, which links peaks of flowering activities to the seasonal variation of limiting factors, such as optimal climate conditions to seed dispersal or seedling development (Ramirez 2002; Wright and Calderon 1995); (2) biotic theory, linking the activity of pollinators to the flowering synchrony (Bomlgren et al. 2003; Pleasants 1980; Sakai 2002); and (3) phylogenetic theory, according to which flowering times are under phylogenetic influence (Johnson 1992, Ollerton and Lack 1992; Wright and Calderon 1995).

According to the climatic theory, flowering phenology is expected to follow predictable variation in environmental factors, such as rainfall, temperature, day length, and insolation (Anderson et al. 2005; Frankie et al. 1974; Ramirez 2002). Wright and Cornejo (1990) found that moisture availability is likely to play a more important role on phenology in areas where water is a limiting factor. Where moisture availability is not limiting, other factors, such as insolation, may be of greater importance, since it is more energy efficient to transfer assimilates directly to growing organs, like flowers, than it is to store them for later use (Wright and van Schaik 1994). Also, sun-related cues are more predictable as they happen regularly at the same time of the year, every year (Borchert et al. 2005). Studies on the reproductive phenology of cerrado communities (Batalha and Martins 2004; Lenza and Klink 2007; Oliveira and Gibbs 2000), as well as of other seasonally dry communities (Borchert 1983; Williams et al. 1999) linked flowering times to the water regime in these areas. Anderson et al. (2005), on the other hand, found evidence of temperature acting as an environmental cue for flowering activities in a rain forest in Ivory Coast. Although climate factors are obvious cues to the synchronization of flowering, they may also serve as indirect cues, acting on the activity of pollinators (Rathcke and Lacey 1985). Moreover, optimal environmental conditions to seed germination were also described as possible determinants of flowering times (Rathcke and Lacey 1985). Until now, works about flowering phenology of cerrado woody species did not test flowering times against sun-related variables, like day length and insolation. In this study, if the climatic theory holds, we expect peak flowering to be annual and linked to rainfall, as the dry season occurs yearly and may limit flower production.

One of the postulates of the biotic theory states that animals that are important to plants are limiting factors, thus flowering events are expected to respond to pollinator activity (Bolmgren et al. 2003; Pleasants 1980). Some authors have said that flowering is likely to be

distributed throughout the year to minimize the effects of competition for pollinators and of interspecific pollination (Bolmgren et al. 2003; Pleasants 1980). Opposed to that, there is the mass action postulate (Rathcke 1983; Thomson 1978), according to which mass flowering patterns would elevate the chances of pollination, since the concentration of resources would attract more visitors. This strategy would also lessen the chances of predation of each individual in the community, because predation would not be concentrated on a few individuals (Augspurger 1981). Wright and Calderon (1995) found very little evidence of pollinator constraints on flowering times. Bolmgren et al. (2003) and Boulter et al. (2006) argued that evidence of the biotic theory is hard to find, as it may be shadowed by phylogenetic constraints. If this theory holds true for our studied community, we expect flowering to be staggered among pollination guilds.

At last there is the phylogenetic theory, according to which flowering times are under phylogenetic constraints (Johnson 1992; Ollerton and Lack 1992). If the phylogenetic theory holds true, phenological patterns are under phylogenetic constraints and, thus, related species are likely to have similar flowering times (Ollerton and Lack 1992). Studying a plant community in a rain forest in Central America, Wright and Calderon (1995) rejected both biotic and climatic theories, but found evidence of phylogenetic constraints in flowering times of congeneric species. Other authors found the same line of evidence for the conservation of flowering patterns inside lineages of related species in communities under either aseasonal climate (Johnson 1992), and seasonally dry climate (Boulter et al. 2006; Johnson 1992; Wright and Calderon 1995).

The very definition of tropical savannas states that their main growth patterns are closely associated with alternating wet and dry seasons (Bourlière and Hadley 1983) and the temporal patterns in reproduction are strongly linked to the climatic seasonality (Williams et al. 1999). So, despite the rejection of the climatic theory in other vegetation types, one could

expect a strong relationship between the peak of flowering of cerrado woody species and some climatic variable. With this study, we tried to answer the following questions: (1) Is the number of flowering species related to temperature, precipitation, or day length?; (2) Are flowering times of species with shared pollinators clustered or staggered?; and (3) Is there a phylogenetic signal in time, concentration, and duration of flowering?

## **Methods**

We carried out this study in a woodland cerrado site located in Itirapina, southeastern Brazil (approximately, 22°13'S and 47°51'W; 760 m asl). Following Köppen's (1948) classification, regional climate is humid subtropical with wet summers and dry winters (Cwa). This area is protected from fire for approximately 20 years. In this site, there is a grid of 200 permanent quadrats, each with 25 m<sup>2</sup> (5 m x 5 m), from which we randomly picked 50. In each quadrat, we sampled all woody individuals, that is, all individuals with lignified stem and diameter at soil level equal to or greater than 3 cm (SMA 1997). We identified all individuals using an identification key based on vegetative characters (Batalha and Mantovani 1999) and comparing collected material to lodged vouchers at the University of Campinas herbarium (UEC). During one year, in monthly field trips, we observed whether each of these individuals was flowering or not. With this data, we constructed a matrix with the number of species flowering in a given month.

### Climatic theory

We obtained climatic data (Fig. 1) from a meteorological station located nearby the study site (Embrapa São Carlos; 22°01'18''S and 47°53'28''W). To test whether there was a

relationship between climatic variables and the proportion of individuals or species flowering in a given month, we used multiple regression analysis. For each month, we calculated average temperature and total rainfall, based on an 11 yr record (1996-2006). To assess mean day length for each month (Fig. 2), we used a website ([http://aa.usno.navy.mil/data/docs/RS\\_OneDay.php](http://aa.usno.navy.mil/data/docs/RS_OneDay.php)).

To estimate the flowering midpoint, we used circular analysis. For every species with at least three flowering events, we calculated the angle of the mean vector,  $\Phi$  (Boulter et al. 2006):

$$\Phi = \arctan\left(\frac{x}{y}\right) \text{ if } x > 0 \text{ or } 180^\circ + \arctan\left(\frac{x}{y}\right), \text{ if } x < 0 \quad (\text{equation 1})$$

in which  $x = \sum n_i \cos \Phi_i$ ,  $y = \sum n_i \sin \Phi_i$ ,  $n_i$  is the number of flowering events in the month  $i$  and  $\Phi_i$  is the midpoint of that month expressed in angles. January, 1<sup>st</sup> was assigned as  $0^\circ$  and all following months start points were determined adding  $30^\circ$  to each. We also calculated the length of the mean vector as a measure of the concentration of flowering times for all species (Zar 1999):

Besides the environmental variables, we also used circular functions as explanatory variables (Anderson et al. 2005) to determine the time gap between the peaks in flowering intensity. We used the following sine ( $X_{sp}$ ) and cosine ( $X_{cp}$ ) functions (Anderson et al. 2005):

$$X_{sp} = \sin\left(\frac{2\pi t}{T}\right) \quad (\text{equation 2})$$

$$X_{cp} = \cos\left(\frac{2\pi t}{T}\right) \quad (\text{equation 3})$$

in which  $t$  is the month (January = 1, February = 2, and so on) and  $T$  is the periodicity of peaks. We searched for the best model using either 6 or 12 months between peaks. We included both circular functions in the models even when only one partial regression coefficient was different from zero, because this procedure allows a more flexible location of our peaks and valleys (Anderson et al. 2005). A regression model with only one of the functions would force the flowering peaks to be at  $t = T$ ,  $t = 2T$ , and so on. We started our analysis with a full model and used a stepwise algorithm to remove explanatory variables. We used adjusted  $R$ -squared ( $R_{aj}^2$ ),  $F$ -statistic, and the significance of partial regression coefficients as criteria to determine the best model (Jongman et al. 1995).

#### Biotic theory

To test whether flowering times were related to pollination system, we calculated the overlapping index for species with the same pollination systems. We used the following pollination guilds: wind, beetles, moths, butterflies, bees, small insects, hummingbirds, and bats (Oliveira and Gibbs 2000). We assessed the main pollinator for each species based on the literature (Barbosa 1997; Gottsberger 1994; Martins and Batalha 2006; Proença and Gibbs 1994). We calculate the overlapping index following Pleasants (1990):

$$\sum \min(p_{ik}, p_{jk}) \quad (\text{equation 4})$$

in which  $p_{ik}$  and  $p_{jk}$  are the proportions of flowering individuals for the species  $i$  and  $j$  in the  $k$ th month. We calculated the mean pairwise overlapping index for all possible

combinations using null model analysis (Gotelli and Graves 1996). To generate the null model, we randomly selected new starting months for the flowering season, retaining the flowering curve, for the species in a given pollination group (Aizen & Vazquez 2006; Pleasants 1990). This procedure was repeated 1,000 times. The flowering curves were randomized inside the flowering season for the group they belonged, which was determined as the time period between the first and last flowering events. To calculate the mean of all possible pairwise combinations, we used an R (R Development Core Team 2008) algorithm written by us and based on an algorithm kindly provided by Aizen and Vazquez (2006). We compared the observed mean overlapping index with the mean of the simulated values. If the observed mean overlapping index was higher than 97.5% of the simulated values (equivalent to a  $P$  of 0.05 in a two-tailed test), flowering was considered to be grouped; if it was lower than 2.5% of the simulated values, flowering was considered to be staggered; if it lied between these limits, flowering was considered to be random. In this analysis we included all species that flowered at least once, since we did not have to calculate flowering midpoints.

### Phylogenetic theory

We searched for evidence of phylogenetic constraints on flowering times with the same analysis we used to answer the question regarding the biotic theory. But here, instead of grouping the species by their pollination systems, we grouped them by genus, family, and order, following the latest APG (Stevens 2008) classification. So, we could determine whether flowering patterns were random in related taxa.

## Results

We sampled 60 woody species and 858 individuals, from which 16 species – those with at least three flowering events – and 585 individuals were included in the regression analysis (Table 1). All species flowered heterogeneously throughout the year (Table 1). The regression model that predicted best the proportion of species flowering in each month was the one with both circular functions and day length as explanatory variables, and periodicity of 12 months ( $R_{adj}^2 = 0.88$ ,  $F = 26.97$ ,  $P < 0.001$ ; Table 2, Fig. 3). When testing both biotic and phylogenetic theories, we included 36 species and 766 individuals (Table 3). Regarding the biotic theory, we were able to group species according to three pollination guilds: bees, moths, and small insects (Table 3). All other guilds had either zero or one species, so they were not included in the analysis. The mean pairwise overlap was higher than expected by chance for bee-pollinated species (Table 4), indicating that the distribution of flowering events in these species was clumped. We did not find, however, evidence of phylogenetic constraints in any of the groups (Table 5), indicating that the distribution of flowering events was random taking in account the phylogeny of the species.

## **Discussion**

We concluded that peak flowering for this community occurs every 12 months. Although flowering was not uniform during the year, we found a maximum of 20% of the sampled species flowering in August and September. These patterns of flowering were also observed in other cerrado communities (Batalha and Mantovani 2000; Batalha and Martins 2004; Lenza and Klink 2006; Oliveira and Gibbs 2000). Likewise, in a study conducted nearby, Tannus et al. (2006) observed year-round flowering of woody species, with weak peaks around August and September, at the end of the dry season. This annual repetition of flowering patterns was expected by us, as the cerrado itself is under a strong alternation of

dry and wet seasons, which seems to influence several ecological functions (Sarmiento 1983) and occurs yearly.

The environmental variable that best explained the variation in flowering midpoints in each month was day length. Even though cerrado areas are usually under strong rainfall seasonality, sun-related environmental factors, such as day length and insolation, are the only reliable environmental cues for flowering synchronization as they do not show variation over the years (Borchert et al. 2005). Studying both vegetative and reproductive phenologies in seasonally dry forests in Central and North America, Borchert et al. (2004) found evidence of photoperiodic and moisture control in flowering times at the community level. There is also evidence of photoperiodic control of flowering in communities under weak climate seasonality for Atlantic rain forest communities in Brazil (Morellato et al. 2000) and for Amazonian rain forests near the Equator (Borchert et al. 2005). Borchert et al. (2005), however, related shifting in times of sunrise and sunset as the environmental cues for flowering synchronization, as in the Equator day length does not vary significantly during a year.

One of the postulates of the climatic theory is that where moisture is limiting, rainfall and soil water availability are expected to drive phenological events, including flowering (Borchert et al. 2005; Boulter et al. 2006; Wright and Calderon 1994). Most cerrado communities are under strong rainfall seasonality, with a well defined dry season (Sarmiento 1983); thus, according to the expectations of this postulate for cerrado communities, flowering phenology would follow rainfall seasonality. Nevertheless, our regression model did not follow our expectations as rainfall was not included as an explanatory variable. Root depths often separate species that are drought-sensitive from those that are not (Wright and van Shaik 1994). Species of the cerrado woody component are predominantly deep-rooted (Rachid 1947; Sarmiento 1983) and can reach soil layers in which there is more water

availability (Oliveira et al. 2005). So, our results are consistent with the predictions of the climatic theory, since even in the dry season, moisture does not seem to limit growth and reproduction (Oliveira et al. 2005).

From our 36 sampled species, 20 were classified as being pollinated mainly or exclusively by bees. Other pollination guilds that had more than two species were moths, with 7 species, and small insects, with 6 species. The distribution of flowering times was different from what was expected by chance only for species pollinated by bees. Bee-pollinated species had clumped flowering times, which did not meet our expectations, since this suggests facilitation, and there is little evidence from previous studies to support it (Boulter et al. 2006; Rathcke and Lacey 1985; Wright and Calderon 1995). Although our results indicated possible facilitation between bee-pollinated species, corroborating the mass-action theory, they have to be interpreted cautiously. Wright and Calderon (1995) and Boulter et al. (2006) did not find evidence of neither facilitation nor competition for pollinators. As long as more than half of our species were pollinated by bees, the presence of aggregated flowering may have been caused by the somewhat seasonal distribution of the whole community. Moreover, it could be argued that both bee activity and flowering phenology are influenced by the same environmental factors. For instance, Hymenoptera species have peaks of abundance around the late dry and early wet season in a cerrado site (Pineiro et al. 2002). This pattern is similar to the flowering patterns we found in our study. It is also difficult to test whether seasonal flowering is a cause or an effect of pollinator seasonality (Rathcke and Lacey 1985). Random flowering distribution may also minimize competition for pollinators, and so the evolution of staggered flowering may not be necessary to avoid competition for pollinators (Boulter et al. 2006).

The results of the phylogenetic restriction analysis did not support the phylogenetic theory, because all groups of related species flowered randomly. Contrary to our results, phylogeny

influenced flowering times in seasonal forests, especially in species of the same genus and family (Wright and Calderon 1995; Boulter et al. 2006). Johnson (1992) also found support for the phylogenetic theory in both seasonally dry and aseasonal areas. Even if there is a phylogenetic signal in flowering times (Ollerton and Lack 1992), local pressures, like climate and pollinator availability, may shade it (Boulter et al. 2006). Thus, as the cerrado is under strong climate seasonality (Sarmiento 1983), phylogenetic factors may have a lower importance in the timing and intensity of flowering. Studies on similar communities at different latitudes and during El Niño events showed flowering closely following differences in solar irradiance (Borchert et al. 2005; Boulter et al. 2006; Wright & Calderon 2006). Future studies could use data from other cerrado communities and under different environmental conditions, with which one could test whether flowering in the cerrado vegetation also tracks variations in these conditions.

Our study area was a small patch of cerrado vegetation surrounded by plantations of *Pinus* spp. and *Eucalyptus* spp. Habitat fragmentation and presence of invasive species have both been described as agents that might disrupt interactions between plants and pollinators by changing pollinator foraging behaviour (Ghazoul 2004; Grindeland et al. 2005; Mustajärvi et al. 2001). Also, environmental-related problems, like climate warming, has been extensively described as a disruptor of plant phenological patterns, such as flowering times (Badeck et al. 2004; Memmott et al. 2007; Miller-Rushing and Primack 2008; Post et al. 2008; Sherry et al. 2007). Moreover, changes in fire occurrence may cause changes in flowering patterns, as some species produce flowers right after fire events (Munhoz and Felfili 2007), what could not be tested here, because the cerrado area we studied has been protected from fire for approximately 20 years. All these variables are also worth to be studied in future works.

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## References

- Aizen MA, Vazquez DP (2006) Flowering phenologies of hummingbird plants from the temperate forest of southern South America: is there evidence of competitive displacement? *Ecography* 29: 357-366.
- Anderson DP, Nordheim EV, Moermond TC, Bi ZBG, Boesch C (2005) Factors influencing tree phenology in Taï National Park, Cote d'Ivoire. *Biotropica* 37: 631-640.
- Ashton PS, Givnish TJ, Appanah S (1988) Staggered flowering in the dipterocarpaceae - new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* 132: 44-66.
- Augspurger CK (1981) Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62: 775-788.
- Badeck F, Bondeau A, Böttcher K, Doktor D, Lucht W, Shaber J, Sitch S (2004) Responses of spring phenology to climate change. *New Phytol* 162: 295-309.
- Barbosa AAA (1997) Biologia reprodutiva de uma comunidade de campo sujo, Uberlândia/MG. PhD thesis.

- Batalha MA, Mantovani W (1999). Chaves de identificação das espécies vegetais vasculares baseada em caracteres vegetativos para a ARIE Cerrado Pé-de-Gigante (Santa Rita do Passa Quatro, SP). *Revista do Instituto Florestal* 11: 137-158.
- Batalha MA, Mantovani W (2000) Reproductive phenological patterns of cerrado plant species at the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and the woody floras. *Revista Brasileira de Biologia* 60: 129-145.
- Batalha MA, Martins FR (2004) Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). *Aust J Bot* 52: 149-161.
- Bolmgren K, Eriksoon O, Peter Linder H (2003) Contrasting flowering phenology and species richness in abiotically and biotically pollinated angiosperms. *Evol* 57: 2001-2011.
- Borchert R (1983) Phenology and control of flowering in tropical trees. *Biotropica* 15: 81-89.
- Borchert R, Rivera G, Hagnauer W (2002) Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica* 34: 27-39.
- Borchert R, Renner SS, Calle Z, Navarrete D, Tye A, Gautier L, Spichiger R, von Hildebrand P (2005) Photoperiodic induction of flowering near the Equator. *Nature* 433: 627-629.
- Bourlière F, Hadley M (1983) Present-day savannas: an overview. In: Goodall DW (ed) *Ecosystems of the world – tropical savannas*. Elsevier, Amsterdam.
- Boulter SL, Kitching RL, Howlett BG (2006) Family, visitors and the weather: patterns of flowering in tropical rain forests of northern Australia. *J Ecol* 94: 369-382.
- Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J Ecol* 62: 881-919.
- Ghazoul G (2004) Alien abduction: disruption of native plant-pollinator interactions by invasive species. *Biotropica* 36: 156-164.

- Gotelli NJ, Graves GR (1996) Null models in ecology. Smithsonian Institution Press, Washington.
- Gottsberger G (1994) As anonáceas do cerrado e sua polinização. Rev Brasil Biol 54: 391-402.
- Grindeland JM, Sletvold N, Ims RA (2005) Effects of floral display size and plant density on pollinator visitation rate in a natural population of *Digitalis purpurea*. Func Ecol 19: 383-390.
- Inouye DW (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89: 353-362.
- Johnson SD (1992). Climatic and phylogenetic determinants of flowering seasonality in the Cape Flora. J Ecol 81: 567-572.
- Jongman RHG, Ter Braak CJF, Van Tongeren OFR (1995) Data analysis in community and landscape ecology. Cambridge University, Cambridge.
- Köppen W (1948) Climatología. Fondo de Cultura Económica, México.
- Lenza E, Klink CA (2006) Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF. Revista Brasileira de Botânica 29: 627-638.
- Martins FQ, Batalha MA (2006) Pollination systems and floral traits in cerrado woody species of the Upper Taquari region (central Brazil). Braz J Biol 66: 543-552.
- Memmott J, Craze PJ, Nickolas MW, Price MV (2007) Global warming and the disruption of plant-pollinator interactions. Ecol. Lett. 10: 710-717.
- Mduma SAR, Sinclair ARE, Turkington R (2007) The role of rainfall and predators in determining synchrony in reproduction of savanna trees in Serengeti National Park, Tanzania. J Ecol 85: 184-196.
- Miller-Rushing AJ, Primack RB (2008) Global warming and flowering times in Thoreau's Concord: a community perspective. Ecology 89: 332-341.

- Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC, Zipparro VB (2000) Phenology of Atlantic Rain Forest Trees: A Comparative Study. *Biotropica* 32: 811-823.
- Munhoz CBR, Felfili JM (2005) Fenologia do estrato herbáceo-subarbustivo de uma comunidade de campo sujo na Fazenda Água Limpa no Distrito Federal, Brasil. *Acta Botanica Brasilica* 19: 979-988.
- Mustajärvi K, Siikamäki P, Rytönen S, Lammi A (2001) Consequences of plant population size and density for plant-pollinator interactions and plant performance. *J Ecol* 89: 80-87.
- Oliveira RS, Bezerra L, Davidson EA, Pinto F, Klink CA, Nepstad DC, Moreira A (2005) Deep root function in soil water dynamics in cerrado savannas of central Brazil. *Funct Ecol* 19: 574-581.
- Oliveira PE, Gibbs PE (2000) Reproductive biology of woody plants in a cerrado community of Central Brazil. *Flora* 195: 311-329.
- Ollerton J, Lack AJ (1992) Flowering phenology: An example of relaxation of natural selection? *Trends Ecol. Evol.* 7: 274-276.
- Pinheiro F, Diniz IR, Bandeira PS (2002) Seasonal pattern of insect abundance in the Brazilian cerrado. *Austral Ecology* 27: 132-136.
- Pleasants JM (1980) Competition for bumblebee pollinators in Rocky Mountain plant communities. *Ecol* 61: 1446-1459.
- Pleasants JM (1990) Null-Model tests for competitive displacement: the fallacy of not focusing on the whole community. *Ecology* 71: 1078-1084.
- Post ES, Pedersen C, Wilmer CC, Forchhammer MC (2008) Phenological sequences reveal aggregate life history response to climate warming. *Ecology* 89: 363-370.
- Proença CEB, Gibbs PE (1994) Reproductive biology of eight sympatric Myrtaceae from Central Brazil. *New Phytol* 126: 343-354.

- R Development Core Team (2008) R: a language and environment for statistical computing. Version 2.8.1. <http://www.r-project.org>. R Foundation for Statistical Computing, Vienna, Austria.
- Rachid M (1947) Transpiração e sistemas subterrâneos da vegetação de verão dos campos cerrados de Emas. Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo. Botânica 5:1-139.
- Ramirez N (2002) Reproductive phenology, life-forms, and habitats of the Venezuelan Central Plain. Am J Bot 89: 836-842.
- Rathcke B (1983) Competition and facilitation among plants for pollination. In: Real L (ed) Pollination Biology. Academic Press, Orlando, pp 305-329.
- Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. Annu Rev Ecol Syst 16: 179-214.
- Sakai S (2002) General flowering in lowland mixed dipterocarp forests of South-east Asia. Biol J Linn Soc 75: 233-247.
- Sarmiento G (1983) The savannas of tropical America. In: Bouliere F (ed) Ecosystems of the world: Tropical Savannas. Elsevier, Amsterdam, Netherlands, pp 79-108.
- Sherry RA, Zhou X, Gu S, Arnone III JA, Schimel DS, Verburg PS, Wallace LL, Luo Y (2007) Divergence of reproductive phenology under climate warming. Proc Natl Acad Sci USA 104: 198-202.
- SMA (1997) Cerrado: bases para conservação e uso sustentável das áreas de cerrado do Estado de São Paulo. Secretaria de Estado do Meio Ambiente, São Paulo.
- Stevens, PF (2008) Angiosperm Phylogeny Website. Version 9. <http://www.mobot.org/MOBOT/research/APweb/>.
- Tannus JLS, Assis MA, Morellato LPC (2006) Reproductive phenology in dry and wet grassland in an area of Cerrado at southeastern Brazil, Itirapina – SP. Biota Neotrop 6.

- Thomson JD (1978) Effect of stand composition on insect visitation in two-species mixtures of *Hieracium*. *Am Midl Nat* 100: 431-440.
- Visser ME, Holleman LJM (2001) Warmer springs disrupt oak and moth phenology. *Proc R Soc Lond* 268: 289-294.
- Williams RJ, Myers BA, Eamus D, Duff GA (1999) Reproductive phenology of woody species in a north australian tropical savanna. *Biotropica* 31: 626-636.
- Wright SJ, Calderon O (1995) Phylogenetic patterns among tropical flowering phenologies. *J Ecol* 83: 937-948.
- Wright SJ, Calderon O (2006) Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol Lett* 9: 35-44.
- Wright SJ, Cornejo FH (1990) Seasonal drought and leaf fall in a tropical forest. *Ecology* 71: 1165-1175.
- Wright SJ, van Schaik CP (1994) Light and the phenology of tropical trees. *Am Nat* 143: 192-199.
- Zar JH (1999) *Biostatistical analysis*. Prentice Hall, Upper Saddle River.

Table 1. Circular statistics of the species observed flowering at least three times in a cerrado site in Itirapina, southeastern Brazil (approximately, 22°13'S and 47°51'W). Number of flowering events (flower), number of flowering individuals (ind), mean angle ( $\Phi$ ), mean date (d; month.day), mean vector length (r), *P* value for the Rayleigh test for uniformity (*P*; NS  $P > 0.05$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ).

species	flower	ind	$\Phi$	d	r	<i>P</i>
<i>Amaioua guianensis</i> Aubl.	5	5	333°	12.06	0.978	**
<i>Anadenanthera falcata</i> (Benth.) Speg.	20	40	258°	09.20	0.999	***
<i>Didymopanax vinosum</i> Marchal	17	6	174°	06.26	0.716	***
<i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns	8	9	218°	08.10	0.835	***
<i>Erythroxylum pelleterianum</i> A.St.-Hil.	3	4	275°	10.07	0.981	*
<i>Eugenia puniceifolia</i> (Kunth) A.DC.	5	9	345°	12.17	0.957	**
<i>Miconia albicans</i> Triana	306	63	197°	07.20	0.479	***
<i>Miconia rubiginosa</i> (Bonpl.) A.DC.	44	28	332°	12.04	0.910	***
<i>Myrcia lingua</i> (O. Berg) Mattos & D.Legrand	68	136	281°	10.13	0.939	***
<i>Ocotea pulchella</i> Mart.	27	41	327°	11.29	0.850	***
<i>Ouratea spectabilis</i> Engl.	11	28	250°	09.11	0.722	**
<i>Pouteria ramiflora</i> Radlk.	13	11	223°	08.15	0.898	***
<i>Pouteria torta</i> Radlk.	68	32	225°	08.17	0.892	***
<i>Serjania lethalis</i> A.St.-Hil.	6	11	250°	09.11	0.948	***
<i>Vochysia tucanorum</i> Mart.	25	43	21°	01.22	0.612	***
<i>Xylopia aromatica</i> (Lam.) Mart.	47	119	312°	11.13	0.883	***

Table 2. Partial regression coefficients ( $\beta$ ) and partial  $F$  values ( $t$ ; \*  $P < 0.01$ , \*\*  $P < 0.001$ ) for the explanatory variables of the model that better explained the periodicity of flowering peak and its relation with temperature, rainfall, and day length for the species observed flowering at least three times in a cerrado site in Itirapina, southeastern Brazil (approximately, 22°13'S and 47°51'W). Sine function ( $X_{sp}$ ;  $T = 12$ ), Cosine function ( $X_{cp}$ ;  $T = 12$ ).

explanatory variable	flowering midpoint	
	$\beta$	$t$
$X_{sp}$	-0.18	-3.12**
$X_{cp}$	-1.09	-3.05*
day length	0.85	3.15*
(intercept)	-10.31	

Table 3. Species observed flowering with their respective number of flowering events (flower), individuals (ind), and exclusive or principal pollinator (pol; si, small insects; bee, bees; mo, moths; hb, hummingbirds; bat, bats) in a cerrado site in Itirapina, southeastern Brazil (approximately, 22°13'S and 47°51'W).

order	family	species	flower	ind	pol
Apiales	Araliaceae	<i>Didymopanax vinosum</i> Marchal	17	6	si
Arecales	Arecaceae	<i>Syagrus petraea</i> (Mart.) Becc.	3	29	bee
Caryophyllales	Nyctaginaceae	<i>Guapira noxia</i> (Netto) Lundell	3	9	si
Ericales	Ebenaceae	<i>Diospyros hispida</i> A. DC.	6	4	mo
Ericales	Sapotaceae	<i>Pouteria ramiflora</i> (Mart.) Radlk.	13	11	mo
Ericales	Sapotaceae	<i>Pouteria torta</i> (Mart.) Radlk.	68	32	mo
Fabales	Fabaceae	<i>Anadenanthera falcata</i> (Benth.) Speg.	20	40	si
Fabales	Fabaceae	<i>Bauhinia rufa</i> (Bong.) Steud.	3	14	bat
Fabales	Fabaceae	<i>Machaerium acutifolium</i> Vogel	1	3	bee
Gentianales	Apocynaceae	<i>Aspidosperma tomentosum</i> Mart.	4	45	mo
Gentianales	Rubiaceae	<i>Amaioua guianensis</i> Aubl.	5	5	mo
Gentianales	Rubiaceae	<i>Palicourea rigida</i> Kunth	3	2	hb
Gentianales	Rubiaceae	<i>Tocoyena formosa</i> (Cham. & Schltld.) K. Schum.	1	5	mo
Lamiales	Bignoniaceae	<i>Jacaranda caroba</i> (Vell.) A. DC.	1	1	bee

Laurales	Lauraceae	<i>Ocotea pulchella</i> (Nees) Mez	27	41	bee
Laurales	Monimiaceae	<i>Siparuna guianensis</i> Aubl.	3	3	bee
Magnoliales	Annonaceae	<i>Xylopia aromatica</i> (Lam.) Mart.	47	119	si
Magnoliales	Myristicaceae	<i>Virola sebifera</i> Aubl.	1	1	bee
Magnoliales	Myrsinaceae	<i>Rapanea guianensis</i> Aubl.	2	6	bee
Malpighiales	Erythroxylaceae	<i>Erythroxylum pelleterianum</i> Griseb.	3	4	bee
Malpighiales	Euphorbiaceae	<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	2	4	si
Malpighiales	Malpighiaceae	<i>Byrsonima coccolobifolia</i> Kunth	5	9	bee
Malpighiales	Malpighiaceae	<i>Byrsonima crassifolia</i> (L.) Kunth	4	1	bee
Malpighiales	Ochnaceae	<i>Ouratea spectabilis</i> (Mart. ex Engl.) Engl.	11	28	bee
Malpighiales	Salicaceae	<i>Casearia decandra</i> Jacq.	1	5	si
Malvales	Malvaceae	<i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns	8	9	bee
Myrtales	Melastomataceae	<i>Miconia albicans</i> (Sw.) Triana	306	63	bee
Myrtales	Melastomataceae	<i>Miconia rubiginosa</i> (Bonpl.) DC.	44	29	bee
Myrtales	Myrtaceae	<i>Blepharocalyx salicifolius</i> (Kunth) O. Berg	1	10	bee
Myrtales	Myrtaceae	<i>Campomanesia pubescens</i> (DC.) O. Berg	1	2	bee
Myrtales	Myrtaceae	<i>Eugenia puniceifolia</i> (Kunth) DC.	5	9	bee
Myrtales	Myrtaceae	<i>Myrcia bella</i> Cambess.	3	2	bee
Myrtales	Myrtaceae	<i>Myrcia lingua</i> (O. Berg) Mattos & D. Legrand	68	135	bee

Myrtales	Vochysiaceae	<i>Qualea grandiflora</i> Mart.	1	24	mo
Myrtales	Vochysiaceae	<i>Vochysia tucanorum</i> Mart.	25	44	bee
Sapindales	Sapindaceae	<i>Serjania lethalis</i> A. St.-Hil.	6	12	bee

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Table 4. Flowering overlapping indices for the species with the same pollination system in a cerrado *sensu stricto* area in a cerrado site in Itirapina, southeastern Brazil (approximately, 22°13'S and 47°51'W). For values higher than 97.5% of the simulated values (equivalent to a *P* of 0.05 in a two-tailed test), flowering was considered to be clustered; for values lower than 2.5% of the simulated values, flowering was considered to be staggered; for values in between; flowering was considered to be random.

<b>pol</b>	<b>n</b>	<b>observed</b>	<b>min</b>	<b>max</b>	<b>distribution</b>
bees	21	0.232	0.143	0.194	clustered
moths	7	0.169	0.071	0.249	random
small insects	6	0.104	0.035	0.256	random

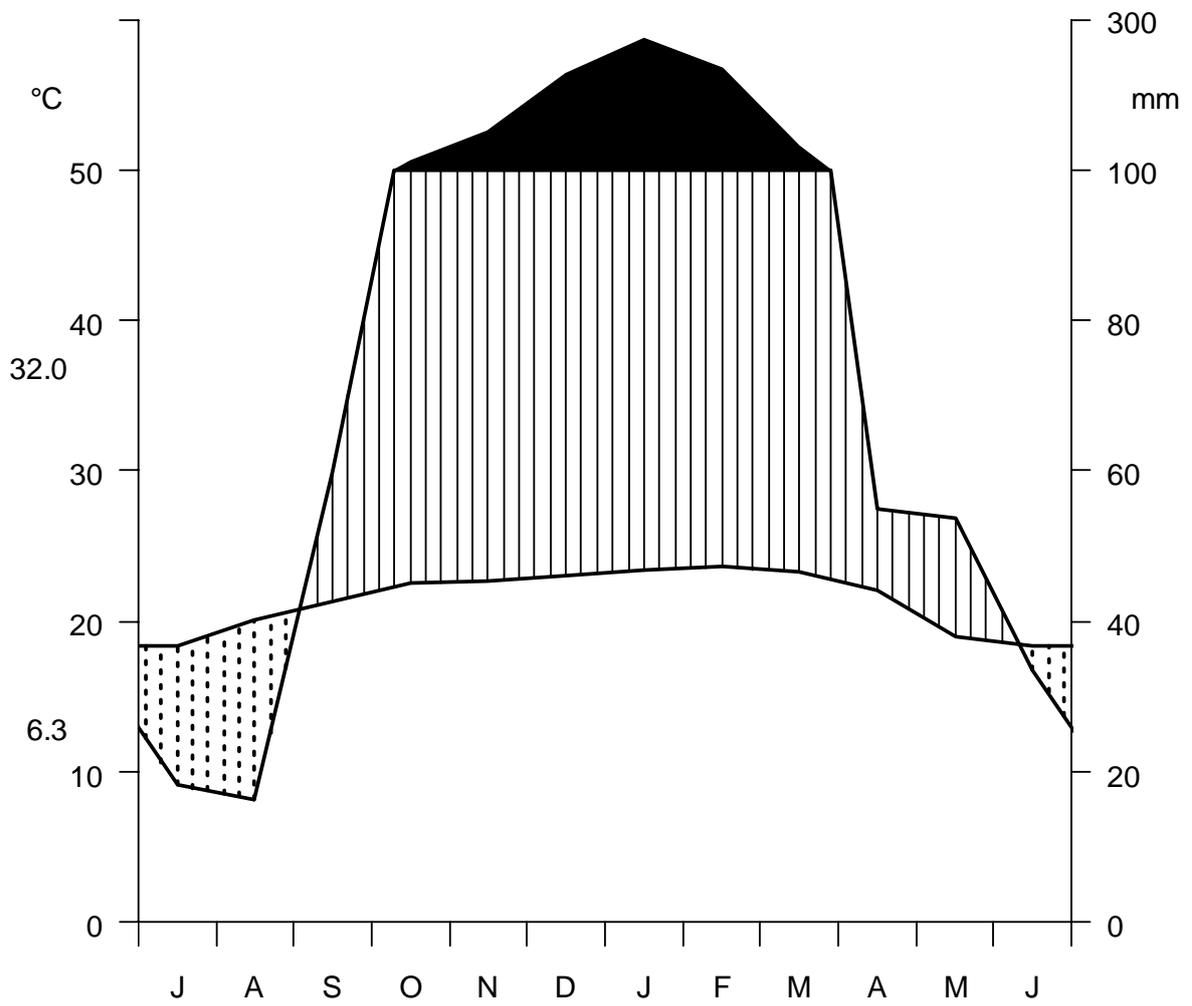
Table 5. Flowering overlapping indices for the species within the same family or order in a cerrado site in Itirapina, southeastern Brazil (approximately, 22°13'S and 47°51'W). For values higher than 97.5% of the simulated values (equivalent to a *P* of 0.05 in a two-tailed test), flowering was considered to be clustered; for values lower than 2.5% of the simulated values, flowering was considered to be staggered; for values in between; flowering was considered to be random.

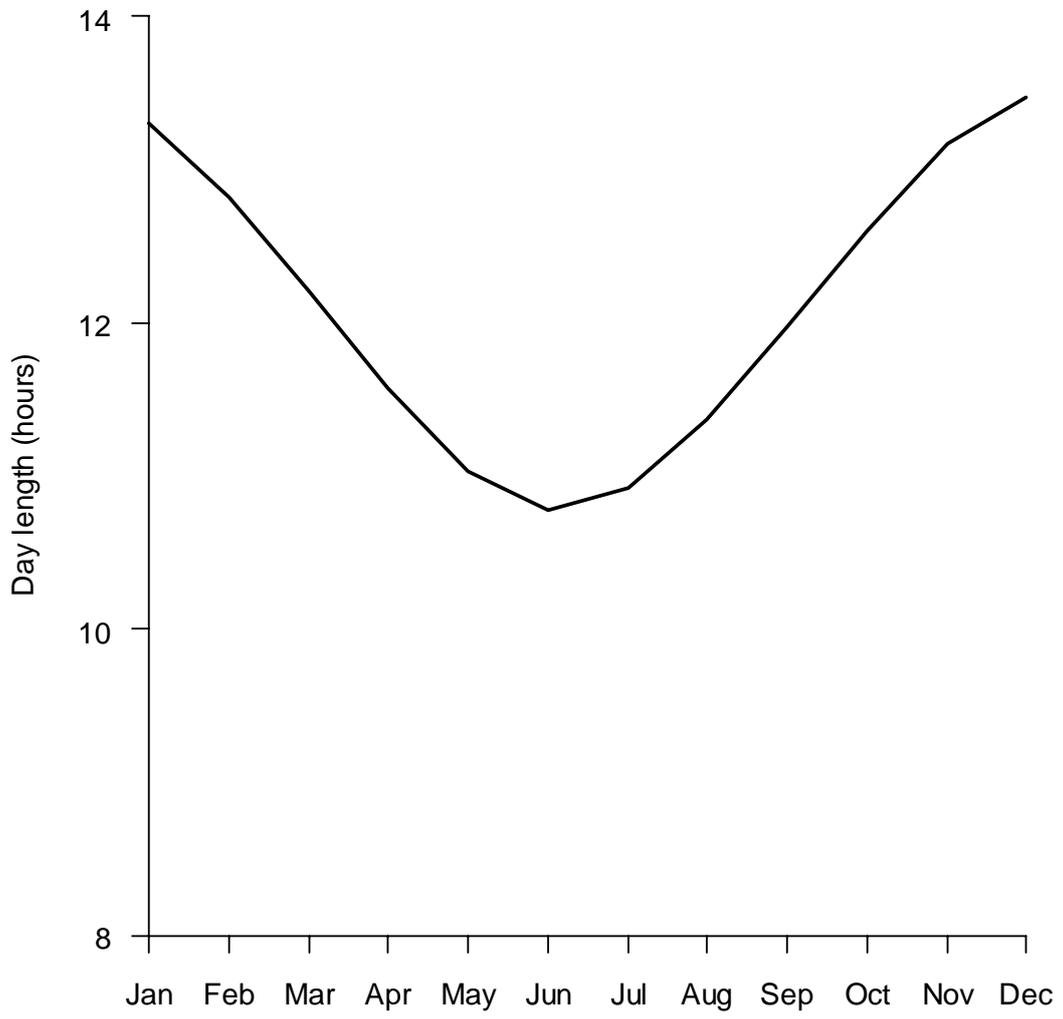
<b>order or family</b>	<b>n</b>	<b>observed</b>	<b>min</b>	<b>max</b>	<b>distribution</b>
Ericales	3	0.426	0.0098	0.541	random
Fabales	3	0.000	0.000	0.333	random
Gentianales	4	0.167	0.000	0.350	random
Lurales	2	0.481	0.000	0.667	random
Magnoliales	3	0.1666	0.000	0.379	random
Malpighiales	6	0.211	0.0978	0.272	random
Sapotaceae	2	0.816	0.000	0.816	random
Fabaceae	3	0.000	0.000	0.333	random
Rubiaceae	3	0.333	0.000	0.422	random
Malpighiaceae	2	0.400	0.200	0.450	random
Melastomataceae	2	0.084	0.0325	0.489	random
Myrtaceae	5	0.269	0.021	0.284	random
Vochysiaceae	2	0.080	0.000	0.320	random

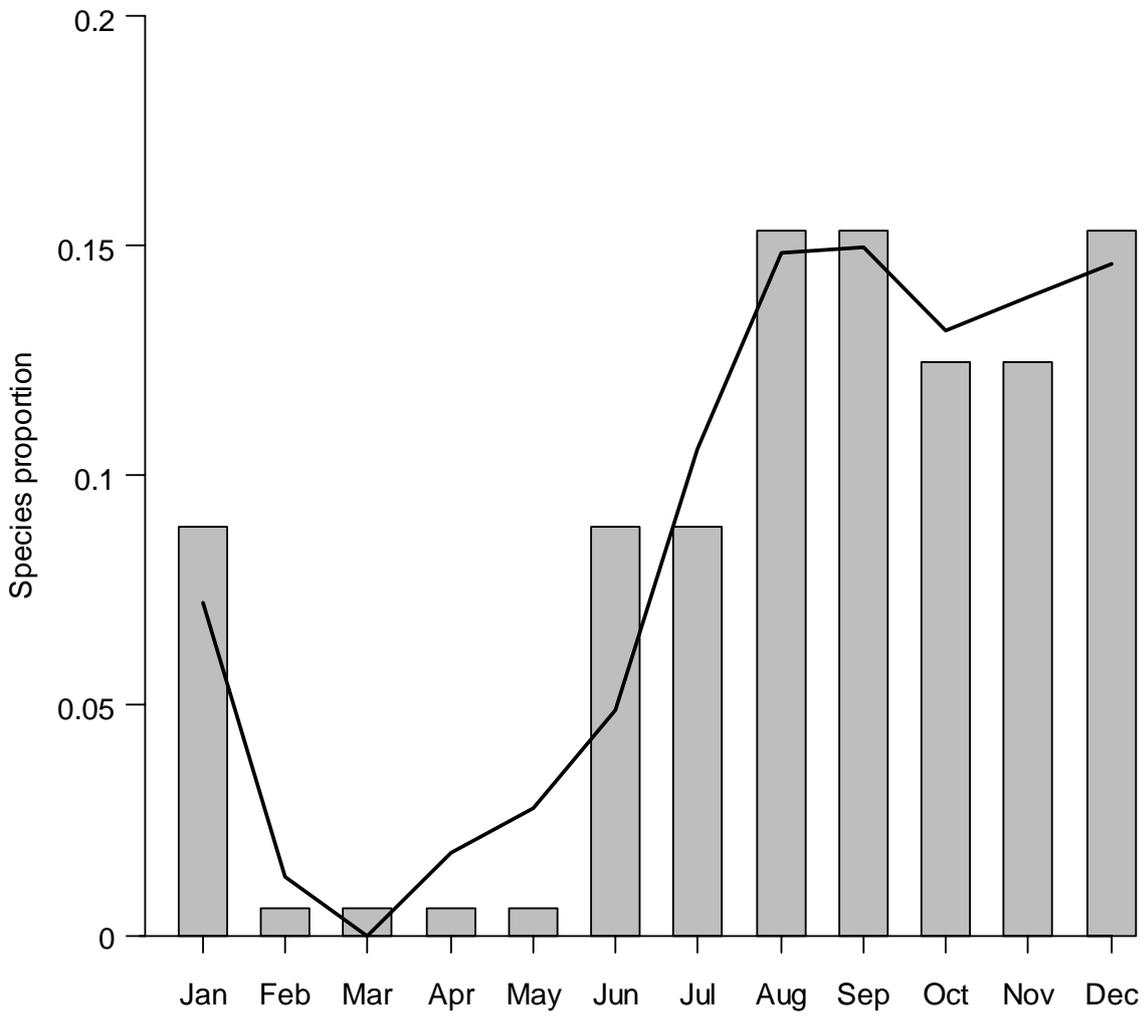
Figure 1 Climatic diagram following Walter (1971). Data obtained at Embrapa São Carlos, São Paulo State, southeastern Brazil (22°01'S, 47°53'W, 856 m asl). Mean annual temperature = 21.5°C, total annual precipitation = 1365 mm.

Figure 2. Yearly day length in a cerrado site in Itirapina, southeastern Brazil (approximately, 22°13'S and 47°51'W).

Figure 3. Regression predicting the proportion of flowering midpoints in each month in a cerrado site in Itirapina, southeastern Brazil (approximately, 22°13'S and 47°51'W). The bold line is the regression model that better explained data ( $R_{aj}^2 = 0.88$ ,  $F = 26.97$ ,  $P < 0.001$ ), with circular functions ( $T = 12$ ) and day length as explanatory variables. Bars are observed values.







# **III – Capítulo 2**

Padrões de floração dos componentes da flora do  
cerrado no Parque Nacional das Emas (GO): relações  
com fatores ambientais estacionais<sup>1</sup>

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<sup>1</sup> Trabalho submetido ao periódico *Biotropica* com o título “Flowering Phenology of the Components of the Cerrado Flora in Central Brazil: Relationships with Seasonal Environmental Factors”.

LRH: Carvalho, Batalha and Martins

RRH: Flowering phenology in a Cerrado Area

**Flowering Phenology of the Components of the Cerrado Flora in Central Brazil:  
Relationships with Seasonal Environmental Factors**

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ABSTRACT – One of the theories that try to explain the influence of several factors on community-wide flowering phenology is the climate theory, which says that flowering events follow predictable variations in environmental factors favorable to flower production, diaspore dispersion, and seedlings development, with water availability playing a crucial role. Where a well defined dry season is not present, it is expected that the species will synchronize their flowering events with environmental factors more predictable than rainfall, such as day length. For the species that suffer from water stress in the dry season, it is expected that the flowering will follow the variation in rainfall. In the cerrado, flowering phenology has been related to rainfall seasonality. However, other environmental factors are seasonal and may influence flowering phenology as well, especially woody species, which usually have deep root systems that provide water even in the dry season. We used data collected in Emas National Park, to determine, by multiple regression analysis with circular functions, the relationships between day length, temperature, rainfall, and the proportion of flowering species. For the herbaceous component, the variables that best explained the flowering patterns were rainfall and temperature, whereas day length and temperature were the best predictors of the flowering patterns for the woody component. Peak flowering of both components were annual. Overall, we corroborated the climate theory, since we found different relationships between flowering and environmental factors for each component: drought does not limit flower production in the woody species, but do so in the herbaceous ones.

*Key words:* climatic theory; day length; herbaceous component; rainfall; savanna; seasonality; temperature; woody component

RESUMO – Uma das teorias que procuram explicar a influência de diversos fatores na floração de comunidade de vegetais é a teoria climática, segundo a qual os eventos de floração acompanham variações previsíveis de fatores ambientais favoráveis à produção de flores, dispersão de diásporos e estabelecimento de plântulas, com a disponibilidade de água tendo papel fundamental. Onde não há estação seca, espera-se que as espécies sincronizem a floração com fatores ambientais mais previsíveis que a precipitação, como o comprimento do dia. Para as espécies que sofrem estresse hídrico na estação seca, espera-se que a floração siga a variação da precipitação. No cerrado, a fenologia da floração tem sido relacionada à estacionalidade da precipitação. Entretanto, outras variáveis ambientais são estacionais e podem influenciar a floração, principalmente das espécies arbustivo-arbóreas, cujas raízes profundas fazem com que tenham acesso à água mesmo na estação seca. Utilizamos dados coletados no Parque Nacional das Emas para determinar, por meio de regressão múltipla com funções circulares, a relação entre comprimento do dia, temperatura e precipitação e o número de espécies florescendo. Para as espécies herbáceo-subarbustivas, as variáveis ambientais que melhor explicaram os padrões de floração foram a precipitação e a temperatura. Para as espécies arbustivo-arbóreas, as variáveis ambientais que melhor explicaram os padrões de floração foram o comprimento do dia e a temperatura. Os picos de floração foram anuais para ambos os componentes. Corroboramos a teoria climática, pois encontramos relações diferentes entre a floração e as variáveis ambientais para cada componente.

THE CERRADO DOMAIN ORIGINALLY COVERED 22 PERCENT (2 MILLION-HA.) OF THE LAND surface of Brazil, mainly in the Central Plateau (Oliveira-Filho & Ratter 2002), but it is now being destroyed and replaced by commercial cultures, such as soybean, sugarcane, and African grasses for cattle ranching (Durigan *et al.* 2007). The cerrado vegetation burns periodically and occurs in oxisols with deep water table, high levels of aluminum and low levels of organic matter (Eiten 1977). There are different physiognomies in the Brazilian cerrado, ranging from open grassland (*campo limpo*) to woodland (*cerradão*) with intermediate savanna physiognomies (*campo sujo*, *campo cerrado*, and *cerrado sensu stricto*). The cerrado vegetation has two distinct components: the herbaceous component constituted by herbs and small subshrubs, and the woody component constituted by shrubs and trees. The importance of the herbaceous component increases towards the *campo limpo*, whereas the importance of the woody component increases towards the *cerradão* (Coutinho 1978).

Flowering is an important step in the reproductive cycle of angiosperms (Wright & Calderon 1995), a fundamental aspect of the interaction between plants and their pollinators (Morales *et al.* 2005), and has great influence on fruit phenology, as well as on diaspora dispersal and seedling development (Wright & Calderon 1995). Flowering time is thus decisive for the reproductive success of a given species (Debussche *et al.* 2004). Flowering times are either under phylogenetic influence with the maintenance of flowering patterns in closely related taxa, or under adaptive influence with the synchronization of flowering patterns to favorable conditions of biotic and abiotic factors, such as the activity of pollinators, seed dispersers, seed predators, herbivores, solar radiation, temperature, and water availability (Boulter *et al.* 2006).

The cerrado vegetation is under strong seasonality, with well defined wet summers and dry winters (Sarmiento 1983). Growth and reproductive patterns are associated with this

seasonality (Bourlière & Hadley 1983; Sarmiento 1983). Most studies concerning the flowering phenology of cerrado communities correlated the variation of flowering events with rainfall. Flowering generally occurs year-round with peaks in late wet season (February and March) for herbaceous species, and in late dry and early wet seasons (August and September) for woody species (Batalha & Mantovani 2000; Oliveira & Gibbs 2000; Batalha & Martins 2004). However, rainfall is not the only seasonal environmental factor that can trigger flowering events in the cerrado. Solar radiation, day length, and temperature are also seasonal. Boulter *et al.* (2006) listed three categories of theories about the influence of different factors on flowering phenology, one of which is the climatic theory. According to this theory, flowering activity follows seasonal variations in limiting factors, with water availability playing a crucial role: where water is limiting, phenological events are expected to follow rainfall variation; where water is not limiting, other factors, such as solar radiation, may play a more important role on phenology.

Although most cerrado areas are under rainfall seasonality, water deficit of upper soil layers during the dry season does not limit the woody species, since their deep root system can reach the water table (Rachid 1947; Oliveira *et al.* 2005). Consequently, cerrado woody species would synchronize their flowering patterns to other seasonal cues, such as day length or solar radiation, which can make flower production more efficient since assimilates would be directly transferred to growing organs (Wright & van Schaik 1994). The shallow root system of cerrado herbaceous species, on the other hand, does not reach deep soil layers and does not provide access to water in the dry season (Rachid 1947). Thus, their reproduction is likely to be related with seasonal changes in rainfall, since water stress may limit the production of flowers and fruits (Wright & Cornejo 1990).

Day length and temperature, both described as major climatic cues for flowering activity (Ashton *et al.* 1988.), were not so far related to community-wide patterns in the flowering of

cerrado species. Here we investigated the flowering phenology of both the herbaceous and the woody components of the cerrado vegetation in relation to environmental variables previously described as possible cues for flowering synchronization in communities under seasonal climate. We put the following questions as guidelines: (1) Is the flowering of the herbaceous component related with day length, rainfall, or temperature? Assuming the climatic theory of phenology, we expect the flowering of the herbaceous component to follow closely the rain seasonality, since the plants in this component have shallow root systems and suffer periodical water restraint during the dry season. (2) Is the flowering of the woody component related with day length, rainfall, or temperature? Since the root system of the shrubs and trees can reach deep soil layers that are water-rich all year long, we expect the flowering of the woody component to not relate to rain seasonality but to other climatic elements. (3) Are flowering peaks annual? If the climatic theory of phenology holds for the cerrado, we expect the flowering peaks to be annual, since the possible climatic cues (“time givers” or “zeitgebers”) show yearly rhythms.

## **METHODS**

We used the same dataset analyzed in Batalha and Martins (2004), obtained in a floristic survey carried out monthly from November 1998 to October 1999 in Emas National Park (ENP), a reserve with about 133,000-ha in the Brazilian Central Plateau (17°49' -18°28'S and 52°39' -53°10'W). Climate is Aw according to (Köppen 1948) classification, with wet summer and dry winter. Annual mean temperature is 24.6°C and mean rainfall varies from 1200 to 2000 mm (Ramos-Neto and Pivello 2000) (Fig. 1). Day length varies from 11 to 13 hours (Fig. 2). Along pre-established trails, with a 50-60 hr monthly sampling effort, we recorded whether a given species was flowering. The observations were simply qualitative,

*i.e.*, in a given month, if we found at least one individual of a determined species producing flowers, we considered the species to be on its flowering period. For a more detailed description of the area and sampling methods, see Batalha and Martins (2004).

To estimate the flowering midpoint for each component, we used circular analysis. We calculated the angle of the mean vector,  $\Phi$  (Boulter *et al.* 2006):

$$\Phi = \arctan\left(\frac{x}{y}\right), \text{ if } x > 0 \text{ or } 180^\circ + \arctan\left(\frac{x}{y}\right), \text{ if } x < 0 \quad (\text{equation 1}),$$

where  $x = \sum n_i \cos \Phi_i$ ,  $y = \sum n_i \sin \Phi_i$ ,  $n_i$  is the number of flowering events in the  $i$ -th month, and  $\Phi_i$  is the midpoint of that month expressed in angles. January 1<sup>st</sup> was set as  $0^\circ$  and all midpoints of the following months were determined adding  $30^\circ$  to the previous midpoint. We also calculated the length of the mean vector as a measure of the concentration of flowering times (Zar 1999):

$$r = \sqrt{(x^2 + y^2)} \quad (\text{equation 2}),$$

To identify the variables that best explained the variation of the flowering times of the herbaceous and woody components, we used multiple regression analysis. We included monthly mean values of day length, rainfall, and temperature as environmental variables in our model. Besides the environmental variables, we used circular functions as explanatory variables to determine the time gap between the peaks in flowering intensity (Anderson *et al.* 2005). We included the following sine ( $X_{sp}$ ) and cosine ( $X_{cp}$ ) functions in our regression models (Anderson *et al.* 2005):

$$X_{sp} = \sin\left(\frac{2\pi t}{T}\right) \quad (\text{equation 3}),$$

$$X_{cp} = \cos\left(\frac{2\pi t}{T}\right) \quad (\text{equation 4}),$$

where  $t$  is the month (January = 1, February = 2, and so on) and  $T$  is the periodicity of peaks. We searched for the best model using 6 and 12 mo between peaks. Both circular functions were included in the models even if their partial regression coefficients were significantly different from zero. As described in (Anderson *et al.* 2005), this allowed a more flexible location of our peaks and valleys. A regression model with only one of the functions would force flowering peak to be at  $t = T, t = 2T$ , and so on. We started our analysis with a full model and used a backward stepwise algorithm to remove explanatory variables (Zar 1999). We used adjusted  $R$ -squared ( $R_{adj}^2$ ),  $F$ -statistic ( $F$ ), and the significance of partial regression coefficients as criteria to determine the best models (Jongman *et al.* 1995). We tested our models for multicollinearity using variance inflation factor (Fox & Monette 1992).

## RESULTS

We sampled 145 woody species of which 130 were found flowering during the sampling period, and 444 herbaceous species of which 428 were found flowering. Neither the woody nor the herbaceous component had uniform distribution of flowering (Table 1). Mean angles were  $30^\circ$  for the herbaceous component, and  $229^\circ$  for the woody one, corresponding respectively to early February and late August. Both the herbaceous and woody components flowered heterogeneously during the year, as indicated by the short mean vectors ( $r = 0.14$  and  $r = 0.20$ , respectively;  $P < 0.001$  for both; Table 1).

The environmental variables that best explained the variation in the proportion of herbaceous species flowering along the year were rainfall and temperature. Our best model also included circular functions with a periodicity of 12 mo. This model explained 96 percent of the variation of the monthly proportion of flowering herbaceous species ( $R_{adj}^2=0.9628$ ,  $F = 72.1$ ,  $P < 0.001$ ; Fig. 3; Table 2). For the woody component the best model included circular functions with 12 mo periodicity, day length, and temperature as explanatory variables ( $R_{adj}^2=0.9394$ ,  $F = 43.65$ ,  $P < 0.001$ ; Fig. 4; Table 3). This model had also a high explanatory capacity (94%) of the variation in the proportion of woody species flowering throughout the year.

## **DISCUSSION**

The flowering pattern of both the herbaceous and the woody cerrado components was similar, as inferred from the circular analysis: flowering occurred non-uniformly all year long and had peaks of activity in different times for each component. Batalha and Mantovani (2000), Oliveira and Gibbs (2000), Munhoz and Felfili (2005) and Lenza and Klink (2006) found the same pattern of flowering in other cerrado communities. They found the peaks to be associated it with rainfall seasonality: woody species peaked flowering at the end of the dry and beginning of the wet seasons, whereas the flowering peak of the herbaceous component occurred in the end of the rainy season. Both patterns were also observed in several studies of flowering times in communities other than the cerrado and under the influence of seasonal environmental variables, especially rainfall (Johnson 1993; Williams *et al.* 1999; Anderson *et al.* 2005; Boulter *et al.* 2006).

The regression model that best explained the flowering variation of the herbaceous component in ENP included rainfall, temperature, and both circular functions with 12 mo period as explanatory variables. The presence of rainfall in this model was expected since above-ground biomass production in the herbaceous component is known to follow the variation in moisture availability in upper soil layers (Silva & Klink 2001). The herbaceous species accumulate carbohydrates throughout the rainy season and use them in the production of flowers and fruits when rainfall decreases (Figueiredo & Dietrich 1981). Also, we expected a high association of flowering with temperature, as we found in our final model, since temperature was previously described as an important environmental factor for the flowering of herbaceous species (Aiming *et al.* 1999). The periodicity of 12 mo of the circular functions in our regression model was probably determined by the seasonality of both rainfall and temperature.

The flowering pattern of the woody component was best explained by day length, temperature, and both circular functions with periodicities of 12 mo. Although the species of this component are under the influence of the same environmental factors as those of the herbaceous component, our best final model did not include rainfall. Rachid (1947) observed that the species of the woody component have roots that can reach deep soil layers, where water is available even in the dry season. Studying the water uptake in two cerrado physiognomies, each dominated by a different component, Oliveira *et al.* (2005) found results that corroborated Rachid's theory. According to them, the woody component, which is predominantly deep-rooted, can take water from deep soil layers in the dry season and thus is able to support growth and reproduction even in the drought.

Water availability in the dry season allows woody species to synchronize their flowering with environmental factors that are more predictable than rainfall, such as day length or solar radiation. Such synchronization minimizes the chance of failure in finding mates and

pollinators (Inouye 2008), especially for the less abundant species. Moreover, the direct transfer of assimilates to the growing organs is more efficient than their storage for later use (van Schaik *et al.* 1993; Wright & van Schaik 1994). This would make advantageous for woody species to flower near the time of the year in which insolation reaches its maximum. In the ENP, the peak in insolation occurs near September (CPTEC 2008). This relationship was highlighted in our regression model for the woody component, which had day length as one of the explanatory variables. Previous studies linked sun-related environmental factors, such as day length, solar position, and irradiation, to flowering patterns of woody species, especially in communities without alternating dry and wet seasons (Johnson 1993; Borchert *et al.* 2004). Overall, our results corroborated the climatic theory, since rainfall seasonality affected both the woody and herbaceous components in different ways. Moisture does not seem to limit flowering in the woody component, contrarily to the herbaceous component. Thus woody species are able to link their flowering patterns to more predictable environmental variables. In a long term community-wide study of reproductive phenology in Uganda, Chapman *et al.* (1999) found that for some species the patterns of flowering recorded in the first 2 yr of the study changed in the remaining years. It is possible that supra-annual patterns occur in cerrado communities as well, so longer periods of data collection are needed in future studies.

## **ACKNOWLEDGMENTS**

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## LITERATURE CITED

- AIMING, Q., R. H. ELLIS, J. D. H. KEATINGE, T. R. WHEELER, S. A. TARAWALI, AND R. J. SUMMERFIELD. 1999. Differences in the effects of temperature and photoperiod on progress to flowering among diverse *Mucuna* spp. *Journal of Agronomy & Crop Science* 182: 249-258.
- ANDERSON, D. P., E. V. NORDHEIM, T. C. MOERMOND, Z. B. G. BI, AND C. BOESCH. 2005. Factors influencing tree phenology in Taï National Park, Cote d'Ivoire. *Biotropica* 37: 631-640.
- ASHTON, P. S., T. J. GIVNISH, AND S. APPANAH. 1988. Staggered flowering in the dipterocarpaceae - new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* 132: 44-66.
- BATALHA, M. A., AND F. R. MARTINS. 2004. Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). *Aust. J. Bot.* 52: 149-161.
- BATALHA, M. A., AND W. MANTOVANI. 2000. Reproductive phenological patterns of cerrado plant species at the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and the woody floras. *Rev. Bras. Biol.* 60: 129-145.
- BORCHERT, R., S. A. MEYER, R. S. FELGER, AND L. PORTER-BOLLAND. 2004. Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography* 13: 409-425.
- BOULTER, S. L., R. L. KITCHING, AND B. G. HOWLETT. 2006. Family, visitors and the weather: patterns of flowering in tropical rain forests of northern Australia. *J. Ecol.* 94: 369-382.
- BOURLIÈRE, F. AND M. HADLEY. 1983. Present-day savannas: an overview. *In* D. W. Goodall (Ed). *Ecosystems of the world – tropical savannas*. Amsterdam: Elsevier.
- CHAPMAN, C. A., R. W. WRANGHAM, L. J. CHAPMAN, D. K. KENNARD, AND A. E. ZANNE.

1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *J. Trop. Ecol.* 15: 189-211.
- COUTINHO, L. M. 1978. O conceito do cerrado. *Revista Brasileira de Botânica* 1: 17-23.
- CPTEC. 2008. Centro de Previsão do Tempo e Estudos Climáticos, Instituto Nacional de Pesquisas Espaciais. <http://satelite.cptec.inpe.br/acervo/imgacervo.jsp?idProd=2027>.
- DEBUSSCHE, M., E. GARNIER, AND J. D. THOMPSON. 2004. Exploring the causes of variation in phenology and morphology in Mediterranean geophytes: a genus-wide study of *Cyclamen*. *Bot. J. Linn. Soc.* 145: 469-484.
- DURIGAN, G., M. F. DE SIQUEIRA, AND G. FRANCO. 2007. Threats to the cerrado remnants of the state of Sao Paulo, Brazil. *Scientia Agricola* 64: 355-363.
- EITEN, G. 1977. Delimitação do conceito de cerrado. *Arquivos do Jardim Botânico* 21: 125-134.
- FIGUEIREDO, R. C. L., AND S. M. C. DIETRICH. 1981. Variações estacionais nos compostos de reserva e no metabolismo do xilopódio de *Ocimum nudicaule* Benth. var. *anisifolia* Giul. (Labiatae). *Revista Brasileira de Botânica* 4: 73-82.
- FOX, J., AND G. MONETTE. 1992. Generalized collinearity diagnostics. *Journal of the American Statistical Association* 87: 178-183.
- INOUE, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89: 353-362.
- JOHNSON, S. D. 1993. Climatic and phylogenetic determinants of flowering seasonality in the Cape Flora. *J. Ecol.* 81: 567-572.
- JONGMAN, R. H. G., C. J. F. TER BRAAK, AND O. F. R. VAN TONGERER. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.
- KÖPPEN, W. 1948. *Climatología*. Fondo de Cultura Económica, Mexico.

- LENZA, E., AND C. A. KLINK. 2006. Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF. *Revista Brasileira de Botânica* 29: 627-638.
- MORALES, M. A., G. J. DODGE, AND D. W. INOUE. 2005. A phenological mid-domain effect in flowering diversity. *Oecologia* 142: 83-89.
- MUNHOZ, C. B. R., AND J. M. FELFILI. 2005. Fenologia do estrato herbáceo-subarbustivo de uma comunidade de campo sujo na Fazenda Água Limpa no Distrito Federal, Brasil. *Acta Botanica Brasilica* 19: 979-988.
- OLIVEIRA-FILHO, A. T., AND J. A. RATTER. 2002. Vegetation physiognomies and woody flora of the Cerrado Biome. *In* P. S. Oliveira, and R. J. Marquis (Eds). *The Cerrados of Brazil: ecology and natural history of a Neotropical savanna*, pp. 91-120. Columbia University Press, New York, U.S.A.
- OLIVEIRA, R. S., L. BEZERRA, E. A. DAVIDSON, F. PINTO, C. A. KLINK, D. C. NEPSTAD, AND A. MOREIRA. 2005. Deep root function in soil water dynamics in cerrado savannas of central Brazil. *Funct. Ecol.* 19: 574-581.
- OLIVEIRA, P. E., AND P. E. GIBBS. 2000. Reproductive biology of woody plants in a cerrado community of central Brazil. *Flora* 195: 311-329.
- RACHID, M. 1947. Transpiração e sistemas subterrâneos da vegetação de verão dos campos cerrados de Emas. *Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo. Botânica* 5:1-139.
- RAMOS-NETO, M. B., AND V. R. PIVELLO. 2000. Lightning fires in a Brazilian Savanna National Park: Rethinking management strategies. *Environ. Manage.* 26: 675-684.
- SARMIENTO, G. 1983. The savannas of tropical America. *In* F. Bouliere (Ed). *Ecosystems of the world: Tropical Savannas*, pp. 79-108. Elsevier, Amsterdam, Netherlands.
- SILVA, D., AND C. A. KLINK. 2001. Dinâmica de foliação e perfilhamento de duas gramíneas C<sub>4</sub> e uma C<sub>3</sub> nativas do Cerrado. *Revista Brasileira de Botânica* 24: 441-446.

- VAN SCHAIK, C. P., J. W. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: adaptative significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* 24: 353-377.
- WALTER, H. 1971. *Vegetationszonen und Klima*. Eugen Ulmer, Stuttgart, Germany.
- WILLIAMS, R. J., B. A. MYERS, D. EAMUS, AND G. A. DUFF. 1999. Reproductive phenology of woody species in a north Australian tropical savanna. *Biotropica* 31: 626-636.
- WRIGHT, S. J., AND O. CALDERON. 1995. Phylogenetic patterns among tropical flowering phenologies. *J. Ecol.* 83: 937-948.
- WRIGHT, S. J., AND F. H. CORNEJO. 1990. Seasonal drought and leaf fall in a tropical forest. *Ecology* 71: 1165-1175.
- WRIGHT, S. J., AND C. P. VAN SCHAIK. 1994. Light and the phenology of tropical trees. *Am. Nat.* 143: 192-199.
- ZAR, J. H. 1999. *Biostatistical analysis*. Prentice Hall, Upper Saddle River.

TABLE 1. *Circular statistics of the species observed flowering in Emas National Park, (17°49'-18°28'S and 52°39'-53°10'W), Goiás State, central Brazil. Number of observations (n), mean angle ( $\Phi$ ), mean date (d; month.day), circular standard deviation (csd), mean vector length (r), P value for the Rayleigh test of uniformity (P; \*P < 0.001).*

Component	$\Phi$	d	csd	r	P
Herbaceous	35°	02.05	109.61°	0.14	*
Woody	229°	08.21	93.47°	0.20	*

TABLE 2. *Partial regression coefficients ( $\beta$ ) and partial F values (t; \* P < 0.01, \*\* P < 0.001) for the explanatory variables of the model that better explained the periodicity of peak flowering and its relation with rainfall and temperature for the herbaceous species observed flowering in Emas National Park, (17°49'-18°28'S and 52°39'-53°10'W), Goiás State, central Brazil. Sine function ( $X_{sp}$ ; T = 12), Cosine function ( $X_{cp}$ ; T = 12).*

Explanatory variable	Proportion of SP	
	$\beta$	T
$X_{sp}$	0.06	7.68**
$X_{cp}$	0	-0.04*
Rainfall	0	1.77
Mean temperature	0.02	3.40
(intercept)	-0.22	-1.35

TABLE 3. *Partial regression coefficients ( $\beta$ ) and partial F values (t; \* P < 0.05, \*\* P < 0.01) for the explanatory variables of the model that better explained the periodicity of peak flowering and its relation with day length and temperature for the woody species observed flowering in Emas National Park, (17°49'-18°28'S and 52°39'-53°10'W), Goiás State, central Brazil. Sine function ( $X_{sp}$ ; T = 12), Cosine function ( $X_{cp}$ ; T = 12).*

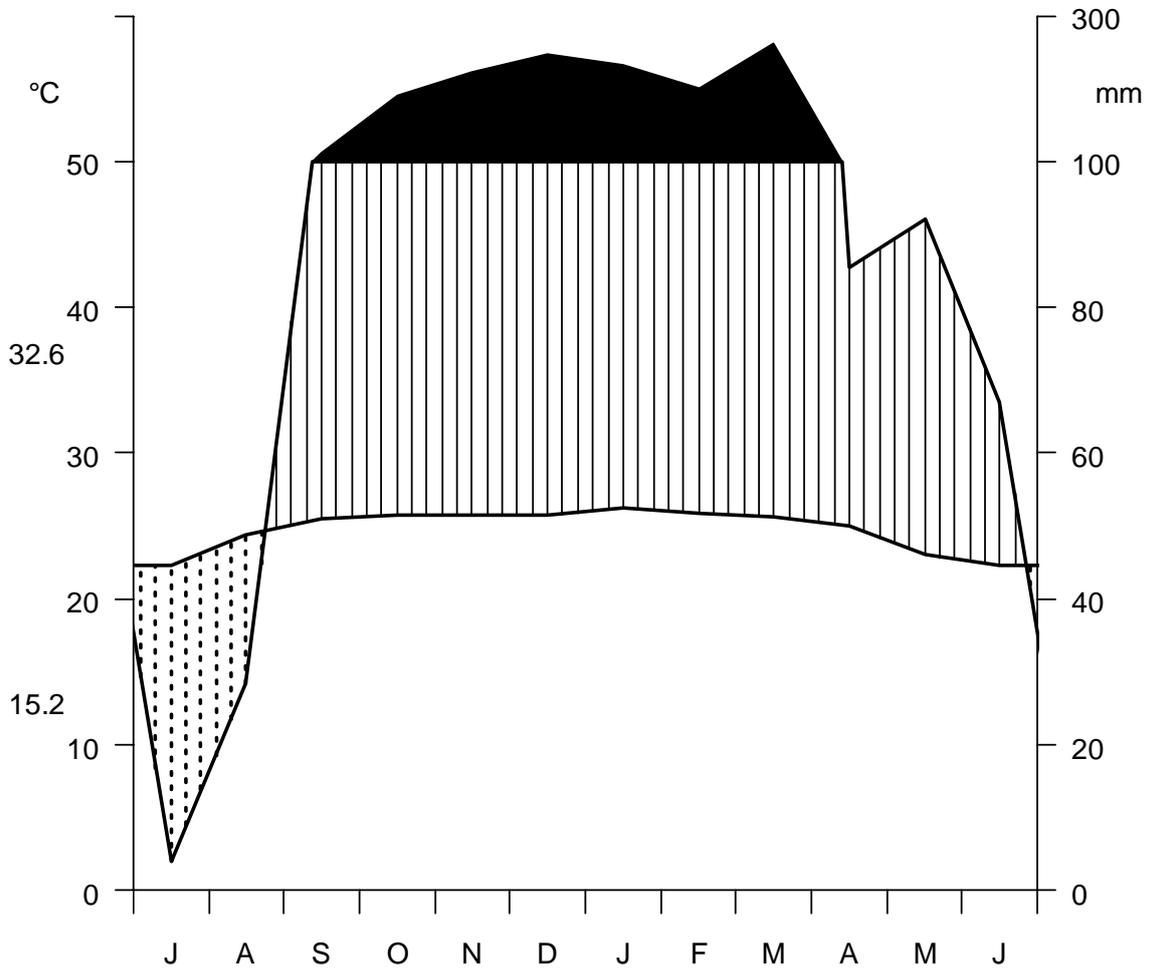
Explanatory variable	Proportion of SP	
	$\beta$	T
$X_{sp}$	-0.1	-2.23*
$X_{cp}$	0.42	0.88
Day length	-0.53	-1.18
Mean temperature	0.04	2.54*
(intercept)	5.95	1.06

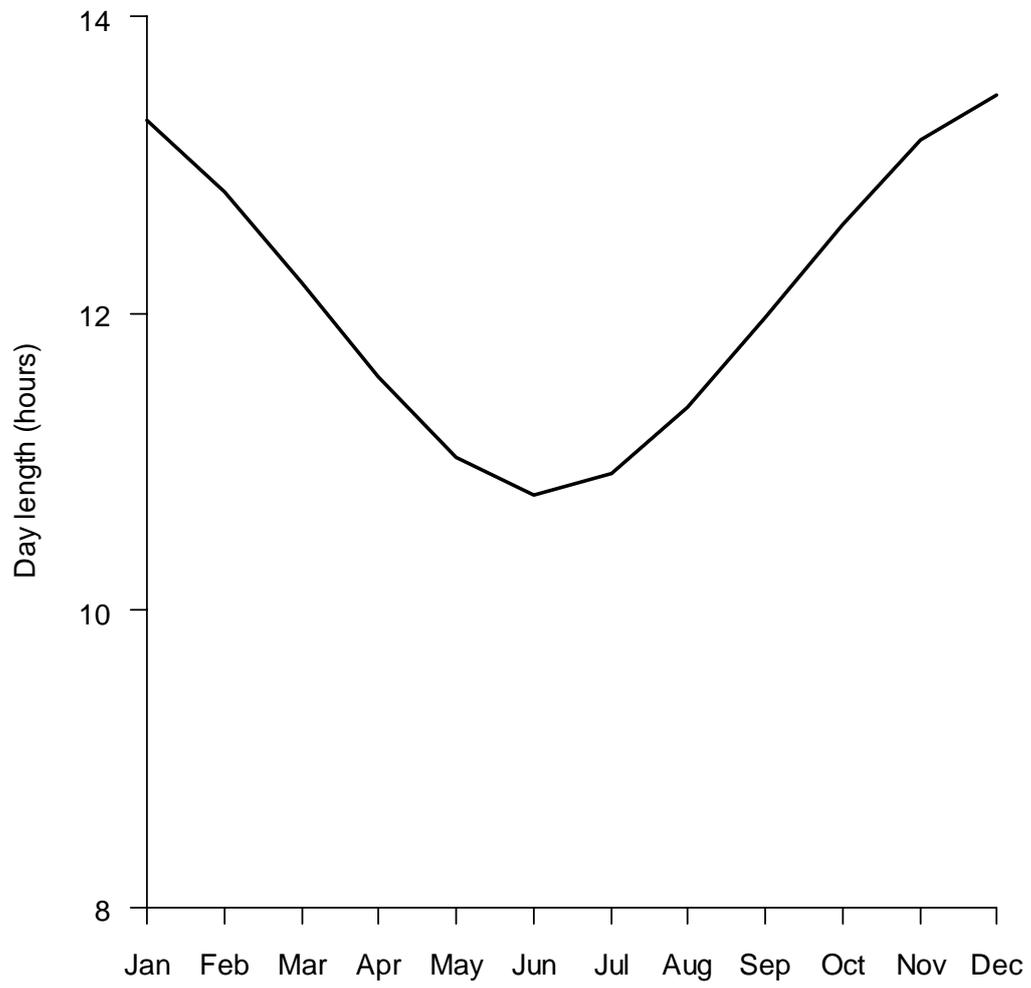
FIGURE 1. Climatic diagram following Walter (1971). Data obtained at the Benedictine Monks Monastery, Mineiros, Goiás State, central Brazil (17°33'25''S, 52°33'05''W, 800 m asl). Absolute temperatures were not available. Mean annual temperature = 24.6°C, total annual precipitation = 1745 mm.

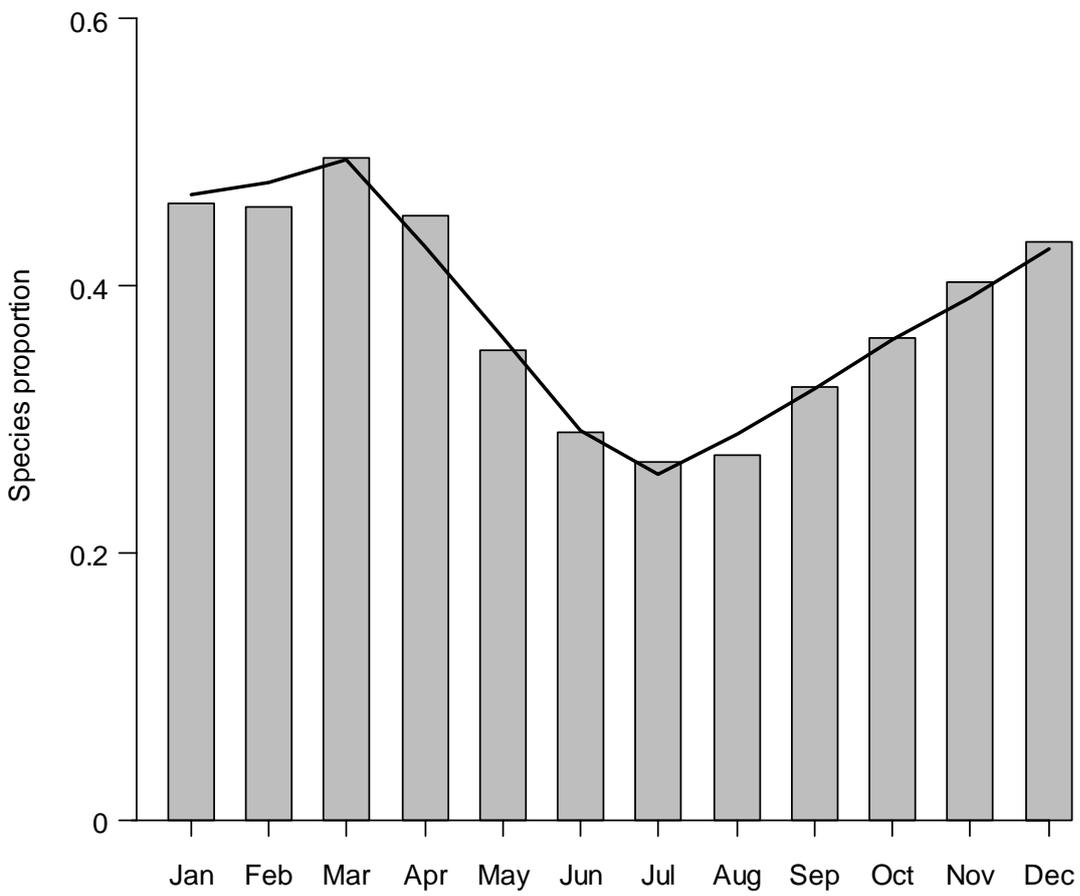
FIGURE 2. Yearly day length in Emas National Park (17°49'-18°28'S and 52°39'-53°10'W), Goiás State, central Brazil.

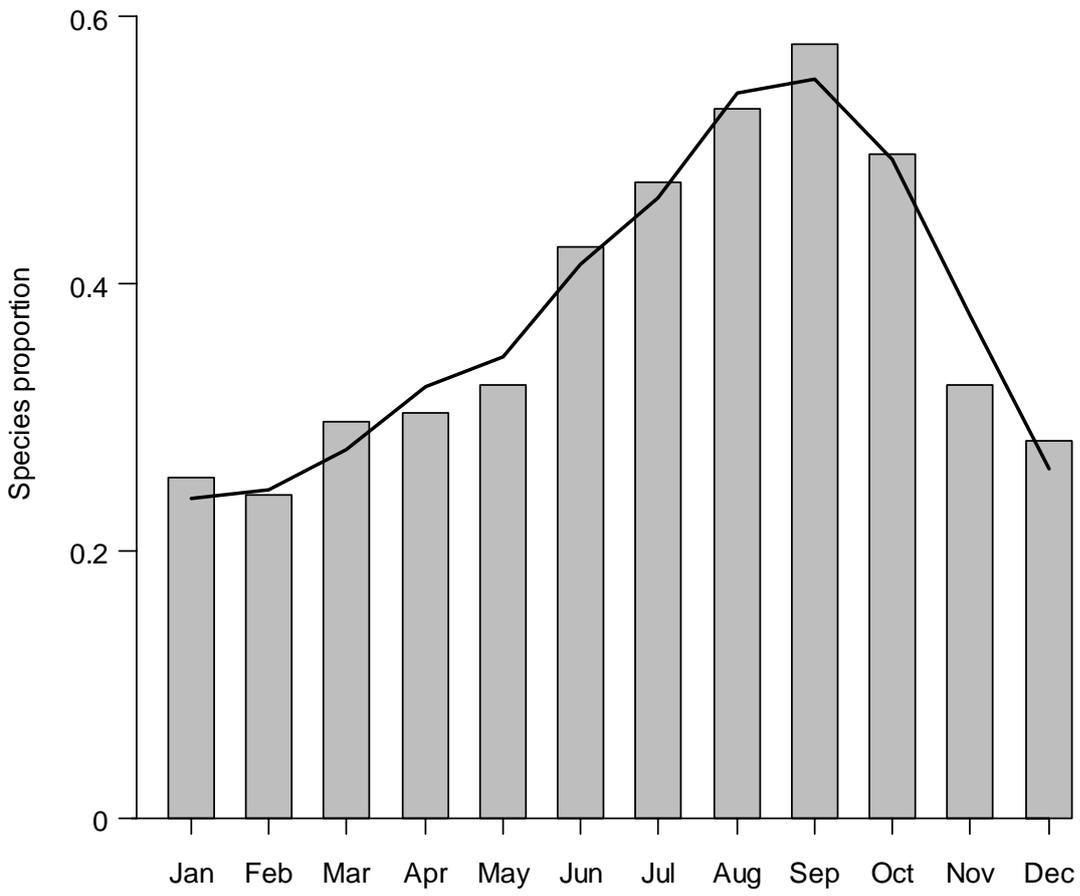
FIGURE 3. Regression predicting the proportion of herbaceous species flowering in each month. The line is the regression model ( $R_{adj}^2=0.9628$ ,  $F = 72.1$ ,  $P < 0.001$ ) with circular functions ( $T = 12$ ), rainfall, and mean temperature as explanatory variables, which best explained data variation. Bars are the observed values. Data collected in Emas National Park, (17°49'-18°28'S and 52°39'-53°10'W), Goiás State, central Brazil.

FIGURE 4. Regression predicting the proportion of woody species flowering in each month. The line was the regression model ( $R_{adj}^2=0.9394$ ,  $F = 43.65$ ,  $P < 0.001$ ) with circular functions ( $T = 12$ ), day length, and mean temperature as explanatory variables, which better explained data variation. Bars are the observed values. Data collected in Emas National Park, (17°49'-18°28'S and 52°39'-53°10'W), Goiás State, central Brazil.









# **IV – Capítulo 3**

Plantminer: uma ferramenta para conferência e busca de  
informações taxonômicas de espécies vegetais na rede  
mundial de computadores<sup>1</sup>

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<sup>1</sup> Trabalho submetido ao periódico *Diversity and Distributions* com o título “Plantminer: a web tool for checking and gathering plant species taxonomic information”.

## **Plantminer: a web tool for checking and gathering plant species taxonomic information**

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## INTRODUCTION

In the past ten years, the popularisation of the Internet allowed an unprecedented availability of biological data worldwide (Bisby 2000; Edwards et al. 2000). Unfortunately, this resulted in the arising of many data formats and independent databases (Bisby 2000) and “the complexity of navigating these databases is a near-insurmountable barrier to bench scientists who often have no programming skills” (Wilkinson et al. 2005). A key problem is the limited ability to access and handle data from several databases in a seamless manner. Therefore, even if many plant taxonomic databases exist elsewhere (e.g., World Checklist of Selected Plant Families – <http://apps.kew.org/wcsp>, Tropicos – <http://www.tropicos.org>, The International Plant Names Index – <http://www.inpi.org>, Plants – <http://plants.usda.gov>), data compilation is a time consuming activity for the final user, that is, the researcher. Researchers, especially those working with meta-analysis or macroecology, find their study subjects through query by navigation as they move from site to site, interacting with different interfaces to extract each different type of data (Karp 1995). Even if all the information needed is available from just one database, compiling this information for a high number of species can take a long time, since these databases often do not allow one to compile data for several species at once. In addition, the different ways in which data are presented and made accessible for many of these databases create an additional burden on researchers who seek to apply the available resources to their research.

Emerging technologies to solve these problems have been suggested, such as the uBio (<http://www.ubio.org>) and The Taxonomic Search Engine (TSE, Page 2005). These initiatives, however, do not completely solve the problem of the integration and availability of taxonomic data. Although the amount of species covered by uBio and other sites are huge, their databases are not as up to date as the ones from more specialized sites, like World Checklist of Selected Plantnames (WCSP), Tropicos, and The International Plant Names

Index (IPNI). Another problem with these sites is that they do not solve some common problems in large datasets, either not allowing the submission of several species at once, or the search for synonyms or duplicated species on the submitted list of species.

Therefore, facilitating and enhancing the integration, processing, and interpretation of the massive amounts of biological data by the research community is a fundamental step (Bisby 2000; Chicurel 2002; Rhee and Crosby 2005). To reduce the effort of compiling, checking, and formatting plants species data, we created an online tool called “Plantminer”. We filled two gaps with Plantminer: (1) the lack of a way to check and compile taxonomic information for several plant species at once and (2) the absence of web services with easily parsed responses to provide simple ways for ecologists to automatize their tasks.

## **HOW PLANTMINER WORKS AND WHAT IT DOES**

Plantminer is a web application designed to do the search for taxonomic information of large amount of species less painful. If you want to search for orders, families, authors, synonyms, and make sure that all species in your list exist or are correctly spelled you will certainly benefit from Plantminer. Plantminer uses the Tropicos and IPNI databases to retrieve taxonomic information, helping you to classify and organize your plant species database.

To gather taxonomic information of the plant species, Plantminer first submits queries to WCSP, where it compiles the desired data by retrieving it from the web page, simulating what a person would do manually. This process is called “screen scraping” and is very sensitive to changes in the source of the data (in this case, the species page on Tropicos). If a given species is not present in the WCSP database, Plantminer will send a query to Tropicos, where it uses a similar process. Finally, the query goes to IPNI if the species was still not found. Plantminer also has a suggestion algorithm, so if a species is not found in any databases, the system will, whenever possible, suggest the closest valid name. Moreover,

Plantminer will crosscheck the user list for synonyms, which are also gathered from the two databases mentioned above. All results are cached for a month to lower both the server resource usage and the number of requests to the above mentioned databases. When the taxonomic information of a given species is present in your cache database, WCSP, Tropicos, and IPNI are not queried. Also, Plantminer classifies your species following the latest APG classification (APG II 2003, Stevens 2001 onwards).

### **AVAILABILITY AND USAGE**

As accessing the Internet requires no specific knowledge, we built Plantminer within a friendly system-user interface web page (<http://www.plantminer.com>) containing step-by-step instructions. Basically, there is a form where the user uploads his or her species list as a text file. After that, Plantminer does the hard work (usually in few minutes – it will depend on the extent of the list) and automatically email the results to the user. To guarantee that the information obtained is updated, cached information is renewed monthly. Moreover, as duplicate entries are frequent in large datasets (especially when they are created from several different sources), Plantminer compares species in pairs warning the user when there are synonyms in the submitted list. Each result message has attached the resulting data, details about how they were obtained, and how they can be exported to other softwares. Resulting files can be compiled in either tab separated columns text files, which are compatible with most of the statistical packages, text editors, and spreadsheets, or in the Phylomatic format (<http://www.phylodiversity.net/phyromatic/>), which is a tool to identify phylogenetic relationships among taxa under different hypothesis. Another way to use Plantminer is by querying its web services. This is often used in automatized tasks and requires some programming skills by the user, like R (<http://www.r-project.org>) programming (R Core Development Team 2008).

## ACKNOWLEDGEMENTS

We thank Jay Page, from the Missouri Botanical Garden, and Alan Paton, from IPNI, for allowing us to use their data. We also thank André Vitor F. Jardim for his help in testing an earlier version of Plantminer. M.A. Batalha has a research grant from CNPq.

## REFERENCES

- APG II. 2003. An update of the Angiosperm Phylogeny Group classification for orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141:399-436.
- Bisby, F. A. (2000). The quiet revolution: Biodiversity informatics and the internet. *Science* **289**, 2309-2312.
- Chicurel, M. (2002). Bioinformatics: Bringing it all together. *Nature* **419**, 751-+.
- Curcin, V., M. Ghanem, et al. (2005). Web services in the life sciences. *Drug Discovery Today* **10**, 865-871.
- Edwards, J. L., M. A. Lane, E. S. Nielsen (2000). Interoperability of biodiversity databases: Biodiversity information on every desktop. *Science* **289**, 2312-2314.
- Karp, P. D. (1995). A strategy for database interoperation. *Journal of Computational Biology* **2**: 573-586.
- Page, R. D. M. (2005). A taxonomic search engine: Federating taxonomic databases using web services. *Bmc Bioinformatics* **6**.
- R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Rhee, S. Y. & B. Crosby (2005). Biological databases for plant research. *Plant Physiology* **138**, 1-3.

Stevens, P. F. (2001 onwards). Angiosperm Phylogeny Website. Version 9, June 2008

<http://www.mobot.org/MOBOT/research/APweb/>

The International Plant Names Index (2008). Published on the Internet <http://www.ipni.org>

[accessed 1 March 2008].

Tropicos. Missouri Botanical Garden. 11 Jan 2009 <http://www.tropicos.org>.

Wilkinson, M., H. Schoof, R. Ernst & D. Haase (2005). BioMOBY successfully integrates

distributed heterogeneous bioinformatics Web services. The PlaNet exemplar case. *Plant Physiology* **138**, 4-16.

# **V – Conclusão geral**

## Conclusão geral

Com este trabalho, chegamos às seguintes conclusões:

- Corroboramos a teoria climática na área disjunta de cerrado em Itirapina, uma vez que a floração do componente arbustivo-arbóreo dessa área parece seguir o comprimento do dia. Esse comportamento é previsto pela teoria climática, já que as espécies desse componente não sofrem tanto com o estresse hídrico na estação seca a ponto de suprimir a reprodução e o comprimento do dia é uma variável ambiental mais previsível que a precipitação. Além disso, é mais eficiente para as plantas produzirem novos órgãos em período de maior disponibilidade de energia.
- Corroboramos um dos postulados da teoria biótica, pois a floração das espécies polinizadas por abelhas na comunidade em Itirapina ocorreu de maneira agrupada, conforme previsto pela teoria biótica seguindo o postulado da floração em massa.
- Não parece haver restrição filogenética na floração das espécies da comunidade em Itirapina. Estudos subsequentes em áreas maiores serão necessários, entretanto, uma vez que encontramos poucas espécies com flores e, conseqüentemente, os grupos de espécies aparentadas possuíram poucas espécies.
- A floração do componente herbáceo-subarbustivo da comunidade no Parque Nacional das Emas parece ser estimulada pela variação da precipitação e temperatura, já que essas duas variáveis explicaram 96% do padrão anual de floração. Esse resultado também corrobora a teoria climática, pois, como as espécies herbáceas têm raízes curtas, não conseguem absorver água do solo suficiente para manterem a floração. Dessa forma, a regime de chuvas restringiria a floração.

- A floração do componente arbustivo-arbóreo da comunidade no Parque Nacional das Emas segue, aparentemente, a variação do comprimento do dia e da temperatura. O modelo de regressão que incluiu essas variáveis explicou 94% do padrão de floração.
- Apesar da fenologia da floração do componente arbustivo-arbóreo do cerrado ter sido recorrentemente relacionada à precipitação em outros estudos, a variação do comprimento do dia e da temperatura são melhores preditoras dos padrões de floração desse componente.
- Não raro há informações conflitantes entre os diversos bancos de dados que fornecem informações taxonômicas de espécies vegetais. Hoje, a melhor solução é buscar informações no World Checklist of Selected Plant Families e, depois, no Tropicos.

Acreditamos que o nosso trabalho contribuiu para o entendimento da fenologia da floração de comunidades de cerrado, especialmente por ter introduzido técnicas diferentes daquelas que têm sido utilizadas em estudos de comunidades de cerrado. Além disso, construímos uma ferramenta bastante útil para a comunidade científica, principalmente para aqueles pesquisadores que trabalham com extensas listas de espécies vegetais. Porém, investigações mais profundas são necessárias, e, assim, sugerimos:

- Estudos com menor espaçamento entre as coletas, para uma melhor identificação dos padrões de floração.
- Aplicações de técnicas que testem as três teorias de maneira conjunta, como o método de contrastes.
- Estudos em comunidades em diferentes latitudes, para observarmos como as espécies florescem em diferentes condições de clima e fotoperíodo.
- Estudos que relacionem a fenologia vegetativa das espécies da comunidade com seus padrões de floração.

- Construção de novas ferramentas para auxiliar nos trabalhos de ecologia de comunidades.

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